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Mayfly larvae preservation from the Early Cretaceous of Brazilian Gondwana: Analogies with modern mats and other Lagerstätten

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ABSTRACT

The Crato Formation paleoentomofauna is noticeable for its high abundance, diversity and morphological fidelity, so the preservational approach of the Ephemeroptera larvae fossils becomes relevant, since they are aquatic insects living in a lacustrine environment of one of the major terrestrial ecosystems of the Early Cretaceous in the Gondwana supercontinent. The mayfly larvae fossils were analyzed under a stereomicroscope and a scanning electron microscope with coupled x-ray spectroscopy (SEM/EDX) for morphological, textural and geochemical purposes. The microfabric analysis confirms the most recent hypothesis that the main factor responsible for the preservation of the Crato Formation fossils was the influence of the microbial mats on the fossilization process. The microscopic signatures left by the mats occur in the insect's cuticle and internal parts, represented by micro cracks and wrinkles, micro spheres, filaments and mineralized EPS. These features have been compared in light with deposits containing Quaternary microbial mats in the Vermelha Lagoon and its associated salt pans, in Brazil. Also, we discussed our results with taphonomic data of other mayfly larvae fossils from the Lagerstätten La Huérguina (Spain) and Yixian (China) Formations, specifically in relation to the taphonomic settings regarding these Early Cretaceous ephemeropterans. This study corroborates to the idea of the fundamental role of the microbial mats in the exquisite preservation of the Crato Formation invertebrate fossils, with an approach that permits some fundamental paleoenvironmental and paleoclimatic inferences for the Aptian of the Araripe Basin, in Brazil.

1. Introduction

The Lagerstätte Crato Formation is an Early Cretaceous lacustrine lithostratigraphic unit of Brazil known throughout the world for its exceptionally preserved specimens, including body fossils of fungi, plants, invertebrates, vertebrates, ichnofossils, such as coprolites, and even fossils in amber (Mohr et al., 2007; Polck et al., 2015; Carvalho et al., 2015; 2019; 2021a, 2021b; Heads and Martins-Neto, 2007; Limaverde et al., 2020; Mendes et al. 2020; Báez et al. 2021; Barros et al. 2021; Beccari et al., 2021; Piovesan et al., 2022; Ribeiro et al., 2021; Carmo et al., 2022; Dias et al., 2022; Nel and Ribeiro, 2022; Ribeiro et al., 2022; Batista et al., 2023). Among all metazoans, insects represent the most numerous and diversified group with 16 orders, representing more than half of the diversity of currently extant orders (Moura-Junior et al., 2018; Ribeiro et al., 2021). The order Ephemeroptera (also known as mayflies) corresponds to about 7% of the paleoentomofauna diversity recorded in the laminated limestone successions of the Crato Formation, with 16 species and nine families (Storari et al., 2020; 2021a; Brandão et al., 2021; Ribeiro et al., 2021). In addition to taxonomic studies of this group,

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Storari et al. (2021b) used these insects as bioindicators of mass mortality events. Mayflies are one of the most important lineages of extant winged insects, appearing in the Carboniferous and reaching the peak of diversity in the Jurassic and Cretaceous. Whilst the larvae are aquatic, their adult forms develop wings for the sole purpose of dispersal and reproduction, leading an ephemeral life, as the name of the group suggests (Grimaldi and Engel, 2005; Sartori and Brittain, 2015).

The preservation process of insect fossils from the Lagerstätte Crato has been topic of study by researchers mainly for the past ten years. Research ranges from more general preservational analyses (Barling et al., 2015; 2020); to the use of a wide range of methodologies for paleoenvironmental purposes (Osés et al., 2016; Prado et al., 2021), including taphonomic analysis with statistical remarks (Bezerra et al. 2021), study of the effect of microbial mats on the preservational process (Iniesto et al., 2021, Dias and Carvalho, 2022), and detailed studies including specific groups of insects, such as cockroaches (Bezerra et al., 2018), ensiferans (Bezerra et al., 2020), crickets (Dias and Carvalho, 2020) and odonatans (Barling et al., 2021).

The exceptionally preserved fossils from the Crato Formation have been analyzed not only to identify soft tissues, but also to use these fossils as palaeobiological tools. In extension of detailed studies with specific taxa, and in view of their high representation among already identified insect fossils, this study analyzed the process of exquisite preservation of a significant amount of the Ephemeroptera larvae fossils from the Crato Formation. The microscopic and geochemical analyses were carried out to determine the morphological completeness and taphonomic alterations of the fossils, focusing mainly in the microfabric and chemical composition. We compared the preservation of the equivalent insect group from another exceptional deposits, the La Huérguina Formation at Las Hoyas, an upper Barremian locality where the presence of microbial mats has been demonstrated (Fregenal-Martínez and Meléndez, 2016; Herrera-Castillo et al., 2022), and the Barremian-Aptian Yixian Formation of Jehol Biota (Pan et al., 2014). To better understand the effect exerted by the environment on the Crato fossil taphonomy, a hypersaline lagoon from the Saquarema city, State of Rio de Janeiro, Brazil, has been selected as a modern analog for comparison of the sedimentary signatures left by the presence of microbial mats.

2. Geological setting

2.1. The Crato palaeoenvironment

The Mesozoic was marked by intense global tectonics and major changes in the configuration of continents and oceans, which shaped the land surface according to the modern geographic context (Benigno et al., 2021). One of the main results of these tectonic processes for the Southern Hemisphere is the emergence of the South Atlantic Ocean as a consequence of the Gondwana rift process (Matos, 1992). This event opened depressions giving rise to a series of intracontinental sedimentary basins, among these, the Araripe Basin (Assine, 2007). This basin is the largest of the interior ones in northeastern Brazil (Fig. 1), with an area of approximately 12,200 km^2 in the south of the state of Ceará and parts of the states of Pernambuco, Paraíba and Piauí (Carvalho et al., 2012; Assine et al., 2014).

Among the Mesozoic sedimentary sequences, the Crato Formation stands out as a lithostratigraphic unit that represents the implantation of a wide range of continental and transitional environments during the late Aptian of the Araripe Basin, including the record of the first marine ingression pulse in the basin (Arai and Assine, 2020; Melo et al., 2020; Varejão et al., 2021a; 2021b; Coimbra and Freire, 2021; Vallejo et al., 2023). The high abundance, diversity, and singular pattern of fossil preservation classify this unit as one of the most important Lagerstätten in the world (Selden and Nudds, 2012; Mendes et al., 2020; Ribeiro et al., 2021; Dias et al. 2022). Following the study of Neumann and Cabrera (2000; 2002) and Neumann et al. (2002), the integrated analysis of sedimentological, stratigraphic, geochemical and paleontological studies by Varejão et al. (2021b) subdivided the Crato Formation into six facies associations (FA-3 to FA-8), that include a variety of paleoenvironments ranging from continental to marine.

The Crato Lagerstätte succession is equivalent to facies association 4 (FA-4 or CKL, Crato Konservat Lagerstätte), representing a hypersaline lacustrine environment with approximately 12 m of laminated limestones containing exceptionally preserved fossils (Varejão et al., 2021b). We confirm that the Ephemeroptera larvae fossils, analyzed in this work, comes from these beds. The microbial nature of laminated limestones from the Crato Formation has already been extensively discussed by Catto et al. (2016) and Warren et al. (2016). These authors identified peloids, amorphous organic matter, coccoid and filamentous cells embedded in extracellular polymeric substances (EPS), as well as horizons of pseudocolumnar and domic stromatolites. In addition, the role of microbial mats (MM) in the fossilization has been widely discussed as a key factor in the formation of the exceptionally preserved fossils recorded in the CKL (Osés et al., 2016; Varejão et al., 2019; Dias and Carvalho, 2020; 2022; Iniesto et al., 2021). On the other hand, other authors consider that the formation of laminated limestones occurred mainly due to the authigenic precipitation of calcite, supporting an inorganic control of the mineralization (Heimhofer et al., 2010).

Lacustrine environments can be very sensitive in response to climate fluctuations. Neumann et al. (2003), Osés et al. (2017), Gomes et al. (2021), Guerra-Sommer et al. (2021) and Dias and Carvalho (2022) have already provided evidence for these climate changes based on faciological, geochemical, cyclostratigraphic and taphonomic studies. It is possible that during drier periods, the MM were more spread in the lacustrine substrate, which resulted in more carbonate precipitation due to the metabolic activity of these microbes (Catto et al., 2016; Varejão et al., 2019; 2021b; Dias and Carvalho, 2022). In contrast, in more humid conditions, the high productivity of the water column also led to the formation of thick carbonate successions, although without a strong influence of the mats (Heimhofer et al., 2010). Thus, it is possible to suggest that the climate control led the deposition of the laminated limestones and, sometimes, in the degree of fossil preservation (Dias and Carvalho, 2022).

2.2. Vermelha Lagoon: A modern hypersaline environment

The Vermelha Lagoon (22°55′46{\Prime}S and 42°22′15{\Prime}W) is a hypersaline and carbonate coastal system (Fig. 2), with shallow and oxygenated waters, developed in the east coast of the Rio de Janeiro State, in Brazil, between the cities of Araruama and Saquarema. It covers an area of approximately 2.5 km2, with an average of two meters of water depth (Vasconcelos et al., 2006; Laut et al., 2017). It records salinities between 43.37% and 63.1% (mean value of 56.8%). with temperatures that ranges from 23.6° C to 31.5° C, pH varying between 7.7 and 9.2 (mean = 8). These values of salinity, temperature and pH were provided during the sampling period recorded by Laut et al. (2017). The water level of the Vermelha Lagoon evolved by fluctuations in the relative sea level because of the climatic changes during the Quaternary period (Suguio et al, 1985). Isotopic analyses of shells from different places of the lagoon provided an age between 3.800 and 4.200 years (Höhn et al., 1986).

