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Exceptionally well-preserved orthopteran proventriculi from the Cretaceous Crato Formation of Brazil

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ARTICLE INFO

Keywords:
Proventriculus
Fossil insect
Orthoptera
Ensifera
Araripe basin
Soft tissue preservation

ABSTRACT

The Crato Formation (Santana Group, Araripe Basin, Brazil) bears a high abundance of fossils in exceptional state of preservation, with insects from the order Orthoptera standing out. However, so far, few studies have explored their preserved inner organs in detail. Here, we provide the first detailed description of fossilized proventriculi from nine Grylloidea (Orthoptera: Ensifera) specimens of the Crato Formation. In all analyzed specimens, the external cuticle of the abdomen is cracked exposing the proventriculi, which are preserved as a tridimensional organ with a globular body and a tubular neck, similar to that of modern crickets. However, in the globular region of all fossils analyzed there are 9–12 rows of parallel divisions, differing from the modern crickets which have, more frequently, six. SEM images of two specimens revealed the exceptional preservation of internal median teeth, folds, and microvilli texture preserved in the organ.

1. Introduction

The digestive tract of insects is morphologically divided into three regions: foregut (or stomodeum), midgut (ventriculus, or stomach), and hindgut (or proctodeum) (Chapman et al., 2013). The foregut, which composes the anterior portion of the digestive tract from the oral cavity to the proventriculus, is lined by exoskeleton consisting of chitin and cuticular glycoproteins (Engel and Moran, 2013). The proventriculus is the last organ through which food passes in the first stage of digestion (Judd, 1948) and is responsible for functions such as storage, grinding, and transport of food (Isely and Alexander, 1949; Liu and Hua, 2009). As the rest of the foregut, it is a sclerotized structure and is composed of several plaques (Chapman et al., 2013). It possesses the same basic structure among insects, but it has diverse modifications associated with

adaptations for different feeding modes (Bland and Rentz, 1991; Engel and Moran, 2013).

The exceptional preservation of the digestive system organs, including proventriculi of fossils of the flea *Saurophthirus longipes* (order Siphonaptera), recovered from the Lower Cretaceous of the Zaza Formation, Baissa locality, Transbaikalia, East Siberia, Russia, have been documented in detail by the researchers Strelnikova and Rasnitsyn (Strelnikova and Rasnitsyn, 2016; Rasnitsyn and Strelnikova, 2018). Recently, Zharkov and Dubovikoff (2023) also presented the first fossil record of ant proventriculi, from Eocene Baltic amber, accessed under Micro-CT scanning. For the Crato Formation of northeastern Brazil, the first mention of fossilized proventriculi was made by Grimaldi et al. (2008) on termites (Isoptera).

The Crato Formation was deposited during the Upper Aptian, Lower

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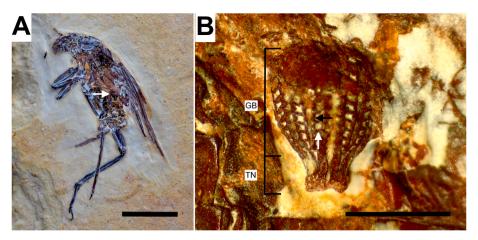


Fig. 1. Araripegryllus cf. Femininus, adult female CAV 0012-I. A) Overview. White arrow points to proventriculus. Scale bar 5 mm; B) Detail of proventriculus. Black arrow points to one longitudinal fold, and the white arrow points to one parallel division. GB – Globular body; TN – Tubular neck. Scale bar 0.5 mm.

