Editors' choice

X-ray computed microtomography as a fundamental piece in the study of microcrinoids

BRUNA POATSKIEVICK-PIEREZAN, ANDREW SCOTT GALE, ANDERSON CAMARGO MOREIRA, BERNARDO VAZQUEZ-GARCIA, LUCAS DEL MOURO, MARCOS ANTONIO BATISTA DOS SANTOS FILHO, SIMONE BAECKER-FAUTH, and GERSON FAUTH

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This study employs X-ray computed microtomography (micro-CT) to investigate the internal structures of microcrinoids, focusing on the roveacrinid *Sergipecrinus reticulatus* from the Aptian–Albian (112–115 Ma) of the Sergipe Basin, Brazil. For the first time, sub-basal balls were observed in situ and in three dimensions, representing the first 3D documentation of these internal structures in a microcrinoid cup. This constitutes both a methodological advance, the first use of micro-CT applied to this group, and a descriptive and taxonomic advance, as it reveals an unprecedented internal morphology. These structures, previously observed only under SEM and identified in fragments of other genera, might be hollow; however, micro-CT analysis reveals they are dense, containing only small and sub-resolution pores. This discovery suggests that their presence may be more widespread across the Roveacrinidae than previously thought, raising questions about their evolutionary and functional significance. As a cladistics trait, the presence of sub-basal balls contributes to the phylogenetic reconstruction of the family. Moreover, this study underscores the value of micro-CT in revealing detailed, non-destructive insights into microfossil morphology and proposes its broader application to uncover the internal structures of other genera within the Roveacrinidae.

Key words: Echinodermata, Roveacrinida, microfossil, Albian, Sergipe-Alagoas Basin, Brazil.

Bruna Poatskievick-Pierezan [brunapp@unisinos.br; ORCID: https://orcid.org/0009-0001-3250-8939], Bernardo Vázquez-García [bernardovg@unisinos.br; ORCID: https://orcid.org/0000-0001-8108-4215], Marcos Antonio Batista dos Santos Filho [abatistas@unisinos.br; ORCID: https://orcid.org/0000-0001-8409-403X], Simone Baecker-Fauth [sbfauth@unisinos.br; ORCID: https://orcid.org/0000-0001-5201-981X], and Gerson Fauth [gersonf@unisinos.br; ORCID: https://orcid.org/0000-0003-2594-1424], Instituto Tecnológico de Paleoceanografia e Mudanças Climáticas, São Leopoldo, 93022-750, Brazil; Universidade do Vale do Rio dos Sinos, São Leopoldo, 93022-750, Brazil.
Andrew Scott Gale [andy.gale@port.ac.uk; ORCID: https://orcid.org/0000-0002-2075-3689], University Portsmouth, Portsmouth, PO13QL, UK; The Natural History Museum, London, SW75BD, UK.
Anderson Camargo Moreira [moreiradr78@gmail.com; ORCID: https://orcid.org/0000-0003-1229-3616], Universidade Federal de Santa Catarina, EMC, Florianópolis, 88040-900, Brazil.
Lucas Del Mouro [lucas.delmouro@gmail.com; ORCID: https://orcid.org/0000-0001-7829-0683], Universidade Federal de Santa Catarina, EMC, Florianópolis, 88040-900, Brazil; Harvard University, Cambridge, 02138, USA.

