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The role of microbial mats in the exquisite preservation of Aptian insect fossils from the Crato Lagerstätte, Brazil

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A B S T R A C T

The insect fossils recorded in the lithographic limestones of the Crato Formation (Aptian of the Araripe Basin, Brazil) have a high degree of morphological fidelity of external and internal anatomical features, including cuticular remains, muscles and organs. The main factor for this exquisite preservation is considered to be the influence of microbial mats in the fossilization process. Petrographic and scanning electron microscope analysis with coupled x-ray spectroscopy (SEM/EDS) showed direct and indirect microbial features associated with the microfabric of the orthopteran insect fossils. We propose a four-steps model for insect fossil preservation, with the capture, protection, creation of the microbial sarcophagus, and mineralization of the organic remains mediated by microbial mats. The confluence of morphological and taphonomic data indicates possible climatic variations on the Aptian of the Araripe Basin, with the exquisitely preserved insect fossils associated with favorable environmental conditions for the installation of microbial mats on the lacustrine substrate.

1. Introduction

During the Cretaceous, the tectonic events related to the Gondwana rifting led to the origin of numerous sedimentary basins in South America and Africa (Matos, 1992; Assine et al., 2014). The Araripe Basin (Fig. 1) is an interior basin in Northeastern Brazil, well-known for its exquisitely preserved fossils, especially in the Crato and Romualdo formations (Martill and Bechly, 2007; Selden and Nudds, 2012; Maldanis et al., 2016; Abreu et al., 2020; Varejão et al., 2021). The genesis of the basin is associated with the Gondwana rifting process, including post-rift stages during which a carbonate deposition occurred in a hypersaline lacustrine system, leading to the formation of the laminated limestones of the Lagerstätte Crato Formation (Brito Neves et al., 2000; Assine et al., 2014; Fambrini et al., 2020; Varejão et al., 2021). Biostratigraphic data suggests an Aptian age for the unit (Arai and Assine, 2020; Melo et al., 2020; Coimbra and Freire, 2021). The Crato Formation fossil record consists of exquisitely preserved fossils, including insects, crustaceans, arachnids, myriapods, fishes, amphibians, turtles, lizards, crocodylomorphs, pterosaurs, dinosaurs, birds, snakes, pteridophytes, conifers, gnetophytes and angiosperms (Martill and Bechly, 2007; Martill et al., 2015; Carvalho et al., 2015a; 2015b; 2019; 2021).

The Crato Formation is considered a wetland ecosystem with seasonal changes from the base level under semiarid conditions (Ribeiro et al., 2021a). According to Varejão et al. (2021), the Crato Formation encompasses six facies associations (FA-3 to FA-8) based on a robust analysis involving geometry, texture, sedimentary structures, paleocurrents, fossil content, taphonomy, and geochemical data. The FA-4 represents the Fossil-Lagerstätte, with approximately 12 m of thick beds of laminated limestones with exquisitely preserved fossils and stromatolites (pseudo-columnar, small to large-sized domal) developed in a hypersaline shallow-water lake system. This interpretation is supported by the widespread microbialites, evaporitic features (halite hoppers and gypsum), and a predominantly terrestrial fauna and flora, as well as by the absence of bioturbation (Varejão et al., 2021).

Concerning the limestone's genesis, sedimentological, petrographic and isotopic data from Heimhofer et al. (2010) suggested

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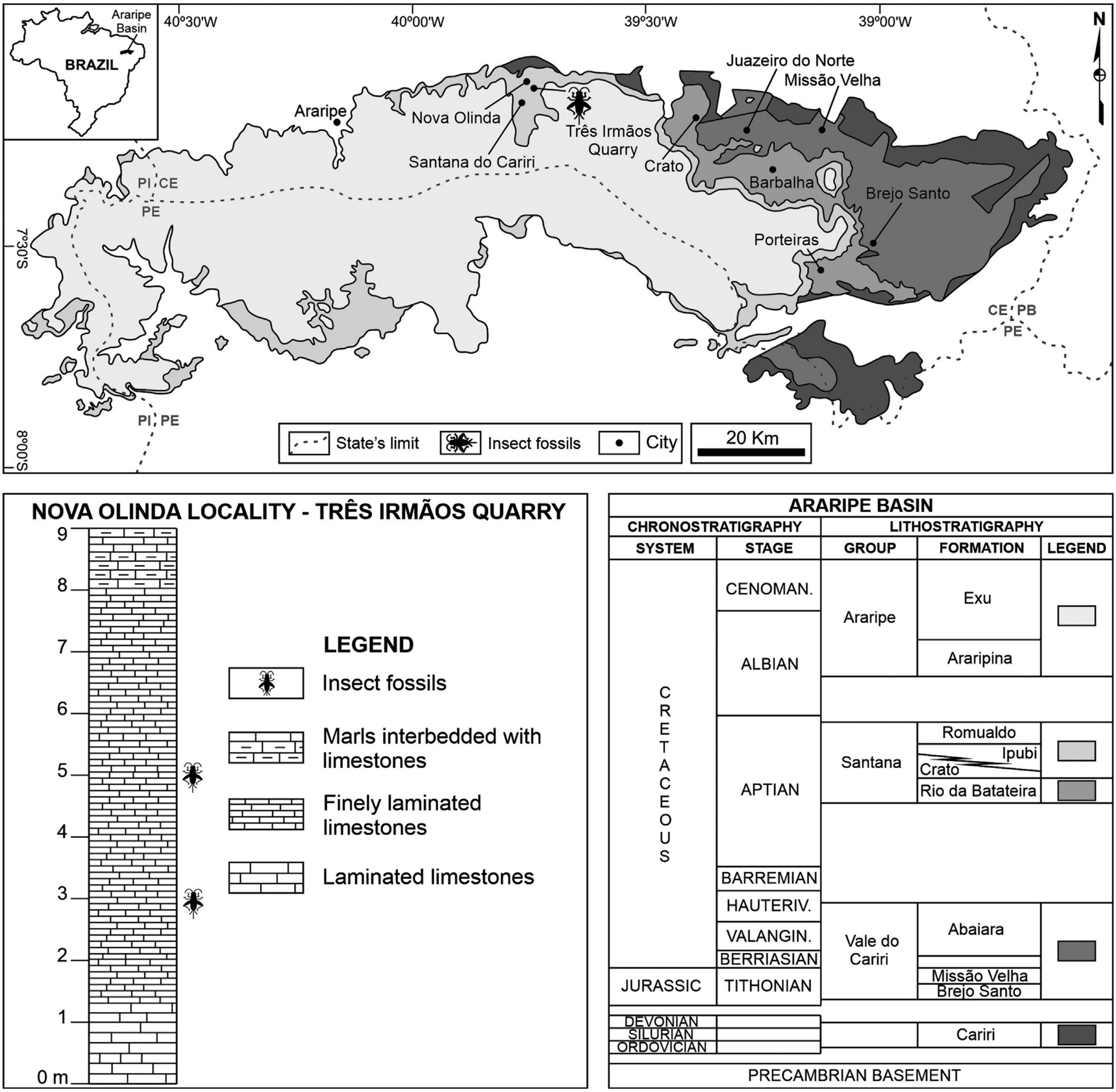

Fig. 1. Geological map of the Araripe Basin and the stratigraphic profile of the Três Irmãos Quarry (7° 6' 9"S and 39° 41' 49"W), where the fossils were collected. Insect fossils commonly occur at the level of finely laminated limestones. The nomenclature of the lithostratigraphic units was based on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

that these deposits were formed due to the authigenic precipitation of calcite in a carbonate lake, without a significant contribution of microbial mats. However, Catto et al. (2016), Warren et al. (2017) and Varejão et al. (2019) presented several lines of evidence in favor of microbial influence on the origin of the laminated limestones, suggesting that the metabolic activity of these microorganisms played a significant role in their formation.