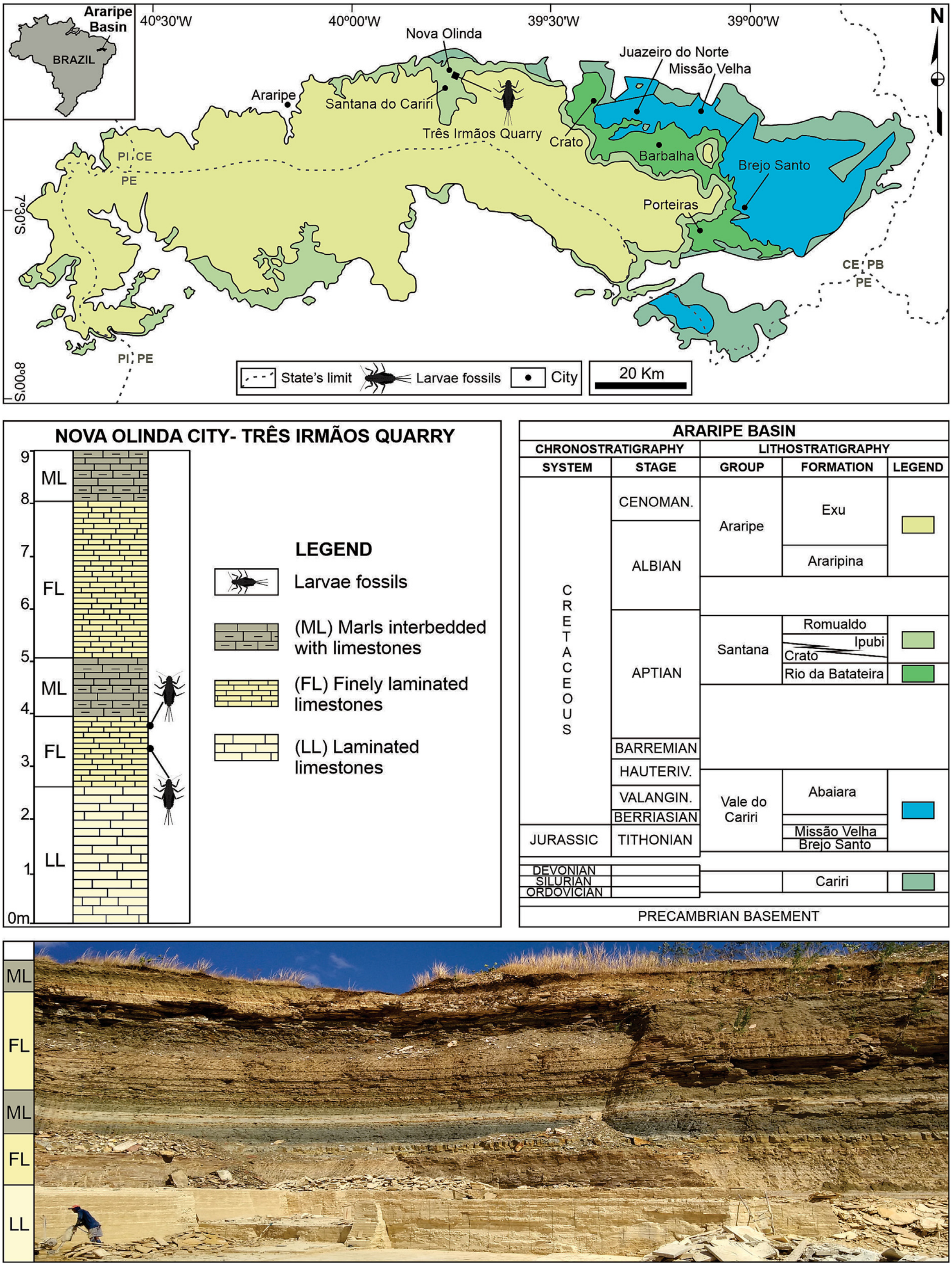


Fig. 1. Geological map of the Araripe Basin, the stratigraphic profile of the Três Irmãos Quarry (7°6′9{\Prime}S and 39°41′49{\Prime}W), and the laminated limestones where the fossils were collected. The mayfly larvae fossils occur at the finely laminated limestone levels. The nomenclature of the lithostratigraphic units was based on Rios-Netto et al. (2012) and Assine et al. (2014). Geological map modified from Assine (2007) and Dias et al. (2022). Abbreviations: PI, Piauí State; PE, Pernambuco State; CE: Ceará State; PB, Paraíba State.

The water balance of Vermelha Lagoon is essentially controlled by low rainfall, high evaporation rate, inflow of fresh groundwater, and input of waters received through the Araruama Lagoon (Höhn et al., 1986). The isolation of the lagoon body of water by sand barriers under conditions of sea regression has created extreme conditions for life, especially associated with high salinity in a more arid

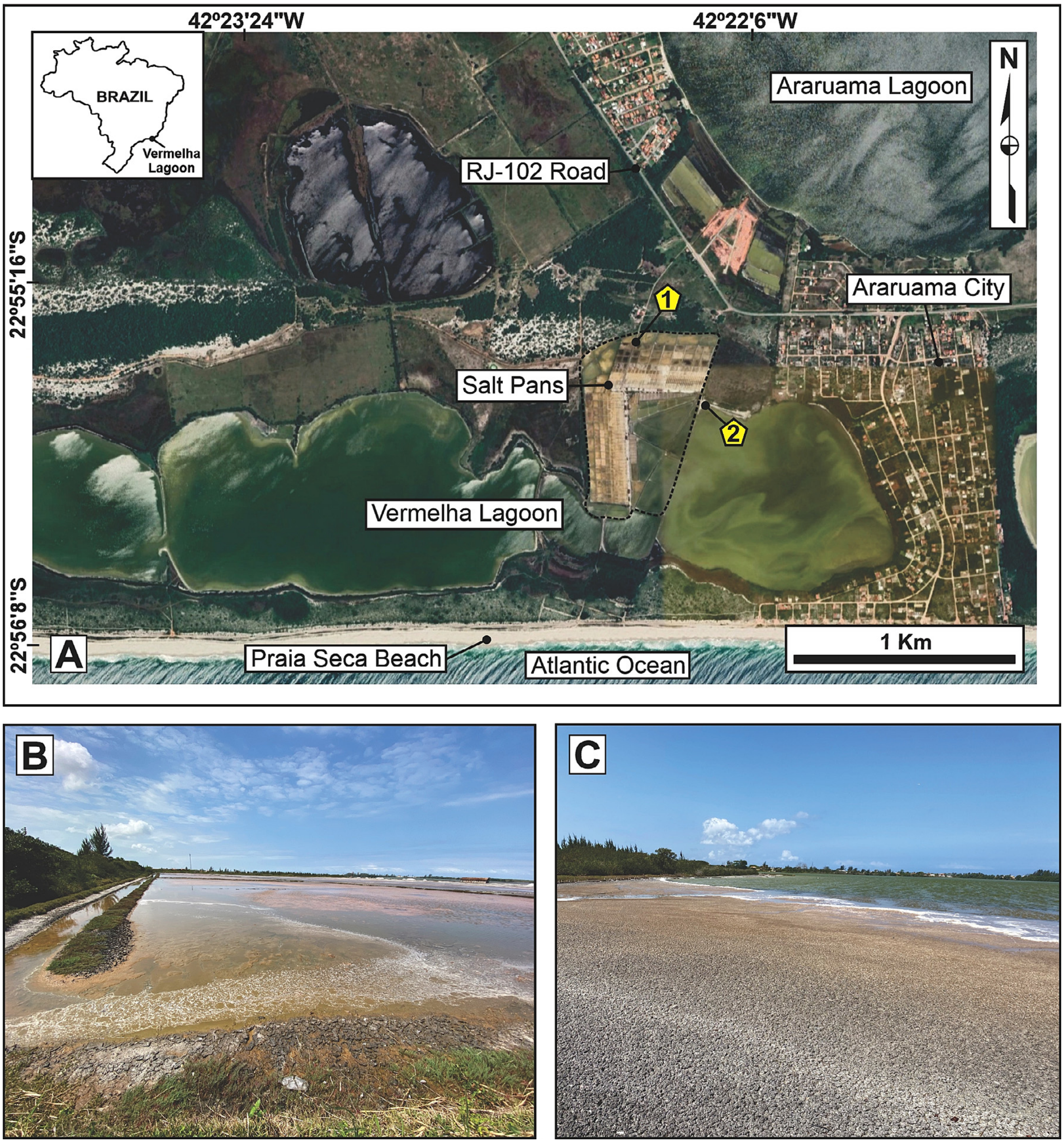


Fig. 2. A: Location map of the Vermelha Lagoon, near the Araruama city on the southeast of Brazil. On the field, it was marked two points, point 1 (22°55′33.31{\Prime}S and 42°22′19.93{\Prime}W) on the salt pans, and point 2 (22°55′33.54{\Prime}S and 42°22′14.05{\Prime}W) on the northeast margin of the Vermelha Lagoon. The satellite image was extracted by the Google Earth Pro software. B: General view of the salt pans of point 1. C: General view of the Vermelha Lagoon and its margin with microbialites associated.

climate (Silva et al., 2004). Generally, these extreme conditions prevent the wide distribution of metazoans, but at the same time it is ideal for the establishment of microbialites (Guedes et al., 2022). Due this, there is a widespread presence of microbial mats in the form of microbially induced sedimentary structures (MISS) and domal stromatolites (Laut et al., 2017). Interestingly, the name of the lagoon refers to the abundance of MM, including the purple bacteria that gives a reddish appearance to the bottom sediment, with differentiation of at least 23 cyanobacteria species (Silva et al., 2004). There is also associated biological debris of mollusks (bivalves and gastropods), ostracods, and foraminiferans (Silva et al., 2004). It is recognized that the exploitation of salt pans (Fig. 2) on the northeastern edge of the lagoon, and the creation of artificial channels to prevent fresh water from entering the body of water, contributes to the increase in salinity. In the field, we marked two points, one that refers to the salt pans (point 1, Fig. 2), and another in the Vermelha Lagoon itself (point 2, Fig. 2).

For more details about biological and physical–chemical parameters of the Vermelha Lagoon, see Vasconcelos et al. (2006), Laut et al. (2017) and Guedes et al. (2022).

3. Material and methods

3.1. Crato Formation

The larvae fossils of mayflies come from the finely laminated limestone levels (Fig. 1) in Tres Irmãos Quarry (7°6′9″S and 39°41′49″W), located in the Nova Olinda city, in the south of the Ceará state. These horizons are equivalent to the planar laminites described for Interval II of the CKL succession of Varejão et al. (2021b), which represents a hypersaline lacustrine environment. The analyzed fossils are available at the Macrofossil Collection of the Institute of Geosciences of the Federal University of Rio de Janeiro (IGEO/UFRJ), and no special permission was required to this study.

A total of 67 specimens of Ephemeroptera larvae from the Crato Formation were analyzed (Supplementary material) using a Zeiss SteREO Discovery V20 stereomicroscope connected to a Zeiss AxioCam MRc5 camera, at the Laboratório de Estudos Paleontológicos, (IGEO/UFRJ). During this phase, our studies were focused on the morphological and taphonomic analysis of the preserved remains, such as the articulation and fragmentation degrees, and three-dimensionality of the fossils. Since the main purpose of this study was to analyze the preservation, we did not use any methods involving mechanical or chemical preparation of fossils to remove the carbonate matrix. The use of hand tools such as compressed air pens, dental instruments, and various types of chemicals, can obliterate or even remove important taphonomic features, especially those that are recognizable at a microscopic level as derivatives of the influence of microbial mats.

Eight samples of Hexagenitidae larvae (Suppelementary material) were analyzed under a scanning electron microscope with X-ray dispersive spectroscopy (SEM/EDX) at the Centro de Tecnologia Mineral (CETEM) in Rio de Janeiro, Brazil. The fossil analysis in SEM aimed to reveal the textural features of the carcass microfabric for a better understanding of the preservational process, complemented by geochemical data provided by EDX. To avoid destruction, the fossils were analyzed in low vacuum, without the need for prior preparation. The images show magnitude up to 4000x at 15 kV and a working distance of 8.5 mm to 10 mm. The main diagnostic characters of these taxa in their nymphal phase are: (1) the dense swimming setae of the caudal filaments, (2) enlarged seventh gill (in contrast to other gills), and (3) the wing pads partially fused medially (Storari et al., 2021a).

3.2. MISS imprints in fossil and sediment

Microbialites are organosedimentary deposits that have accreted as a result of a benthic microbial mats trapping and binding detrital sediment and/or forming the locus of mineral precipitation (Burne and Moore, 1987). The microbial mats are vertically bedded benthic communities, in which millions of microorganisms (specially bacteria) are immersed in a polysaccharide matrix called extracellular polymeric substance (or EPS). The EPS matrix has a sticky nature that helps in the adhesion of microbial cells to the substrates, a cohesive function that keeps the sedimentary particles connected to each other, and acts as a nucleation site of minerals (Decho, 2000; Bolhuis et al., 2014; Prieto-Barajas et al., 2018). The microbialites can be stromatolites and correlates (thrombolites, dendrolites and leioliths), consisting of three-dimensional deposits formed by the precipitation of organominerals; and microbially induced sedimentary structures (MISS), which are two-dimensional structures associated with the presence of these mats in an aqueous substrate (Noffke, 2010; Noffke and Awramik, 2013; Grey and Awramik, 2020). In microbial mats, there is a direct interaction between the microbes involved, the colonized surface, and the environment with the physicochemical and biological variables that determine their formation (Stolz, 2000; Konhauser, 2007).