Cretaceous (Assine et al., 2014; Neumann and Assine, 2015), and is of worldwide importance due to its outstanding fossil record. Several studies have already explored the taphonomy of Crato insects (Menon and Martill, 2007; Barling et al., 2015, 2020; Osés et al., 2016; Bezerra et al., 2018, 2020a, 2020b, 2023; Dias and Carvalho, 2020, 2022; Iniesto et al., 2021; Storari et al., 2021; Dias et al., 2023), with orthopterans figuring as the most studied insect clade from that unit in respect to exceptional preservation (Barling et al., 2015; Osés et al., 2016; Bezerra et al., 2020a; Dias and Carvalho, 2020; Mendes et al., 2020; Ribeiro et al., 2021). They constitute one of the most expressive groups of arthropods found in this lithostratigraphic unit due to their abundancy and preservation, with several fossils belonging to the suborders Ensifera (commonly known as crickets and katydids) and Caelifera (grasshoppers and locusts) (Menon and Martill, 2007). From those, grylloids (Ensifera) are the most diverse and are often well-preserved (Heads and Martins-Neto, 2007).

Recent orthopterans figure as one of the most prominent groups in terms of morphological variety of the proventriculus, presenting diverse patterns among its clades (Judd, 1948; Bland and Rentz, 1991; Szinwelski et al., 2009), but this structure has yet to be morphologically described in detail in their fossils. Here, we provide a detailed description of the oldest orthopteran proventriculi known so far, recovered from several fossil crickets (Orthoptera: Ensifera: Grylloidea) of the Crato Formation.

2. Material and methods

2.1. Geological setting

The Araripe Basin crops out in Brazil's northeast region, covering areas of the states of Piauí, Pernambuco and mostly Ceará (Saraiva et al., 2007, 2021). While its units range from the Paleozoic through the Mesozoic eras (Assine et al., 2014), the Aptian deposits were formed by post-rift units associated with the separation of South America and Africa, and are known as the Santana Group, being subdivided into the Barbalha, Crato, Ipubi and Romualdo Formations, from bottom to top (Neumann and Cabrera, 1999; Assine et al., 2014).

From those units, the Crato Formation, a ca. 90 m thick succession, is formed by meter-scale horizontal strata of limestone that are interbedded with shales, siltstones and sandstones (Neumann and Cabrera, 1999; Castro et al., 2007; Assine et al., 2014). Most of its outcrops are exposed in commercial quarries or river margins, particularly between the Nova Olinda and Santana do Cariri municipalities, as well as on the Batateiras River banks, all located in the state of Ceará (Viana and Neumann, 2002).

Due to the absence of true marine fossils, there is strong indication

that the Crato Formation strata were deposited under lacustrine conditions (Neumann et al., 2003; Heimhofer et al., 2010; Varejão et al., 2021), though the presence of halite pseudomorphs in some sections suggests that the basin experienced salinity variations with increased arid and evaporitic conditions (Martill, 2007; Warren et al., 2017; Heimhofer et al., 2010; Storari et al., 2021).

The layers of the Crato Formation have received several stratigraphic classifications to date. The most recent work addressing Nova Olinda's stratigraphy is from Corecco et al. (2022), in which the authors report the most common layer where insects are found with the informal name "veio do besouro", commonly used by local mine workers. For formal classifications, the most recent names the level with the exceptionally preserved fossils as facies association 4 (FA-4 - sensu Varejão et al., 2021), with insects usually found in its upper beds (Varejão et al., 2021). A previous classification by Varejão et al. (2019) pointed out that the stratigraphic position of most of insects is a layer called Interval III, consisting the upper 2-m part of the Lagerstätte succession and characterized by finely laminated, rhythmic, laminites. Finally, the Crato Formation has also been divided in six carbonate intervals, designated C1 to C6 by Neumann and Cabrera (1999), with C6 encompassing the Lagerstätte succession (Neumann and Cabrera, 1999; Storari et al., 2021). However, since the C6 is not further subdivided, no specific profile has been associated with the presence of well-preserved insects.

2.2. Material

We analyzed nine specimens from the Crato Formation: CAV 0012-I (from the Paleontological collection of the Centro Acadêmico de Vitória, Universidade Federal de Pernambuco, Vitória de Santo Antão, Brazil) (Fig. 1); LPU P1–P4, and LPU P6 (from the Paleontological collection of the Universidade Regional do Cariri, Crato, Brazil) (Figs. 2 and 3); and GP/1 E 7268, 8691, and 8910 (from the Scientific Paleontological Collection of the Institute of Geosciences of the Universidade de São Paulo, São Paulo, Brazil) (Fig. 4).

