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Remarkable fossil crickets preservation from Crato Formation (Aptian, Araripe Basin), a *Lagerstätten* from Brazil

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ABSTRACT

The paleoentomofauna recorded in the Crato Formation laminated limestones (Araripe Basin, Aptian) represents one of the most important *Konservat-Lagerstätten* deposits globally documented. Among the insects, the high morphological fidelity, abundance and diversity of the Grylloidea superfamily allows a more refined study of the external and internal cuticular morpho-anatomical features and preserved soft tissues. Scanning electron microscope analysis with coupled energy dispersion x-ray spectroscopy (SEM/EDS) show that the carcasses of the grylloids are predominantly replaced by three distinct mineral phases with occurrence of features hardly preserved in the fossil record such as the ommatidia's polygonal facets of compound eyes, cuticular layers differentiation (epi and procuticle), internal anatomical microstructures of digestive tract, ovarian fragments, eggs, and visceral and locomotor muscle tissues. The identification of significant microbial evidence associated with the cricket's carcasses allow us to interpret that the main factor responsible for the exceptional cricket's preservation is the influence of microbial mats in the fossilization process.

1. Introduction

Konservat-Lagerstätten deposits are important sources of evolutionary and paleoecological information of past ecosystems. Their genesis is associated with different geological time intervals (Seilacher et al., 1985; Seilacher, 1990; Allison and Briggs, 1993). During the Phanerozoic, these deposits tended to migrate from onshore to lacustrine and deep marine environments (Allison and Briggs, 1993; Briggs, 2003a). However, according to Muscente et al. (2017), variations in ocean chemistry, oxygenation, and bioturbation rates resulted in dramatic decrements in exceptionally well-preserved assemblages in the marine environments, except in periods with widespread development of ocean floor anoxia.

Consequently, the largest diffusion of *Konservat-Lagerstätten* deposits has occurred in non-marine environments since the Mesozoic. It involved the preservation of faunas and floras in essentially thin and laminated rocks, such as lithographic limestones (Allison, 1990; Allison and Briggs, 1993; Muscente et al., 2017). This is corroborated by the Aptian lake deposits of the Crato Formation of Araripe Basin (Brazil). They consist essentially of laminated limestones and successions of siliciclastic rocks (Martill, 1989; Heimhofer and Martill, 2007).

The paleoentomofauna recorded in these limestones represents one of the most important globally documented *Konservat-Lagerstätten* deposits. It comprises the most abundant, diverse, and exceptionally well-preserved Cretaceous insect fauna (Martill, 1993; Selden and Nudds, 2012; Assine et al., 2014). In addition to insects, the Crato Formation includes fossils of crustaceans, arachnids, fishes, amphibians, chelonians, lizards, pterosaurs, woody plants and algal fragments (Martill, 1993, 2003; Martill and Bechly, 2007; Carvalho et al., 2019).

According to Heads and Martins-Neto (2007), Orthoptera are the most abundant fossil elements recorded in the Crato Formation paleoentomofauna (approximately 27% of all recognized insects). Menon and Martill (2007) considered that this high numerical representativeness may be associated with the actual abundance of the original population. Aptian crickets from the Araripe Basin are included in the third stage of evolution of Orthoptera by Gorochov and Rasnitsyn (2002). This stage is characterized by a wide cricket diversification owing to their morphology, which is favorable for the occupation of different ecospaces. The high diversity is indicated by recent researches into the Brazilian paleoentomofauna by Moura Júnior et al. (2018). It shows that the Grylloidea superfamily is abundant and diverse in the Aptian of the Araripe Basin, with two families (†Baissogryllidae and Gryllidae), 14 genera, and 31 species.

The first taxonomic description of an Araripe Basin cricket was

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provided by Martins-Neto (1987) through the creation of the genus *Araripegryllus* and its type species *A. camposae*. Over the next two decades, the cricket paleofauna of this unit was broadly classified, described, and illustrated by Martins-Neto (1987; 1991a; 1991b; 1995; 1999; 2002) and Martins-Neto and Tassi (2009).

With regard to preservational studies, Barling et al. (2015) and Osés et al. (2016) analyzed multiple orders of insects from the Crato Formation. They described the preserved anatomical features and used paleometry techniques to define the chemical composition of the cuticle and its soft tissues. Regarding to specific fossil-diagenetic studies with grylloids, only Oliveira (2018) analyzed the chemical and mineral composition of three specimens in microscale. This enabled a better understanding of the mineral transformations involved in their preservation.

The high-fidelity preservation, abundance and diversity of the Crato Formation cricket paleofauna enables a more detailed study of the external and internal morpho-anatomical features preserved at the macro and microscopic levels, by focusing on the anatomical parts hardly preserved in the fossil record. Therefore, the scope of this work is the illustration and description of soft tissues, organs, and other external and internal structures of cricket fossils dated at 110 million years. In addition, an overview of taphonomic factors responsible for the high-fidelity preservation is developed.

2. Geology

The Araripe Basin is a large continental basin in northeastern Brazil (Fig. 1). It covers approximately 12 200 km^2 on the south of the Ceará State and portions of Pernambuco, Paraíba and Piauí states (Assine, 1992, 2007; Carvalho et al., 2012). Its sedimentation pattern was strongly controlled by the reactivation of Pre-Cambrian basement structures with the propagation of tectonic stresses related to the continental rifting processes of the Gondwana Supercontinent (Matos, 1992; Camacho and Sousa, 2017). Biostratigraphic analysis based on palynological data reveals that the whole Santana Group, which includes Crato Formation, is dated as late Aptian (Fig. 1) (Rios-Netto et al., 2012; Arai and Assine, 2018).

The Crato Formation consolidates lacustrine depositional system implementation during the Aptian on the basin, and comprises sequences of up to 70 m thick, which contain laminated micritic limestones, shales, and fine-to-coarse sandstones (Martill and Bechly, 2007; Assine et al., 2014). The strata outcrops are present on the north, east, and southeast of the Araripe plateau flanks, between the Nova Olinda, Santana do Cariri, Tatajuba and Barbalha cities (Martill and Heimhofer, 2007; Assine et al., 2014). One of the most important *Konservat-Lagerstätten* fossil records are in the laminated limestones, making these Aptian deposits one of the most diverse Cretaceous terrestrial biotas in the world. It was formed while Gondwana was still geomorphologically intact (Martill and Bechly, 2007; Menon and Martill, 2007).

The presence of micritic limestones with fine-scale plane parallel lamination indicates calm and protected environments with low benthic activity, absence of bottom currents, and deposition of sediments below the wave baseline at depths of approximately 50 m. The absence of bioturbation indicates that the lacustrine hypolimnion was hostile and possibly anoxic, forming an area where only highly specialized microbial communities could settle. In addition, the occurrence of halite pseudomorphs reveals episodes of bottom water hypersalinity under extremely dry conditions (Heimhofer and Martill, 2007). Taphonomic analyses using the variation in flexure on the Crato Formation spiders' appendices indicate that the salinity of the lake alternated between low and hypersaline periods (Araújo-Júnior and Carvalho, 2015; Downen et al., 2016). On the basis of the intercalation of laminated limestone levels with lutaceous and arenaceous siliciclastic rocks, Silva and Neumann (2003) indicate that the lithofaciological association of the unit represents a lacustrine system associated with fluvio-deltaic environments.

The intercalation of discontinuous laminated limestone banks with shales and sandstones may be indicative of climatic variations between hot and dry and hot and humid periods, accompanied by expansion and retraction events of the lake. The abundance of continental fossils is representative of a depositional site enlarged beyond the boundaries of the sedimentary successions of the rift phase, with depositions over the Precambrian crystalline basement (Heimhofer and Martill, 2007; Martill and Bechly, 2007; Assine et al., 2014).

3. Material and methods

One hundred and seventy eight specimens of grylloids were analyzed. They ranged from the yellowish laminated limestone to the yellowish/grayish laminated limestones (Fig. 2) from Pedra Branca and Três Irmãos quarries localized in Nova Olinda city, south Ceará State (Fig. 1). The fossils are part of the macrofossil collection of the Institute of Geosciences, in the Rio de Janeiro Federal University.

Prior to analysis, the specimens were mechanically prepared to remove excess matrix and expose previously covered anatomical parts. In addition to a Zeiss SteREO Discovery V20 stereomicroscope coupled to a Zeiss AxioCam MRc5 camera, dentist instruments, such as spatulas, exploratory probe, tweezers, and diggers; brushes; and needles were used. The specimens were macroscopically illustrated by a NIKON D600 camera with a 60 mm NIKKOR Micro lens and aperture of scale 1:2.8, and regulated using a tripod. Alcohol was applied with a plastic pipette at the surface of certain fossils for better visualization of anatomical features.

The elements 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 1053-Ins, UFRJ-DG 1057-Ins, UFRJ-DG 1923-Ins, UFRJ-DG 1925-Ins, UFRJ-DG 1926-Ins, UFRJ-DG 1927-Ins, UFRJ-DG 1928-Ins and UFRJ-DG 1929-Ins) were selected for chemical analysis and illustration of microscopic anatomical features by using Scanning Electron Microscope (SEM) Hitachi TM3030 Plus coupled with energy dispersive x-ray spectroscopy (EDS). To minimize fossil destruction, the specimens were analyzed under low vacuum without prior preparation. The spectroscopic chemical analyses were performed preferably punctually, and then, secondarily in the form of chemical mappings. Initially, the analyses were focused on the external cuticular regions. Subsequently, they were focused on the internal cuticles and soft tissues. For three-dimensional specimens, the empty spaces identified in the fossils were analyzed to locate possible internal features of fossilized muscle tissues and/or organs, without manual fragmentation. The microbial features were identified and interpreted primarily using guides on the biogenicity of microbial fossils extracted from Tomescu et al. (2016).

4. Exceptional preservation

The Aptian crickets of the Araripe Basin exhibit a high degree of morphological fidelity. They display macro and microscopic anatomical features and mineralization of cuticular regions and internal soft tissues (Fig. 3). Commonly, the specimens are articulated and poorly fragmented, with folded wing-like shapes (Fig. 3A), open wings (Fig. 3B), or isolated tegmina. Moreover, they are preserved in different positions, providing ventral (Fig. 3D), dorsal (Fig. 3A), or lateral views (Fig. 3B), and two- or three-dimensionally individualization of the head, thorax and abdomen. The morpho-anatomical features identified here will be grouped, described, and illustrated under three categories: i) cuticle; ii) head; and iii) thorax and abdomen.

4.1. Cuticle

The cuticle is a chitinous natural biocomposite secreted by plasma membrane plaques from the upper portion of insect epidermal cells (Merzendorfer, 2013). Its composition is chitin-protein, occasionally

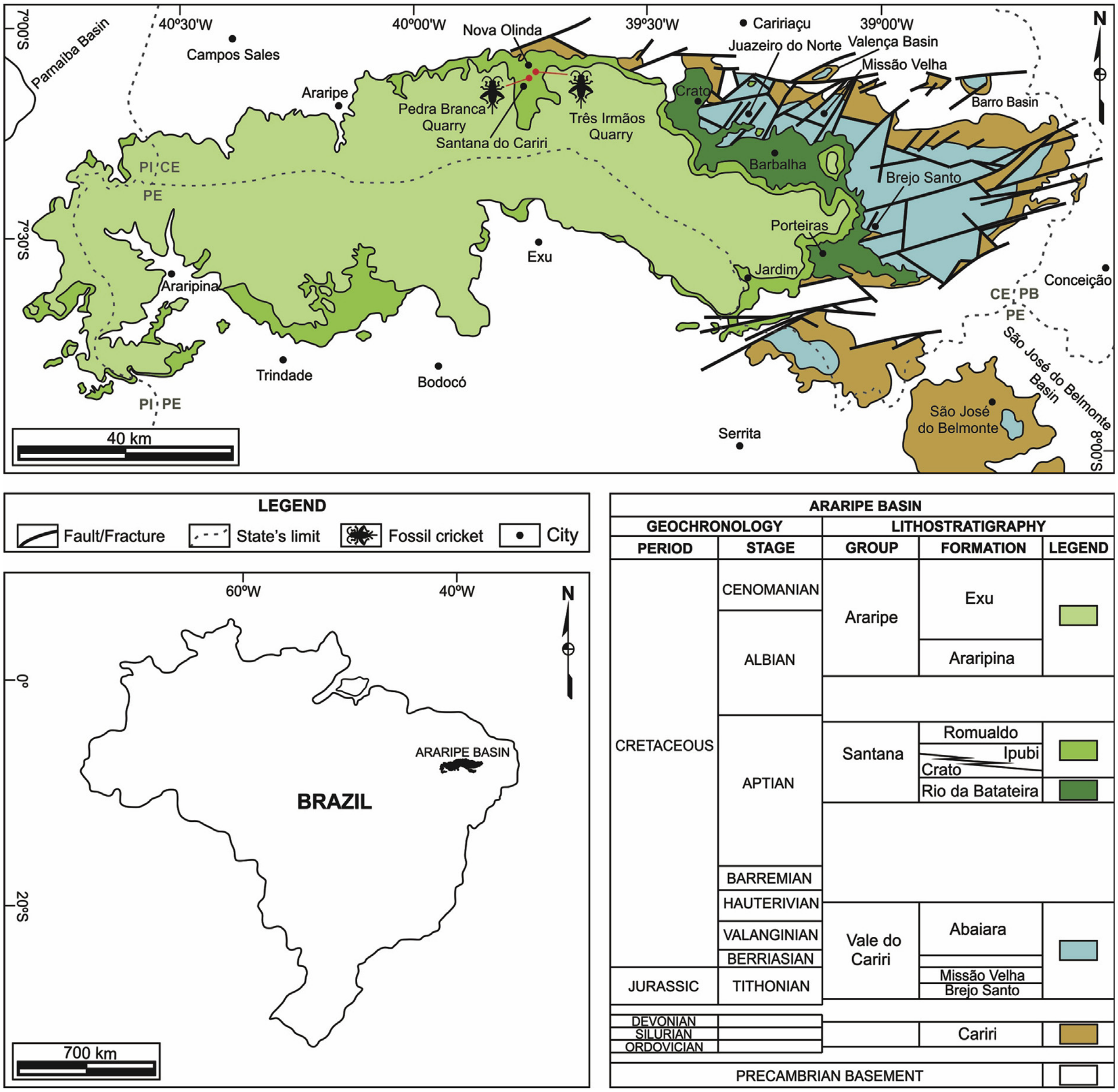

Fig. 1. Simplified geological map of Araripe Basin with its position on northeastern Brazil. The fossil cricket's symbol shows the localization of the Pedra Branca and Três Irmãos quarries, where the specimens herein analyzed were collected. The nomenclatures of the lithostratigraphic units followed Rios-Netto et al. (2012) and Assine et al. (2014). Geological map modified from Assine (2007).

impregnated with carbonate and/or calcium phosphate; and coated with sclerites, which are rigid sclerotized plates (Davies, 1988). It comprises the outermost portion of an insect, covering almost its entire body, as well as invaginations such as proventriculus, posterior intestine and tracheal breathing system (Merzendorfer, 2013).