Thus, the observation of microbial mats formed in modern environments allows researchers to draw conclusions about the relationship of microorganisms and their habitat in the geological record (Noffke, 2010). Moreover, in carbonate sedimentary systems, microbial signatures have more potential to be preserved due to earlier cementation of sediments (Bose and Chafetz, 2012; Choudhuri, 2020). This latter feature qualifies the Vermelha Lagoon and its associated salt pans as a potential environment for observing microbial mats and their record in carbonate deposits.

4. Results

4.1. Preservation features of the Crato Formation mayflies' larvae

The analyzed fossils were mostly preserved in a dorsal view, and only a few were visualized ventrally. The specimens are poorly fragmented and well-articulated with some three-dimensionality (Fig. 3). All fossils studied show a high degree of morphological fidelity, with clear differentiation of the three tagmas, head, thorax, and abdomen, as well as other distinguishable external morphologies (Fig. 3A). In the head, there is the preservation of the bulging compound eyes (Fig. 3B), the three median ocelli (Fig. 3B), as well as the short cetacean antennae. The diverse morphologies of the masticatory apparatus were not commonly observed due to the dorsal side of preservation that cover most of the oral components. In the thorax, locomotory appendages are easily visualized, especially the intermediate and posterior ones, with slight differentiation of the femur, tibia, and tarsus (Fig. 3A).

The gills (Fig. 3C-3E) are flat, rounded or bilaminated, attached to the lateral parts of the abdomen and, apparently, mobile, with the identification of internal filamentous tracheae. In aquatic insects, respiration is provided by the movement of tracheal gills in the lateral parts of the abdomen (Sartori and Brittain, 2015). In one specimen (UFRJ-DG 376-Ins) it was possible to observe in the lateral part of a distal abdominal segment (Fig. 3F and 3G) a mineralized fragment that would represent the filamentous trachea. As expected, this structure has a tubular shape with a major axis of about 220 μm and a minor axis of up to 30 μm, internally subdivided into smaller filamentous plates perpendicular to the major axis. The preservation of tracheal tubes in insect fossils is made possible by a greater degree of sclerotization relative to other internal parts, which increases their potential for preservation in the fossil record (Förster and Woods, 2012).

In the abdomen, the cerci and median caudal filament (typical morphology of Ephemeroptera larvae) are usually covered by numerous setae preserved, mineralized, or as impressions in laminated limestones (Fig. 3E). According to Sartori and Brittain (2015), the abundance of setae on the cerci is directly related to the greater swimming efficiency of these larvae, and can also be used as a defense mechanism against predators, mimicking the behavior of scorpions. In some larvae, it was also possible to observe the holes for attachment of setae directly preserved on the massive external cuticle (Fig. 4G).

4.2. Textural and geochemical analysis of the Crato Formation mayflies

The vast majority of the Crato Formation fossil are at the levels of the Lagerstätte succession (CKL), in yellowish or grayish laminated limestones (Osés et al., 2017; Bezerra et al., 2021; Varejão et al., 2021b; Dias and Carvalho, 2022). A peculiarity of the Ephemeroptera larvae fossils is that 66 of the 67 specimens analyzed in this work were preserved only in yellowish limestones. Analyzing recent works on the taxonomy of these insects (Brandão et al., 2021; Storari et al., 2021a), as well as images of larvae fossils displayed in the mass mortality horizon interpreted by Storari et al. (2021b), all of which also occur only in yellowish limestones. Compared to other fossil groups, insects of the order Orthoptera (Dias and Carvalho, 2020; 2022) and fish (Osés et al., 2017) are in both yellowish and grayish limestones.

When the fossils are analyzed under a stereomicroscope, two main textures are discernible (Fig. 4A-4C): 1) massive, reddish-

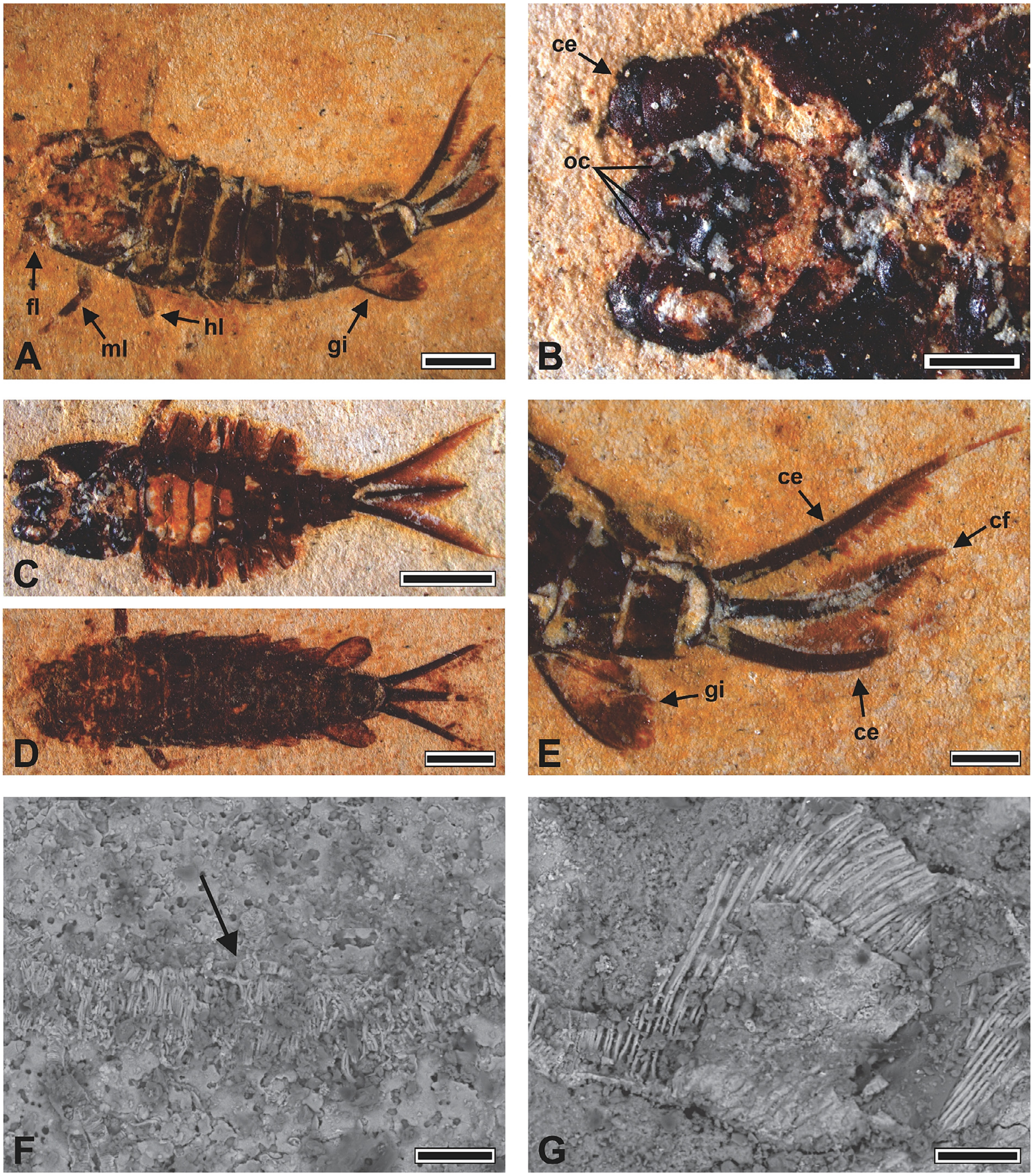


Fig. 3. Morphological features of the Crato Formation mayflies' larvae. A: Dorsal view of the UFRJ-DG 172-Ins specimen with differentiation of the three tagmas, head, thorax and abdomen, fore (fl), median (ml) and hind legs (hl), and lateral gills (gi). Scale bar: 2 mm. B: Detailed view of the head of the UFRJ-DG 441-Ins specimen, with bulging compound eyes (ce) and median ocelli (oc). Scale bar: 1 mm. C and D: General view of the well-articulated and poorly fragmented UFRJ-DG 441-Ins specimen (C) and UFRJ-DG 326-Ins (D), with lateral gills, cerci and median caudal filament well preserved. Scale bars: 2 mm. E: Detailed view of the abdominal features of the UFRJ-DG 376-Ins specimen, with lateral gills (gi), cerci (ce) and median caudal filament (cf) covered by numerous setae. Scale bar: 1 mm. F and G: SEM image of the mineralized fragment of the filamentous trachea (indicated by arrow) identified in the UFRJ-DG 376-Ins specimen. Scale bars: 200 μm in F and 50 μm in G.

brown and with difficult to individualize crystals, replacing the external cuticular features associated with the larvae exoskeleton; and 2) granular, very fine-granulated, yellowish-red in color, replacing internal features of the carcasses, mostly seen in three-dimensional fossils.

In SEM, the massive texture has polygonal cracks, similar to desiccation cracks but on a smaller scale and limited to the insect cuticle (Fig. 4D). For instance, in sample UFRJ-DG 34-Ins, a massive texture is found with wrinkle-like structure in addition to accompanying the polygonal microcracks (Fig. 4E-4G). In 3D fossils, broken parts of the massive texture reveal an internal granular texture (Figs. 5 and 6 and Table 1) composed of round or nearly round microspheres, which occurs densely packed and approximately equidimensional, ranging in size from less than 1 to 3 μm, but never exceeding 5 μm (Fig. 5A-5D). In some sections, the microspheres appear to be internally hollow (Fig. 5D). Additionally, in the middle of the microfabric, there are also smallest mineralized filaments with a major axis size of up to 4 μm (Fig. 5E, 5F and