CAV 0012-I was collected in 2009 during a field trip of biology students of the Centro Acadêmico de Vitória (Universidade Federal de Pernambuco) in the renowned limestone mine, Mina do Demar, on the road that connects Nova Olinda and Santana do Cariri municipalities, Ceará state. The LPU specimens lack exact locality information as they have been collected by mine workers and donated to that collection. The GP/1 E specimens also lack exact locality information because they were recovered by the Brazilian federal police during an operation against fossil smuggling. Although those specimens lack exact locality details they were probably collected from upper portions of the FA-4 (or C6) layer.

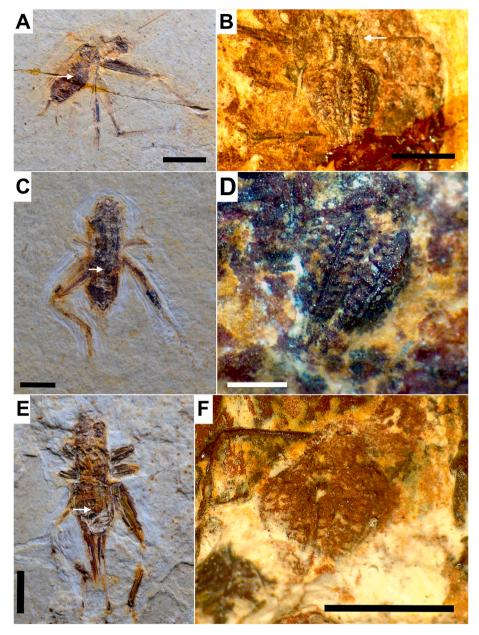


Fig. 2. Grylloidea specimens. A) Specimen LPU P4 overview, adult female, Grylloidea indet., white arrow points to proventriculus. Scale bar 5 mm; B) Detail of proventriculus of specimen LPU P4; white arrow points to long, curved tube, that connects the proventriculus to the gastric crop. Scale bar 0.5 mm; C) Specimen LPU P1 overview, Grylloidea indet., white arrow points to proventriculus. Scale bar 3 mm; D) Detail of proventriculus of specimen LPU P1. Scale bar 0.2 mm; E) Specimen LPU P2 overview, Gryllidae indet., white arrow points to proventriculus. Scale bar 4 mm; F) Detail of proventriculus of the specimen LPU P2. Scale bar 0.5 mm.

2.3. Methods

The specimens were prepared mechanically under a stereomicroscope, and the sediment was removed with ultrafine needles and a brush. All figures were made with the software Autodesk Version 8.6.1, and the photos were taken with a Nikon D800 digital camera or an Olympus DSX110 microscope (Laboratório de Estudos Paleobiológicos, Instituto de Geociências, Universidade de São Paulo, São Paulo, Brazil). The descriptive morphological terminology follows Judd (1948), Bland and Rentz (1991), and Wang et al. (2012). The specimens LPU P5, GP/1 E 7409, and GP/1 E 8827 were analyzed only for biostratinomic features since their proventriculi are not well preserved. Micro morphological analyses were conducted on specimens CAV 0012-I and LPU P6 using the scanning electron microscope (SEM) FEI Quanta 650 FEG at the Instituto de Geociências, Universidade de São Paulo (São Paulo, Brazil), after a gentle bath of alcohol 70%. The specimens were kept uncoated and

analyzed under low vacuum (environmental scanning electron microscope), with images taken at 20 kV of acceleration voltage, spot size 6, and variable working distances (as shown in each SEM image). The micrographs were taken with the microscope's secondary electron detector (LFD) and backscattered electron detector (CBS).