According to Davies (1988), the cuticle can be subdivided into the outermost epicuticle and innermost procuticle. The latter is subdivided into the exocuticle and endocuticle. In the Crato Formation crickets, the epicuticle is preserved as a highly thin film with a reddish-brown color, massive texture, and thickness less than 5 μm, without microtextural differentiation inside, and with sensilla insertion holes in the surface region (Fig. 4A and B).

The low preservation of the epicuticle in most specimens is owing to the minimal degree of sclerotization of this layer compared to the exocuticle, as well as the essentially protein composition. The exception occurs in specimens with surface micro-cracking features, possibly indicating exoskeleton dryness under extremely arid conditions (Fig. 4C and D). The best cuticular preservation of those crickets could possibly occur by increasing the epicuticle wax (cement layer) in more arid periods to minimize water loss to the environment.

Owing to the higher degree of sclerotization and chitin-protein composition, the procuticle is commonly preserved in fossils as a layer with incipient lamination and occasional microfibrils recognition (Fig. 4E and F). Exceptions are the regions with higher skeletal flexibility such as joints, where the exocuticle is reduced or absent; this favors the disarticulation of post-mortem remains. According to Moussian (2010), microfibrils are the result of crystallization of chitin polymers, which associated with other cuticular proteins form a high strength supramolecular chitin-protein complex responsible for the mechanical rigidity of the cricket cuticle. The massive texture of the epicuticle, laminate exocuticle, and membranous endocuticle were observable on a cross-section (4E,F).

McNamara et al. (2012) also recognized the exceptionally preserved characters of the cuticle layers on the basis of scanning electron microscopy (SEM) studies of the color pattern of Cenozoic beetles of various *Konservat-Lagerstätten* deposits. According to these authors, the

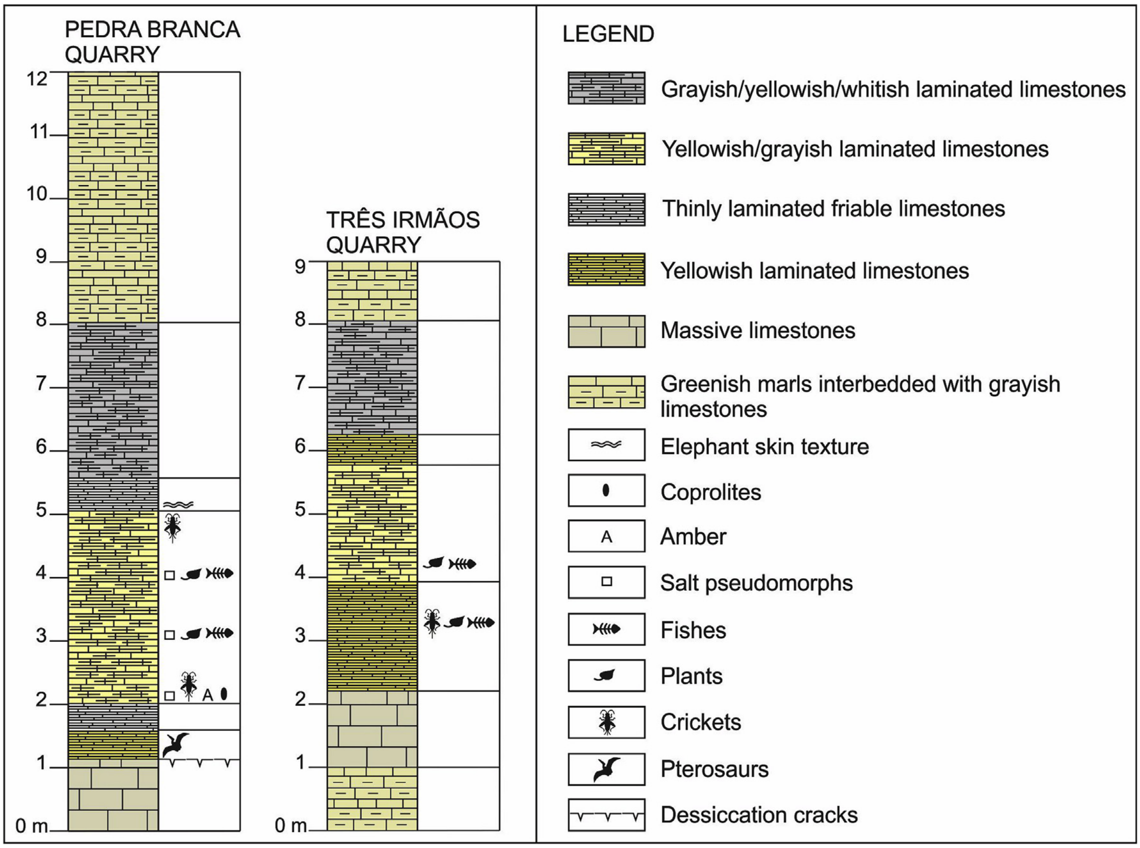

Fig. 2. Stratigraphic surface profiles of the locations where the cricket specimens were collected, with two different levels from Pedra Branca Quarry (7° 7′ 11″S and 39° 41′ 56″W) and one from Três Irmãos Quarry (7° 6′ 9″S and 39° 41′ 49″W). Fossil crickets commonly occurs associated with other insects, as well as coprolites, plant fragments, fishes, ambers and salt pseudomorphs.

preservation of the cuticle's ultramicroscopic textures as well as the insect staining pattern is directly associated with the low rate of soft tissue decomposition and chemical weathering.

Another factor that influences the preservation of the ultrastructure of insect cuticular layers is the sclerotization rate. It varies between different stages of development or in different parts of the same insect. According to Merzendorfer (2013), the sclerotization of insects occurs by the formation of crosslinking between cuticular proteins, forming a rigid matrix into which chitin microfibrils can be inserted. Depending on the region of the cricket, different amounts and types of proteins can interconnect with chitin, thereby generating regions with different resistances in the same individual (Gullan and Cranston, 2014; Rafael and Marques, 2016).

4.2. Head

The insects' compound eyes comprise hundreds to thousands of units called ommatidia (Fig. 5A). Each ommatidium is composed of light-collecting sensory devices. These transform light into electrical pulses that aid the insects' vision (Alexander and Otte, 2003; Gillot, 2005; Triplehorn and Johnson, 2005; Land and Chittka, 2013). In the Crato Formation crickets, the compound eyes are robust and well developed, with densely packaged polygonal facets corresponding to the ommatidia inside (Fig. 5B and C). A lateral ocelli was also identified, a small light-sensitive structure located between the compound eyes as a tiny hole partially filled with sediment (Fig. 5F).

In addition to compound eyes, a morphological feature commonly preserved on the head of the Araripe Basin Aptian grylloids is the long filiform antenna, mainly identified in the Gryllidae family specimens (Fig. 5A). The basal escape, pedicel, and a multiarticulated flagellum are visualized and divided into several annuli with fibrous microstructure (Fig. 5D and E). According to Simpson (2013), membranous tissues interconnect the flagellum articles of the antenna. Therefore, their movement occurs by sensory pulses generated by the muscles of the escape and pedicel, radiating to the antenna's extremity.

Although grylloids are hypognathous insects, with mouthpieces that are well pronounced and directed to the ventral portion of the head, the chewing apparatus is hardly visualized, with mandible and maxillary palp differentiation in only one specimen (Fig. 5F). Mouthparts, such as the labrum, hypopharynx, and other palps may be covered by sediments. This is because more delicate features of the head, such as the polygonal facets of the ommatidia or filiform antennas exhibit exceptional preservation, whereas naturally highly sclerotized features, such as mandibles occur in only one specimen. Owing to weather variations, the cuticle of these grylloids is commonly highly friable, hindering a deeper mechanical treatment of the specimens without eventual fragmentation.

4.3. Thorax and abdomen

The thorax is the intermediate tagma of insects. It consists of three segments: prothorax (anterior), mesothorax (intermediate) and metathorax (posterior). Each has a pair of legs, and the third has two pairs of wings. The membranous region between the head and thorax, called the cervix, is equivalent to a neck in the vertebrates. The pronotum, the dorsal region of the first thoracic segment, is a differentiated intermediate region of the thorax rather than an individualized segment. It is well pronounced in grylloids (Grimaldi and Engel, 2005; Capinera, 2008; Gullan and Cranston, 2014). The preservation of the extended and pronounced pronotum is common in the analyzed specimens, although it is not conveniently distinguishable from the other thoracic segments.

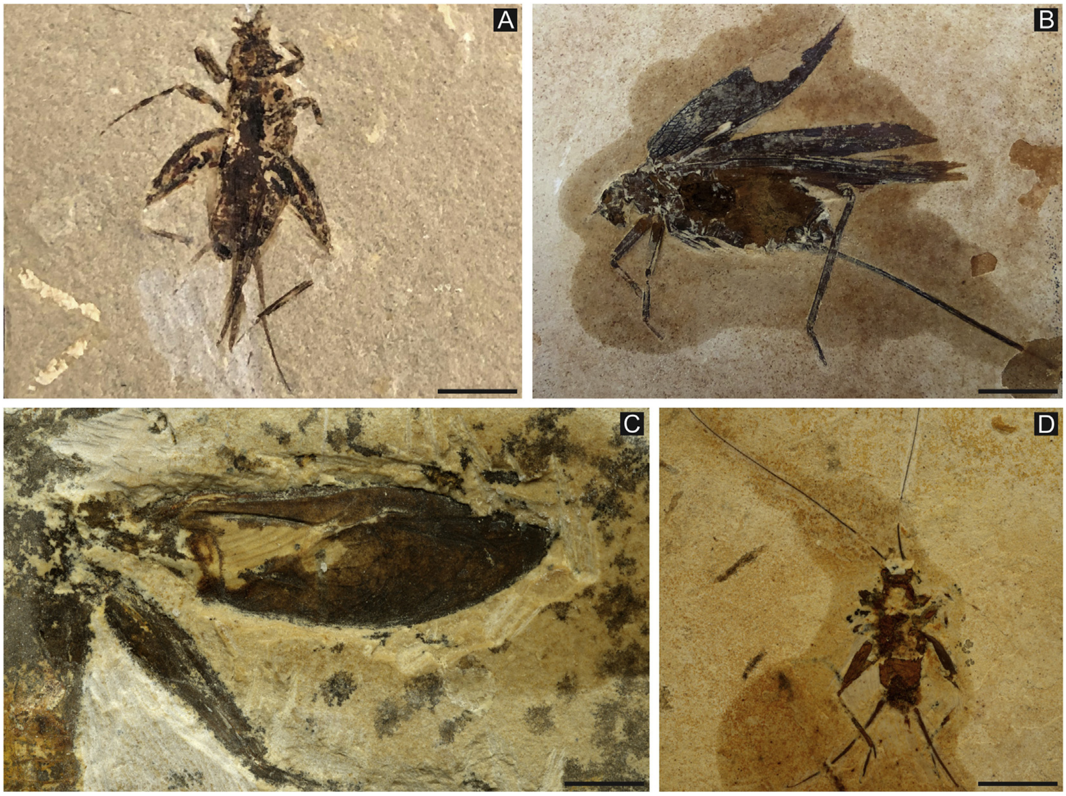

Fig. 3. Fossil crickets from the Crato Formation and its macro-view of anatomical parts with high morphological fidelity, articulated and poorly fragmented carcasses: **A.** Dorsal view of female Gryllidae specimen with wings folded close to the body and head, thorax, abdomen, legs, cerci and ovipositor well preserved (UFRJ-DG 1507-Ins). Scale bar: 5 mm. **B.** Lateral view of female Baissogryllidae specimen with open wings and exceptional preservation of the long and tubular ovipositor, tympanic organ located in the early portion of the anterior tibia, tegminas and membranous wings with venation pattern well stablished (UFRJ-DG 882-Ins). Scale bar: 9 mm. **C.** Dorsal view of male Baissogryllidae specimen with focus on well preserved tegmina showing the longitudinal and transversal venation pattern, as well as the stridulatory apparatus (UFRJ-DG 1923-Ins). Scale bar: 5 mm. **D.** Ventral view of female Gryllidae specimen with long and filiform antenna and well-preserved cerci (UFRJ-DG 1929-Ins). Scale bar: 7 mm.