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Introduction

X-ray computed microtomography (micro-CT) has become a powerful tool for the three-dimensional visualization of internal structures in modern organisms and fossils, enabling significant advances in the study of the morphology of tiny marine organisms (Chen et al. 2009; Hickman-Lewis et al. 2017). Previous studies highlight the relevance of computational techniques in fossil modeling (Rahman and Smith 2014; Rahman 2017; Rahman and Zamora 2023), as well as the application of micro-CT in microfossil analysis, including within the Sergipe-Alagoas Basin (Karch et al. 2017; Hermanová et al. 2020; Kachovich and Aitchison 2020; Becker-Kerber et al. 2021; Mouro et al. 2021). Among them, the family Roveacrinidae, a group of microcrinoids, exhibits anatomical characteristics that are crucial for the reconstruction of its phylogenetic tree. Traditional studies

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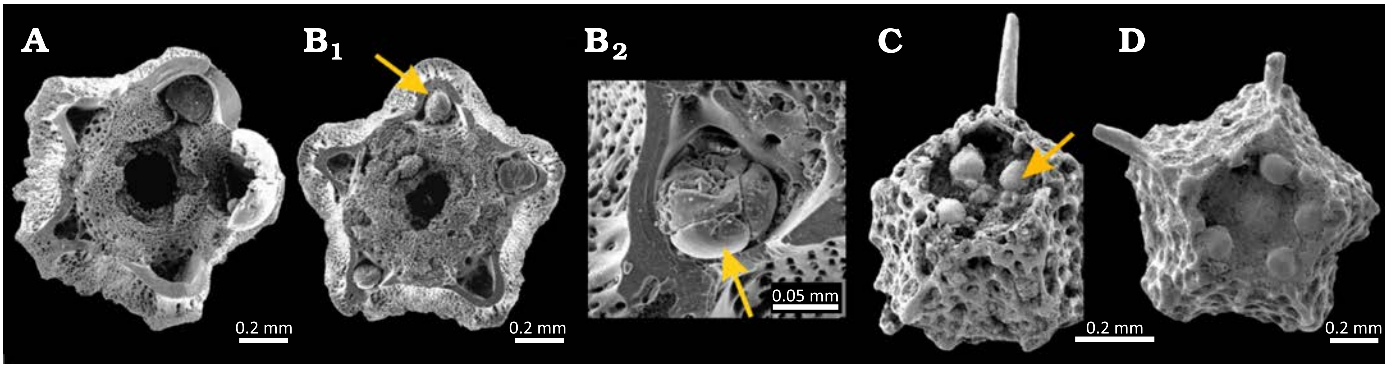

Fig. 1. Broken cups of roveacrinoids showing the position of sub-basal balls (arrows). **A**, **B**. *Hyalocrinus magnezii* Destombes, 1984, from the middle Albian (Lower Cretaceous), Gault Formation, Folkestone, UK (after Gale 2019: pl. 38: 2, 3). **A**. NHMUK PI EE 16062. **B**. NHMUK PI EE 16063. A, B_1, transverse sections of broken cups: B_2, enlargement of the subradial ball. **C**, **D**. *Euglyphocrinus pyramidalis* Peck, 1943, from the upper Albian (Lower Cretaceous), Duck Creek Formation, Fort Worth, Texas, USA (after Hess 2015: fig. 9). Transverse sections of broken cups: **C**, M11595; **D**, M11594.

of fossil crinoids are often constrained by the preservation of isolated and fragmented ossicles, limiting access to internal morphological characters (Salamon and Feldman-Olszewska 2018). Consequently, micro-CT has become an increasingly valuable tool for investigating the internal architecture of these organisms.One of these characteristics is the presence or absence of the sub-basal balls, enigmatic spherical structures located radially, immediately aboral to the basal plates within the cup. These features have previously been observed in several genera of the subfamily Orthogonocrininae (*Hyalocrinus*, *Orthogonocrinus*, and *Styracocrinus*) and in the plotocrininae genus *Euglyphocrinus*, recovered in broken cups (Figs. 1, 2; Gale 2019, 2020, 2023; Gale and Matrion 2021). Here, we report for the first time the presence of sub-basal balls in the Aptian–Albian species *Sergipecrinus reticulatus* Poatskievick-Pierezan, Gale & Fauth, 2023, expanding the known distribution of these structures within the Roveacrinidae. This finding not only underscores the value of micro-CT as a powerful tool to explore the internal structures of microcrinoids but also raises important questions about the evolutionary history of the family. The discovery of sub-basal balls in *S. reticulatus* suggests that these structures may have appeared much earlier than previously thought, indicating a broader distribution across genera. Moreover, the presence of these structures in one of the oldest known roveacrinid genera implies that they could be synapomorphic for the family, with significant implications for the understanding of its evolution and diversity. Thus, this study highlights the potential of micro-CT to reveal previously inaccessible morphological traits, providing new insights into the phylogeny and internal anatomy of Roveacrinidae.