3. Results

Most analyzed specimens could be identified just as Grylloidea indet., given the poor preservation of diagnostic structures (such as the wings) at less inclusive levels (Table 1). Most of them are preserved flattened, dorso-ventrally, with the legs spread out and wings absent. CAV 0012-I is preserved in lateral aspect with the wings folded over the abdomen in a characteristic 'rest position' (Martins-Neto, 1992) (Fig. 1), while LPU P4 is also preserved in lateral view but its wings are absent (Fig. 2A). GP/1 E 8910 has its wings open laterally, as typical of

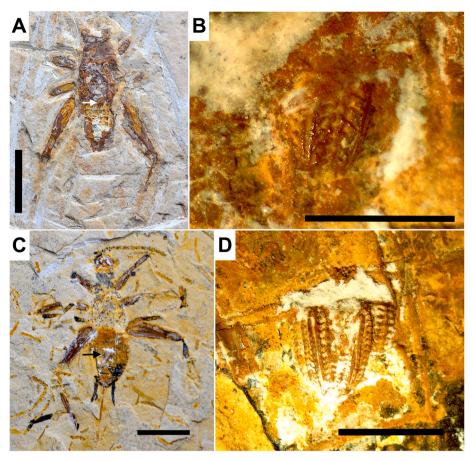


Fig. 3. Grylloidea specimens. A) Specimen LPU P3 overview, Grylloidea indet., white arrow points to proventriculus. Scale bar 5 mm; B) Detail of proventriculus of specimen LPU P3. Scale bar 0.5 mm; C) Specimen LPU P6 overview, *Cearagryllus* sp. Indet., adult female, black arrow points to proventriculus. Scale bar 10 mm; D) Detail of proventriculus of specimen LPU P6. Scale bar 1 mm.

individuals who died in the depositional environment, possibly owing to asphyxiation and drowning after exhaustion (Martins-Neto, 1992; Martínez-Delclòs et al., 2004) (Fig. 4E). The posterior limbs are preserved in all specimens. For their general morphological description, see Appendix Table A1.

The analyzed specimens are compressed with their cuticles cracked in their abdominal plates, fully exposing the inner cavity and proventriculi, except in GP/1 E 8691, which presents the proventriculus partially covered by external cuticle (Fig. 4C and D).

The proventriculi are three-dimensionally preserved and, as in modern crickets, consist of an anterior globular body (GB) and a posterior tubular neck (TN), a structure that connects with the gastric caeca of the midgut (Bland and Rentz, 1991; Li et al., 2011) (Fig. 1). At the globular region, there are rows formed by groups of sclerotized appendices (parallel divisions) united to each other by sclerotized partitions (longitudinal folds). The specimens LPU P4 and GP/1 E 8910 also present, anteriorly to the GB, a long, curved tube, similar to the TN in morphology, that connected to the gastric crop (Fig. 2B and 4D).

SEM images of CAV 0012-I revealed internal median teeth, as well as microvilli texture throughout the GB and TN (Fig. 5). In that specimen, the upper part of the proventriculus has a flat external wall, unlike other areas, which are preserved in three dimensions. SEM images of LPU P6 show some preserved remains of the inner cavity of the foregut, which consist of several small denticles that could be associated with the crop cavity (Fig. 6B and C). Finally, as in specimen CAV 0012-I, LPU P6 also preserves some of the folds that form internally the median and lateral teeth of the proventriculus (Fig. 6D–F).

4. Discussion

Grylloids from the Crato Formation can show three types of fossilization processes: pyritization, phosphatization, and kerogenization (Bezerra et al., 2020a, 2020b; Dias and Carvalho, 2020). The fossils we analyzed have iron-oxide preservational microfabrics, which suggest oxidation after pyritization (Osés et al., 2016, 2017; Bezerra et al., 2023). Pyritization depends on the concentration of sulphate and iron ions within the decaying carcass, and on their subsequent reduction and pyrite precipitation, that are controlled by microbial mats (Osés et al., 2016, 2017). If fissures are present in the insect cuticle, solutes can penetrate and facilitate the mineralization of both external cuticle and inner soft tissues (Osés et al., 2016, 2017).