The insect fossils recorded in the lithographic limestones of the Crato Formation have been generally analyzed as far as their taxonomy and paleobiology is concerned, mainly due to the preservation of external and internal features, including muscles, organs and other soft tissues (Barling et al., 2015, 2020, 2021; Osés et al., 2016; Bezerra et al., 2018, 2020, 2021; Dias et al., 2019; Dias and Carvalho, 2020; Moura-Júnior et al., 2020; Nel and Pouillon, 2020; Pouillon and Nel, 2020; Prado et al., 2020; Ribeiro et al., 2021b; Santos et al., 2021). Experimental studies of Iniesto et al. (2020) on the decay of insect larvae and its relationship with microbial mats allowed a comparative analysis between textural aspects of the larvae carcasses and the insect fossils' microfabric from the Crato Formation. The fossilization mediated by these microbes is a significant factor leading to the origin of the Crato Lagerstätte (Dias and Carvalho, 2020).

Given the high relevance of the preservation studies of the Fossil-Lagerstätten, this paper focuses on the influence of microbial mats in the exquisite preservation of the insect fossils from the Crato Formation. We present a more detailed approach based on microtextural and geochemical data that support the control of these microorganisms on the fossilization process. Also, we used preservational data of the insect cuticle as criteria for paleoclimatic inferences for this Cretaceous Fossil-Lagerstätte from Brazil.

2. Material and methods

The study analyzed twenty-five specimens (see Supplementary Material) of insect fossils of the order Orthoptera from the finely laminated limestone levels of the Três Irmãos quarry, Nova Olinda city, south of the Ceará State (Fig. 1). The insect fossils of the Crato Formation are distributed in 16 orders, representing more than half of the diversity of the living orders (Moura-Júnior et al., 2018). It is the most diverse insect paleofauna recorded on a global level. According to Heads and Martins-Neto (2007), the orthopterans are the most abundant fossil elements among the Crato Formation insects, constituting approximately 27% of all forms described. Menon and Martill (2007) considered that this high numerical representation may be associated with an actual abundance of the original population, which justifies the choice of the analyzed material. The fossils are available at the Macrofossils Collection, Institute of Geosciences, Geology Department of Federal University of Rio de Janeiro (IGEO/UFRJ).

The specimens with the highest degree of morphological fidelity (UFRJ-DG 15-Ins, UFRJ-DG 29-Ins, UFRJ-DG 36-Ins, UFRJ-DG 58-Ins, UFRJ-DG 882-Ins, UFRJ-DG 1082-Ins, UFRJ-DG 1503-Ins, UFRJ-DG 1507-Ins, UFRJ-DG 1582-Ins, UFRJ-DG 1661-Ins, UFRJ-DG 1923-Ins, UFRJ-DG 1925-Ins, UFRJ-DG 1926-Ins, UFRJ-DG 1927-Ins, UFRJ-DG 1928-Ins, UFRJ-DG 1929-Ins, UFRJ-DG 1942-Ins) were selected for microscopic and geochemical analysis in a scanning electron microscope (SEM) Hitachi TM3030 Plus with coupled energy dispersion x-ray spectroscopy (EDS). The analyses were carried out at the Centro de Tecnologia Mineral (CETEM) in Rio de Janeiro, Brazil. To avoid their destruction, the fossils were analyzed in a low vacuum, without prior preparation. The specimens were analyzed under voltages of 15 kV average, and the work distance varied between 8.5 mm and 10 mm.

The petrographic analysis was performed through 14 thin sections of eight specimens (UFRJ-DG 1930-Ins, UFRJ-DG 1931-Ins, UFRJ-DG 1932-Ins, UFRJ-DG 1933-Ins, UFRJ-DG 1934-Ins, UFRJ-DG 1935-Ins, UFRJ-DG 1936-Ins, UFRJ-DG 1937-Ins) in an AXIO Scope A1 Zeiss petrographic microscope at the IGEO/UFRJ Biosedimentology Laboratory. The cross sections were produced in two main orientations, head-thorax-abdomen and hind femur, which presents a robust morphology in orthopterans insects. The analysis was made in sections of the organic remains to identify any pieces of evidence that point to the role of microbial mats in the fossilization process. During the preparation of the thin sections, some fossils were completely damaged due to their delicate and friable nature, and could not be identified in the photomicrographs.

The identification of the direct (microbial morphotypes) and indirect (remaining structures of microbial activity) microbial features followed the criteria provided by Tomescu et al. (2016), which will be detailed in the following sections.

3. Insect fossils from the Crato Formation

The insect fossils from the Crato Formation are found in finely laminated limestones, also called the lithographic limestones or plattenkalk, according to Selden and Nudds (2012). These deposits are poorly weathered, with high lateral continuity, tabular geometry, very fine to fine granulation, well-marked presence of planar to undulating lamination, and vertical color variation from yellow to gray (Fig. 2A–C). The lamination is expressed by an alternation of lighter and darker portions within the limestone beds. In the bedding plane, there are microbially-induced sedimentary structures (MISS), such as wrinkles and wavy marks (Fig. 2D).

It is well known that these insect fossils present a high degree of morphological fidelity, with cuticle and soft parts preserved (Barling et al., 2015; Dias et al., 2019; Dias and Carvalho, 2020). The orthopteran fossils are generally preserved dorsally and laterally, with few specimens preserved ventrally. Usually, the fossils are poorly fragmented and well-articulated, with antennae, head, thorax, abdomen, cerci and ovipositor identified (Fig. 2E–F). Due to the higher preservational potential, the posterior locomotory appendices (especially hind femur) are well preserved, including delicate structures such as claws, tibial spines and spurs (Fig. 2F). The high sclerotization of the anterior wings enhances their preservation, and few specimens have posterior membranous wings visualized.

When observed under SEM/EDS, the carcasses may show two main types of preservation: pyritization and kerogenization, associated with different types of laminated limestone (Fig. 3). Pyritized specimens (secondarily replaced by iron oxide according to Osés et al., 2016) mainly occur in yellowish laminated limestones (Fig. 3A), while kerogenized ones are preserved in grayish laminated limestones (Fig. 3B). Replications of internal morphological features by calcium phosphate are also subordinately present (Fig. 3).

The pyritized insect fossils are better preserved than the kerogenized ones. In the yellowish laminated limestones, insect fossils present details of the cuticular and internal features in three-dimensional preservation (Fig. 2E). In the grayish limestones, there is only a massive carbonaceous film on the carcasses' surface, with an absence of soft tissues and few three-dimensional fossils (Fig. 2F).

4. Microbial nature of the Crato Formation insect fossils

The microbial nature of the exquisitely preserved Crato insects can be attested by direct and indirect microbial features. These features are abundant and evenly concentrated in both the fossilized insect carcasses and in the framework of laminated limestones. Direct pieces of evidence are microbial morphotypes and textural features of mineralized EPS visualized on SEM due to their micrometric scale. Indirect pieces of evidence are micro laminations with abundant organic matter, micropeloids, and index minerals that point to a biologically induced mineralization. Due to their higher scale, the indirect features were visualized on the petrographic microscope. The MISS structures are also considered indirect evidence (Fig. 2D).

As direct evidence, coccoids, filaments and needles are occasionally found immersed in a network-shaped texture. Coccoids are spherical to sub spherical, with the same dimension and with sizes measuring, in general, less than 5 μm in length (Fig. 4A–B). Filaments are slightly larger than coccoids, but not as abundant, ranging from 5 to 15 μm in their largest axis, or length (Fig. 4B). Needles are less than 5 μm in length (Fig. 4C) and usually occur associated with the network-shaped texture. Another diagnostic microbial feature is the presence of coccoids with evidence of cell division, which is a strong suggestion of bacterial binary fission, the reproduction process of these prokaryotes (Fig. 4D).