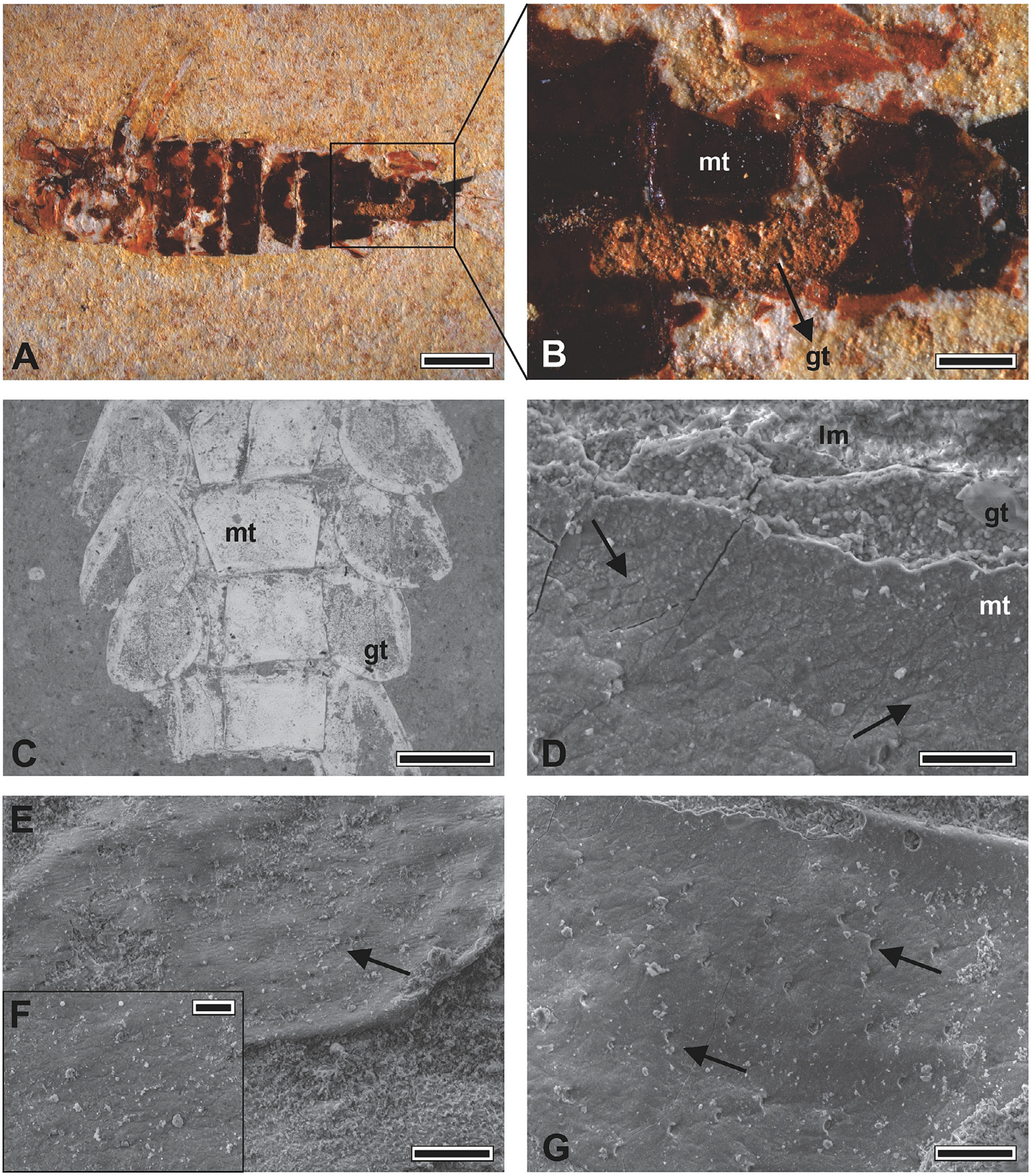


Fig. 4. Textural features of the Crato Formation mayflies' larvae. A: General view of the UFRJ-DG 59-Ins specimen with two differentiated textures exposed in B. Scale bar: 2 mm. B: Detailed view of the selected area in A, showing the reddish-brown massive texture (mt) replacing external cuticular features, and the yellowish-red granular texture (gt) replacing internal portions of the larvae. Scale bar: 500 μm. C: SEM image of the UFRJ-DG 34-Ins specimen showing the massive (mt) and granular texture (gt). Scale bar: 1 mm. D: Textural relations of the UFRJ-DG 59-Ins specimen, showing polygonal cracks (indicated by arrow) in the massive texture (mt), the granular texture (gt) in the internal parts of the fossil and the surrounding laminated limestone (lm). Scale bar: 30 μm. E and F: Massive texture of the UFRJ-DG 34-Ins specimen with wrinkle-like structures (indicated by arrow). Scale bars: 100 μm in E and 20 μm in F. G: Massive texture of the UFRJ-DG 59-Ins specimen with holes for the attachment of setae (indicated by arrow) and polygonal cracks. Scale bar: 60 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

6D). In some specimens, a network-shaped texture was revealed, directly associated with the microspheres of the granular texture (Fig. 6), some of them with evidences of a possible cell division, which is a strong suggestion of bacterial binary fission (Fig. 6D). In addition, in the granular texture there is pseudo-framboids after pyrite with irregular margins and signs of dissolution, that formed aggregates up to 25 μm in size (Fig. 6F).

The outer massive texture and the inner granular texture consisted of microspheres, filaments, network-shaped texture, and pseudo-framboids show iron and oxygen peaks in the EDX analysis, suggesting iron oxide as the current chemical composition (Fig. 7A). In one specimen (UFRJ-DG 376-Ins), the internal granular texture observed in the area of the cercus shows peaks of phosphorus and calcium, indicating a punctual phosphatization process (Fig. 7B).

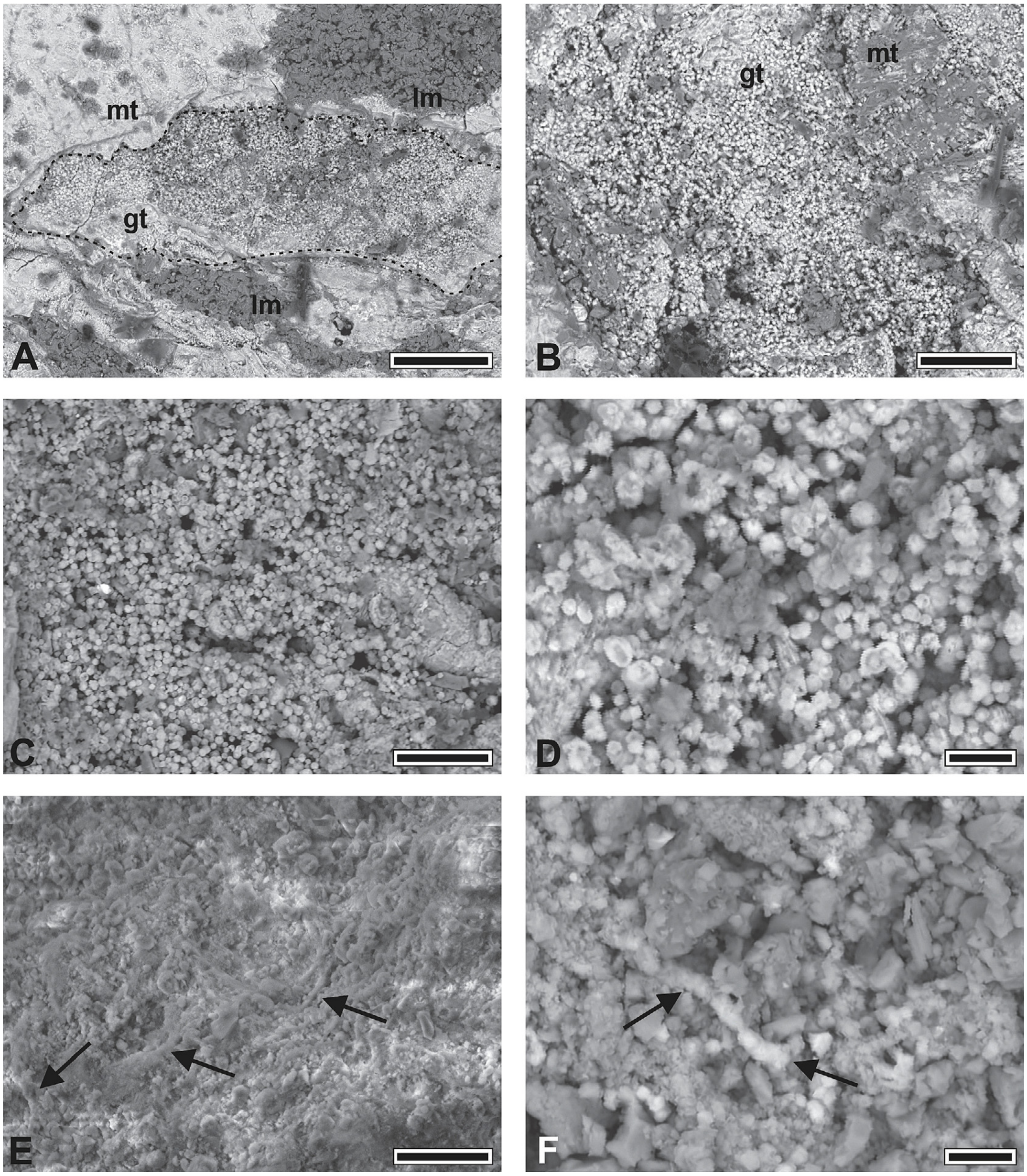


Fig. 5. Textural features of the Crato Formation mayflies' larvae visualized in SEM. A and B: Microfabric of the UFRJ-DG 441-Ins specimen with clear differentiation of the massive texture (mt) with polygonal cracks, granular texture (gt) and the calcium rhombohedra of the laminated limestones (lm). Scale bars: 100 μm in A and 50 μm in B. C and D: Detailed view of the granular texture exposed in A and B composed of hollow, round or nearly round microspheres densely packed. Scale bars: 20 μm in C and 5 μm in D. E: Granular texture of the UFRJ-DG 376-Ins specimen with microspheres and subordinated mineralized filaments (indicated by arrow). Scale bars: 30 μm in E and 5 μm in F.

4.3. Preservation features of the Lá Huérguina Formation mayflies' larvae

The Las Hoyas insect fossils could be preserved as an organic film; as an authigenic mineral, often calcium carbonate, with isolated parts in calcium phosphate; as a cast replicated in a secondary mineral, such as pyrolusite, calcite and silica; and as a mold of the exoskeleton (Briggs et al., 2016; Delclòs and Soriano, 2016). The specimen MUPALH-7048, correspond to a nymph of the subfamily Mesonetinae (Fig. 8A, Morphotype A in Delclòs and Soriano, 2016). It is preserved as a very thin, soft-tissue imprint, somewhat darker than the surrounding matrix (Fig. 8B). The fossil is poorly fragmented and well-articulated, without three-dimensionality. There is the preservation of external morphologies, i.e., the head, thorax, abdomen, locomotory appendices, gills, cerci, and the caudal filament (Fig. 8).

The darker material of the fossil exhibits a characteristic smooth texture, with cracking, similar to that of kerogen (that contrast with the texture of the matrix) (Fig. 8D). The elemental mapping by EDX analysis of the carbonaceous flakes of the body have an elementary composition of sulfur and carbon, while the matrix is predominantly calcite. MUPALH-7048 shows more than one type of preservation, because the intestinal tract is, otherwise, phosphatized (calcium phosphate), with a whitish color in the specimen (Fig. 8C). Details of the digestive tract evidence the presence of areas with densely packed round microspheres of about 1 – 3 μm (Fig. 8E), as well as patches of network-shaped structures.