Although the insect fore and hindguts are highly sclerotized, as they are of ectodermic origin (Fantazzini et al., 1998; Douglas, 2013), their organs are rarely preserved in the fossil record and to date were only mentioned for Orthoptera by Rust (1999) and Dias and Carvalho (2020). Rust (1999) revealed the presence of a proventricular structure in a fossil specimen of Gryllidae from the Paleogene of the Ølst Formation in Denmark, but it was not well-preserved, and Dias and Carvalho (2020) reported anatomical microstructures such as cutaneous plaques and denticles as associated with the proventriculus of a female Baissogryllidae from the Crato Formation. However, their location in the specimen was not described nor it was possible to observe in the image provided the whole globular organ preserved, perhaps due to taphonomic imprints, or simply because they recovered only fragments of the putative proventriculus associated with the foregut region. Our SEM results show similar cutaneous plaques and denticles as those found by Dias and Carvalho (2020) preserved in LPU P6 but associated with a

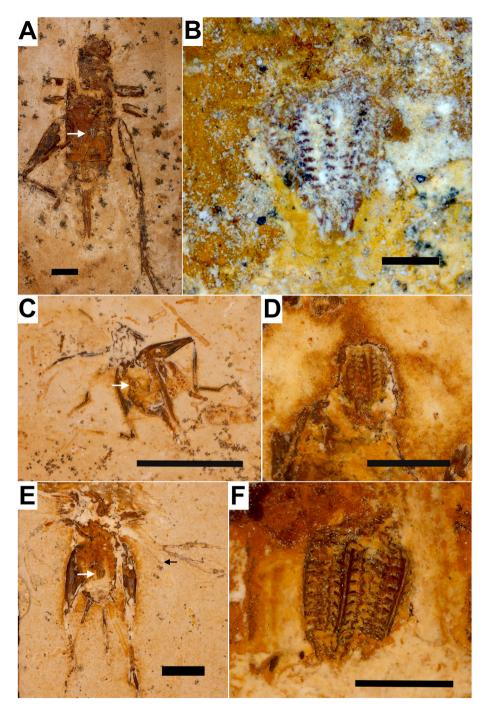


Fig. 4. Grylloidea specimens. A) Specimen GP/1 E 7268 overview, Grylloidea indet., white arrow points to proventriculus. Scale bar 5 mm; B) Detail of proventriculus of specimen GP/1 E 7268. Scale bar 0.2 mm; C) Specimen GP/1 E 8691 overview, Grylloidea indet., white arrow points to proventriculus. Scale bar 10 mm; D) Detail of proventriculus of specimen GP/1 E 8691. Scale bar 1 mm; E) Specimen GP/1 E 8910 overview, *Araripegryllus* sp. Indet., adult female, white arrow points to proventriculus; and black arrow pointing to antennae. Scale bar 5 mm; F) Detail of proventriculus of specimen GP/1 E 8910. Scale bar 1 mm.

different body area than that of the proventriculus that, based on their location and seemingly sclerotized appearance, we interpret as remains of the foregut's internal surface, most possibly of the crop, which is situated anteriorly to the proventriculus (Chapman et al., 2013) (see Fig. 6). Therefore, to our knowledge, the orthopteran proventriculi we present here are the oldest known, and the first ones described in detail.

In most cricket fossils from the Crato Formation, the proventriculi are not preserved; for instance, they were preserved in only seven out of the 208 orthopteran specimens in the Scientific Paleontological Collection of the Institute of Geosciences of the Universidade de São Paulo, although only three were investigated in details in the present work

since the remaining four were badly preserved. Interestingly, even in specimens with well-preserved proventriculi, their bodies are frequently not well-preserved at hand-scale. To explain the exceptional preservation of this internal organ but not of the remaining of the carcass, we hypothesize that despite the proventriculus being an extremely hard organ, it can only be observed in the fossils if exposed after the decomposition and/or cracking of the overlying body exoskeleton. This cuticle cracking could be related to decaying processes due to longer exposure time of carcasses after death in the waterbody, following a short period of decay on land (Martínez-Delclòs et al., 2004). Alternatively, the proventriculi could simply be observed because the outer

Table 1
Summary of the main characters of the analyzed grylloids. '?' unknown.