In the insect fossils, direct microbial evidence occurs on the head, thorax and abdomen, covering the surface of the cuticle, as in the polygonal facets of compound eyes, or immersed in the internal

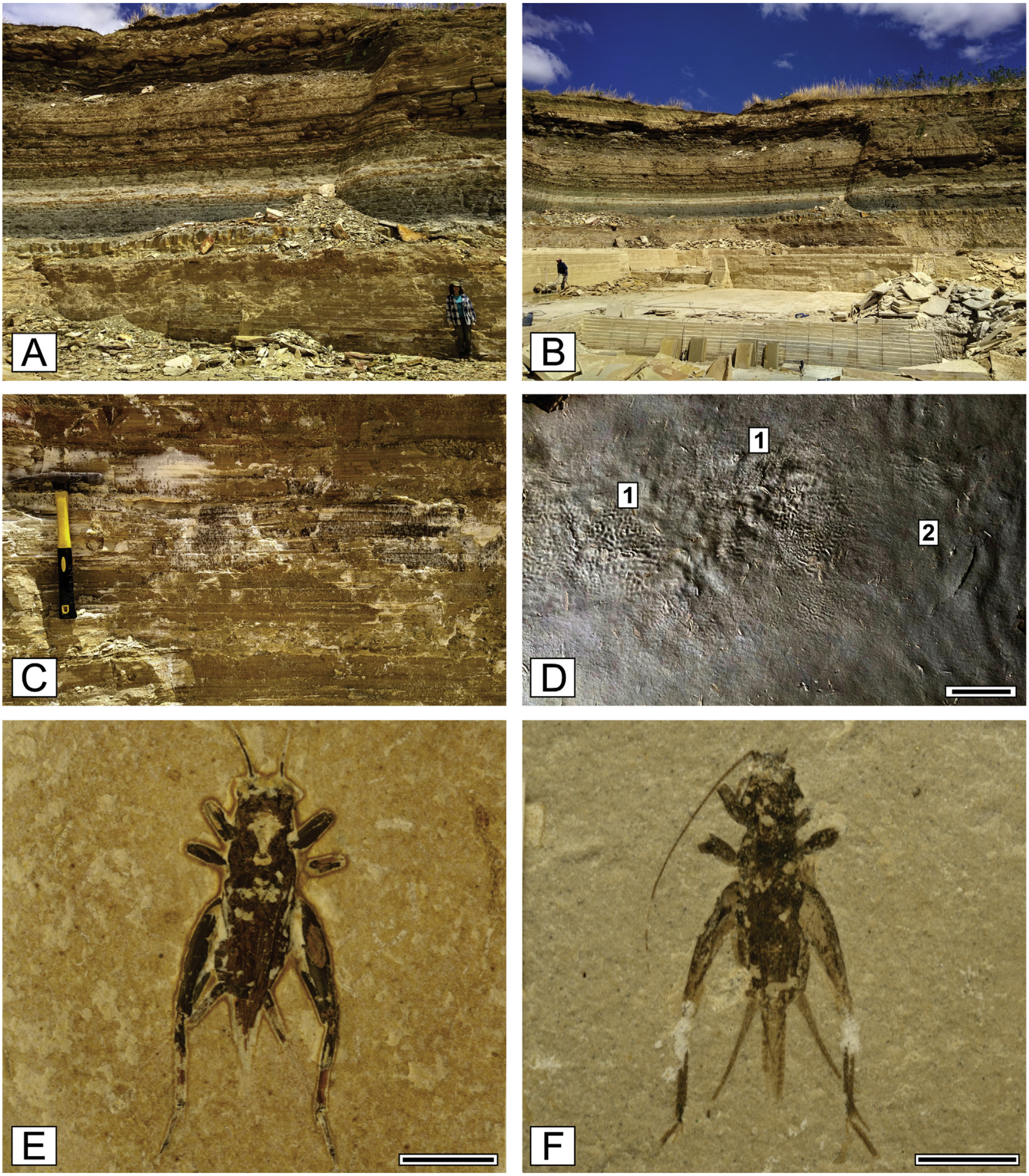

Fig. 2. A, B. Três Irmãos Quarry, Nova Olinda (Araripe Basin, Crato Formation), where the carbonate succession presents lateral continuity, tabular geometry and prominent color changes. C. The finely laminated limestones in which fossil insects occur. D. Wrinkled (1) and wavy structures (2) on the bedding surface of a laminated limestone. E, F. Orthopteran insect fossils with exquisite preservation. The color variation can be observed in the yellowish sample E (UFRJ-DG 1926-Ins) and grayish sample F (UFRJ-DG 1927-Ins). Scale bars: D. 2 cm; E, F. 4 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