The roveacrinid cup is made up of a circlet of five radial plates, surrounding a central radial cavity, and the bases of the arms articulate with the adoral surfaces of these. Basal plates are very variably developed within the family, and in Orthogocrininae these are fused to form a small polygonal plug in the base of the radial cavity (Gale 2023: text-figs. 5D–G, 6A) and the top of the basal cavity. Sub-basal balls are spherical to ellipsoidal structures which fit into five radially positioned depressions in the roof of the basal cavity.

These are illustrated in Fig. 1, and their position within the proposed phylogeny of the Roveacrinidae is shown in Fig. 2. They are solid subspherical structures, made up of discrete components (Fig. $1B_2$).

Institutional abbreviations.—M, Naturhistorisches Museum Basel, Augustinergasse, Basel, Switzerland; NHMUK, Natural History Museum, South Kensington, London, UK; ULVG, Life and Earth Laboratory, Unisinos University, São Leopoldo, Brazil.

Geological setting

The Sergipe-Alagoas Basin is a passive margin basin located in northeastern Brazil that developed during the brake-up of Gondwana and the opening of the South Atlantic Ocean in the Early Cretaceous (Feijó 1994). Its stratigraphic succession record the transition from continental rift deposits to fully marine sedimentation associated with the post-rift stage of basin evolution.

The suited material derives from the Riachuelo Formation (upper Aptian–Albian) (Fig. 3), which represents the first fully marine carbonate succession deposited during the post-rift phase of the basin (Feijó 1994). The establishment of open marine conditions and the development of extensive carbonate sedimentation during this interval have been widely documented (Berthou and Bengston 1988; Koutsoukos 1989). According to the microfacies and deposited framework proposed by Luft-Souza et al. (2023), the Riachuelo Formation corresponds to a shallow marine carbonate ramp system developed under warm-water conditions and composed predominantly of limestone and marls containing diverse marine invertebrate assemblages, including microcrinoids.