4.4. The microbial mats from Vermelha Lagoon

In the Vermelha Lagoon salt pans (Fig. 9A), microbial mats (Fig. 9B) biostabilize the substrate and preserve sedimentary

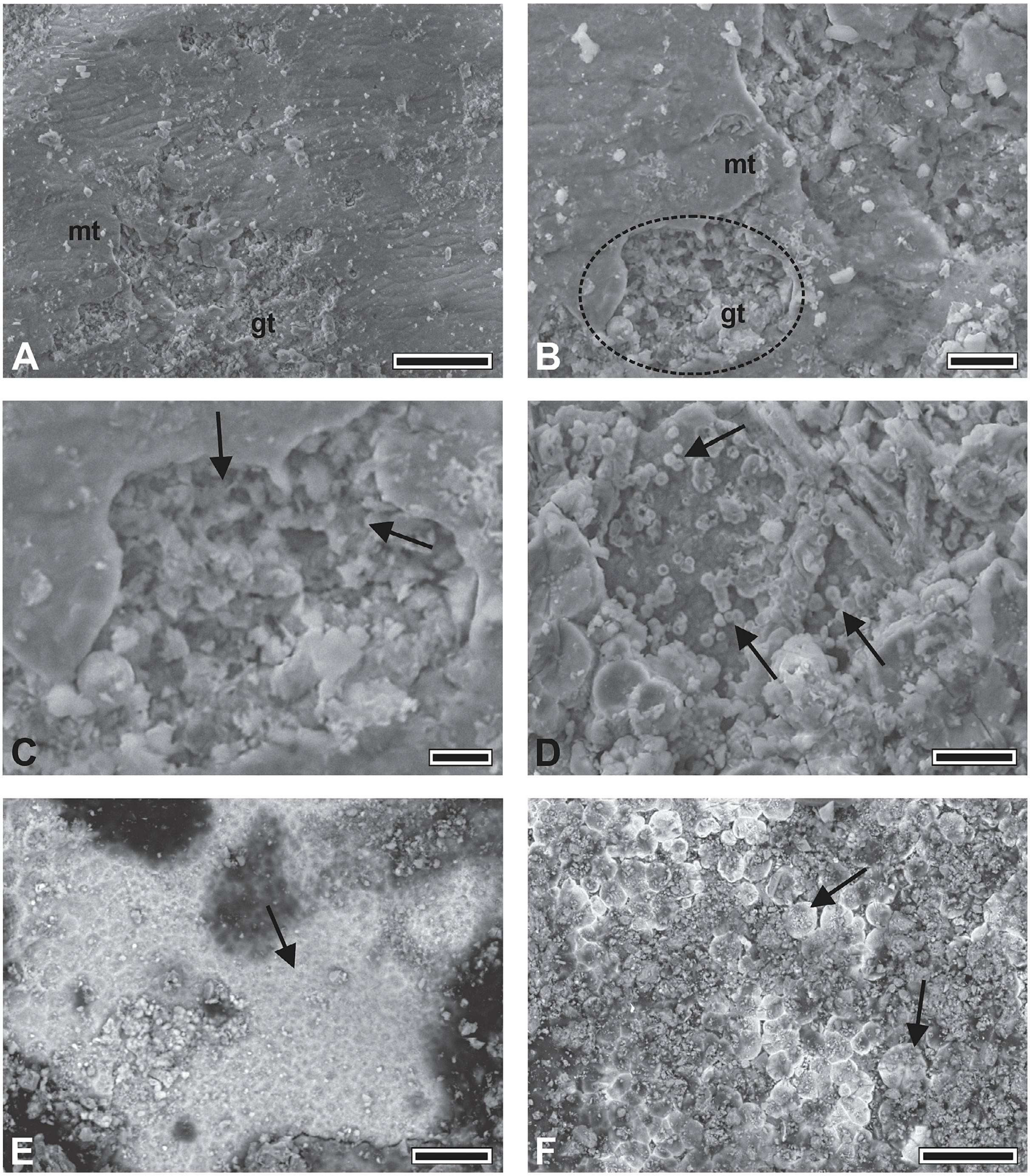


Fig. 6. Textural features of the Crato Formation mayflies' larvae visualized in SEM. A and B: Microfabric of the UFRJ-DG 34-Ins specimen with the massive texture (mt) with wrinkle-like structures, and the granular texture (gt) replacing internal parts, with a network-shaped structure associated (selected section). Scale bars: 50 µm in A and 10 µm in B. C. Detailed view of the network-shaped structure (indicated by arrow) visualized in B. Scale bar: 5 µm. D. Granular texture of the UFRJ-DG 34-Ins specimen with filaments and mineralized and hollow microspheres with a possible evidence of cell division (indicated by arrow). Scale bar: 10 µm. E: Detailed view of the UFRJ-DG 113-Ins with granular texture associated with a network-shaped structure (indicated by arrow). Scale bar: 20 µm. F: Granular texture of the UFRJ-DG 326-Ins specimen with potential pyrite pseudo-framboids (indicated by arrow). Scale bar: 50 µm.

structures in a very shallow aquatic environment, resulting in the formation of MISS at a macroscopic scale on field (Fig. 9). The mats' signatures are consisted of desiccation cracks (Fig. 9C and 9D) and wrinkle marks at the margins of the lagoon (Fig. 9G). Also, these microbial consortium structures can enhance the preservation of aerial wave marks and footprints (as seen in Fig. 9E and 9F). For instance, this was associated with the mechanism responsible for track preservation of non-avian dinosaurs in the Souza Basin of the Early Cretaceous of Brazil (Carvalho, 2004; Carvalho et al., 2013), as well as in the preservation of vertebrates and invertebrate ichnofossils from the same basin (Carvalho et al., 2017). The sealing effect of the microbial mat can be visualized when it grows over the plant fragments that eventually embeds them in a mucous matrix mostly composed of EPS (Fig. 9H). This

Table 1
The average dimensions of the mineralized morphotypes (microspheres and filaments) and pyrite pseudo-framboids identified in the granular texture of the insect fossil microfabric from the Crato Lagerstätte.

Granular texture	Average dimensions	Number of analyzed contents
Microspheres	<1 – 3 µm	400
Filaments	4 µm in the major axis; µm in the minor	50
Pyrite-pseudo framboids	20 – 25 µm	200

microenvironment created by the mats has specific geochemical gradients favorable for the mineralization of soft parts (Iniesto et al., 2016; 2018).

5. Discussion

The exceptional preservation of the Crato Formation fossils has been well-documented in other arthropods, and a strong microbial influence has been proposed (Barling et al., 2015; Osés et al., 2016; Varejão et al., 2019; Dias and Carvalho, 2020; Bezerra et al., 2021; Iniesto et al., 2021; Prado et al., 2021; Dias and Carvalho, 2022). This impact includes four main steps: capture, protection, creation of a microbial sarcophagus, and mineralization of the organic remains (Briggs, 2003). Herein, we examined the fossilization of 67 specimens of ephemeropterans to emphasize the mat influence in their preservation by associating with MISS structures (Noffke, 2010), and the particular environment of these microorganismal communities. We aimed the identification of possible mat signatures in the mayfly exoskeletons that can be used to infer its influence in insect preservation. In addition, we discuss that the pyritization observed in the Crato mayflies, that preserved inner organs in three-dimensions (Barling et al., 2015; Dias and Carvalho, 2020), can be also explained by the mediation of the mat community. As a consequence, the studied ephemeropterans led us to recognize their preservation and some environmental conditions that acted upon their fossilization. Thus, in order to get a better understanding of the taphonomic and paleoecological factors involved in the fossilization of the Crato mayflies, we discuss the taphonomic equivalence (isotaphonomy, *sensu* Behrensmeyer et al., 2000) of three Early Cretaceous localities, placed at La Huérguina (upper Barremian), Yixian (Barremian-Aptian) and Crato (Aptian) Formations.

5.1. The mayfly larvae preservation from the Crato Formation in light of the microbial mats from Vermelha Lagoon

The cuticle of the Ephemeroptera larvae fossils registers microscopic cracks and wrinkles, which could be originated in three possible ways: 1) the breakdown by mechanical factors (such as the transport in life and post-mortem), 2) they could correspond to morphologies of the larvae itself; and 3) by the process of dehydration of microbial mats during the fossilization process. The more

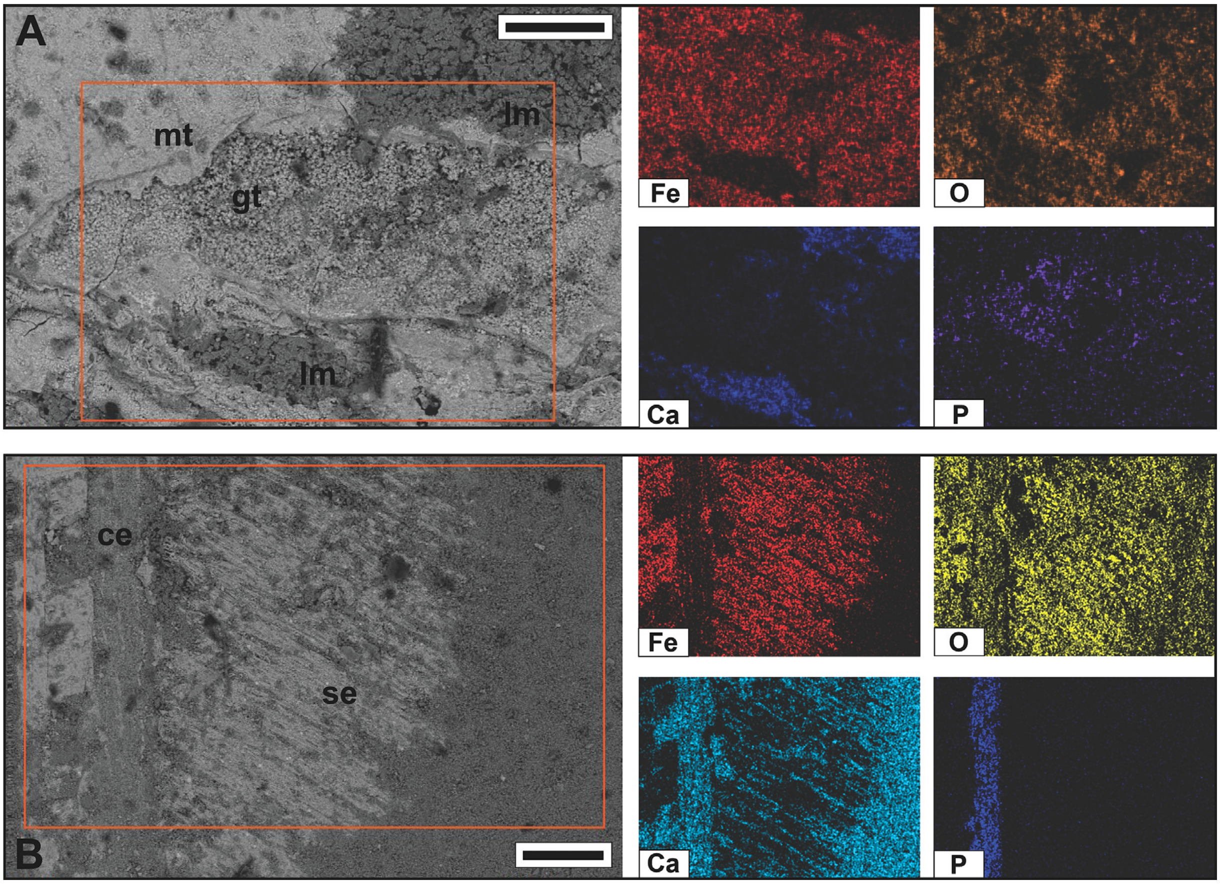
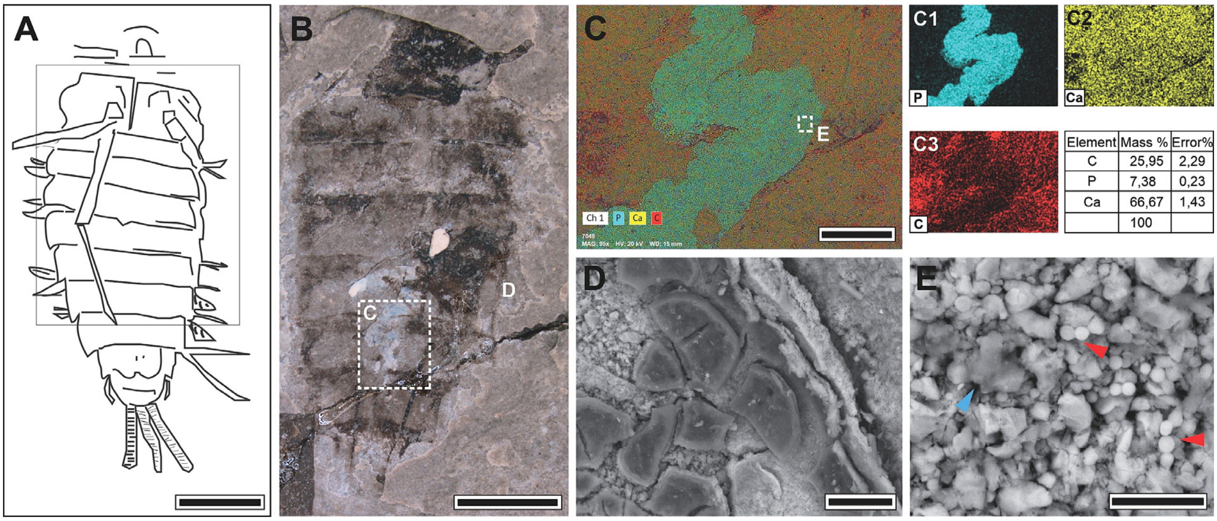