The first and second pairs of legs are cursorial and used for predation. They are covered by the matrix in specimens with dorsal view and conveniently visualized when they are preserved laterally. The long saltatorial hind legs are commonly visualized, with individualization of the dilated femur with dense fibrous muscles, long tibia with ornamentation, tarsus, and post-tarsus. Highly delicate structures are also recognized, such as claws at the post-tarsus terminations, tibial spines (Fig. 6A), spurs and opening of the tympanic organ, located in the early portion of the anterior tibia and capable of detecting the direction of sound over long distances (Fig. 3B).

Insect wings are flap-shaped cuticular projections, supported by tubular sclerotized ribs that constitute characteristic venation systems (Gillot, 2005; Sperber et al., 2012; Gullan and Cranston, 2014). In the analyzed grylloids, the presence of thick, narrow and well-preserved tegmina is common, with clear visualization of the longitudinal and transversal venation pattern, stridulatory apparatus, and cells formed between the veins. (Figs. 3C and 6B). In certain specimens, the mirror area may be obliterated, because the cuticle in this region is naturally thinner and less sclerotized to permit vibration and generation of the classic sound of crickets. Similarly, the lower degree of sclerotization of the posterior membranous wings hinders their preservation. These generally occur only as impressions on embedding rock. However, it was identified in a specimen with well-stablished longitudinal and transversal venation patterns (Fig. 3B).

The segmented abdomen is the tagma with the highest degree of morphological fidelity owing to the higher sclerotization rate (Fig. 6C). The ovipositor is commonly well exposed, ranging from the long and tubular forms of *Cearagrylloides* (up to 1.5 x longer than the body length) to the shorter and thicker form, typical to *Araripegryllus* (approximately half of the body length). In the post-abdominal region, a pair of unisegmented and flexible cerci is identified. They are ornamented by numerous sensory sensilla (Fig. 6D).

In one of the specimens, it was feasible to identify exceptionally preserved internal anatomical structures equivalent to the alimentary canal and female reproductive system. According to Douglas (2013), the alimentary tract of insects exists in the form of a continuous tube limited by a mouth and anus at the opposite ends, with differentiated regions and invaginations inside. It is divided into three main regions: foregut, midgut, and hindgut. The first and last are highly sclerotized as they are of ectodermic origin. Meanwhile, the second is of endodermal origin, which hinders their preservation in the fossil record owing to the low sclerotization rate.

Anatomical microstructures associated with the foregut terminal regions were recognized, specifically the proventriculus, a highly sclerotized region that anticipates the passage of food into the midgut. Extensive cutaneous plaques and denticles are identified as being inserted in a mosaic with microvilli that correspond to the proventriculus covering (Fig. 7A and B). The presence of these cuticular projections in this region of the alimentary tract is directly associated with the mechanical disruption of the proventriculus, which decreases the contact surface of the food, thereby favoring its better absorption by specialized digestive glands located in the microvilli (Douglas, 2013).

The female reproductive system of crickets consists of a pair of ovaries and lateral oviducts interconnected with a median oviduct, which ends in a reception chamber called as spermatophore or vagina. The spermatheca is attached to the spermatophore. It is a storage structure used for reproduction and accompanied by a pair of accessory glands (Simmons, 2013). Two ovarian fragments (Fig. 7C) were

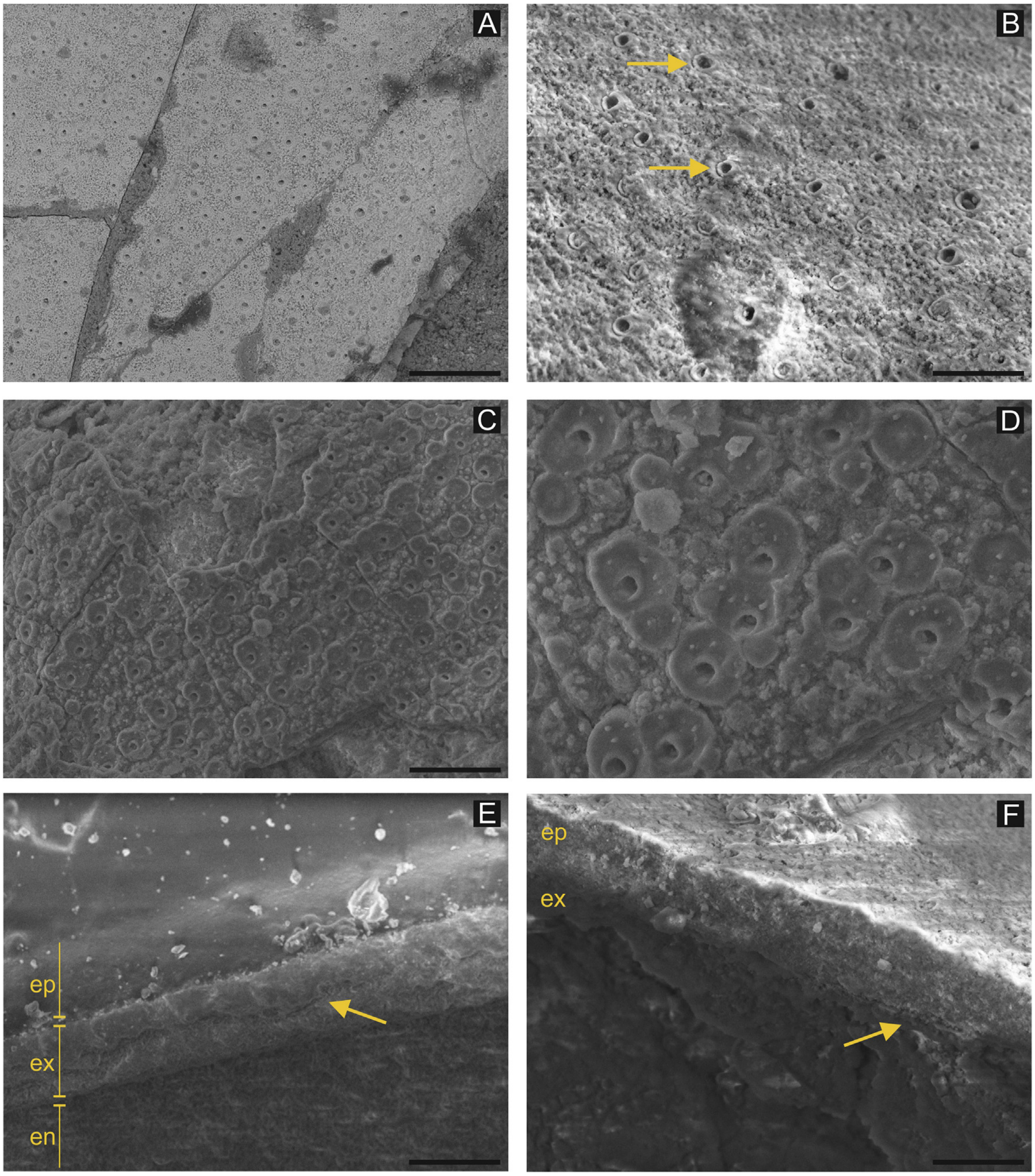

Fig. 4. Morpho-anatomical features of grylloid's cuticle visualized on scanning electron microscopy: **A.** A portion of massive epicuticle with sensilla insertion holes on its surface (UFRJ-DG 1926-Ins). Scale bar: 120 μm. **B.** Detail of the sensilla insertion holes illustrated in A (UFRJ-DG 1926-Ins). Scale bar: 30 μm. **C.** Surface micro-cracking features of epicuticle, a possible indication of extremely arid conditions with dryness of exoskeleton before the fall of carcasses on the lacustrine system (UFRJ-DG 58-Ins). Scale bar: 40 μm. **D.** Detailed view of micro-cracking exhibited in C showing sensilla insertion holes of epicuticle (UFRJ-DG 58-Ins). Scale bar: 20 μm. **E.** Cross section showing massive texture of the epicuticle (ep), microfibrils (setae) of exocuticle (ex) and membranous endocuticle (en), the last one thicker than the other layers (UFRJ-DG 36-Ins). Scale bar: 70 μm. **F.** Poorly preserved fragment with incipient laminar (setae) texture of exocuticle (ex) and well-preserved massive epicuticle (ep) (UFRJ-DG 1926-Ins). Scale bar: 30 μm.

identified in the abdominal region of a female specimen (UFRJ-DG 882-Ins). The fragments have a membranous texture (Fig. 7D) consisting of numerous egg-tubes equivalent to the ovarian follicles aligned and neatly arranged (Fig. 7E). Associated with the ovaries, there is a structure of apparent organic nature. It is possibly equivalent to a spermatheca fragment, which is used to store material from the moment that a female is inseminated by the male until the eggs are fertilized (Fig. 7F). The ectodermal origin with the high rate of spermatheca sclerotization would increase its preservation potential in the fossil record. Small micrometric and tridimensional elements (between 20 and 40 μm) were also identified. Approximately equidimensional, sub elliptic, and predominantly smooth, they are interpreted as cricket's eggs (Fig. 8A and B).

In addition to the proventriculus and ovarian fragments, other delicate anatomical features are also identified in the thoracic and abdominal regions of various grylloid specimens, such as visceral muscle tissues and mechanoreceptors. Insect visceral muscles are characteristically striated (Fig. 8C), and incorporate microfilaments identify their organic nature. They are highly important for air pumping respiratory movement to the spiracles (Taylor, 2013). Meanwhile, mechanoreceptors are evidenced by rod-shaped sensilla adorned by longitudinal lines to the largest axis (Fig. 8D). They are originally coupled to

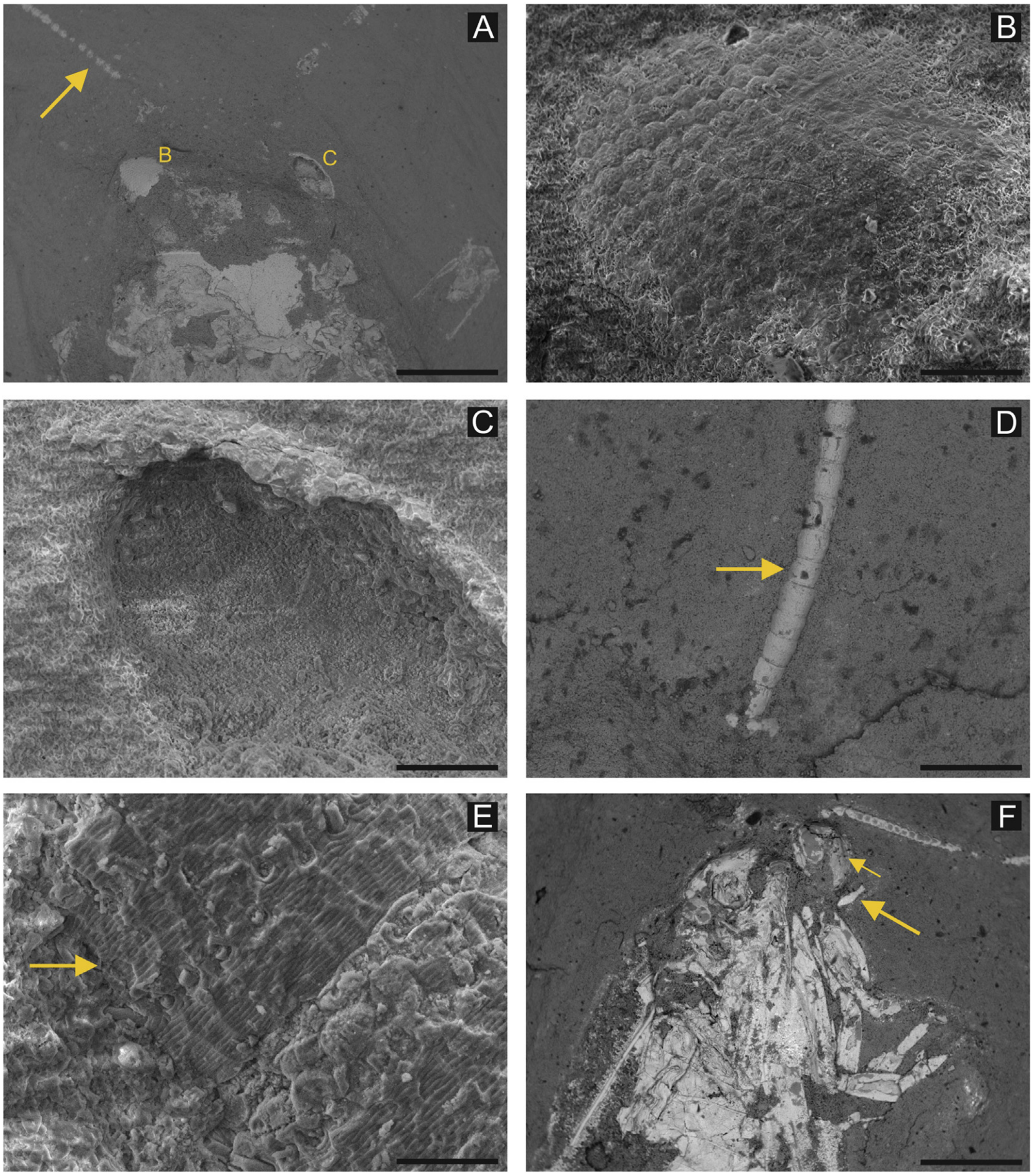

Fig. 5. Morpho-anatomical features of grylloid's head visualized on scanning electron microscopy: **A.** Dorsal view showing cricket's compound eyes and a fragment of filiform antenna (setae) (UFRJ-DG 1925-Ins). Scale bar: 1 mm. **B.** Detailed view of compound eye depicted in A, with densely packaged polygonal facets referent to the ommatidia (UFRJ-DG 1925-Ins). Scale bar: 100 μm. **C.** Detailed view of compound eye depicted in A, with polygonal facets on the outside and very fine internal ommatidia texture (UFRJ-DG 1925-Ins). Scale bar: 80 μm. **D.** Long and filiform antenna (setae) with multiarticulated flagellum divided into several annuli or articles (UFRJ-DG 1926-Ins). Scale bar: 700 μm. **E.** Annuli microstructure with fibrous texture (UFRJ-DG 1929-Ins). Scale bar: 30 μm. **F.** Lateral view of grylloid with very well-preserved antenna, mandible and maxillary palp (big setae) differentiation and a tiny orifice equivalent to lateral ocelli (small setae) (UFRJ-DG 58-Ins). Scale bar: 1 mm.

the surface of the thorax, abdomen, or appendages for sensory functions. However, they are also being identified in the internal regions (Fig. 11A) of the crickets owing to their disarticulation from their original position.