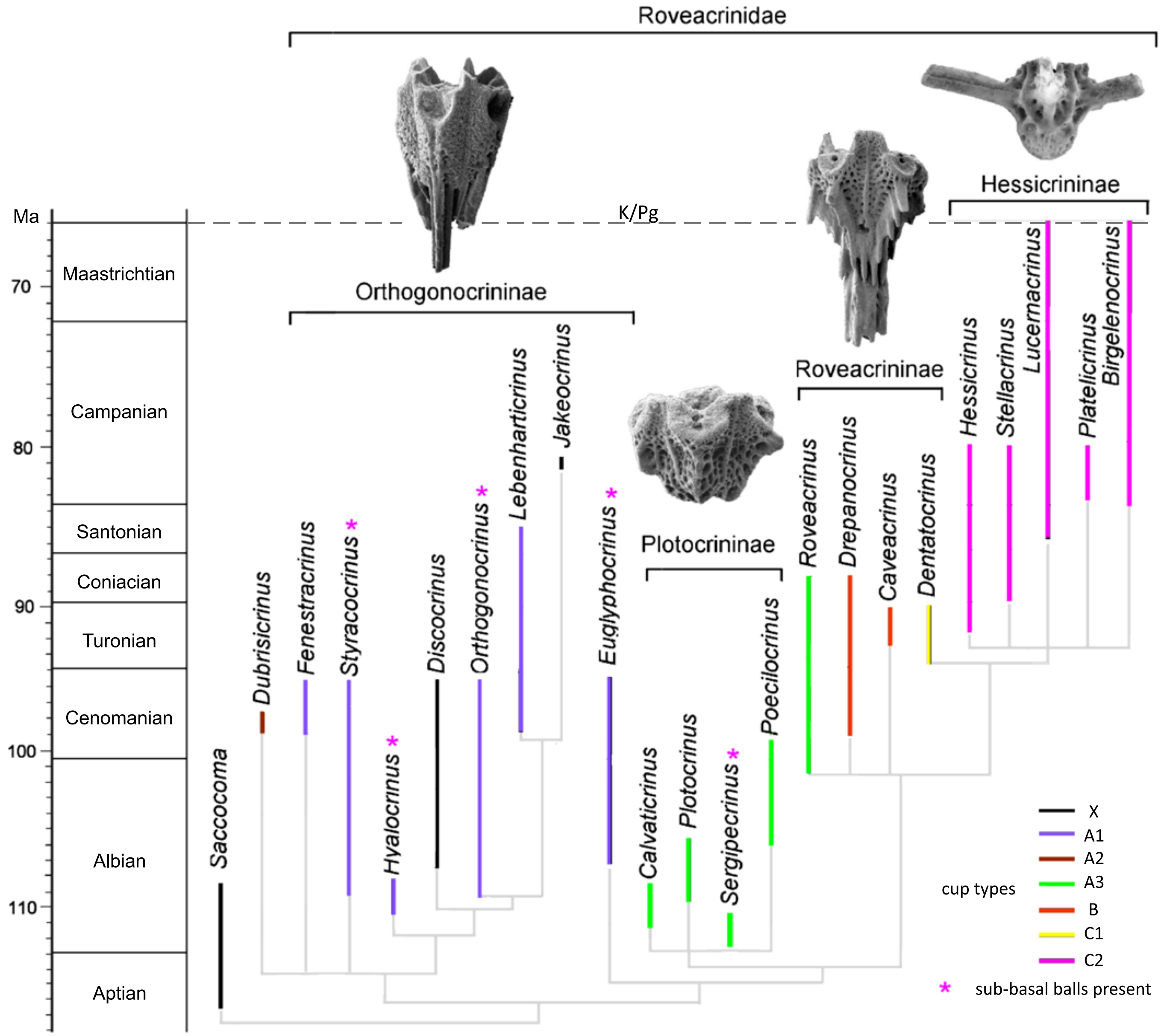

Fig. 2. Phylogeny of Roveacrinidae, highlighting the occurrence of sub-basal balls within the family. Modified from Gale (2023: text-fig. 8), for a comprehensive description of cup morphologies and phylogenetic framework, see Gale (2023).

Material and methods

The analysed specimen, belonging to the species *Sergipecrinus reticulatus* Poatskievick-Pierezan, Gale, & Fauth, 2023, was selected from one of the samples of the SER-03 core in the Sergipe-Alagoas Basin. The specimen chosen for imaging was taken from the 132-meter depth (see Fig. 3D), which represents the level of highest abundance of these organisms, where the greatest number of individuals was observed (Poatskievick-Pierezan et al. 2023, 2024). The holotype of the species was not used, as the gold coating for scanning electron microscopy (SEM) imaging was applied non-uniformly, which would compromise the micro-CT analysis. The analysed specimen is another well-preserved cup and is deposited in the Museu de História Geológica do Rio Grande do Sul under the catalogue number ULVG 15894.