Fig. 7. Elemental analysis of the Crato Formation mayflies' larvae. A. UFRJ-DG 441-Ins specimen showing the massive texture (mt), granular texture (gt) and laminated limestone (lm). The EDX analysis shows a concentration of iron (Fe) and oxygen (O) for the fossil, suggesting iron oxide as the chemical composition. The calcium (Ca) peaks refer to the laminated limestones, and phosphorous (P) occur subordinately in the granular texture of the fossil. Scale bar: 100 µm. B: Detailed view of the UFRJ-DG 376-Ins specimen showing the cercus (ce) with numerous setae (se). The setae are composed by iron (Fe) and oxygen (O), and the cercus by calcium (Ca) and phosphorous (P). Scale bar: 100 µm.



Element	Mass %	Error%
C	25,95	2,29
P	7,38	0,23
Ca	66,67	1,43
	100	

Fig. 8. A. Schematic drawing of Mesonetinae Morphotype A in ventral aspect from Las Hoyas (Spain). Scale bar 5 mm. B. Photograph of specimen MUPALH-7048 with high degree of articulation and low degree of fragmentation. Scale bar 2 mm. The boxes correspond to the figured details. C. Color mapping of the elementary composition of the specimen and digestive tract (note that the photograph is up-down turned with respect to the specimen). Scale bar: 300 µm; C1. Phosphorous; C2. Calcium; C3. Carbon. D. SEM image of the exoskeleton showing the carbonaceous film as kerogenous flakes. Scale bar: 20 µm. E. Detail of the microspheres (red arrows) and network-shaped patches (blue arrows) inside the digestive tract. Scale bar: 10 µm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

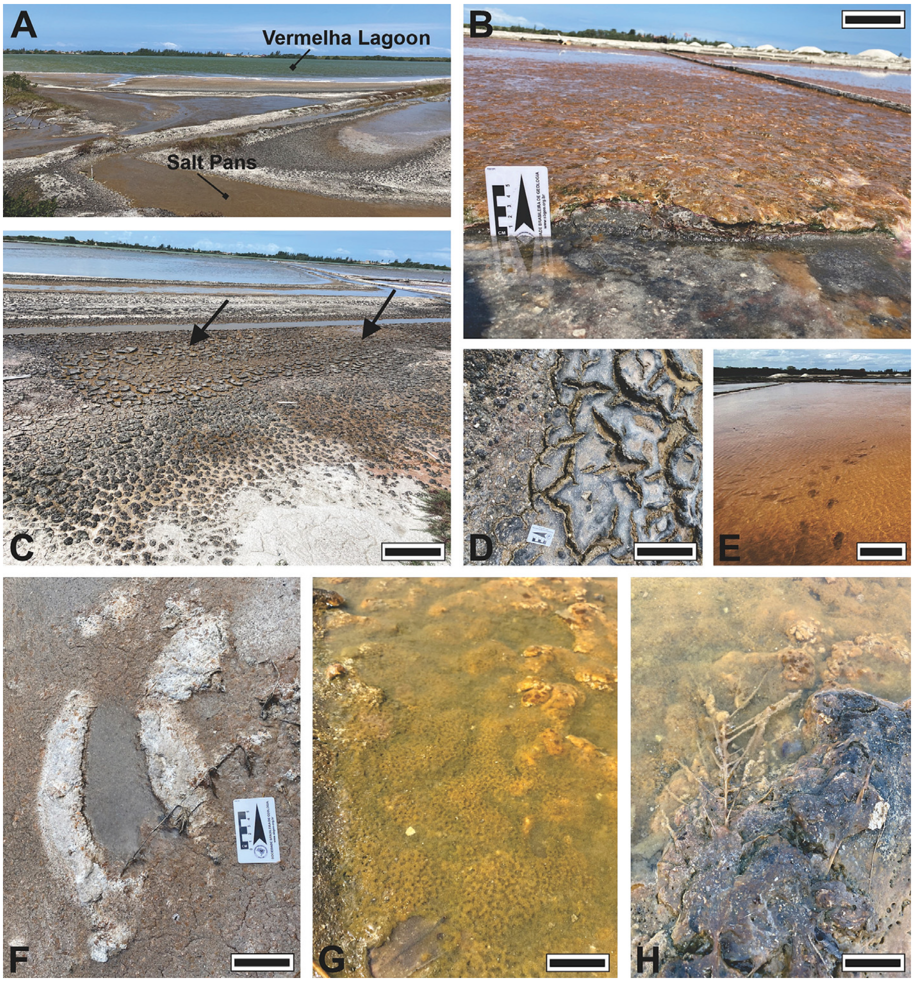


Fig. 9. A. General view of the Vermelha Lagoon and the associated Salt Pans. B: Microbial mats identified on the Salt Pans. Scale bar: 5 cm. C and D: Desiccation cracks visualized on the marginal environments. Scale bars: 1 m in C and 20 cm in D. E: Aerial wave marks and human footprints visualized in the Salt Pans. Scale bar: 50 cm. F: Human footprint lithified by the microbial mats with desiccation cracks associated. Scale bar: 8 cm. G: Wrinkle marks generated by the microbial mats at the margins of the lagoon. Scale bar: 5 cm. H: Plant fragment coated by mats with a very sticky nature associated with the EPS secretion. Scale bar: 1 cm.

organized arrangement of the polygonal micro cracks and the absence of other features that could indicate a high transport rate (fragmentation and disarticulation), makes the first hypothesis unfeasible. Also, there is no register of a mechanical disruption in the form of a wrinkle surface in the cuticle of a living or fossil insect, especially Ephemeroptera larvae. The second hypothesis is more plausible than the first one, since the insect cuticle could register a variety of protuberances (Richards and Richards, 1979). The presence of three-shaped microtrichia in living Ephemeroptera of the Caenoculini tribe (Malzacher and Sangpradub, 2017) resembles slightly the structures we described here. However, these body components have more rounded surfaces, not like the polygonal micro cracks seen in the Crato fossils. Furthermore, to the best of our knowledge, there is no register of wrinkled surfaces in the cuticle of living Ephemeroptera, as a consequence, this places this second hypothesis to be highly unlikely. The third hypothesis is related to the sealing effect created by the mats in the coating of the carcasses, with the posterior dehydration during the diagenesis. We suggest that the third hypothesis is the more adequate to explain the genesis of these microstructures, especially when they are associated with the other identified microscopic features that suggest the presence of the mats.

On one hand, the massive texture described for the outer regions of the cuticle that captures the polygonal micro-cracks and wrinkle structures, might be associated with the coating by the mats (Fig. 4D-4F and 6A). On the other hand, in the microfabric there are circular to subcircular microspheres (mostly smaller than 1 μm), mineralized filaments, and a network-shaped texture probably reminiscent of the EPS-rich mucosal matrix (Figs. 5 and 6). These features, together with the presence of pyrite pseudo-framboids, were associated with the presence of a microbial community growing in the hypersaline lacustrine succession of the Crato Formation. The microbial mat influence on the genesis of the Crato laminated limestones was pointed out by Catto et al. (2016) and Warren et al. (2016). Moreover, the spatial relationship between the Crato fossils with mats was also exemplified in petrographic studies with decapods done by Varejão et al. (2019), and crickets by Dias and Carvalho (2022). As expected, both studies provided strong supporting for this coating process as already described.

Therefore, the cuticle of the larvae would have acted as a substrate for the mat's establishment. As a result, the microstructures in the cuticle accompanied by other textural evidences (e.g., microspheres, filaments, pseudo-framboids, and remains of the EPS-rich mucosal matrix) would be formed during the coverage of the carcasses in shallow water depth (cf. Varejão et al., 2021b) and extreme aridity. Indeed, the arid climate is supported by mass mortality events reported by Storari et al. (2021b) with the accumulation of 40 Ephemeroptera larvae in one layer of laminated limestone. According to these authors, this horizon also contained pseudomorphs of halite, indicating high evaporation, probably caused by the high aridity, which directly affected the autochthonous fauna of the lake environment, and possibly led to the death of the Ephemeroptera larvae in addition to *Dastilbe* fishes.

Pyrite pseudo-framboids also indicate the effect of microbial mats, especially sulfate-reducing bacteria (SRB). From a geological point of view, SRBs are a group of bacteria that play an important role in mineral precipitation and mat lithification. They are capable of reducing sulphates to sulphides, which are very reactive and combine with metals and subsequently precipitate (Baumgartner et al., 2006; Prieto-Barajas et al., 2018). According to Noffke (2010), pyrite framboid is an indicator mineral for the process of cell replication in microbial mats. The high potential of the micropyrite in capturing microbial signatures of sulfur, as well as how sulfur isotope composition can map the microenvironment created by the mats, has been demonstrated by analyzing the pyrite isotopes in the microbial mats of the hypersaline lagoon in Cayo Coco, Cuba (Marin-Carbonne et al., 2022). Moreover, the calcium phosphate minerals, visualized replacing the interior of the cercus of one of the specimens (Fig. 7), may also indicate the nucleation of crystals under the influence of microbes (Noffke, 2010). Therefore, the granular texture in Ephemeroptera larvae fossils may be due to bacteria-mediated organomineralization (Dupraz et al., 2009) and/or self-lithification of these microbes (Tomescu et al., 2016).

5.2. Taphonomy of the Crato mayflies' larvae

The larvae of Ephemeroptera are aquatic, i.e., they live in a lacustrine setting with no signs of serious transport after death. This is evidenced by the high degree of articulation and the low degree of fragmentation of the analyzed fossils. After death, once the larvae reach the lake substrate, it becomes a nucleus for microbial attachment and agglutination, with continuous secretion of EPS that envelopes them. For the Crato insects, this latter feature is determined by the network-shaped texture identified in the fossil microfabric.