Specimen	CAV 0012-I	LPU P1	LPU P2	LPU P3	LPU P4	LPU P6	GP/1 E 7268	GP/1 E 8691	GP/1 E 8910
Taxonomical identification	Araripegryllus sp. Indet.	Grylloidea indet.	Gryllidae indet.	Grylloidea indet.	Grylloidea indet.	Cearagryllus sp. Indet.	Grylloidea indet.	Grylloidea indet.	Araripegryllus sp. Indet.
Text figure	1 and 5	2C,D	2 E,F	3 A,B	2 A,B	3C,D and 6	4 A,B	4C,D	4 E,F
Sex	Female	Male	Female	?	Female	Female	?	?	Female
Body length: proventriculus length	1:16	1:16	1:16	1:20	1:17	1:20	1:21	1:10	1:14
Position of proventriculus within body length	2/3	3/5	3/4	3/5	2/3	3/4	2/3	1/2	2/3
Proventriculus length	0.7 mm	0.6 mm	0.6 mm	0.5 mm	0.7 mm	1.2 mm	0.6 mm	1.0 mm	1.5 mm
Proventriculus diameter (widest point)	0.5 mm	0.4 mm	0.5 mm	0.5 mm	0.6 mm	1.2 mm	0.5 mm	0.7 mm	1.0 mm
Globular body to tubular neck proportion	4× wider than tubular neck	3.5× wider than tubular neck	5× wider than tubular neck	?	3× wider than tubular neck	5.5× wider than tubular neck	4× wider than tubular neck	?	4.5× wider than tubular neck
Number of proventricular parallel divisions	10 rows	10 rows	10 rows	10 rows	10 rows	12 rows	10 rows	9 rows	9 rows
Number of proventricular longitudinal folds	12	13	15	9	13	16	12	10	14

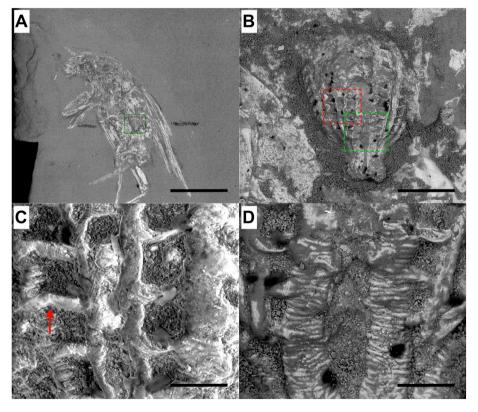


Fig. 5. Araripegryllus cf. Femininus, adult female CAV 0012-I. Morpho-anatomical features of proventriculus visualized on scanning electron microscopy; A) Overview, CBS detector. Green square delimits proventriculus showed in detail in figure B. Magnification $7\times$. Scale bar 5 mm; B) Detail of proventriculus, CBS detector. Red square evidencing region magnified in figure C, and green square delimiting part of proventriculus under magnification in D. Magnification $80\times$. Scale bar 500 μ m; C) Part of the GB, LFD detector. Red arrow points to fold, indicating an internal median tooth. Magnification $450\times$. Scale bar 100 μ m; D) Part of the GB and TN with preserved microvilli texture. Magnification $400\times$. Scale bar 100 μ m.

cuticle was cracked open during sampling and/or preparation of the material; unfortunately, counterparts of the analyzed material are not available. In any case, since insects with well-developed wings such as

grylloids most often die, decompose, disarticulate, and/or fragment/crack while floating on the lake surface, but seldom sink and are buried (Martínez-Delclòs and Martinell, 1993), cases as the present ones are