The specimen was imaged using a Zeiss the X-ray microtomography scanner (Versa XRM-500) with the following specifications: the X-ray source operating at 50kV/4W, an exposure time of four seconds, and a 360° sample rotation capturing the amount of 1600 projections. Due to the small size of the sample (~0.9 mm), no beam-hardening filters were used. The resolution of the resulting 3D image is 1.2 µm/voxel. The image was analyzed using FIJI open-source software (Schindelin et al. 2012). Two main tools were employed in this analysis: the feature classifier Trainable Weka Segmentation (Arganda-Carreras et al. 2017) and

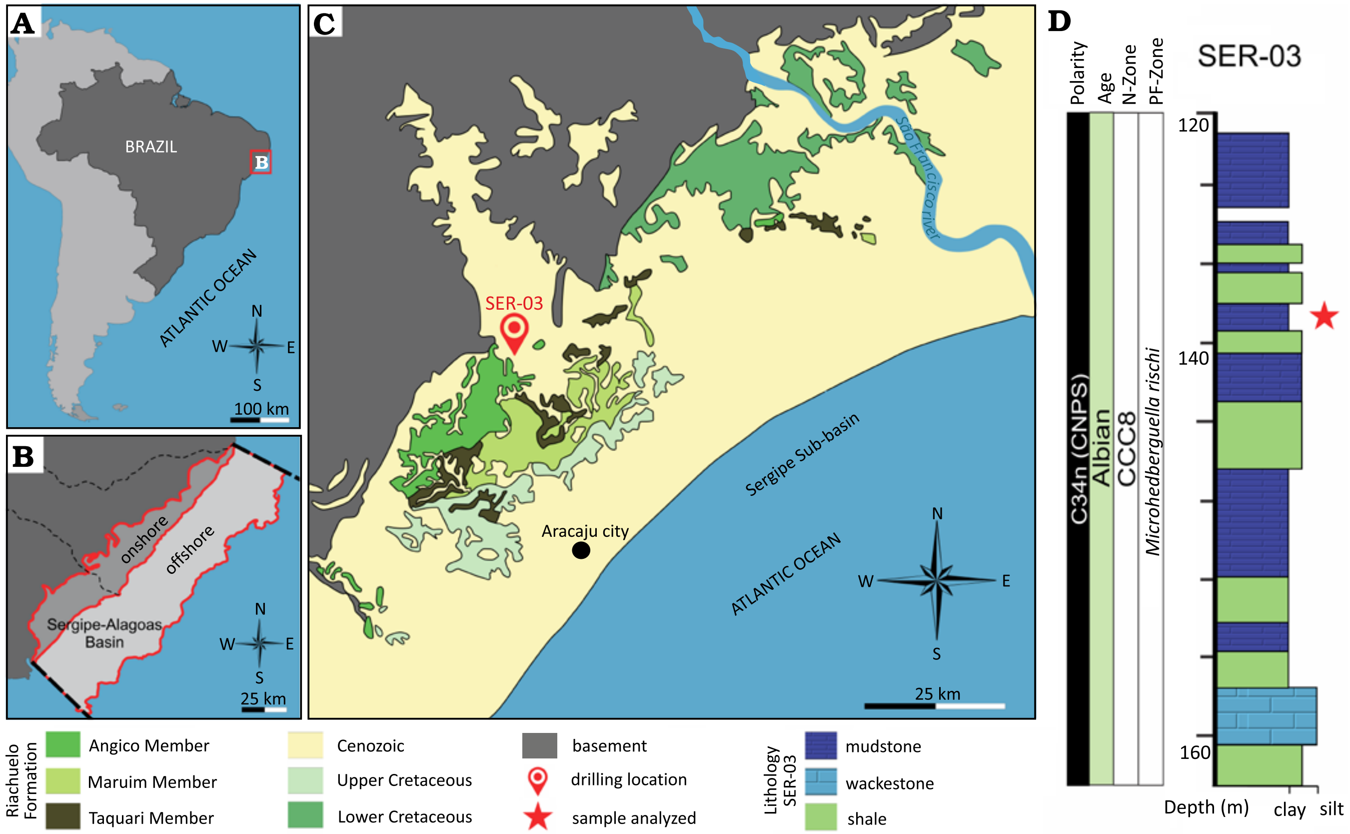

Fig. 3. **A**. Location of the study area in northeastern Brazil, highlighting the states of Sergipe and Alagoas, on the eastern margin of South America. **B**. Regional setting of the Sergipe-Alagoas Basin, showing its onshore and offshore portions. **C**. Geological map of the area near the drilling site, indicating the main lithostratigraphic units and the location of core SER-03. **D**. Detail of the stratigraphic section of core SER-03, corresponding to the interval between 120 and 165 m depth (adapted from Fauth et al. 2021, 2022), presented to emphasize the level at 132 m, from which the analyzed specimen was collected. N-Zone, Nanoplankton Zone; PF, Planktonic Foraminifera Zone.

the smoothing filter Non-Local Means Denoising (Buades et al. 2011). The Weka plugin is based on machine-learning algorithms, allowing users to train the system to recognize patterns in the image. This method serves as an alternative to those based on selecting a threshold in the histogram. The Non-Local Means filter was applied due to its ability to smooth images while preserving edges and interfaces.

Results