5. Mineralization and microfabric

An analysis using a stereomicroscope and scanning electron microscope with coupled EDS reveals that the crickets of the Crato Formation carcasses have been replaced by three main mineral phases: 1) very fine to fine iron oxide, reddish orange, replaces outer and inner portions (Figs. 3B and 9A); 2) grayish black carbonaceous material, identified in external and internal portions (Figs. 3A and 12A); and 3) very fine pale-yellow calcium phosphate, replaces internal features, particularly soft tissues (Fig. 9A). The specimens substituted by iron oxide occur preferentially in yellowish limestones, whereas the carbonaceous ones are identified mainly in greyish limestone. Specimens with calcium phosphate occur in both types of limestone.

These types of preservation are consistent with those already described by Menon and Martill (2007), Barling et al. (2015), and Osés et al. (2016) for different orders of insects of the Crato paleoentomofauna. In these cases, francolite and apatite replaced the internal muscle tissues, and goethite replacing internal and external cuticular features. According to Barling et al. (2015), specimens replaced by goethite mark a weathered phase of fossils originally replaced by iron sulfide. Paleometric microtextural analyses using RAMAN spectroscopy by Osés et al. (2016) revealed that the insects microfabric of the Crato unit is essentially composed of framboidal pyrite pseudomorphs, with goethite and

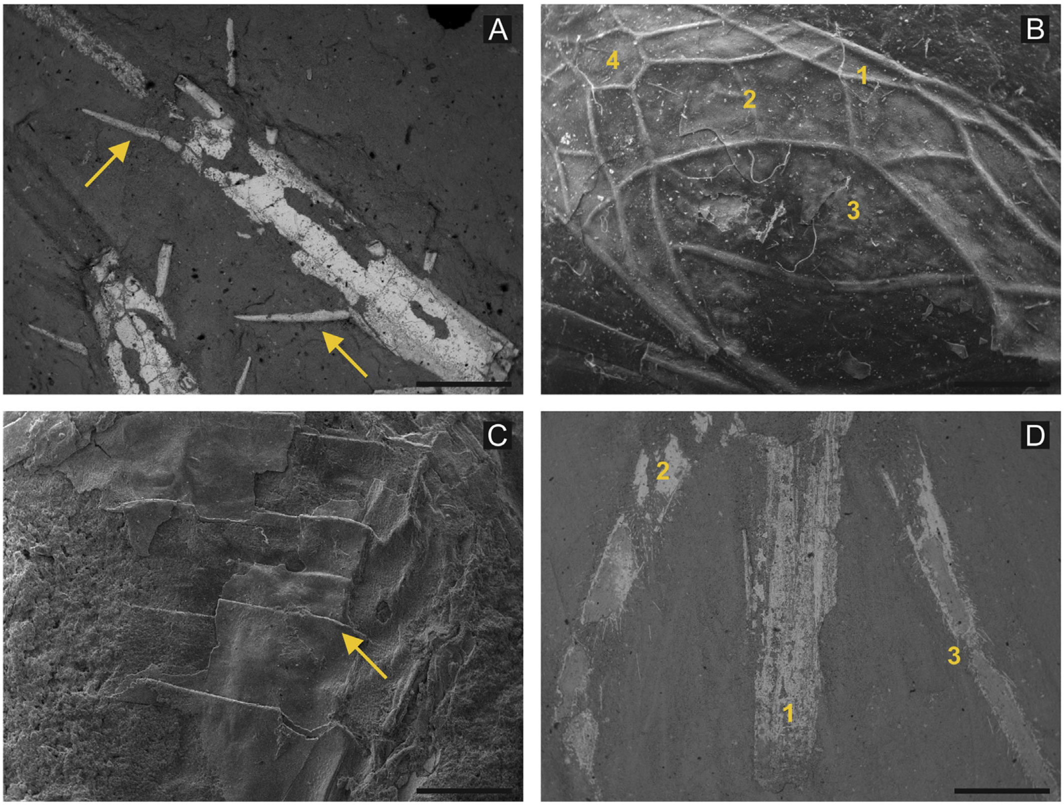

Fig. 6. Morpho-anatomical features of grylloid's thorax and abdomen visualized on scanning electron microscopy: **A.** Detail of tibial spines (setae) on fossil cricket's carcasses (UFRJ-DG 1082-Ins). Scale bar: 1 mm. **B.** Grylloid's tegmina, showing longitudinal (1) and transversal (2) venation pattern, mirror of stridulatory apparatus (3) and cells formed between the veins (UFRJ-DG 15-Ins). Scale bar: 1 mm. **C.** Detailed view of segmented abdomen, a very common feature preserved, possibly due to the high sclerotization rate of this tagma (UFRJ-DG 1928-Ins). Scale bar: 800 μm. **D.** Post-abdominal features also commonly preserved, with ovipositor (1), cerci (2) and numerous sensory sensilla transversal to the cerci (3) (UFRJ-DG 1925-Ins). Scale bar: 1 mm.

amorphous hematite as secondary mineral phases. Similarly, on the basis of fossil-diagenetic studies of fish from the same lithostratigraphic unit, Osés et al. (2017) revealed that the replacement of specimens occur by the processes of pyritization and kerogenization, generating fossils with distinct preservational fidelity. Using three specimens of Ensifera from the Crato Formation, Oliveira (2018) determined that the preservation of these insects (apart from that of fishes) could occur place in two distinct stages with the replacement of the cuticle and soft tissue with framboidal pyrite or kerogen.

Geochemical mappings using EDS analyses were performed in different specialized regions of cricket specimens. From analyses of the internal and external portions of features associated with the head, antenna, eyes, thorax, legs, abdomen, proventriculus, ovaries, and mechanoreceptor sensilla, a uniform concentration of iron and oxygen was identified in the fossil in comparison to the matrix, presenting up to 58% iron in its chemical composition (Fig. 9). The appearance of the occasional phosphorus and calcium peaks refers to calcium phosphate. It preferentially replaces soft tissues associated with the internal regions of the specimens, such as the muscle tissues intrinsic to the digestive tract, muscle fibers within the femur (Fig. 9), and interior regions of the compound eyes. It is common to identify the presence of zinc associated with the head region. This is because this element is highly concentrated in the chewing apparatus of hypognathous insects, for the food maceration process. The appearance of subordinate sulfur peaks (Fig. 10) is possibly associated with the remaining iron sulphides of the primary pyritization process, or the presence of other types of sulphides (galena and sphalerite), as attested by Osés et al. (2016). The presence of silicon, magnesium, and aluminum may be related to the secondary formation of weathering clay minerals. This is because the manganese peaks are associated with the formation of dendritic pyrolusite (Fig. 10). The higher carbon concentration in fossils inserted in gray limestone is directly associated with the kerogenization process of these specimens (Fig. 12C).

The pyrite pseudo framboids in the form of iron oxide compose most of the grylloid microfabric. Inequidimensional and spherical to subspherical micro-cryptocrystals (Fig. 11A) replace the external cuticular features such as the head's surface, thorax, abdomen, compound eyes, antennae, tegmina, legs, cerci and ovipositor, and internal cuticular features and soft tissues such as the interior of the compound eyes, proventriculus, ovaries and muscle tissues. Whereas pyrite's pseudomorphs are densely packed in the outer regions of the carcasses, the packing is more dispersed in the inner portions with larger size divergence between the crystals (Fig. 11B).

As identified by Barling et al. (2015) and Osés et al. (2016), dissolution cavities (Fig. 11C) previously occupied by crystals were recognized with the generation of empty structures after oxidation reactions. Crystal aggregates that result in an alveolar habit (Fig. 11D) with partially corroded surfaces (Fig. 11E), as well as compact and amorphous regions without individualization of crystals in and/or over the microfabric (Fig. 11F) are also present. These microtextural features are evidence that indicates the secondary origin of iron oxide as a product of oxidation reactions of framboidal pyrite (Osés et al., 2016).

There is a homogeneous, isotropic, and amorphous material in the gray limestone. It does not have crystal identification even at increases above 1000x and has web-like structures embedded in carbonaceous material (Fig. 12). The absence of microfabric and the carbonaceous composition of the specimen indicate the kerogenization process associated with the preservation of these grylloids, as described for fish on the same unit by Osés et al. (2017). In this process, the preservational fidelity of the fossils generated is lower when compared to fossils

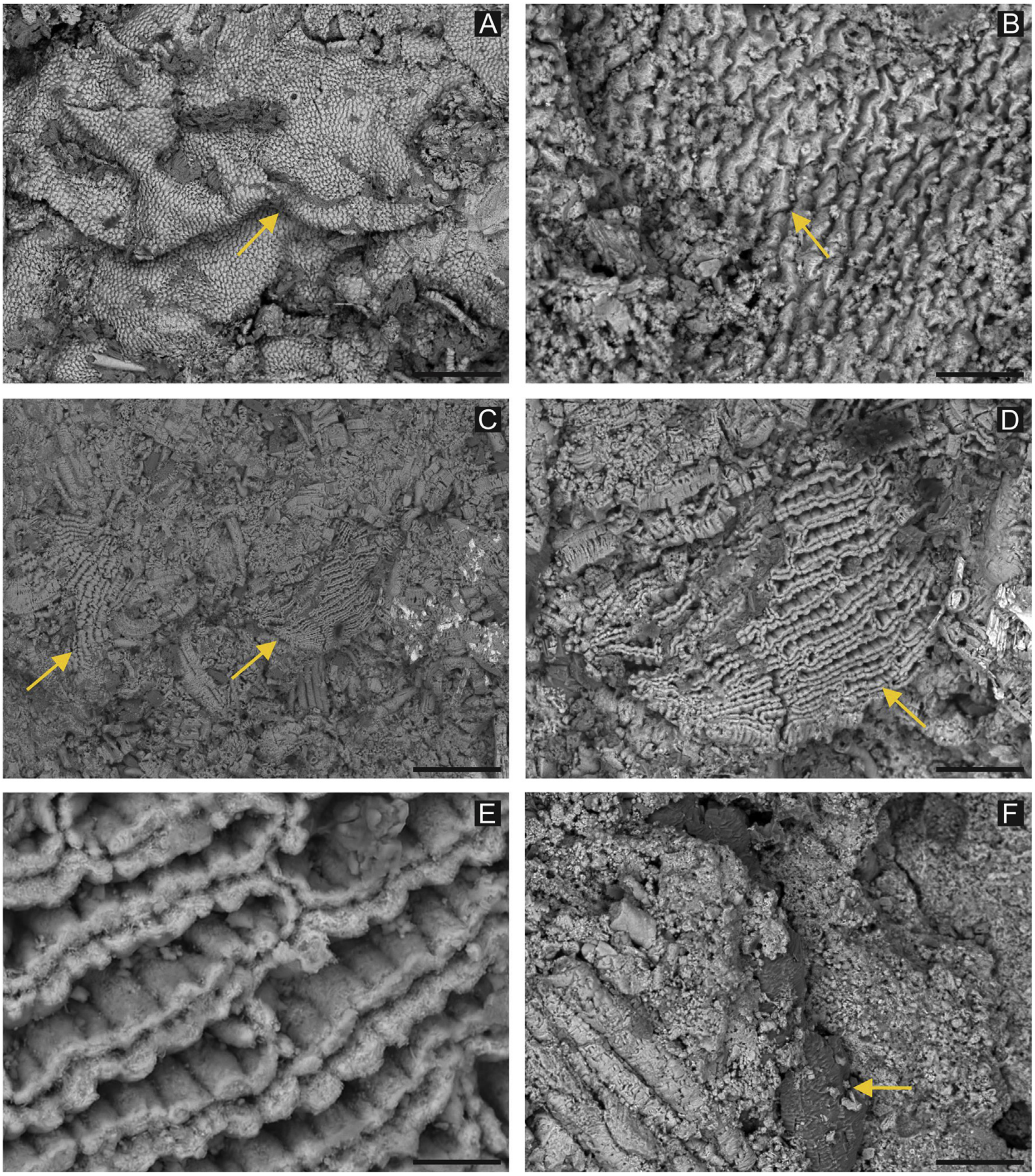

Fig. 7. Micro-features identified on internal parts of grylloid specimens: **A.** Fragment of proventriculus, with extensive cutaneous plaques inserted in a mosaic with microvilli (setae) (UFRJ-DG 882-Ins). Scale bar: 150 μm. **B.** Detailed image showing several denticles (setae) identified in proventriculus, directly associated with mechanical disruption of food for digestion (UFRJ-DG 882-Ins). Scale bar: 30 μm. **C.** Fragments of ovaries (setae) included in the abdominal region (UFRJ-DG 882-Ins). Scale bar: 150 μm. **D.** Membranous texture of ovaries, with numerous tubes aligned and systematically arranged (UFRJ-DG 882-Ins). Scale bar: 50 μm. **E.** Detailed view of ovaries' egg-tubes depicted in B (UFRJ-DG 882-Ins). Scale bar: 10 μm. **F.** Organic structure possibly equivalent to spermatheca fragment, very close of two ovarian fragments on abdominal region of the same specimen (UFRJ-DG 882-Ins). Scale bar: 60 μm.

initially pyritized and secondarily replaced by iron oxide.