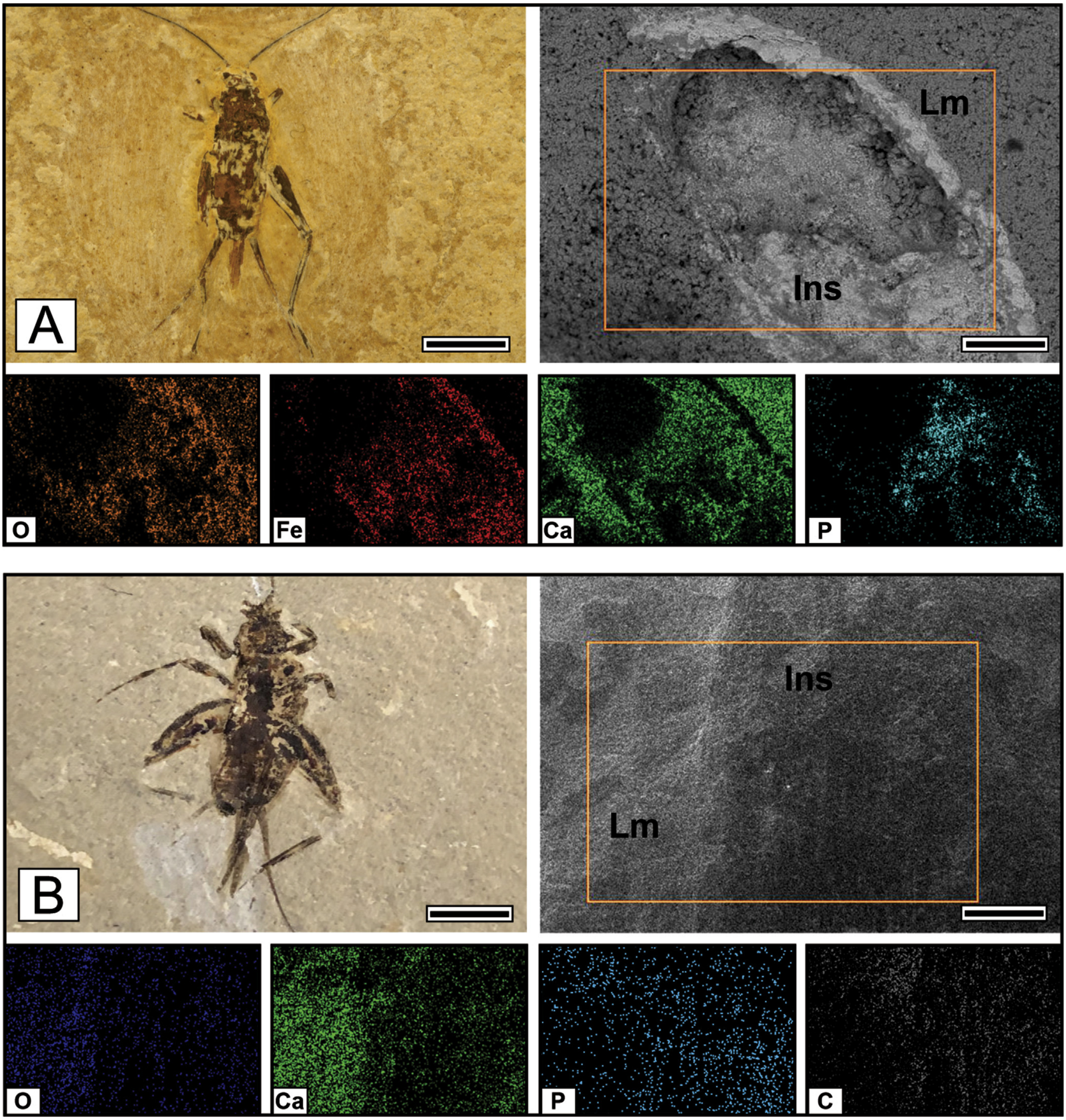

Fig. 3. Insect fossils analyzed in SEM/EDS: A. UFRJ-DG 1925-Ins (Ins) specimen identified in yellowish laminated limestone (Lm) with chemical analysis performed in one compound eye. The analysis enabled the identification of the microfabrica that fills the carcass interior. In this specimen, EDS analyses indicate the presence of iron (Fe) and oxygen (O) in the external and internal portions, and phosphorus (P) and calcium (Ca) in the internal portions. Iron oxide represents a secondary phase of originally pyritized fossils, while the occurrence of P and Ca indicates phosphatization of internal soft tissues. B. UFRJ-DG 1507-Ins (Ins) specimen identified in grayish laminated limestone (Lm), with carbonaceous composition (C) indicating the kerogenization of the carcass, in addition to the presence of phosphorus (P) and calcium (Ca) related to subordinated phosphatization processes. Scale bars: A. 5 cm (left), 100 μm (right); B. 5 cm (left), 600 μm.

parts, like muscle tissues (Fig. 5A–E). In the laminated limestones framework, there are calcium carbonate micro rhombohedra with smooth margins and acicular crystals associated with a network-shaped texture (Fig. 5F–I).

The indirect features are textures, structures and/or minerals indicative of the influence of microbial mats on the fossilization process and/or laminated limestones genesis. Macroscopically, the intercalation of light and dark laminations and the occurrence of wrinkle and wavy structures on the bedding surface suggest a microbial nature for the host deposit (Fig. 2). Microscopically, the laminated limestones exhibit planar to undulated laminations with amorphous organic matter, micritic microfilms, micropeloids and

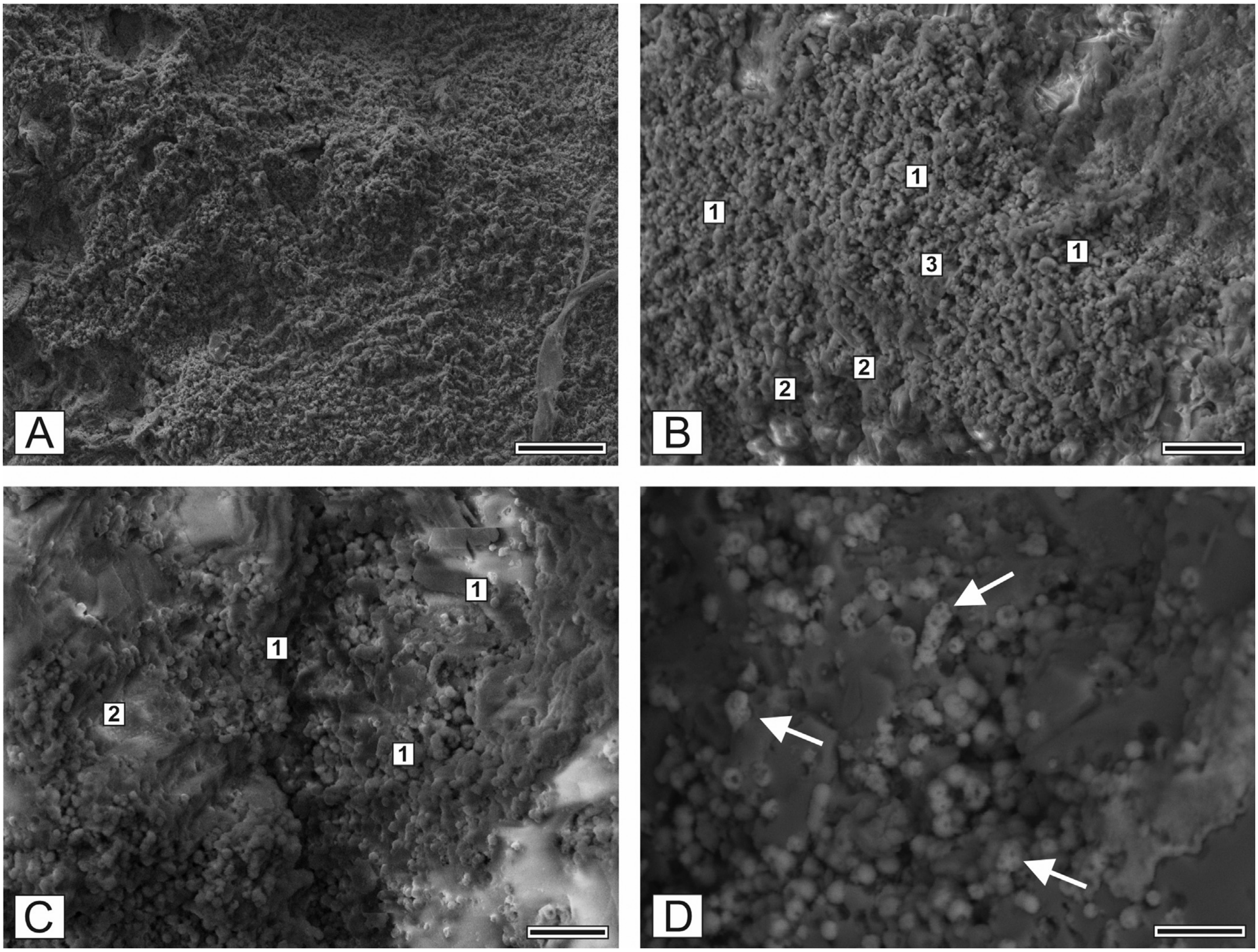

Fig. 4. Direct microbial evidence in insect fossil carcasses from the Crato Formation observed in SEM: A, B, C. General view of the microfabric in the abdominal segment of UFRJ-DG 882-Ins specimen. Presence of coccoids (1), filaments (2) and needles (3) of approximately same dimension and uniformly distributed. D. UFRJ-DG 1929-Ins specimen with tiny coccoids with evidence of cell division (indicated by arrows) that points to the bacterial reproductive process of binary fission. Scale bars: A. 100 μm; B. 20 μm; C. 10 μm; D. 5 μm.

few siliciclastic grains (Fig. 6). The laminations occur as intercalations of lighter-thicker and darker-thinner laminae, with small domes occasionally associated (Fig. 6A and B). The micropeloids are more frequent in the darker, circular to sub circular, well selected, partially flattened and without a recognizable internal structure microbands (Fig. 6C and D). The micritic microfilms are curved to crenulated, discontinuous and parallel to the lamination (Fig. 6B). The orthopteran remains (Fig. 7A–F) occur wrapped in laminations with these curved and crenulated microfilms. Directly associated with the organic remains, there is a higher concentration of micropeloids and microfilms compared to the rest of the rock framework (Fig. 7C and D). This is suggestive of a biogenic control in the entombment of these insects during the fossilization process.

In addition to the textures and structures already mentioned, another indirect evidence is the presence of index minerals, such as pyrite. According to Noffke and Awramik (2013), framboidal pyrite is commonly formed in the cell replication process on microbial mats. The insect carcasses in yellowish laminated limestones were replaced by iron oxide (Fig. 3), which is a secondary phase of the framboidal pyrite. In addition to pyrite, the occurrence of calcium phosphate (Fig. 3), when associated with other microbial features, can also be an indicator of the effect of microbial mats (Noffke and Awramik, 2013; Prieto-Barajas et al., 2018).