The sample (Fig. 4A_1, A_2) presents aggregates attached to its structure, as can be seen in the chart of Figure 4. A 2D slice, in its original format (Fig. 4A_2), taken from the specimen's 3D image (Fig. 4A_1), shows reconstruction artifacts and internal infill material accumulated within the cavities. In Figure 4A_3, a region within a cavity showing an apparent accumulation of fine-grained diagenetic material, possibly micritic is highlighted. Using Trainable Weka Segmentation, the fine material accumulated were segmented from the rest of the specimen to create a mask. The mask was then subtracted from the original image, resulting in the microstructure of the microcrinoid free of diagenetic coverage accumulation. The image was subsequently smoothed with Non-Local Means (Fig. 4A_4). This procedure was applied to each 2D slice, covering the entire 3D image. The 3D images were rendered using Volume Viewer, another tool available in FIJI.

In Figure 5, a small sub-volume cropped from he processed 3D image (Fig. 5A_1) is shown, along with two cropped 2D slices taken from different depths of the volume. The 3D formation of the balls (Fig. 5A_1) can be identified in the 2D images (Fig. 5A_2, 5A_3).

A difficulty in characterizing the balls lies in separating them from each other and from the structure of the microcrinoid. The sub-basal balls 4 and 5 (Fig. 5A_1) have boundaries between them and theyare visually distinguishable (Fig. 5A_3). However, this is not the case for balls 1, 2, and 3. It is also a challenge to recognize the boundaries between the balls 1 and 2 (Fig. 5A_2), and the microcrinoid radials.

Therefore, to estimate the volume of each ball, 2D slices were examined in the three orthogonal planes to locate the slices where the boundaries were either visible or presumable. The balls are ellipsoidal structures, and the major and minor-axis were estimated, as shown in the ball 3 example (Fig. 5A_3).