Phosphatization occurs preferentially in association with soft tissue replication and generation of exceptionally preserved structures in the fossil record (Briggs et al., 1993). Within the hind femur of a specimen there is a fibrous texture equivalent to the muscle fibers used in the displacement and jumping of the cricket (Fig. 9A). Under approximately 300x magnification, the replication process of these fibers is observed to form a highly fine granular texture with densely packed equidimensional calcium phosphate cryptocrystals that result in high morphological fidelity (Fig. 9B). According to Briggs et al. (1993), the smaller is the precipitated calcium phosphate particle aggregates, the higher is the morphological fidelity of preservation.

In addition, there are numerous, predominantly small, spherical and sub-spherical grains associated with the microfabric. They are moderately to densely packed, and exhibit highly similar shapes, isotropic texture, absence of crystalline faces, and sizes less than 5 μm (Fig. 13). Subordinate to the grains, tiny tubular and three-dimensional features of lengths less than 10 μm were also identified (Fig. 13B). These elements were interpreted as fossilized bacteria in the form of coccoids and tubular filaments. They were identified in internal features of the thorax and abdomen as well as between the antenna segments and compound eyes. Thy occasionally exist immersed in a net-like structure called web-like texture (Fig. 14A and B) that partially covers the polygonal facets of one of the compound eyes (Fig. 14C and D).

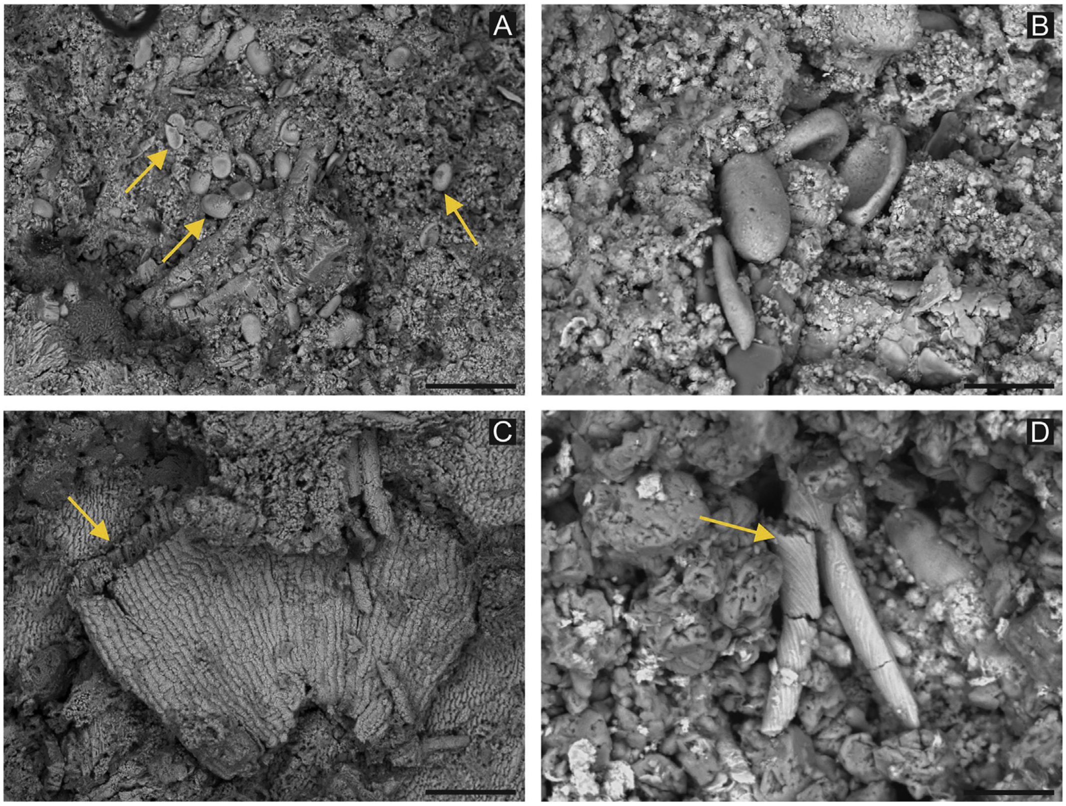

Fig. 8. Exceptionally preserved internal anatomical features identified on grylloids: **A.** Cricket's eggs (setae) associated with grylloid ovaries (UFRJ-DG 882-Ins). Scale bar: 70 μm. **B.** Detailed view of eggs depicted in C (UFRJ-DG 882-Ins). Scale bar: 30 μm. **C.** Striated visceral muscle with microfilaments neatly arranged (UFRJ-DG 882-Ins). Scale bar: 100 μm. **D.** Rod-shaped sensilla with longitudinal lines, identified on cricket's internal parts, but originally coupled on surface regions (UFRJ-DG 882-Ins). Scale bar: 20 μm.

Alternatively, they are related to the acicular remnants present inside the thorax, abdomen and tegmina of different specimens (Fig. 13D). In addition, spherical and filamentary impressions with mildly negative reliefs were observed on the outer cuticle of cricket carcasses (Fig. 14F). These were similar to those identified by Gupta et al. (2008) in fish from the Las Hoyas Formation, Lower Cretaceous of Spain. It is also associated with fossilized bacteria.

The presence of expressive coccoids and subordinate filaments immersed in a web-like texture in the grylloid microfabric is a strong indication of the influence of microbial communities on the fossilization process of these insects. These textures are associated with mineralized extracellular polymeric substances (EPS), also called mucilage. These are typically secreted by the activity of microbial mats and biofilms. In addition, the acicular remnants directly related to the coccoids and filaments can be identified as remains of the EPS matrix. Spherical and filamentary impressions on cricket cuticles are also associated with the mineralization of bacteria in coccoid and filament shapes. Other evidence of microbial and biofilm activity is the carbon peaks in regions with direct presence of coccoids and web-like texture on kerogenized specimens.

6. Taphonomic and paleoenvironmental implications

A more detailed study of the paleoenvironmental context in which these fossils are observed is required for a better understanding of the preservation of Crato Formation crickets. According to Heimhofer and Martill (2007), the unit was constituted by a meromictic lacustrine environment composed of a highly productive epilimnion and a stagnant, anoxic, and hypersaline hypolimnion. The anoxia of a lake bottom may decrease the rate of aerobic decomposition and disarticulation of the remains and inhibit the presence of benthic and bioturbating organisms that could function as bioerosive agents (Martin, 1999). Hypersaline episodes, identified by widespread pseudomorphs of salt in carbonate-siliciclastic strata, also contribute to the reduced activity of benthic organisms. Therefore, carcass decomposition is essentially anaerobic, and is significantly less efficient than aerobic processes (Heimhofer and Martill, 2007).

Among the Crato Formation insects, Orthoptera are the most abundant. They exhibited terrestrial forms that needed to be transported from their original habitat to the waters of the lacustrine environment. As indicated by the exceptional preservation, the transport must have occurred over short distances and non-aggressive regimes. This, in turn, indicates the relative proximity between the lake and the cricket habitat. While taphonomically and paleoecologically interpreting a paleofauna of insects identified in the Purbeck Group limestones, Southern England Cretaceous, Coram (2003) stated that Orthoptera, identified by predominantly articulate and poorly fragmented forms, live in regions very close to the lagoon with wide fields and spaced vegetation characterized by the presence of conifers, gnetophytes, and occasional ferns.

According to Sperber et al. (2012), crickets are more abundant and diverse in tropical and subtropical regions. Here, they live in crevices, tunnels, underground, or associated with vegetation, preferably in open areas. The presence of an abundant and diverse grylloid paleofauna in the Crato Formation strata is indicative of the presence of environments with more spaced vegetation and climate marked by seasonality (alternating between wetter and more arid periods). The epicuticle microcracking in certain specimens may be related to the aridity episodes. Alternatively, the crack propagation can be associated with a large decrease in the fracture toughness with age (according to O'Neill et al. (2019)), which causes the cuticle to be more sensitive. The high degree of articulation and low degree of fragmentation of the fossils indicate

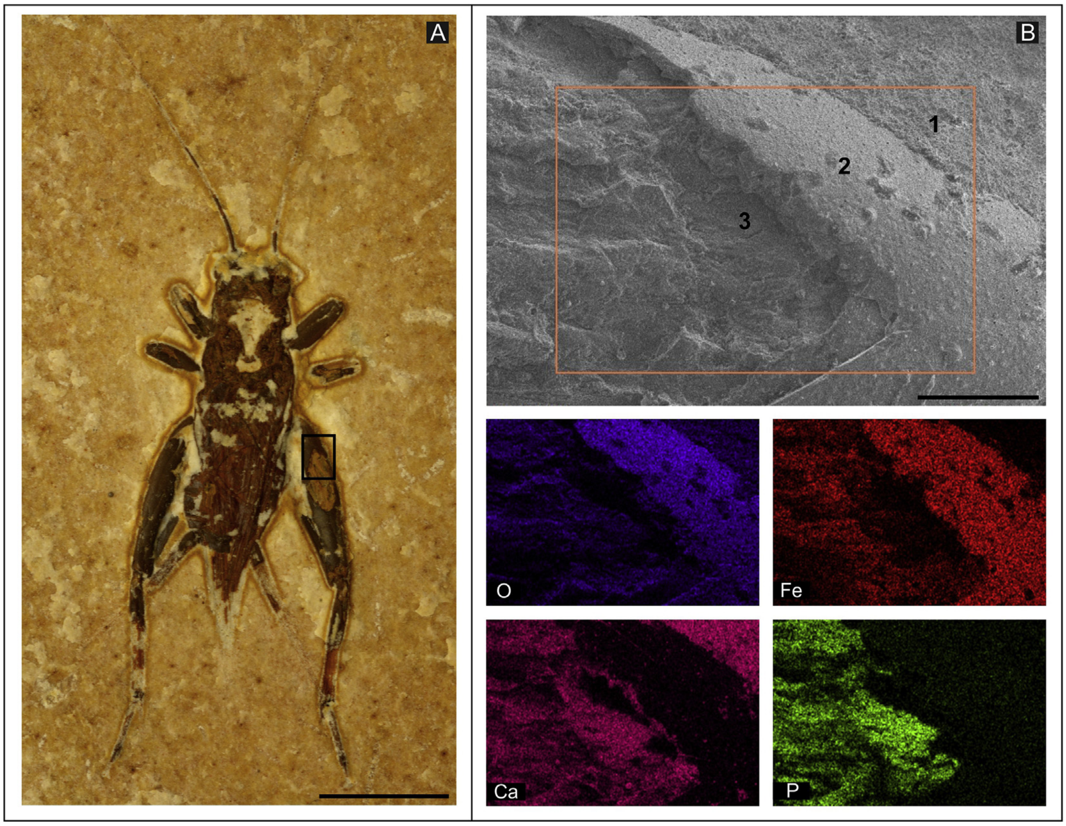

Fig. 9. Gryllidae specimen on yellowish laminated limestone submitted in energy dispersion x-ray spectroscopy for elaboration of geochemical maps: **A.** Cuticle replaced for a reddish orange thin pellicle, and internal parts of hind femur for a very fine pale-yellow granular material (UFRJ-DG 1926-Ins). Scale bar: 5 mm. **B.** Demarked area exhibited in A used for spectroscopic analysis with geochemical mapping for elements oxygen (O), iron (Fe), calcium (Ca) and phosphorous (P) elements. On rock matrix (1) the composition is essentially Ca and O, referent to laminated limestones. On cuticle parts (2), there are peaks for O and Fe corresponding to iron oxide. On internal soft parts, it is possible to identify a fibrous texture equivalent to the muscle fibers of hind femur, all of them replaced for Ca and P, referent to calcium phosphate. These phosphatized parts are characterized the presence of densely packed equidimensional grains that result in exceptional preservational fidelity. Scale bar: 300 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that the living environment of these crickets was very close to the lake, possibly in the peripheral areas, with very short or no transport to the deposition site and short exposure time of carcasses after death.

The occurrence of terrestrial insects in lake carbonates is generally associated with water dependence for ecological reasons such as habitat, search for food, or oviposition (Martínez-Delclòs et al., 2004). The significant presence of grylloids in lacustrine limestones may be associated with the proximity between the deposition and oviposition sites. Herein, females use the ovipositor to penetrate the substrate and inject their eggs into the sediment or vegetation. This is verified by paleoethological data from Martins-Neto and Tassi (2009). The data includes those on specimens of the genus *Cearagrylloides* from the Crato Formation. Their ovipositor length is larger than the body length (Fig. 3B), indicating a habitat close to the sedimentation environment and an oviposition site on the sandy margins of the paleolake.

The presence of wingless or laterally folded wing specimens indicates death around the lake and subsequent transportion to the lake environment. However, this transport may have occurred over short distances, as these specimens are poorly fragmented. Meanwhile, open-winged specimens represent individuals who died in the deposition environment, possibly owing to asphyxiation and drowning after exhaustion. According to Zhehikhin (2002), Orthoptera insects are unlikely to escape from aquatic environments because they do not have the anatomy necessary for swimming. The morphological fidelity of specimens that died in the deposition environment is higher than those that were transported.