5. The role of microbes in the exquisite preservation

Microbial mats are vertically bedded benthic communities, in which millions of microorganisms (essentially, bacteria) are immersed in a polysaccharide matrix called extracellular polymeric substance, or EPS (Gerdes, 2010; Bolhuis et al., 2014; Prieto-Barajas et al., 2018). From a paleontological point of view, the metabolic activity of these microbes can be one of the dominant factors responsible for the genesis of Lagerstätten around the world (Seilacher et al., 1985), as observed in the Upper Jurassic-Lower Cretaceous Pastos Bons Formation (Cardoso et al., 2020), Lower Cretaceous Dabeigou, Yixian and Jiufotang formations (Wang et al., 2012) and Lower Cretaceous La Huérguina Formation (Buscalioni et al., 2016).

The influence of microbial mats on fossil preservation has been widely discussed since the 1990s (Briggs et al., 1993; 1996; 1997; 2005; Briggs and Kear, 1993; Duncan and Briggs, 1996; Wilby et al., 1996; Duncan et al., 1998; Peñalver et al., 2002; Pinheiro et al., 2012; Wang et al., 2012; Carvalho et al., 2013; 2017; Schiffbauer et al., 2014; Iniesto et al., 2015; 2016; 2017; 2018; 2020; Guerrero et al., 2016; Bustillo et al., 2019; Varejão et al., 2019; Cardoso et al., 2020; Dias and Carvalho, 2020; Gäb et al., 2021).

In the insect microfabric of the Crato Lagerstätte, coccoids and filaments are strong evidence of the influence of microbial mats in

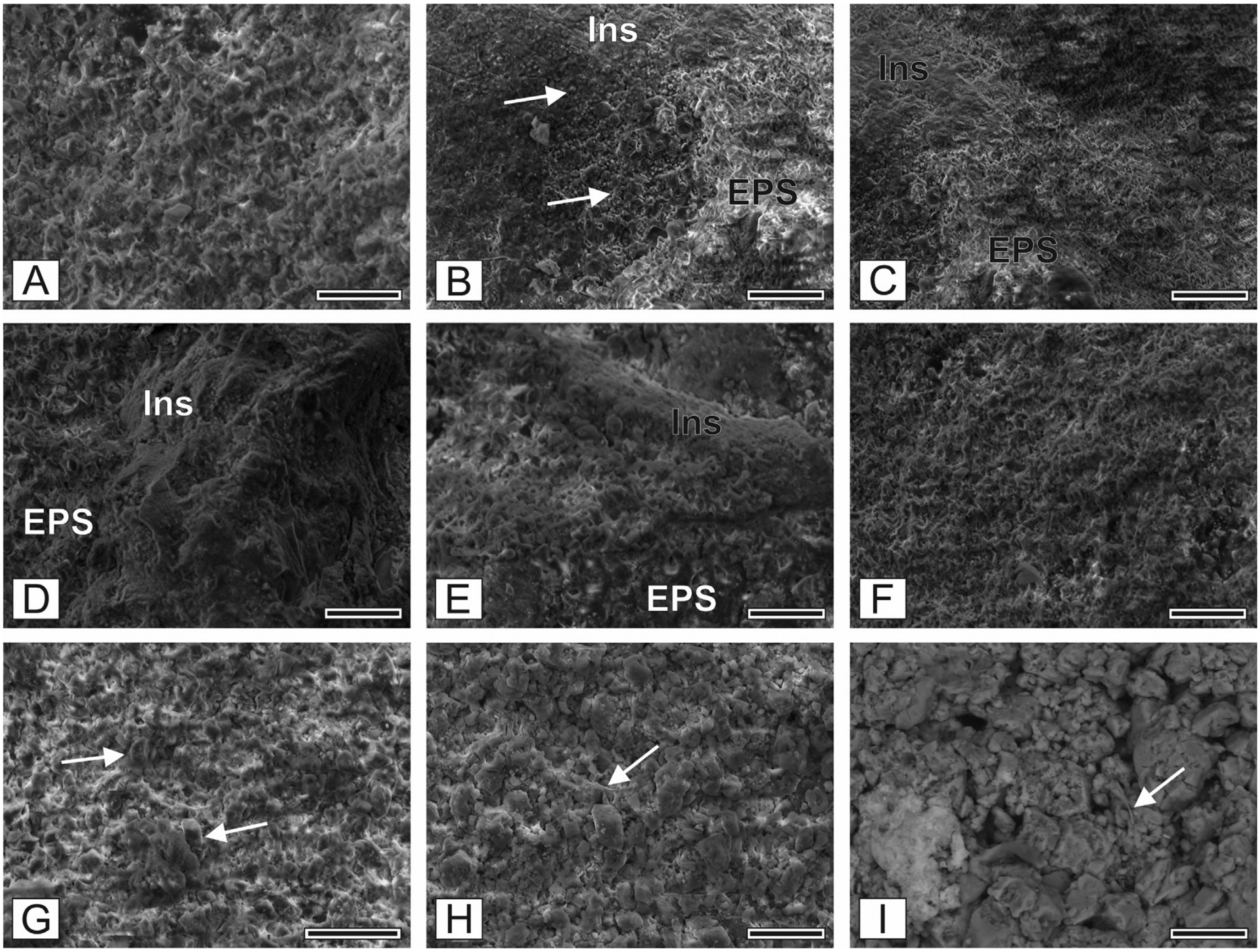

Fig. 5. Direct microbial evidence identified in insect fossil carcasses visualized in SEM: A. Specimen UFRJ-DG 1925-Ins with network-shaped texture, which is indicative of EPS mineralization secreted by bacteria. B, C. UFRJ-DG 1925-Ins specimen with network-shaped texture (EPS) over the compound eye (Ins), with tiny associated coccoids. D, E. UFRJ-DG 1925-Ins specimen with mineralized EPS features associated with insect fragments (Ins), possibly indicating carcasses' trapping by microbial mats, allowing the formation of the microbial sarcophagus. F. UFRJ-DG 882-Ins specimen with network-shaped texture in the laminated limestone framework. G. UFRJ-DG 1926-Ins specimen with calcium carbonate micro rhombohedrons with smooth margins (arrow) identified in the limestone matrix. H, I. Acicular features (arrows) associated with micro rhombohedrons in specimens UFRJ-DG 1926-Ins (H) and UFRJ-DG 1082-Ins (I). These features were interpreted as remnants of mineralized EPS. Scale bars: A. 30 μm; B, C, D, F, G. 50 μm; E. 30 μm; H. 15 μm; I. 10 μm.

the fossilization process (Fig. 4). These morphotypes can originate from organomineralization mediated by these microbes (Dupraz et al., 2009). According to Tomescu et al. (2016), the preservation of microbial body fossils is a cell-to-cell process on a very small scale, in which there is mineral precipitation inside the microbial cell with direct replication of its content. The precipitates can aggregate on the walls of the microbial cells or through the EPS matrix.

Peñalver et al. (2002) considered that the secreted EPS allows the mats to become rigid, adhered to a substrate by a web-like structure. This structure is associated with the network-shaped texture and acicular crystals widely identified both in the fossils and laminated limestones of the Crato Formation (Fig. 5). For Lagerstätten, the main importance of this polysaccharide matrix is that it acts as the nucleation site of organominerals, besides maintaining specific physical-chemical gradients inside the mats (Decho, 2000; Stolz, 2000; Konhauser, 2007). This mineralization was evidenced by the EPS texture, with mineralized coccoids and filaments on the insect microfabric. In addition to the fossils, the EPS texture was also identified next to the calcium carbonate micro rhombohedrons with smooth margins on the limestone framework (Fig. 5). According to Dupraz et al. (2009), this type of crystals could be suggestive of the influence of microbial mats on the precipitation process of carbonates.

5.1. A model for insect fossil preservation from Crato Lagerstätte

In this study, microbial features identified in orthopteran insect fossils from the Crato Formation point to a close relationship between microbial mats and the exquisite preservation of fossils. Since orthopterans are essentially terrestrial insects, the carcasses had to be transported to the lacustrine environment. The high articulation and low fragmentation rates suggest that this transport occurred over short distances. Once the carcasses reached the lake water, the microbial influence on the fossilization process began. We propose four different processes adapted from Briggs (2003), which are perfectly applicable to the exquisite preservation of the insect fossils studied here: capture, protection, microbial sarcophagus and mineralization.