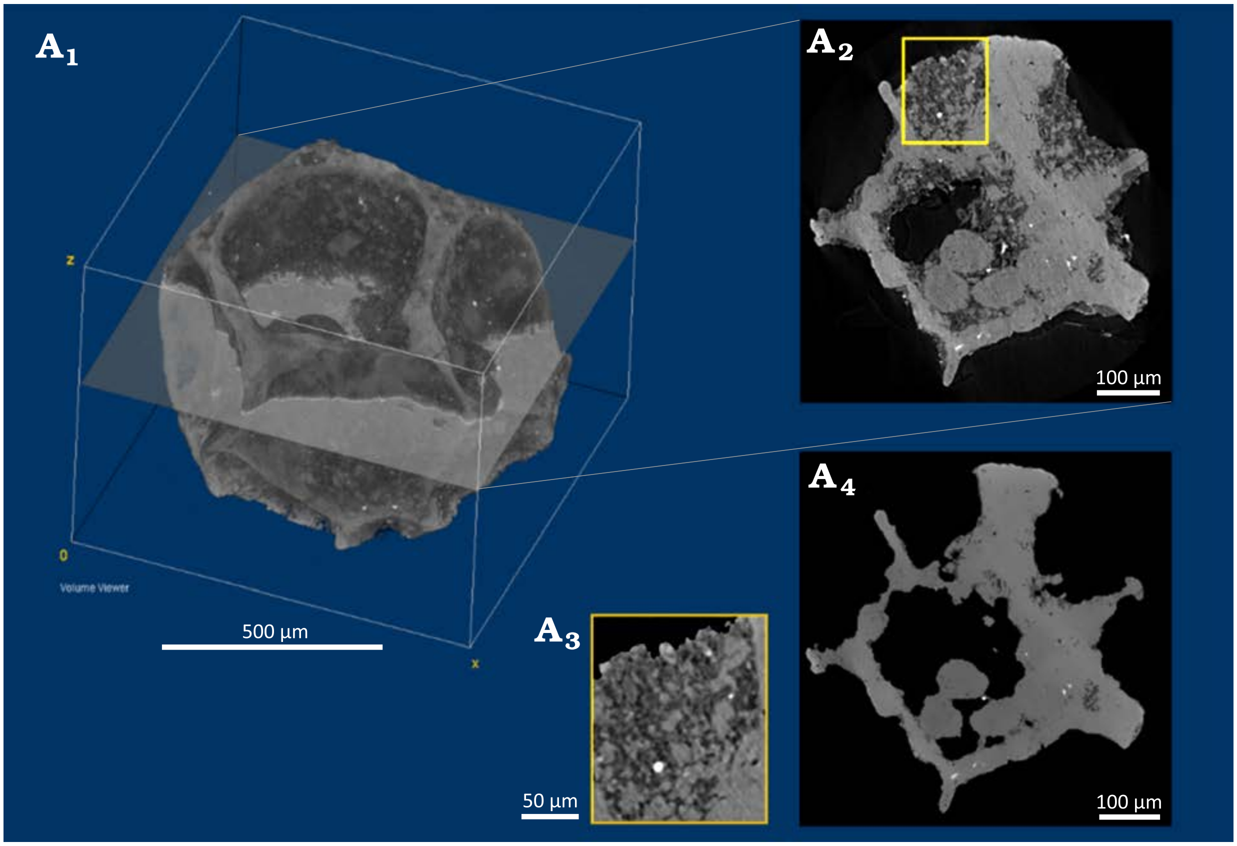

Fig. 4. Roveacrinid crinoid *Sergipecrinus reticulatus* Poatskievick-Pierezan, Gale & Fauth, 2023 (ULVG 15894) from Albian, Sergipe–Alagoas Basin, Brazil. Original 3D microtomography image of ULVG 15894 (A_1) and a 2D slice (A_2). Accumulation of diagenetic cover attached to the cavities of the sample (A_3) and the processed image (A_4).