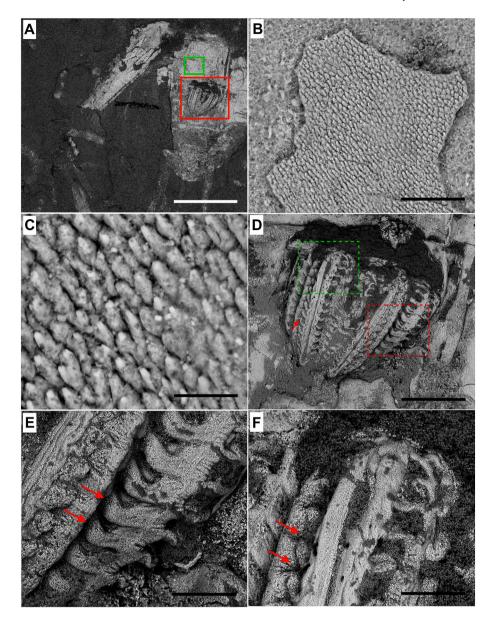


Fig. 6. Cearagryllus sp. Indet., adult female LPU P6. Morpho-anatomical features of inner cavity of foregut visualized on scanning electron microscopy, CBS detector; A) Overview of abdomen. Green square evidencing region detailed in figures B and C, and red square evidencing region detailed in figure D. Magnification $8\times$. Scale bar 5 mm; B,C) Detail of remains of inner cavity of foregut under $450\times$ and $2000\times$ magnifications, with surface consisting of several denticles. Scale bars $100 \mu m$ and $30 \mu m$; D) Detail of proventriculus. Red square shows part of proventriculus under magnification in figure E, and green square delimits part of proventriculus under magnification in F. Red arrow points to fold indicating internal median tooth. Magnification $40\times$. Scale bar 1 mm; E) Part of GB. Red arrows point to fold indicating internal median teeth. Magnification $150\times$. Scale bar $400 \mu m$.

rare in the fossil record.

All proventriculi analyzed are tridimensionally preserved structures (albeit to different degrees), even though internal organs are easily affected by compression by the overlying sediments. However, in most specimens we could only recognize proventricular external features: their length and diameter, the general number of sclerotized appendices preserved on each longitudinal fold, and the number and width of preserved sclerotized partitions between adjacent rows. Other characters useful for taxonomical attributions among extant groups, such as anatomical features of the lateral and median teeth (Li et al., 2011; Wang et al., 2012), could not be evaluated in detail since they are only visible on the internal surface of the proventriculus, although we could identify in two of the analyzed specimens the folds that form internally the median and lateral teeth of the proventriculus.

Regarding the rows of parallel divisions, in the fossils we analyzed

there are 9–12, while in all the recent 102 orthopteran species whose proventriculi have been studied so far (belonging to the Ensifera families Trigonidiidae, Gryllidae, and Tettigonidae; and also the Caelifera family Acrididae) there are six (Judd, 1948; Bland and Rentz, 1991; Szinwelski et al., 2009; Li et al., 2011; Wang et al., 2012). These data, although limited, suggests a possible trend of decreasing number of parallel divisions in modern taxa, while the overall size of the proventriculus increased (e.g., body/proventriculus proportions between 1/8 to 1/12 in extant taxa—see Wang et al., 2012). This could represent an evolutionary tendency to lose parallel divisions while increasing the overall size of the organ, but more data on fossil and recent grylloids are needed to test this hypothesis.