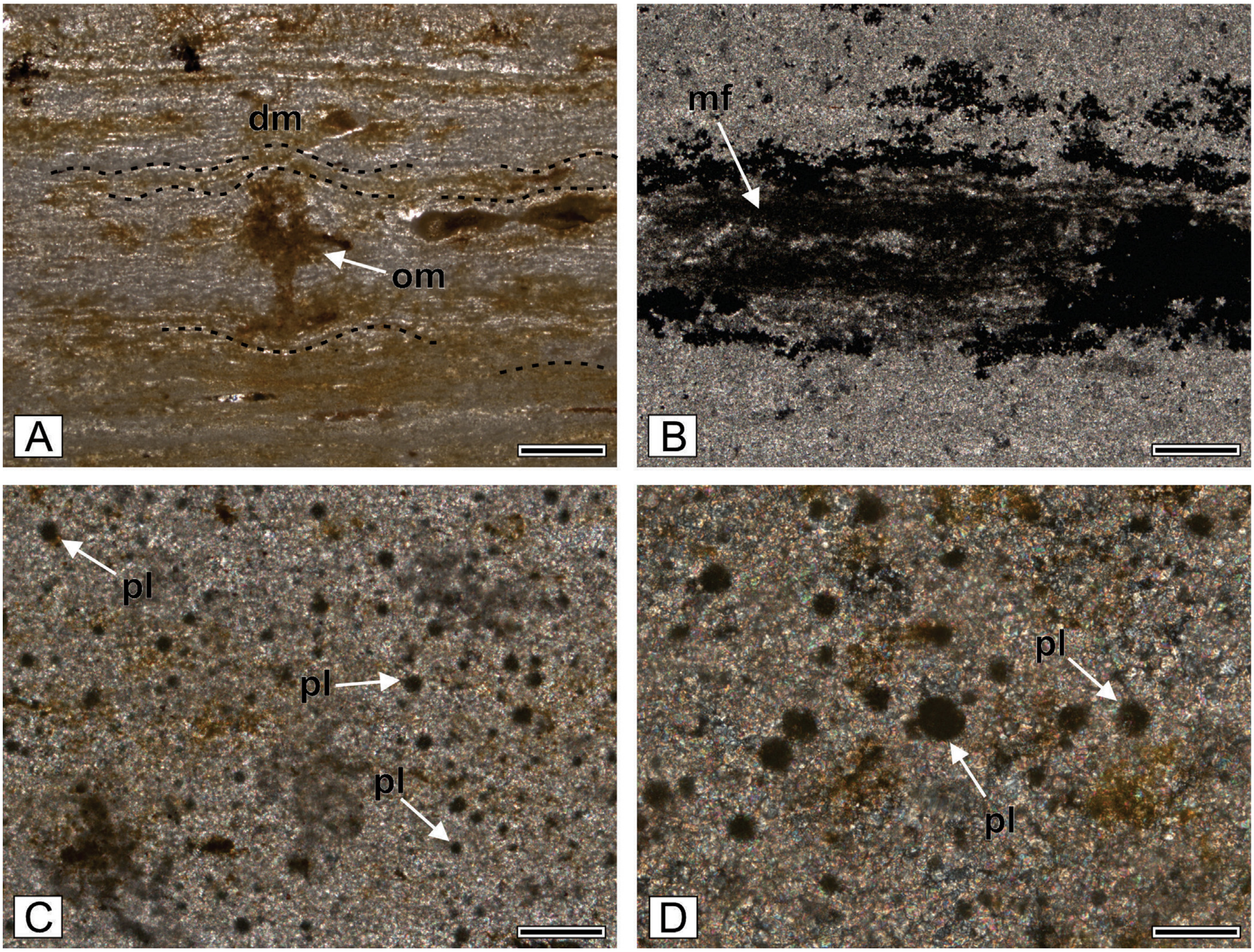

Fig. 6. Petrographic slices of the laminated limestones of Crato Formation showing indirect microbial evidence: A. Planar to smoothly undulated laminations with amorphous organic matter (om) and small domes (dm) associated in sample UFRJ-DG 1934-Ins. B. Curved to crenulated micritic microfilms (mf) produced by biofilms and/or microbial mats in sample UFRJ-DG 1932-Ins. C. and D. Sample UFRJ-DG 1934-Ins with abundance of circular to subcircular and well-selected micropeloids (pl). Scale bars: A. 1 mm; B. 300 μm; C. 400 μm; D. 200 μm.

5.1.1. *Capture*

The capture consists of the carcasses' imprisonment in the water by planktonic microbes, preventing its prolonged fluctuation on surface waters. Water input into the carcasses (through natural openings, such as the tracheal breathing system), associated with the infestation of microbes, increases the carcass' density. This leads to faster sinking, protecting the carcasses from fragmentation by waves and predation, the latter primarily by fishes, widely described in the Crato Formation.

5.1.2. *Protection*

In the petrographic microscope, the insect carcasses appear wrapped in laminations with curved and crenulated micritic microfilms and a higher concentration of micropeloids (Fig. 7). The spatial relationship between laminations, microfilms, micropeloids and fossils, despite the compression, suggests that the insect carcasses deformed the substrate (Fig. 7A and B), pointing to substrate plasticity, probably due to mucilage (directly associated with the EPS) secreted by the microbial mats. According to Decho (2000), this mucilage ensures the attachment of the microbial cells on the surface, acting as a cohesive glue that keeps the particles connected. The high amount of mucilage from the mats reduces high rates of particle suspension, even under the action of waves or currents.

The cohesive action provided by mucilage secretion stabilizes and protects the carcasses, which are subsequently covered by mats. This covering involves the formation of microbial films around insect carcasses on the lacustrine substrate, protecting against fragmentation, disarticulation and erosive action by biotic and non-biotic agents. According to Noffke and Awramik (2013), the sticky nature given by the constant production of mucilage helps in the trapping of organic remains by microbial mats. In the Crato Formation insect fossils, this is associated with the EPS texture with mineralized coccoids and filaments covering cuticle features, as in the polygonal facets of compound eyes (Fig. 5B and C).

5.1.3. *Microbial sarcophagus*

The sealing effect of microbial mats also generates the formation of a microenvironment which, according to Iniesto et al. (2016), is similar to a sarcophagus. The microbial sarcophagus has specific conditions for the mineralization of cuticular remains and soft parts, acting as a chemical barrier that traps and concentrates ions