Well-developed winged insects such as grylloids and odonatans cannot penetrate the surface tension of water. They tend to decompose, disarticulate, and/or fragment on the lake surface (Martínez-Delclòs and Martinell, 1993). Therefore, the preservation of three-dimensional, articulate and, poorly fragmented crickets also indicates a short period of flotation of their carcasses before they reached the paleolake substrate. The entry of water into the tracheal breathing system in association with carcass infestation by microbial communities increases the density of the remains and enables them to reach the paleolake substrate faster. According to Briggs (2003b), microbial mats may be present on the surface or bottom of the water in aquatic environments. Therefore, insect carcasses are trapped and enveloped by microbial communities from their initial fall into the water body to the substrate. This protects the carcass from disarticulation, erosion, and predation, particularly by fish. The presence of isolated tegmina could have resulted from disarticulation outside the lake with posterior transport into the lacustrine system. In addition, these disarticulated elements could be directly associated with predation. This is because crickets tend to flap their wings to escape when they fall into the water, generating surface waves that attract predators such as fishes, crocodiles, pterosaurs, and turtles (Martínez-Delclòs and Martinell, 1993). Whereas they tend to swallow the carcasses entirely, they spit the more sclerotized anatomical features such as tegmina. For Martínez-Delclòs et al. (2004), fishes are one of the main taphonomic filters for the preservation of insects in lake, lagoon, and river environments.

According to Osés et al. (2016), the high morphological fidelity of Crato Formation insects is a response to the association of environmental, biological, and diagenetic factors that continuously functioned to form the exceptionally preserved fossils that characterize the unit as a *Konservat-Lagerstätte* deposit. In combination with the low

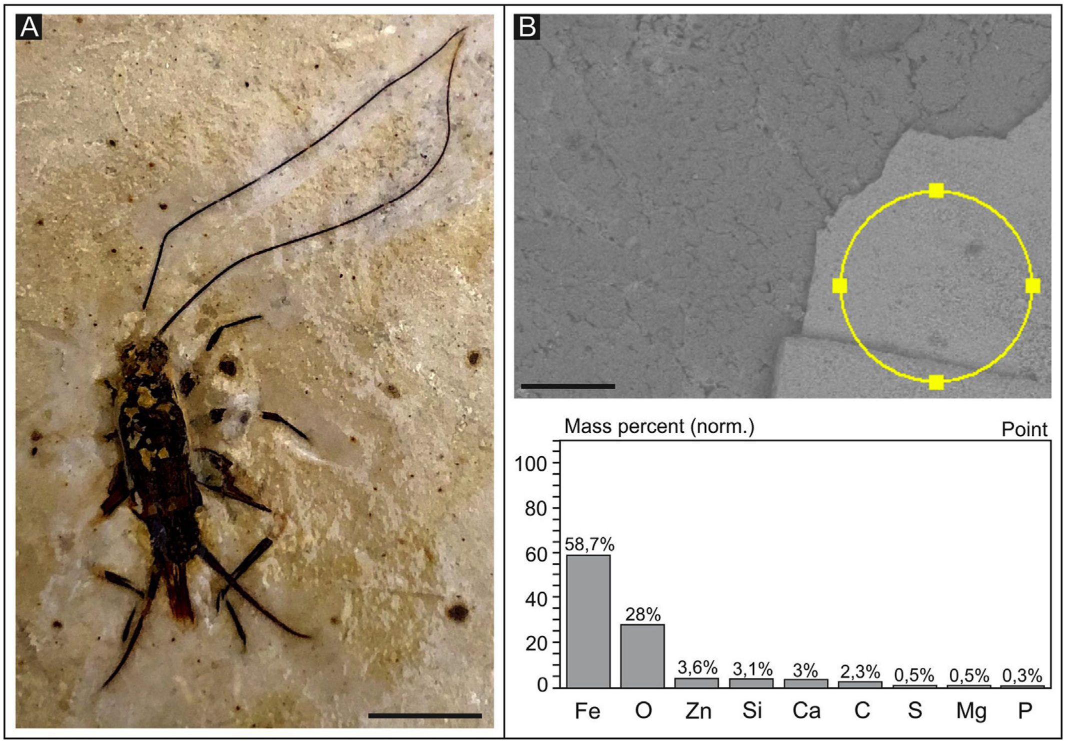

Fig. 10. Gryllidae specimen on yellowish laminated limestone submitted in energy dispersion x-ray spectroscopy for quantitative geochemical analysis: **A.** Cuticle replaced for reddish orange thin pellicle. A small portion of cricket's head was used for quantitative geochemical analysis exposed in B (UFRJ-DG 625-Ins). Scale bar: 5 mm. **B.** Demarked area used for spectroscopic analysis with equivalent graphic of chemical elements that replaced cricket's cuticle. Iron (Fe) and oxygen (O) are the most abundant ones, equivalent to iron oxide. The high concentration of zinc (Zn) on cricket's head can be associated with the common presence of this element on chewing apparatus for food maceration process. The occurrences of silicon (Si) and magnesium (Mg) may be related to weathering clay minerals, and the presence of sulfur (S) can be associated with remaining iron sulphides of the pyritization process. The low quantities of calcium (Ca) and phosphorous (P) probably refers to small phosphatized areas, and the subordinate occurrence of carbon (C) can be related to calcite grains of host carbonate rock or small querogenized areas. Scale bar: 100 μm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

decomposition and high carcass mineralization rate, these factors can generate fossil assemblages with high morphological fidelity, including soft tissue preservation, as identified in the Crato Formation. Specifically in relation to grylloids, the iron oxide-substituted specimens identified in yellow limestones exhibit higher morphological fidelity than those preserved in gray limestone. Calcium phosphate can occur in either type of limestone, with replication of soft tissue such as muscle tissue.

This preservation pattern is analogous to that explained by Osés et al. (2017) in the preservation of soft tissues of fish from the same unit by pyritization and kerogenization, generating fossils with different degrees of preservation. The difference is controlled predominantly by sedimentological factors such as the sedimentation rate, and microbial factors such as the type of zone of microbial mats on which the crickets are deposited. From lithofaciological studies of the Crato unit, Neumann et al. (2003) determined that the laminated limestones facies (here associated with the yellowish limestones) have negligible content of organic matter and associated terrigenous, indicating a low sedimentation rate. This is verified by isotopic signatures of Heimhofer et al. (2010). It may indicate the reduced throughflow of water in a confined basin, probably with stagnant conditions and low input of plant or soil to the lake. However, in clay-carbonate rhythmite facies, which are associated with gray limestone, there is a high content of organic matter and higher input of terrigenous. This indicates a high sedimentation rate with higher contribution of siliciclastics to the paleolake. Under high sedimentation rates, there is a higher burial rate and longer residence time of the carcasses in the methanogenic bacteria zone, with consequent kerogenization of the specimens. Under low sedimentation rates, the residence time of carcasses in the microbial zone of sulfate-reducing bacteria (which is the superficial portion of a microbial mat in relation to the methanogenic zone) is longer, with consequent fossil pyritization. According to Allison (1990), pyritization is an important eodiagenetic mechanism mediated by the metabolic activities of sulfate-reducing bacteria. In this process, carcasses need to be buried rapidly in sediments with low organic matter content and significant amounts of reactive iron and sulfate (Briggs et al., 1996; Briggs, 2003c). If the amount of organic matter is high and the burial velocity is low, the sulfate reduction will be uniform throughout the surrounding sediment. The pyrite formation would be spread throughout the framework, rather than only the carcasses. However, if the organic matter content is low and the burial velocity high, the pyrite precipitation is confined to decomposition sites, concentrating on carcasses (Allison, 1988). Thus, Freire et al. (2013) concluded that the Crato paleolake presented periods with low organic matter content as well as high amounts of iron and sulfate, thereby enabling the fossil pyritization.

Neumann et al. (2003) also verified the influence of microbial mats on the pyritization of Crato Formation fossils, which contributes to their high morphological fidelity. For Heimhofer and Martill (2007), the likely microbial character of the unit was evidenced only by structures such as oncoids, vugular porosities, and ripples. Heimhofer et al. (2010) proposed that the genesis of the carbonate succession of the Crato unit is associated with the authigenic inorganic precipitation of calcite crystals, which is induced by biochemical processes caused by the presence of phyto and picoplankton on the paleolake water surface, without association with microbial communities.

However, Catto et al. (2016) gathered strong microbial evidence of the Crato Formation strata. They identified abundant coccoids and calcified filamentous cells, alveolar structures associated with extracellular polymeric matrix (EPS), amorphous organic matter,

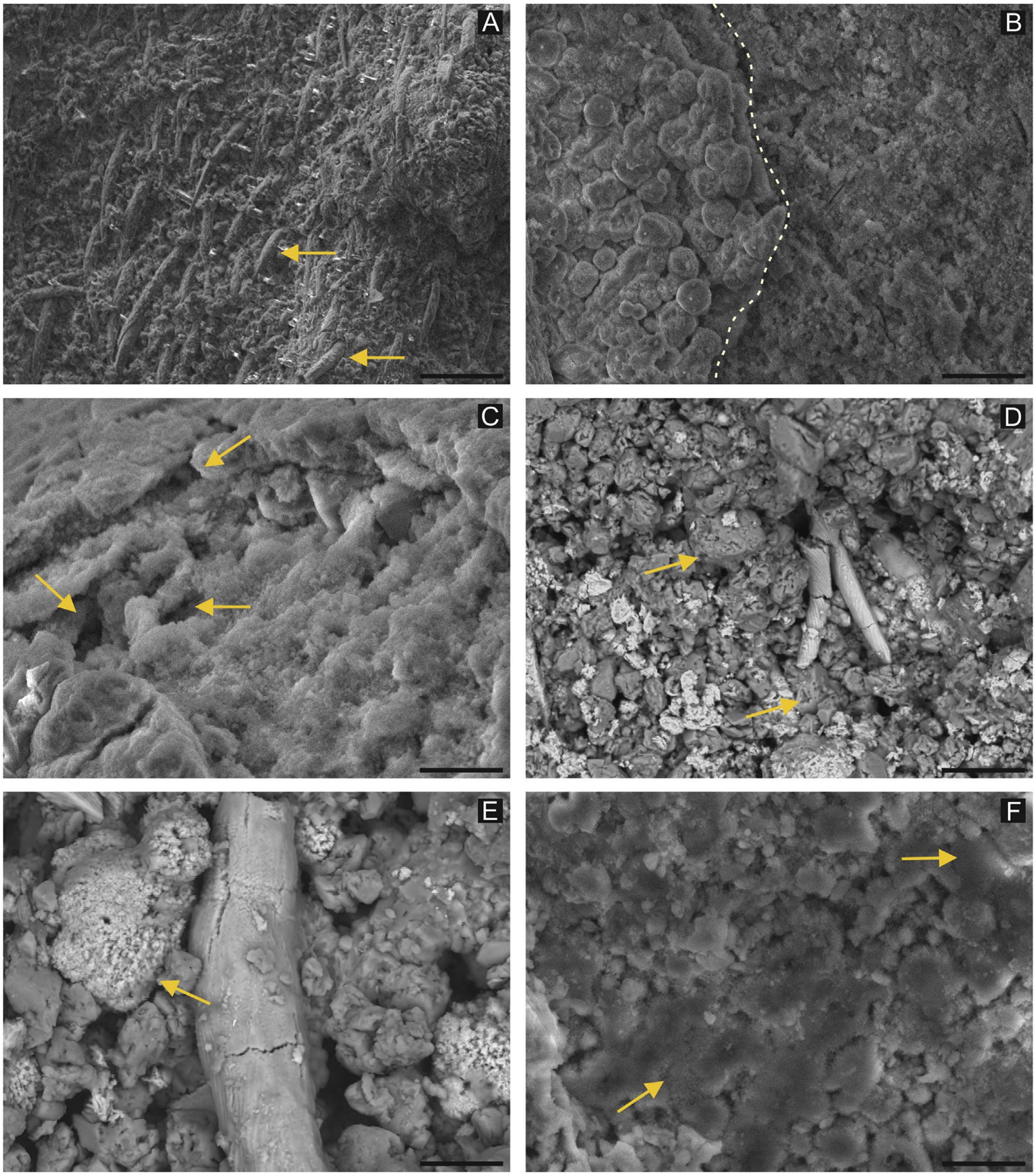

Fig. 11. Detailed cricket's microfabric of specimens replaced for iron oxide: **A.** Small pseudo framboids directly associated with disarticulated sensilla (setae) on internal parts of abdominal region (UFRJ-DG 882-Ins). Scale bar: 90 μm. **B.** Inequidimensional and spherical to sub-spherical micro-cryptocrystals showing greater size divergence between them, replaced internal parts of cricket's carcass (UFRJ-DG 58-Ins). Scale bar: 20 μm. **C.** Empty structures of dissolution cavities (setae) generated by oxidation reactions of original framboidal pyrite microfabric (UFRJ-DG 58-Ins). Scale bar: 10 μm. **D.** Alveolar aggregates (setae) of iron oxide crystals embedded on cricket's microfabric (UFRJ-DG 882-Ins). Scale bar: 30 μm. **E.** Detailed view of disarticulated sensilla and alveolar aggregates with corroded surfaces (setae), another evidence of posterior oxidation process, as discussed by Osés et al. (2016) (UFRJ-DG 882-Ins). Scale bar: 10 μm. **F.** Compact and amorphous regions predominantly identified on cuticle external parts of cricket's carcass (UFRJ-DG 1926-Ins). Scale bar: 6 μm.

microspheres, pellets, spherulites, needles and calcite micro-rhombohedrons within the EPS matrix. The latter was interpreted as a product of the organomineralization induced by biofilm and microbial mats. Warren et al. (2016) complemented the observations of Catto et al. (2016) on the basis of the identification of three stromatolitic levels in the intermediate portions of the Crato unit. This indicated that the formation of laminated limestone was at a certain point, strongly influenced by microbial activity, with the organomineralization induced by the metabolic activity of these microorganisms.