Once the microbial sarcophagus, caused by EPS enveloping, is formed, the mineralization of organic remains increases the potential for insect preservation in the fossil record. Bacteria promotes mineral precipitation by releasing metabolic products that interact with ions in the environment (Hoffmann et al., 2021), describing as the organomineralization process, with mineral precipitation in soils and sediments mediated mainly by SRB (Dupraz et al. 2009). Precipitates can aggregate on the walls of microbial cells or through extracellular polymeric substances, and the presence of solid bacterial bodies such as coccoids and filaments, may indicate this auto-lithification process with direct replication of its external contents (Tomescu et al., 2016). The differentiation of the products resulting from the organomineralization and the bacterial self-lithification is yet practically impossible in the fossil record, but the microbial shapes (Figs. 4-6) analyzed in this work strongly suggests the microbial nature of the fossilization process, including those from the organism itself (endogenous bacteria), and those derived by the microbial mats (exogenous bacteria).

According to Janssen et al. (2021), organic residues become sites for ion release, and when covered by mats, these residues become effective nuclei for mineral nucleation. This is the case of Ephemeroptera larvae from the Crato Formation whose pyritization was the main fossilization process, with a subordinate phosphatization. The analyzed mayflies follow the same taphonomical model described by Osés et al. (2016) for other insects of the Crato Formation: initially mineralized with framboid pyrite and secondarily transformed into iron oxide, as evidenced by EDX analyzes and identification of pseudo-framboids with dissolution textures. Sulfate-reducing bacteria can induce pyrite deposition due to the redox conditions of the microenvironment formed by the microbial mat (Marin-Carbonne et al., 2022), not necessarily under the same physicochemical conditions as the lake environment. Drawing a parallel with the Crato Formation, although the lacustrine environment can be oxygenated (Varejão et al., 2019), the reducing and anoxic conditions inside the microbial sarcophagus delaying the rate of autolysis, contributing to the mineralization of the remains (Butler et al., 2015). However, it should be noticed that the microbial sarcophagus may not be anoxic during the whole stages of decay. Experiments of actualistic taphonomy involving the decay of fish in microbial mats show that during the first week, the anoxic conditions prevail, with a significant depletion of oxygen caused by heterotrophic aerobic respiration, and the pH profile changed from basic to slightly acid (Iniesto et al., 2015). After three months, the dissolved oxygen exceeding its initial value and the pH increased, resulting in an oxygenated and alkaline microbial sarcophagus. This data is also supported by synchrotron-based analysis of phosphatized fishes and crustaceans from a Cretaceous Lagerstätte in Morocco (Gueriau et al., 2020). The phosphatized tissues and mineralized biofilms composed of iron oxides were interpreted as concomitant, which suggest an oxygenated microenvironment during the decay stages. In relation to the metabolism of SRB, analysis in microbialites of the hypersaline Great Salt Lake in Utah, United States, point that the sulphate-reduction action of these bacteria in the organomineralization process could occur in both oxygenated and anoxic zones of a microbial mat (Pace et al., 2016). In all cases, the exceptional preservation of fossils is enhanced by the covering of the carcasses by microbial mats, creating an anoxic and/or oxygenated microbial sarcophagus.

In the mayfly fossils of this work, it was identified two types of chemical processes in the same specimen, pyritization and phosphatization (Fig. 7B). The pyritization process occurs either in the outer parts associated with the massive texture, or in the inner parts associated with the granular texture. Interestingly, secondary chemical modifications of fossils from pyrite to iron oxide have not destroyed the preservation of primary features associated with the exceptional preservation of fossils. In contrast to pyritization, the phosphatization is subordinate and limited to some areas, as identified on the cercus (Fig. 7B). The lack of preserved internal soft parts in Ephemeroptera larvae fossils may simply be a taphonomic bias, or the result of a higher rate of decay. According Iniesto et al. (2015), after the initial period of decay under anoxic conditions, what remains of the carcass is more difficult to decay, and therefore the decomposition proceeds slower. Thus, the internal granular texture of the Crato mayfly fossils must have been formed by a posterior infilling following the decomposition of the soft parts, as organs and other soft tissues, with pyrite organomineralization under the action of SRB.

The preservation types of the Crato Formation fossils provide information on the paleoenvironmental conditions (Osés et al., 2017; Varejão et al., 2019; Dias and Carvalho, 2022). With regard to orthopteran fossils, Dias and Carvalho (2022) proposed two different paleoenvironmental and paleoclimatic conditions based on the analysis of their preservation, especially the cuticle analysis: the three dimensional pyritized fossils predominantly found in yellowish laminated limestones, and the two-dimensional kerogenized fossils, preserved as an amorphous carbonaceous microfilm, and mostly associated with grayish limestones. Pyritized fossils may indicate drier climatic conditions in a shallow, saline, and stagnant lacustrine environment. Kerogenized fossils, on the other hand, would be associated with more humid conditions, with the lake environment susceptible to large sediment discharge brought in by river influxes, likely to increase depth and decrease water salinity. The environmental and climatic conditions associated with the yellowish limestones are more favorable for the formation and spread of the microbial mats, directly increasing the potential for exceptional fossil preservation.

5.3. Climatic control of the fossilization

The preservational control of the Ephemeroptera larvae from the Crato Formation is excellent evidence that the coloration of the laminated limestones may reflect paleoenvironmental changes, and not simply being the result of recent weathering processes. For Menon and Martill (2007) and Barling et al. (2015; 2020), grayish limestones (blue-gray limestones) are unaltered rocks, while yellowish (pale cream) are their weathered versions. Ephemeroptera larvae fossils clearly "prefer" yellowish limestones, and there is very little chance that this is only equivalent to sampling bias. In addition, geochemical studies of fish fossils from the Crato Formation by Osés et al. (2017) demonstrated that the several patterns of fossil preservation are in fact not the result of weathering processes alone, and were later supplemented by an analysis by Dias and Carvalho (2022) of the orthopteran fossils from the same lithostratigraphic unit.

In this work, 66 of the 67 analyzed fossils of the Crato Ephemeroptera larvae are recognized in yellowish limestones and, as discussed earlier, there is a clear association of the fossils of these groups with this specific type of limestone, visualized even in the images of other works published by other authors. The predominance of the Ephemeroptera larvae fossils only in yellowish limestones may indicate that these insects prefer shallower and more saline environments, which is currently noted in some recent insects of this order (Kondratieff, 2008; Sartori and Brittain, 2015). However, the analysis of orthopteran fossils from the same unit shows that fossils preserved in yellowish limestones have a higher degree of preservation, since they represent more favorable conditions for better development of the microbial mats in the substrate (Dias and Carvalho, 2020; 2022). Thus, there is possibly a climate control in the exceptional preservation of the Crato Formation fossils, and the "preference" of the larvae fossils in yellowish limestones may reflect this.

This climatic influence is also supported by Storari et al. (2021b) by the identification of a stratigraphic horizon of mass mortality of mayflies' larvae and *Dastilbe* fishes. However, it should be noted that not all the Crato Formation fossils, and even not all Ephemeroptera fossils, are necessarily preserved by a mass mortality event. The uniqueness of the preservation of the Crato Formation fossils is primarily a reflection of the influence of microbial mats on capture, protection, microbial sarcophagus creation, and mineralization of the remains, with the influence of these microbes being greatest during the more arid periods. Even the process of natural death (rather than catastrophic events) can lead to the exceptional fossil preservation because, as discussed earlier, the insect carcass functions as a site for ion release and subsequent mineral nucleation in a microenvironment created by a microbial mat.

5.4. Mayfly larvae fossils from other exceptionally Early Cretaceous localities

Other relevant Early Cretaceous localities with fossil ephemeropterans are the ones from China in Yixian and Liaoning Formations (Pan et al., 2014), Iberian Peninsula in Tremp and La Huérguina Formations (Whalley and Jarzembowski, 1985; Delclòs and Soriano, 2016), the Koonwarra Formation from Australia (Poropat et al., 2018) and the Purbeck Group from Southern England (Coram and Jarzembowski, 2021). Herein, we summarized the environmental and taphonomical settings of the La Huerguina locality of Las Hoyas, and of the Chinese ephemeropterans from the Sihetun area in the Zhangjiagou, Erdaogou, and Jianshangou localities. Then, we compare these data with the environmental and preservational patterns observed in the fossil ephemeropterans from the Crato Lagerstätte.

5.4.1. Las Hoyas

Sedimentary environment. The upper Barremian Las Hoyas fossiliferous site is characterized by deposits of finely laminated limestones, which are composed almost entirely of calcium carbonate, with a small fraction of clays and organic matter (Fregenal-Martínez and Meléndez, 2016). The nature of the lacustrine water, climate and seasonality has been isotopically contrasted in rocks, fish, plant cuticles and coprolites from Las Hoyas locality (see for a summary Barrios de Pedro et al., 2020). The δ13C and δ18O values (δ13C = -2.72 ± 0.23‰; δ18O = -4.81 ± 0.17 ‰) and their covariances, collected from a 1.25 m thick section at the fossil site, indicated the prevalence of lacustrine conditions in a groundwater-dominated, relatively small, hydrologically open lake, and strongly influenced by carbon dioxide release by the karstic water, the metabolism of the microbial mat, and the organic matter degradation (Poyato-Ariza et al., 1998). There are a set of microfacies that indicate drier and wetter periods. The drier ones are composed of densely packed calcium carbonate with a stromatolitic lamination, and the wetter ones are made up of positively graded millimetric laminae deposited under a persistent shallow lamina, with decantation of allochthonous to parautochthonous shells and vegetal debris (Fregenal-Martínez and Meléndez, 2016).

Fossil assemblages and preservation. The collected aquatic insects have been characterized as auchthotonous fossils, and endemic (i.e., dwellers of the Las Hoyas small lake) (Buscalioni and Fregenal-Martínez, 2010). The Las Hoyas ephemeropterans include mostly larvae forms (91%), with few adults (9%). All the Las Hoyas Ephemeroptera (N = 48) appear isolated, without evidence of mass mortality clusters, and commonly associated with tiny and small sized plant debris (Fig. 8). The larvae fossils are mostly articulated, with variable sizes between the specimens, and about 20% of them are fragmented. The adult ones are mostly represented by isolated wings.

Diversity. The Las Hoyas Ephemeroptera are not abundant, representing only a 9% of the reported Hexapoda (Delclòs and Soriano, 2016). The collection is placed at the Museo de Paleontologia (MUPA) in Cuenca, Castilla-La Mancha. Ephemeroptera have been attributed to the Leptophebidae and Euthyplociidae families (Martinez-Delclòs, 1992). The Leptophebidae is characterized by two larvae morphotypes of the Mesonetinae subfamily, whereas the Euthyplociidae is represented by just one larvae morphotype.

Fossilization. About 20% of the Las Hoyas ephemeropterans are carbonaceous compression. Previous analyses on insects and crustaceans from Las Hoyas showed the presence of organic constituents, but traces of original chitin and protein were not detected. The overall composition was found to be predominantly aliphatic and resembled kerogen, with the original components having been altered by *in situ* polymerization (Stankiewicz et al., 1997; Gupta et al., 2008). Given these previous reports of pyrolysis–gas chromatography-mass spectrometry (Py-GC–MS) analysis on arthropods, including insects, from the same locality, it is likely that extensive alteration has taken place.