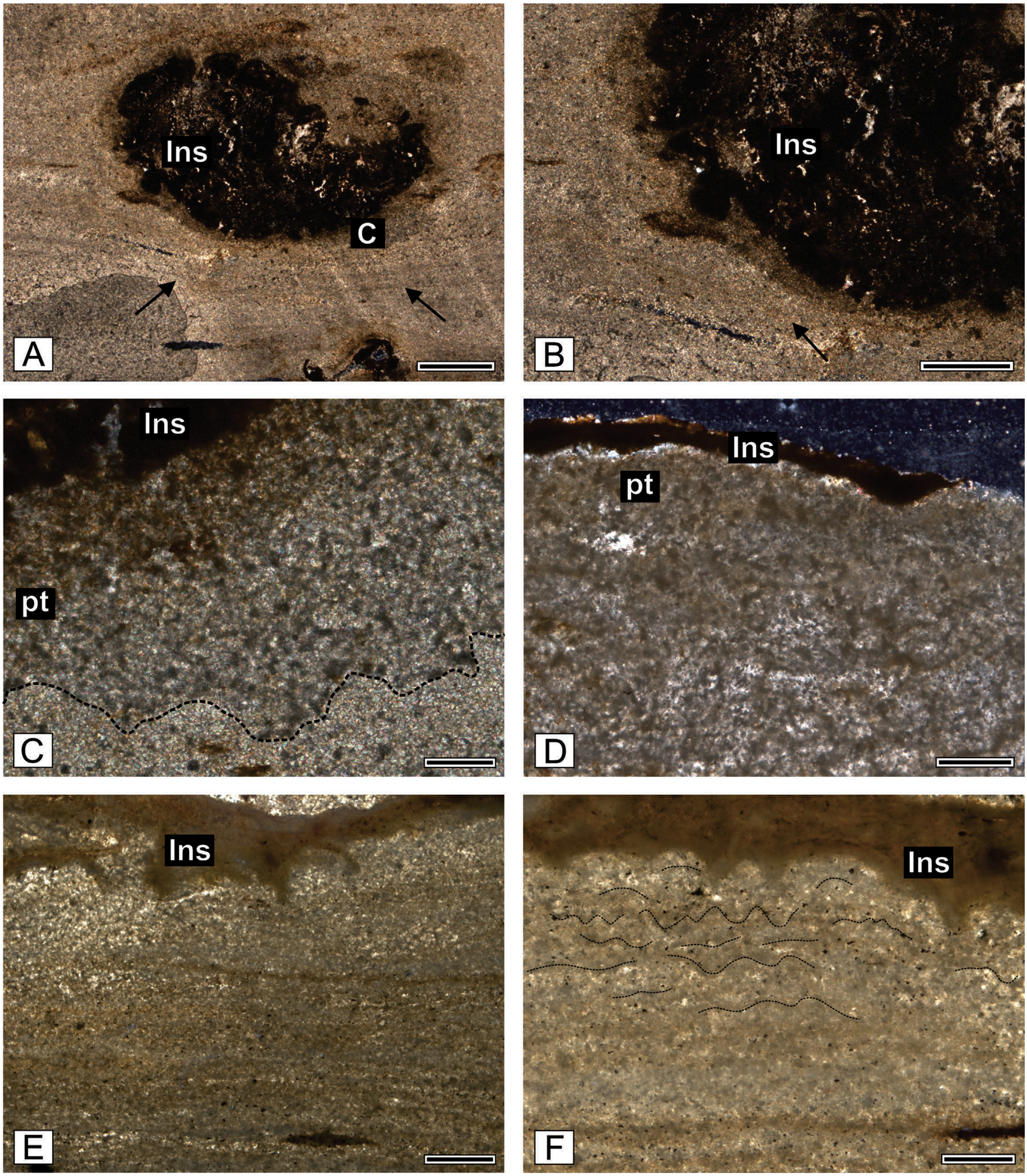

Fig. 7. Petrographic slices of laminated limestones from the Crato Formation showing indirect microbial evidence associated with the insect fossil carcasses: A, B. UFRJ-DG 1937-Ins specimen cross-section of the hind femur (Ins) surrounded by undulated laminations. C, D. Specimens UFRJ-DG 1937-Ins and UFRJ-DG 1933-Ins showing a peloidal texture (pt) close to the insect carcass (Ins). E, F. Insect carcass (Ins) of specimen UFRJ-DG 1931-Ins wrapped in laminations with curved to crenulated microfilms associated. Scale bars: A. 2 mm; B. 500 μm; C. 100 μm; D. 200 μm; E. 400 μm; F. 200 μm.

within the carcasses. Inside the mats, the geochemical gradients could be sharply distinct from the surrounding environment (Gerdes, 2010; Iniesto et al., 2016; 2020). The lacustrine environment of the Crato Formation was commonly inferred to have an anoxic hypolimnion, mainly because the fossil pyritization process was associated with reducing environments (Barling et al., 2015; Osés et al., 2016, 2017; Bezerra et al., 2020, 2021; Dias and Carvalho, 2020). However, anoxia required for pyritization is not necessarily associated with all the lacustrine environment, but rather with microbial sarcophagus within the microbial mats. Therefore, the lacustrine environment could be oxygenated, but the geochemical conditions created on the microbial sarcophagus must be anoxic and reducing, enabling a high rate of mineralization and a low rate of decomposition of organic remains.

5.1.4. Mineralization

For the mineralization process mediated by the microbial mats, we follow the model proposed by Schiffbauer et al. (2014) and Osés et al. (2017), in which there are different taphonomic patterns according to different residence times of the carcasses in sulfate-reduction and methanogenesis zones of the microbial mats, providing fossil pyritization and kerogenization, respectively. Following Saleh et al. (2020), the iron and phosphorous could come from biological tissues themselves, released inside the microbial sarcophagus during the decomposition of the insects. For the kerogenization process, the insects' organic tissues transform into more resistant polymeric compounds with large aliphatic chains, like kerogen, visualized as dark carbonaceous films (Fig. 3B) on the insect fossils (Osés et al., 2017; Iniesto et al., 2020).

Although the exogenous bacteria derived from the microbial mats are essential for this mineralization process, the importance of endogenous microbes must be considered. Experimental taphonomy data involving the fossilization of a decapod crustacean indicated that endogenous bacteria, present in the animal's intestine, were the main controllers of the mineralization process of internal parts (Butler et al., 2015). The data allows us to suggest that the exquisite preservation of internal parts in the Crato insect fossils may have been the result of this process. The well-preserved internal parts, such as ovaries, digestive tract and muscles, in cricket fossils described by Dias and Carvalho (2020), associated with microbial features described in this paper, point to the role of endogenous bacteria in the fossilization process. The reducing and anoxic conditions within the microbial sarcophagus created by exogenous bacteria decreases the autolysis rate (the natural fermentation processes that occur within the cells of an individual after death), allowing the organs and internal tissues to remain intact until they are mineralized by microbes. When the insect carcass is covered by the microbial mat, the bacteria from its digestive tract begin to form microbial biofilms inside the body cavity, initiating the mineralization process of internal remains. This is the main reason that the digestive tract is commonly preserved in fossiliferous locations around the world, while other internal morphologies are lost (Butler et al., 2015).

6. Microbial mats and the lacustrine paleoenvironment

The paleoenvironment where the microbial mats developed was interpreted from petrographic, taphonomic and morphological data of the orthopteran insects themselves. The presence of very fine-grained micritic limestones with planar to undulated laminations, micritic microfilms, amorphous organic matter, micropeloids and few siliciclastic grains (Fig. 6) suggests an aqueous and calm environment with alkaline waters and limited presence of benthic organisms. The wrinkle marks are indicative of low energy environments with reduced waves/current activity and substrate replete with microbial mats (Sarkar et al., 2016). When these structures are associated with the wavy marks and the intercalation of lighter/darker carbonate layers, an intermittent growth of mat layers is suggested. The spatial relation between insect fossil and the laminated limestone framework visualized in petrography (Fig. 7) is also suggestive of a soft substrate with a microbial component.

We consider that the lake substrate of the Crato Formation was proliferated by microbial mats. These very specialized benthic communities are indicative of important environmental particularities. According to Prieto-Barajas et al. (2018), the main source of energy and nutrition of a microbial mat is photosynthesis, which is a limiting factor for its occurrence and distribution across a hypersaline lacustrine environment. Therefore, it is assumed that the waters should be shallow enough for appropriate luminosity to reach the substrate, allowing the photosynthesis reaction of these benthic communities. The data obtained here supports the hypothesis of Varejão et al. (2019; 2021) that microbial mats were widely spread across an oxygenated and shallow lacustrine environment.

The understanding of the nature of insect fossilization in Fossil-Lagerstätten can provide valuable data in paleoecology and in the depositional environment of the analyzed deposit (Smith, 2012). According to Sperber et al. (2012), an insect fauna with abundant and diversified orthopteran insects is suggestive of tropical and subtropical regions, with a climate marked by seasonality between more humid and arid periods. This sensitivity can be measured, for example, by the varying thickness of the insect cuticle (Gullan and Cranston, 2014). We used the fossil preservation rate and three-dimensionality of the specimens as criteria for indirect measures of the cuticle thickness, which points to possible climate oscillations on the Aptian of the Araripe Basin (Fig. 8).