In this work, it was identified that microbial features such as coccoids and filaments in internal and external portions, bacteria impressions in negative relief on the cuticle, and web-like texture and acicular remains corresponding to mineralized extracellular polymeric mineralization (EPS) are directly associated with cricket's carcasses. In fish eyes from the Eocene of Denmark, Lindgren et al. (2012) identified micrometric spherical body masses interpreted as melanosomes. These are intracellular corpuscles that store melanin pigments, are highly similar to coccoids associated with microbial activity, and may occur in fossil eyes, feathers, and hair-like structures. The microspheres identified inside the compound eyes of Crato Formation crickets are directly associated with the web-like structures linked to the mineralization of the EPS of microbial mats (Fig. 14C and D). They differ from the

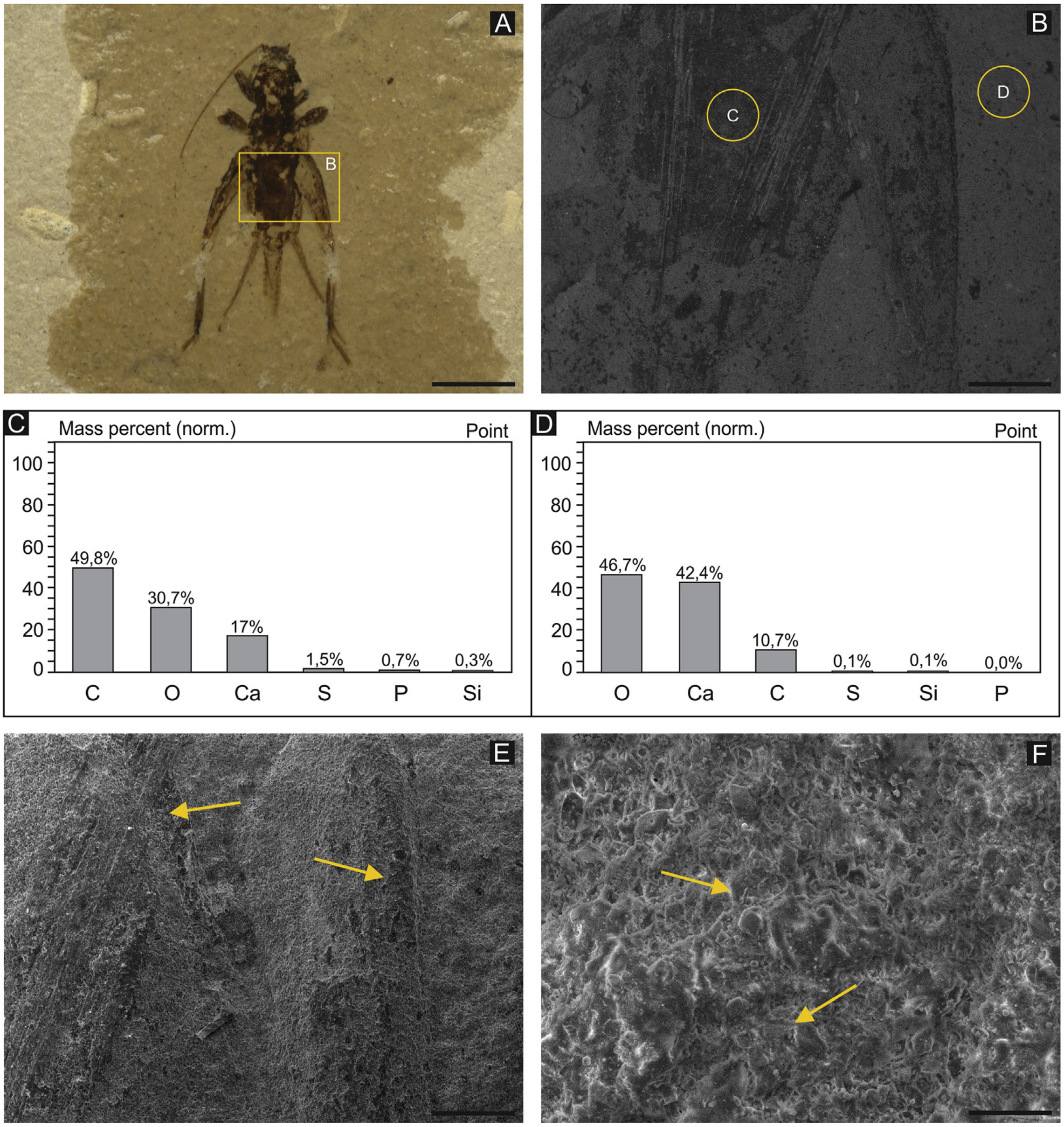

Fig. 12. Gryllidae specimen on grayish laminated limestone submitted in energy dispersion x-ray spectroscopy for quantitative geochemical analysis: **A.** Cuticle replaced for grayish black carbonaceous material (UFRJ-DG 1927-Ins). Scale bar: 4 mm. **B.** Detailed area of abdomen demarked in A, with better view of wings folded close to the body and selected areas utilized for quantitative geochemical analysis of the fossil (C) and rock matrix (D) (UFRJ-DG 1927-Ins). Scale bar: 1 mm. **C.** Equivalent graphic of demarked area in B showing chemical elements that replaced fossil cuticle. The high abundance of carbon (C) and oxygen (O) on the fossil points to the kerogenization process as described for the Crato Formation fishes by Osés et al. (2017). **D.** Equivalent graphic of chemical analysis of rock matrix. The high abundance of oxygen (O) and calcium (Ca) and moderate quantities of carbon (C) refers to the carbonate nature of the laminated limestones. **E.** Detailed of cricket's microfabric on kerogenized specimen, with isotropic and amorphous material (setae) replacing morpho-anatomical structures (UFRJ-DG 1927-Ins). Scale bar: 400 µm. **F.** Web-like texture (setae) embedded in carbonaceous material on hind femur (UFRJ-DG 1927-Ins). Scale bar: 40 µm.

possible melanosomes and are strong evidence of the influence of microbial mats on a cricket's fossilization process.

Seilacher et al. (1985) list three dominant factors for the genesis of *Konservat-Lagerstätten* deposits: 1) anoxia (stagnation); 2) rapid burial (obruption); and 3) microbial mats activity. For the Crato Formation cricket fossils, it is interpreted that the main factor responsible for the high morphological fidelity of the specimens is the activity of the microbial communities, and the episodes of anoxia form the secondary factor. Exceptional preservation of fossils is not necessarily associated with anoxic episodes of the entire water column, rather with microenvironments developed by the activity of microbial communities in paleolake hypolimnion. The presence of highly fine laminated micritic limestone indicates a gradual and continuous deposition without significant rapid burial events directly associated with the fossil's preservation.

The role of microbial mats in the exceptional preservation of fossils 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; Carvalho et al., 2013, 2017; Schiffbauer et al., 2014; Iniesto et al., 2015, 2016; 2017; Becker-Kerber et al., 2017). Biofilms are ecologically simpler and thinner microbial communities, whereas microbial mats are constituted by successions of different microbes with high ecological complexity and thickness (Briggs, 2003b; Gall, 2003). These communities group populations of microorganisms that excrete extracellular polymeric substances (EPS), a gelatinous material also called mucilage, and capable of mobilizing solutions and altering the

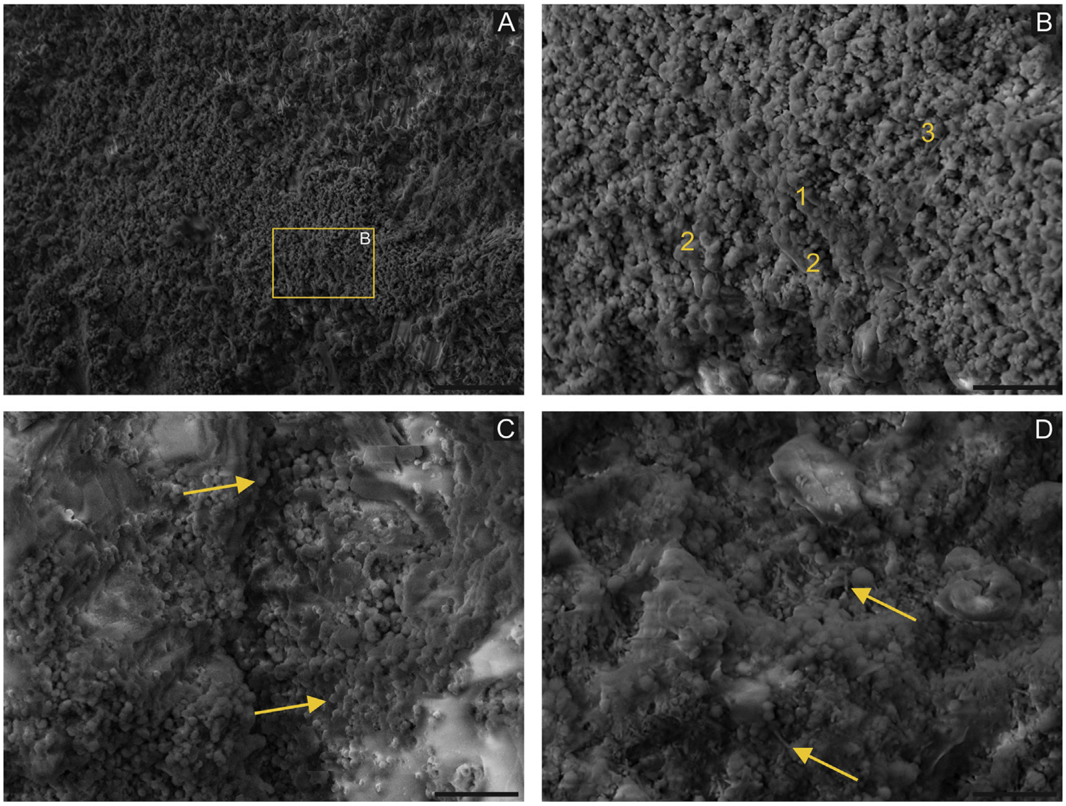

Fig. 13. Microbial evidences identified on internal and external parts of cricket's carcasses: **A.** Numerous coccoids with very similar shape and isotropic texture (UFRJ-DG 882-Ins). Scale bar: 60 μm. **B.** Detailed view of depicted area in A, with abundant coccoids (1), subordinate filaments (2) and acicular remnants (3) associated with extracellular polymeric substances (UFRJ-DG 882-Ins). Scale bar: 20 μm. **C.** Numerous coccoids embedded on grylloids' microfabric (UFRJ-DG 58-Ins). Scale bar: 15 μm. **D.** Coccoids with subordinate acicular filaments associated (setae) (UFRJ-DG 882-Ins). Scale bar: 10 μm.

biogeochemistry of sedimentary environments (Gerdes, 2003). They are composed of cyanobacteria, heterotrophic bacteria, green and purple bacteria, sulfate-reducing bacteria, and methanogenic bacteria, as well as unicellular algae and other microorganisms (Martínez-Delclòs et al., 2004; Konhauser, 2007).

For the Crato unit grylloids, the influence of microbial mats on the fossilization process is directly associated with the process described by Gall (1990, 2003) and Briggs (2003b). The process has hour four main aspects: 1) entrapment, infiltration, and faster transport of carcasses for the water sediment interface; 2) trapping of the remains and consequent reduction of the disarticulation rate; 3) protection of biogenic remains from erosion by non-biotic agents such as waves and currents, as well as by bioerosive agents and decomposers; and 4) development of particular microenvironments that enable the mineralization of the carcasses, resulting in environments similar to “sarcophagus”, which permits the concentration and transfer of ions, thereby mineralizing the more resistant and soft parts and/or the microbial mat infiltrated in the carcass.

According to Briggs (2003b), the average speed to erode a sediment trapped by biofilms and microbial mats is two-five times higher than that of a “sterile” sediment. This increases the preservational potential of articulated fossils. Presently, microbial communities are widespread in confined lake environments with extreme conditions such as hypersalinity and anoxia. This is similar to that proposed for the Crato paleolake (Martin, 1999; Gerdes, 2003; Catto et al., 2016; Warren et al., 2016).

The presence of preserved cricket in different positions (ventral, dorsal or lateral) is also an indication of the activity of microbial mats. According to Martínez-Delclòs et al. (2004), only insects trapped by microbes in the water column tend to be preserved exceptionally with different substrate orientations. When they reach the bottom of the paleolake, microbial mats develop microenvironments that are conductive to the mineralization of the anatomical features of grylloids, with pyritization, phosphatization and kerogenization induced by microbial community activity and replication of external and internal portions, including soft tissues such as muscle fibers and features associated with the eyes. The presence of coccoids immersed in web-like textures in the middle of the microfabric resembles the self-lithification of the biofilms that infiltrated the carcass, because of the extracellular polymeric substances mineralization and three-dimensional fossil generation. The high degree of sclerotization of certain anatomical parts such as ovaries and proventriculous, also supports the exceptional preservation.

7. Conclusions

The Crato Formation crickets exhibit a high degree of morphological fidelity, with mineralization of external and internal anatomical features such as the compound eye ommatidia, epi and procuticle, internal anatomical microstructures associated with the digestive tract, reproductive system and visceral and locomotor muscle tissues. The carcasses were replaced by three main mineral phases: i) iron oxide; ii) carbonaceous material; and iii) calcium phosphate. The presence of dissolution cavities, crystal aggregates with alveolar habits and corroded surfaces, and compact and amorphous regions provide evidence that indicate the secondary origin of iron oxide as a product of the oxidation of fossils originally replaced by framboidal pyrite.