5.4.2. Yixian Formation

Sedimentary environment. The Barremian-Aptian Yixian Formation is formed by finely laminated siliciclastic sediments, dominated by shales and low-energy sandstones, with extrusive basalts and tuffs intercalated, and crosscut by dykes and sills. In the Sihetun area of the lacustrine Yixian Formation, frequent and often severe volcanic activity, represented by the abundant tuff layers, influenced the water quality, causing repeated collapse of the aquatic ecosystem that was most probably controlled by fluctuations of oxygen level related to climate (Pan et al., 2011). The Sihetun area comprises the Lujiatun and Jianshangou units, with the last one being subdivided into four beds corresponding to four phases of the lake evolution (see Hethke et al., 2013). Six microfacies (Mf 1–6) were distinguished within the most fossiliferous beds 2 and 3. The pyritized ephemeropterans are restricted to the Phase 2, which encompass allochthonous siliciclastic laminae, cyst accumulations, and tuffaceous sediments, with occurrences of biofilms and framboids (pyrite pseudomorphs) in a lacustrine setting with meromictic conditions and stratified waters (Hethke et al., 2013). Palynological evidence in the Yixian Formation points to a warm and dry climate with seasonal rainfall (Li and Batten, 2007), however, palaeobotanical analysis sustains a warm and wet climate (Ding et al., 2003).

Fossil assemblages and preservation. The studied mayflies have been characterized as accumulated *in situ*, and buried under low energy conditions. The Yixian ephemeropterans include mostly articulated specimens, while disarticulated and distorted samples comprise a very low proportion of the total (less than 1%). The mayflies from Liaoning concurred with the conchostracean *Eosestheria*, and clusters of mass mortalities were documented (Fürsich et al., 2007).

Diversity. The collected ephemeropterans from the Yixian includes mostly genera from the Hexagenitidae family, and to lesser extent the Mesonetidae. The species *Hexagenites* (=*Ephemeropsis*) *trisetalis* represents the most common giant mayfly larvae from the Yixian Formation from the western Liaoning (Huang et al., 2007; 2011; Pan et al., 2014).

Fossilization. The Yixian Formation has been characterized as two modes of insect preservation, three-dimensionally pyritized insects, and carbonaceous compressions. The three-dimensionally preserved fossils underwent authigenic mineralization, following the process described as "clay-polymer interactions" denoting the association of clay and pyrite in soft-tissue preservation. The primarily pyritized fossils were extensively weathered, forming crystals of iron hydroxide. The carbonaceous compressions show no trace of authigenic minerals, and the EDS spot indicates a relative peak of carbon with compositional differences between the fossils and matrix (Pan et al., 2014).

5.4.3. The Crato ephemeropterans in light of Las Hoyas and Yixian

The Lagerstätten deposits of Crato, Las Hoyas and Yixian exhibit some similar and distinct patterns regarding the preservation of the mayfly larvae fossils. During the Early Cretaceous, the greatest diversity of mayflies was concentrated in Eurasian deposits (especially in China, with more than 30 species, Huang et al., 2007; 2011), with the exception of the Gondwanan deposits of the Crato Formation in Brazil, with 16 formally described species in nine families. Both units show a predominance of the Hexagenitidae family between the collected specimens (Huang et al., 2011; Brandão et al., 2021; Storari et al., 2021a). At Las Hoyas, however, the mayflies are not so abundant and diverse, being distributed only in two families, Leptophebidae and Euthyplociidae (Martinez-Delclòs, 1992).

The mayfly fossils from the Crato, Las Hoyas, and Yixian deposits usually occur as articulated and poorly fragmented specimens, with a predominance of aquatic larval morphotypes. In Las Hoyas and Crato, fossils are recognized in finely laminated limestones, while in Yixian, in finely laminated siliciclastic and tuffaceous rocks. The taphonomic signatures of these three localities indicate that these insects were fossilized in their proper aquatic environment, with no significant post-mortem transport, and low-energy conditions. This calm condition is supported by the predominance of lacustrine settings in all of the aforementioned units. For Las Hoyas, there is a relatively small and hydrologically open lake (Fregenal-Martínez and Meléndez, 2016); in Yixian, a meromictic lacustrine environment influenced by volcanic activity, and with the occurrence of biofilms (Hethke et al., 2013); and in the Crato Formation, a lacustrine environment with hypersaline and shallow waters, and the presence of microbial mats and stromatolites (Varejão et al., 2021b).

Although the paleoenvironmental contexts are similar, the mode of preservation of the mayfly larvae fossils has distinct patterns and processes: 1) pyritization, for the Crato and Yixian ephemeropterans; 2) kerogenization, for Las Hoyas; and 3) occasional phosphatization in the Crato and Las Hoyas fossils. In addition, horizons of mass mortality of mayfly larvae fossils were identified in the Crato and Yixian Formations, with no report at Las Hoyas. For the Crato Formation, the mass mortality event was associated with a water hypersalinity during dry conditions (Storari et al., 2021b), while in the Yixian Formation, the mortality was related with anoxia of the lake waters at high temperatures, resulting in water stratification, surface algae blooms, and oxygen depletion even in the shallower parts of the lake (Fürsich et al., 2007). Another possibility that increases the mortality events at Yixian is the recurrent sudden outgassing events derived by the volcanic and hydrothermal activity (Hethke et al., 2013).

Pyritization. Fossils of the pyritized larvae from the Yixian Formation bear a resemblance to those of larvae from the Crato Formation. Both contain three-dimensional specimens with mineralization of the external and internal parts. In addition, the Crato fossils were originally pyritized and are currently composed of iron oxyhydroxide due to secondary replacement. The Yixian fossils are currently composed of iron hydroxides, also being the result of late replacement by weathering reactions. However, the exceptional preservation of the mayfly larvae fossils from Yixian was not associated with the influence of mats (Pan et al., 2014), despite the reported biofilms for the rocks of the phase 2 (Hethke et al., 2013). For the Yixian larvae fossils, the carcasses were covered by sediments in the lake substrate, with the absorption of suspended clay particles by the cuticle of the insects, inhibiting or slowing down the decay. The pyritization in this case occur in the void spaces created by degradation of the carcasses, with an infilling of authigenic pyrite in an environmental context of low oxygenation, high concentrations of iron and sulfides (probably derived by the volcanic activity reported), and a relatively low organic matter (Pan et al., 2014).

The exceptional fossil preservation of vertebrates and invertebrates (including the mayfly larvae) of the Yixian Formation is mainly correlated with the frequent volcanic activities developed in the volcanic lakes (Jiang et al., 2011). For the Crato Formation, however, there is no evidence of a volcanic nature in the sedimentary succession. The pyritization in the Crato fossils are currently associated with the envelopment of the carcasses by microbial mats in the lake substrate, with organomineralization by the SRB (Osés et al., 2016; Varejão et al., 2019; Dias and Carvalho, 2022).

Kerogenization. The mayfly fossil from Las Hoyas analyzed in this paper (MUPALH-7048) occurs as a kerogenized film with a smooth texture, resulting in a bi-dimensional specimen with poor visualization, distinguished from the calcareous matrix by its darker color. In the Crato Formation, the kerogenization process has not yet been identified in the ephemeropterans' larvae, but this could only correspond to a preservational bias, since this mode of preservation has already been identified in fossil fishes (Osés et al., 2017), and crickets (Dias and Carvalho, 2020). In those kerogenized specimens from the Crato Formation, there are also bi-dimensional fossils occurring as dark films with a smooth texture, and the preservational fidelity is lower than the pyritized fossils (see Dias and Carvalho, 2022). The kerogenized nature of the mayfly larvae fossil from Las Hoyas is the responsible factor for its lower preservational fidelity when compared with the pyritized and three-dimensional ephemeropterans fossils from the Crato and Yixian Formations. Although there was previous report of microbial mats associated with a theropod trackway preservation from Las Hoyas (Herrera-Castillo et al., 2022), in the MUPALH-7048 specimen there was no substantial evidence that attests to the influence of the mats in the fossilization. The microspheres and the network-shaped structures visualized are localized, and more analysis needs to be done.

Phosphatization. In the Las Hoyas specimen, the elemental mapping by EDX showed that the caudal part of the digestive tract of the mayfly larvae fossil has peaks of calcium and phosphorous, indicating a local phosphatization, since the rest of the carcass is kerogenized. In the specimen UFRJ-DG 376-Ins from the Crato Formation, there is also a localized phosphatized process restricted to the cercus, and the rest of the fossil were pyritized. The phosphatized digestive tract and cerci could correspond to the mineralization of soft parts, probably during the early diagenetic stages. According to Briggs et al. (1993), the phosphatization occurs preferentially in association with soft tissue replication, explaining why it generates exceptionally preserved structures. However, it is also necessary to analyze more specimens, both from the Las Hoyas and Crato localities, to understand exactly how this process occurs.

6. Conclusions

The mayfly larvae fossils from the Crato Formation exhibit poorly fragmented, well-articulated, and two- to three-dimensional specimens with a high degree of morphological fidelity. The textural analysis of the fossils indicates an external massive texture associated with the insect cuticle, and a granular texture related to the inner parts. SEM analysis shows irregular polygonal cracks and wrinkle-like structures in the massive texture, which we suggest it could be interpreted as microscopic signatures of microbial mats in the insect cuticle. These features have been visualized in field at the Vermelha Lagoon and its associated salt pans, where there are extant microbial mats with current development of MISS, such as desiccation cracks and wrinkle marks. In the fossil microfabrica, there are mineralized microspheres (some of them with binary fission) and filaments, sometimes associated with a network-shaped texture reminiscent of the mucous matrix composed of the EPS secreted by the mats. These morphotypes have been interpreted as self-lithified bacteria, or simply organomineralized crystals under the influence of these microbes.

We propose that the role of microbial mats in the fossilization of the Ephemeroptera larvae from the Crato Formation was the key factor for the exceptional preservation. The insect carcasses could become a nucleus for microbial agglutination in the lake substrate, with continuous secretion of EPS until the organic remains have been coated. The microenvironment created by the mats provides the organomineralization of the organic remains, and may not necessarily correspond to the gradients of the surrounding oxygenated lacustrine environment. SEM/EDX analysis of the larvae showed that the carcasses were pyritized, with only punctual phosphatization. Currently, the fossils consist of iron oxide as a result of the secondary replacement of originally pyritized fossils, as indicated by EDX analysis, and also the presence of framboidal pyrite pseudomorphs in the microfabric. The exceptional preservation is also possible due to the fact that these larvae are aquatic and already live in the lacustrine environment. Taphonomic signatures support very short or an absent transport in a low-energy environment. In addition, the extensive domain of the larvae fossils in yellowish laminated limestones, associated with the cracks in the insect cuticles, suggests a possible climate control in the fossilization. A more arid climate is propitious for the development of microbial mats in the lake substrate, enhancing their subsequent influence on the trapping, protection and mineralization of the organic remains.

Comparisons with others Early Cretaceous Lagerstätten deposits that also contain fossils of mayflies' larvae provide some imprints regarding the taphonomic settings in which these insects were fossilized. The Yixian (China), La Huérguina (Spain) and Crato (Brazil) Formations all share a lacustrine environment, despite some different physical–chemical parameters. The diversity and abundance of the ephemeropteran fossils are higher in the Yixian and Crato localities. The Crato ephemeropterans share the primary mode of preservation with the Yixian mayflies, which is pyritization, but in the Chinese fossils there is no evidence of microbial mats influencing the fossilization. On the other hand, the Las Hoyas specimen is kerogenized, and shares a phosphatization process with one of the Crato fossils, probably associated with the mineralization of soft tissues and formation of a microenvironment that favored this mode of preservation. All things considered; this study shows that although diversity and taphonomic pathways differ among deposits, we showed that ephemeropteran larvae can indeed be used as a taphonomic and paleoenvironmental tools. This feature may be due to the fact that these animals are highly endemic and subject of environmental changes, consequently, they are able to add new information to the understand of the ancient paleobiology and paleoecology systems.

CRediT authorship contribution statement

J.A.F.G. de Andrade: Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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