The better preservation of cuticular features and the three-dimensionality in pyritized insects preserved in the yellowish limestones could indicate more arid conditions, with thicker cuticles to prevent water loss. Arid periods can be associated with shallower, saline and stagnant waters, with a reduced discharge of material into the basin by river influx. These conditions are favorable for the broader development of microbial mats on the lacustrine substrate. On the other hand, low preservation in kerogenized insects in the grayish limestones is associated with more humid conditions and thinning of the cuticle. Humid periods are associated with a greater discharge of material into the basin by river influx, increasing depth and decreasing water salinity. In these conditions, the development of microbial mats was limited compared to dryer periods, which would explain the lower degree of fossil preservation identified in the grayish limestones.

Climate seasonality during the Aptian of the Araripe Basin was pointed by Guerra-Sommer et al. (2021) based on fragments of permineralized woods of the Crato and Romualdo formations. The climatic oscillations were already suggested by taphonomic, isotopic and sedimentological studies (Varejão et al., 2021; Ribeiro et al., 2021a), and cyclostratigraphic analysis (Gomes et al., 2021). Also, Osés et al. (2017) pointed out that different preservation patterns of fish fossils of the Crato Formation are associated with sedimentation rates in different climatic conditions. During humid periods, there are high sedimentation rates, a greater burial of the carcasses and longer residence time in the methanogenic bacteria zone, a lower portion of the microbial mat. These conditions permit fossil kerogenization. Likewise, pyritization is associated with more arid periods, low sedimentation rates and longer residence time of carcasses in the SRB zone.

This relation between climatic oscillations associated with different fossil preservation patterns is also identified in other Cretaceous Lagerstätten, like the lithographic limestones of Las Hoyas in Spain. As we proposed herein, the greatest potential for

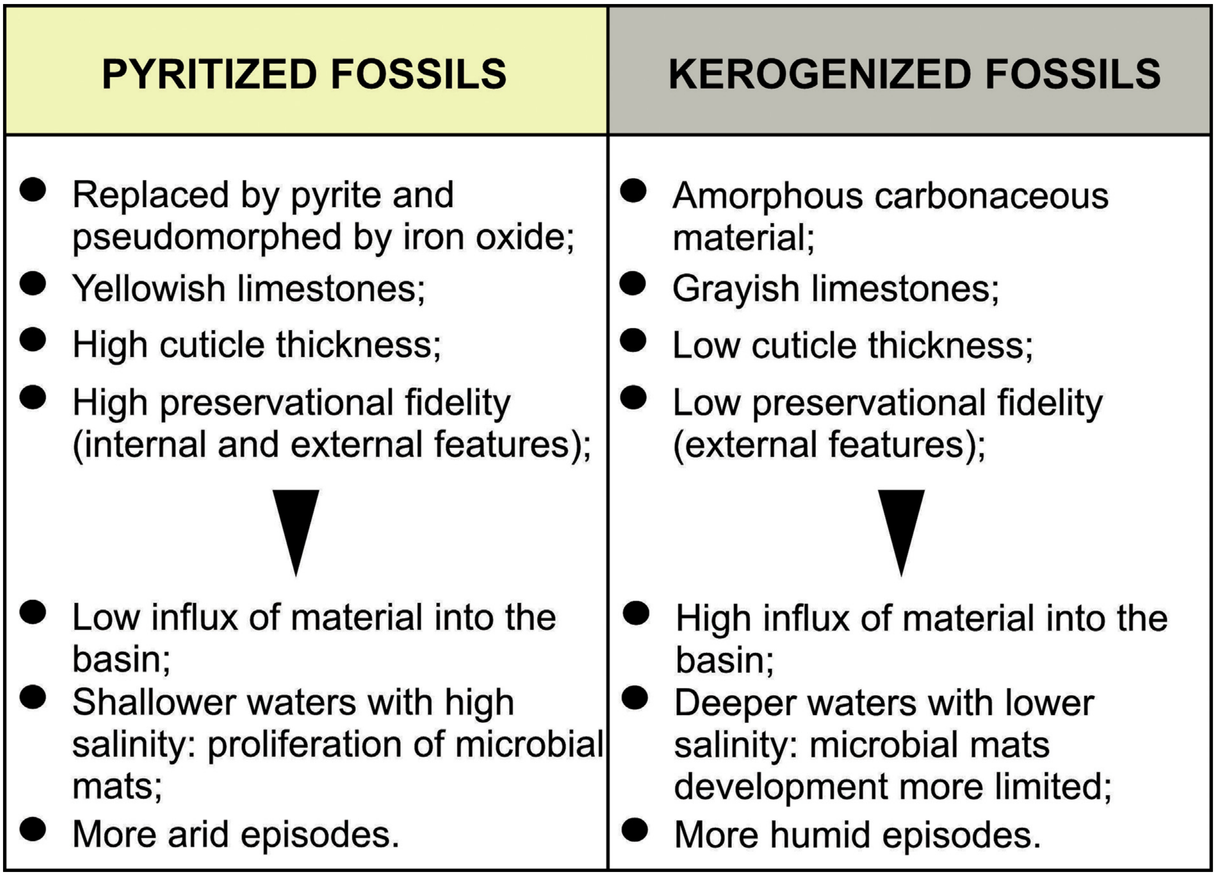

Fig. 8. Summary of the distinct fossil preservational patterns (pyritized and kerogenized) and morphological data involving the insect cuticle preservation, which may indicate environmental and climatic oscillations in the Aptian of the Araripe Basin.

fossil preservation in this locality would be associated with arid periods, when microbial mats proliferated on the substrate. During wetter times, the increase of rainfall and the consequent higher level of lake water were not favorable for the broad development of the mats, decreasing fossil preservation potential (Selden and Nudds, 2012; Buscalioni et al., 2016; Guerrero et al., 2016). In the Lower Cretaceous Yixian Formation of the Jehol Lagerstätte, there are distinct preservational types (pyritization and carbonaceous compression) of *Ephemeropsis trisetalis* remains in a lacustrine environment that records climatic changes during the evolution of the basin. The transition of meromictic conditions of phase 2 to holomictic conditions of phase 3 was accompanied by a turnover from a dryer climate to a humid one (Hethke et al., 2013; Pan et al., 2014).

7. Conclusions

The direct and indirect microbial features identified in the orthopteran fossils of the Lagerstätte Crato Formation allowed us to interpret that the microbial mats were the main agents that enabled the exquisite preservation of insect fossils. The direct microbial features are represented by coccoids, some of them with binary fission, filaments and needles immersed in a network-shaped texture equivalent to the mineralized EPS. The indirect features are planar to undulated laminations, wrinkled and wavy structures, high concentration of amorphous organic matter, micritic microfilms, and abundant micropeloids.

The spatial relation between organic remains and indirect microbial features visualized in petrography (Fig. 7), associated with macroscopic wrinkled and wavy structures, suggest a lake substrate full of microbial mats, with a more plastic and soft nature due to the mucilage secretion by these microbes. The mats acted in the capture and protection of insect carcasses when they reached the lake waters, in the creation of the microbial sarcophagus trapping the carcasses, and in the mineralization of cuticular and soft parts by exogenous and endogenous bacteria. The anoxic and reducing conditions necessary for the mineralization of organic remains are not associated with the full water depth, but with the inside of the microbial sarcophagus.

The morphological analysis of the insect cuticle associated with petrographic and taphonomic data indicates possible climatic changes on the Aptian of the Araripe Basin. Pyritized fossils in yellowish laminated limestones could be associated with more arid periods, with thicker cuticles to prevent water loss, while the kerogenized specimens in grayish limestones indicate more humid conditions, with thinner cuticles. The better preservation of insect fossils in yellowish limestones is favored by thicker cuticles and environmental particularities for the installation of microbial mats on the lacustrine substrate. Arid periods and shallower, saline and stagnant bodies of water are favorable for the installation of these microbial communities and, consequently, for the generation of exquisitely preserved fossils.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2021.105068.