Numerous tiny coccoids and subordinate filaments are associated with the microfabric. They are occasionally immersed in a web-like texture, reflecting the mineralization of the remaining EPS, or as slightly negative impressions and reliefs on carcass surface regions. We interpret that the main factor responsible for the exceptional

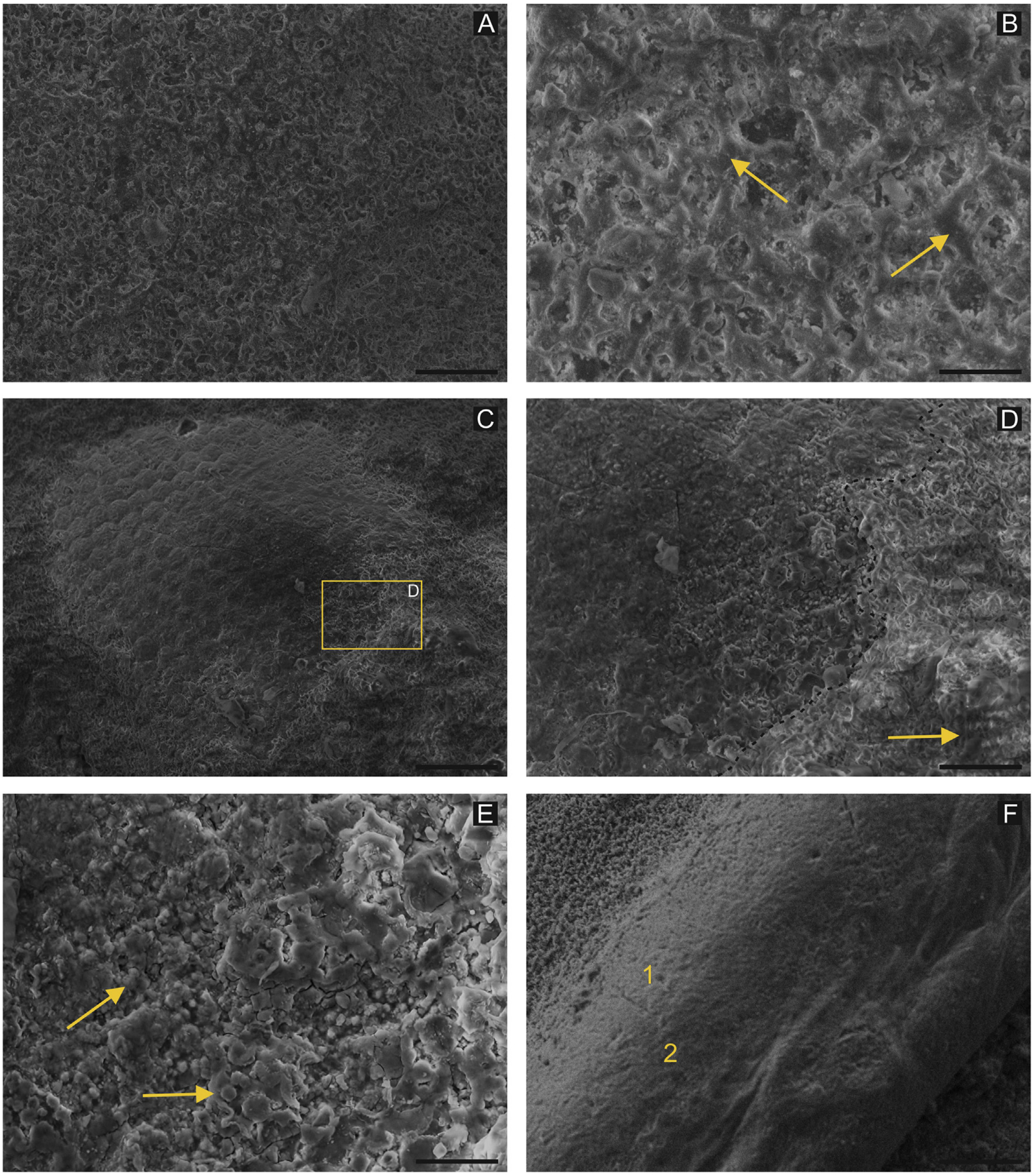

Fig. 14. Microbial evidences identified on internal and external parts of cricket's carcasses: **A.** Net-like structure called web-like texture, which is directly associated with mineralized extracellular polymeric substances (EPS), a mucilage secreted by microbial mats and biofilms (UFRJ-DG 1927-Ins). Scale bar: 100 μm. **B.** High magnification view of web-like texture exhibited in A (UFRJ-DG 1927-Ins). Scale bar: 30 μm. **C.** Web-like texture partially covering polygonal facets of cricket's compound eyes, a direct evidence of microbial mats influencing fossilization process (UFRJ-DG 1925-Ins). Scale bar: 100 μm. **D.** Detailed view of image depicted in C, with web-like texture (right) "invading" the surface of compound eyes (left), assisting on cricket's exceptional preservation (UFRJ-DG 1925-Ins). Scale bar: 40 μm. **E.** High magnification view of polygonal facets with disperse coccoids (setae) on its surface (UFRJ-DG 1925-Ins). Scale bar: 20 μm. **F.** Spherical (1) and filamentary (2) impressions on external parts of cricket's cuticle, possibly related to occurrence of bacteria, as identified by Gupta et al. (2008) (UFRJ-DG 1926-Ins). Scale bar: 60 μm.

preservation of the Aptian crickets in the Araripe Basin is the activity of microbial mats, with entrapment of carcasses in the water column and substrate, protection of debris from decomposition and bioerosion, and formation of microenvironments that permit mineralization. These microenvironments are similar to that of a sarcophagus, with low decomposition and high mineralization rates. Microbial mats may induce mineralization by pyritization, kerogenization and phosphatization processes, or self-lithification by infiltrating carcasses by the mineralization of EPS.

Other factors that enable high morphological fidelity are episodes of anoxia and hypersalinity of lacustrine hypolimnion (these inhibit the presence of bioerosive agents and aerobic decomposers), short distance transport of biogenic remains under non-aggressive regimes to the lake sedimentation environment, and the low period of flotation of the carcasses before they reach the paleolake substrate. The latter two are indicated by the high degree of articulation, low degree of fragmentation, and three-dimensional preservation of carcasses. Therefore, the living environment of crickets was very close to the lake, possibly in the peripheral regions, with some individuals using the marginal regions as an oviposition site. The significant presence of these insects in the Crato Formation strata is indicative of environments with more dispersed vegetation and climatic seasonality, alternating between wetter and more arid periods.

Given the preservational study of Crato Formation grylloids, it is necessary to conduct a more detailed analysis that focuses exclusively upon the role of microbial mats in the exceptional preservation, and based on petrographic, geochemical, and biological information. It is also necessary to refine the biostratinomic processes associated with the preservation of these insects, and seek feasible paleoenvironmental and taxonomic controls that interfere with the fossilization process.

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Appendix A. List of analyzed specimens

UFRJ-DG 3-Ins, UFRJ-DG 4-Ins, UFRJ-DG 11-Ins, UFRJ-DG 14-Ins, UFRJ-DG 15-Ins, UFRJ-DG 23-Ins, UFRJ-DG 29-Ins, UFRJ-DG 36-Ins, UFRJ-DG 58-Ins, UFRJ-DG 67-Ins, UFRJ-DG 68-Ins, UFRJ-DG 107-Ins, UFRJ-DG 108-Ins, UFRJ-DG 114-Ins, UFRJ-DG 141-Ins, UFRJ-DG 224-Ins, UFRJ-DG 242-Ins, UFRJ-DG 244-Ins, UFRJ-DG 255-Ins, UFRJ-DG 266-Ins, UFRJ-DG 274-Ins, UFRJ-DG 287-Ins, UFRJ-DG 295-Ins, UFRJ-DG 301-Ins, UFRJ-DG 308-Ins, UFRJ-DG 316-Ins, UFRJ-DG 351-Ins, UFRJ-DG 353-Ins, UFRJ-DG 361-Ins, UFRJ-DG 365-Ins, UFRJ-DG 383-Ins, UFRJ-DG 385-Ins, UFRJ-DG 396-Ins, UFRJ-DG 418-Ins, UFRJ-DG 419-Ins, UFRJ-DG 478-Ins, UFRJ-DG 484-Ins, UFRJ-DG 488-Ins, UFRJ-DG 507-Ins, UFRJ-DG 514-Ins, UFRJ-DG 526-Ins, UFRJ-DG 538-Ins, UFRJ-DG 554-Ins, UFRJ-DG 559-Ins, UFRJ-DG 561-Ins, UFRJ-DG 564-Ins, UFRJ-DG 572-Ins, UFRJ-DG 577-Ins, UFRJ-DG 580-Ins, UFRJ-DG 592-Ins, UFRJ-DG 594-Ins, UFRJ-DG 595-Ins, UFRJ-DG 600-Ins, UFRJ-DG 602-Ins, UFRJ-DG 610-Ins, UFRJ-DG 625-Ins, UFRJ-DG 629-Ins, UFRJ-DG 631-Ins, UFRJ-DG 632-Ins, UFRJ-DG 644-Ins, UFRJ-DG 649-Ins, UFRJ-DG 655-Ins, UFRJ-DG 657-Ins, UFRJ-DG 664-Ins, UFRJ-DG 710-Ins, UFRJ-DG 718-Ins, UFRJ-DG 723-Ins, UFRJ-DG 736-Ins, UFRJ-DG 739-Ins, UFRJ-DG 741-Ins, UFRJ-DG 759-Ins, UFRJ-DG 785-Ins, UFRJ-DG 787-Ins, UFRJ-DG 788-Ins, UFRJ-DG 789-Ins, UFRJ-DG 790-Ins, UFRJ-DG 826-Ins, UFRJ-DG 844-Ins, UFRJ-DG 847-Ins, UFRJ-DG 854-Ins, UFRJ-DG 864-Ins, UFRJ-DG 868-Ins, UFRJ-DG 875-Ins, UFRJ-DG 882-Ins, UFRJ-DG 898-Ins, UFRJ-DG 902-Ins, UFRJ-DG 907-Ins, UFRJ-DG 946-Ins, UFRJ-DG 952-Ins, UFRJ-DG 980-Ins, UFRJ-DG 993-Ins, UFRJ-DG 1013-Ins, UFRJ-DG 1019-Ins, UFRJ-DG 1022-Ins, UFRJ-DG 1029-Ins, UFRJ-DG 1044-Ins, UFRJ-DG 1048-Ins, UFRJ-DG 1058-Ins, UFRJ-DG 1063-Ins, UFRJ-DG 1071-Ins, UFRJ-DG 1072-Ins, UFRJ-DG 1075-Ins, UFRJ-DG 1082-Ins, UFRJ-DG 1085-Ins, UFRJ-DG 1088-Ins, UFRJ-DG 1109-Ins, UFRJ-DG 1118-Ins, UFRJ-DG 1141-Ins, UFRJ-DG 1149-Ins, UFRJ-DG 1155-Ins, UFRJ-DG 1162-Ins, UFRJ-DG 1189-Ins, UFRJ-DG 1200-Ins, UFRJ-DG 1221-Ins, UFRJ-DG 1234-Ins, UFRJ-DG 1240-Ins, UFRJ-DG 1243-Ins, UFRJ-DG 1258-Ins, UFRJ-DG 1298-Ins, UFRJ-DG 1312-Ins, UFRJ-DG 1323-Ins, UFRJ-DG 1336-Ins, UFRJ-DG 1345-Ins, UFRJ-DG 1359-Ins, UFRJ-DG 1392-Ins, UFRJ-DG 1433-Ins, UFRJ-DG 1436-Ins, UFRJ-DG 1439-Ins, UFRJ-DG 1445-Ins, UFRJ-DG 1460-Ins, UFRJ-DG 1461-Ins, UFRJ-DG 1474-Ins, UFRJ-DG 1475-Ins, UFRJ-DG 1477-Ins, UFRJ-DG 1493-Ins, UFRJ-DG 1503-Ins, UFRJ-DG 1507-Ins, UFRJ-DG 1518-Ins, UFRJ-DG 1525-Ins, UFRJ-DG 1527-Ins, UFRJ-DG 1532-Ins, UFRJ-DG 1546-Ins, UFRJ-DG 1562-Ins, UFRJ-DG 1570-Ins, UFRJ-DG 1572-Ins, UFRJ-DG 1592-Ins, UFRJ-DG 1593-Ins, UFRJ-DG 1597-Ins, UFRJ-DG 1607-Ins, UFRJ-DG 1625-Ins, UFRJ-DG 1674-Ins, UFRJ-DG 1677-Ins, UFRJ-DG 1683-Ins, UFRJ-DG 1685-Ins, UFRJ-DG 1709-Ins, UFRJ-DG 1711-Ins, UFRJ-DG 1724-Ins, UFRJ-DG 1733-Ins, UFRJ-DG 1748-Ins, UFRJ-DG 1772-Ins, UFRJ-DG 1797-Ins, UFRJ-DG 1864-Ins, UFRJ-DG 1913-Ins, UFRJ-DG 1923-Ins, UFRJ-DG 1924-Ins, UFRJ-DG 1925-Ins, UFRJ-DG 1926-Ins, UFRJ-DG 1927-Ins, UFRJ-DG 1928-Ins, UFRJ-DG 1929-Ins, 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 and UFRJ-DG 1937-Ins.

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