The specimens LPU P2 and LPU P6 presented their proventriculi located more posteriorly in the body than other specimens. Wang et al.'s (2012) results showed that recent Phaneropterinae (Tettigonidae) with a

short foregut and a longer midgut and hindgut are carnivorous or omnivorous since the main place for grinding food is the foregut, so herbivorous species have a larger one. One could thus hypothesize that specimens LPU P2 and LPU P6 were phytophagous because they have a longer foregut. However, considering the possibility that the proventriculi as well as the entire intestine may be displaced due to decomposition [as similarly noted for termites of Crato Fm. By Grimaldi et al. (2008)], we cannot attest that this character is related to a specific feeding habit, though Crato orthopterans are frequently associated to phytophagy (Grimaldi, 1990; Martins-Neto, 2005; Santos Filho et al., 2017). On the other hand, carnivores and omnivores present high degree of chitinization in their proventriculi (as all the specimens analyzed by us), and big and numerous teeth on their proventriculi (as specimen LPU P6), due to processing hard parts of food (Gibbs, 1967; Muralirangan, 1979; Wang et al., 2012). Based on the latter we could hypothesize that the fossils analyzed here are carnivorous or omnivorous. But for that, it would be important to consider many additional characters (e.g. structure of mouthparts, forelegs, degree of chitinization of foregut), which are, unfortunately, unavailable in our specimens.

5. Conclusion

The proventriculi of Crato Formation grylloid specimens described above are the oldest known (Lower Cretaceous) for this group, and the first characterized in detail. They show that these extinct orthopterans had an overall similar proventricular morphology compared to recent taxa, with a globular body and a posterior tubular neck. However, in the globular region of all the fossils analyzed, there are between 9 and 12 rows of parallel divisions, differing from all the modern crickets studied so far, which usually have only six. Since here we only worked with nine specimens, it is not possible to provide a statistical analysis to test for evolutionary hypotheses that could explain the observed differences among extant and extinct taxa, though it remains open to debate.

The cuticle of all the grylloids analyzed here are cracked in their abdominal plates, exposing the inner cavity and proventriculi, which are highly sclerotized and robust. The exposure and 3-D preservation of the proventriculi is, probably, related to a short preservational window, in which the carcasses needed to decay before exposition to favorable environment for the exceptional preservation. Additionally, two of the specimens analyzed with SEM revealed preserved internal median teeth and folds, as well as microvilli texture, revealing astonishing internal preservation.

CRediT authorship contribution statement

Arianny P. Storari: Writing - review & editing, Writing - original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Gabriel L. Osés: Writing - review & editing, Validation, Methodology, Investigation, Formal analysis. Débora Soares de Almeida-Lima: Writing - original draft, Investigation, Formal analysis. Marcia A. Rizzutto: Methodology. Renan Alfredo Machado Bantim: Writing - review & editing, Visualization, Resources, Investigation, Data curation. Flaviana Jorge de Lima: Writing - review & editing, Visualization. Taissa Rodrigues: Writing - review & editing, Visualization, Validation, Supervision, Project administration, Funding acquisition. Juliana Manso Sayão: Writing - review & editing, Visualization, Validation, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

Acknowledgements

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, 001), to APS. GLO thanks Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for his Post-doctoral scholarship, grant #2021/07007–7. RAMB thanks the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP, grants BMD-0124-00302.01.01/19 and PV1-00187-00052.01.00/21). TR thanks Fundação de Amparo à Pesquisa e Inovação do Espírito Santo and Conselho Nacional de Desenvolvimento Científico e Tecnológico (FAPES/CNPq, grant 509/2020), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant 314260/2021–8). JMS acknowledge Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ, grant 260003/001185/2023).

We thank the CTG-UFPE Biostratigraphy Laboratories, and CB-UFPE insectary for their technical support. We acknowledge three anonymous reviewers for their helpful comments in a previous version of the manuscript. We also thank Gustavo Pinho, Elis Santana and Lenart Lucena for helping to identify specimens from URCA. We also thank the Centro de Pesquisas em Geocronologia e Geoquímica Isotópica, Universidade de São Paulo, and particularly Isaac Jamil Sayeg for support during SEM analyses. We acknowledge Juliana Leme and Ivone Cardoso Gonzales for the permission to use samples from the Paleontological Scientific Collection, University of São Paulo, as well as for research support. GLO thanks the Programa de Pós-Doutorado, Instituto de Física, Universidade de São Paulo for research support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2023.104737.

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