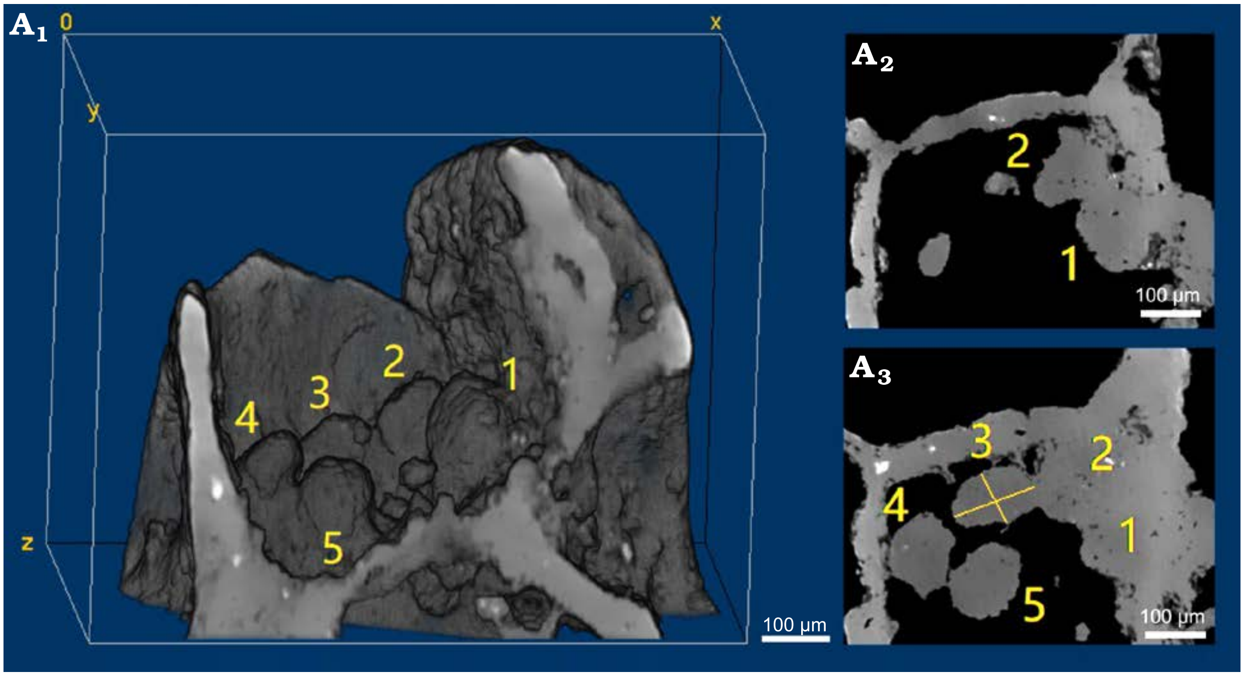

Fig. 5. Roveacrinid crnoid *Sergipecrinus reticulatus* Poatskievick-Pierezan, Gale & Fauth, 2023 (ULVG 15894) from Albian, Sergipe–Alagoas Basin, Brazil. Sub-basal balls in a cropped 3D volume, showing the five sub-basal balls visible within the lower cavity the cup (A_1) and corresponding 2D slices (A_2, A_3), showing the same structures in 2D sections. In all panels, the individual sub-basal balls are labeled 1–5; their respective volumes were measured using the same labels and are reported in Table 1.

Table 1. The volume of the sub-basal balls. Volume (voxel³): volume expressed in cubic voxels obtained from X-ray microcomputed tomography (micro-CT) data; volume (mm³): volume expressed in cubic millimetres after conversion from voxel measurements.

Sub-basal ball	Volume (voxel³)	Volume (mm³)
1	59035.7	1.02E+05
2	51035.2	8.82E+04
3	44861.9	7.75E+04
4	50139.8	8.66E+04
5	44568.7	7.70E+04

Table 1 presents the estimated volumes for each sub-basal ball in the Figure 5A$_1$, and the modelling of the cup based on X-ray micro-computed tomography (micro-CT) of the roveacrinid *Sergipecrinus reticulatus* Poatskievick-Pierezan, Gale, & Fauth, 2023 (SOM: fig. 1), is available for free download in the SOM (Supplementary Online Material available at http://app.pan.pl/SOM/app71-PoatskievickPierezan_etal_SOM.pdf).

Discussion

The discovery of sub-basal balls in *Sergipecrinus reticulatus* Poatskievick-Pierezan, Gale, and Fauth, 2023, using the X-ray computed microtomography adds an important new dimension to the understanding of the internal skeletal organization of this genus and of the Roveacrinidae as a whole. The presence of these structures, previously documented in other roveacrinid genera (Hess 2015; Gale 2016, 2023, Gale et al. 2021), is potentially significant for reconstructing phylogenetic relationships within the family. The occurrence of sub-basal balls in one of the oldest known roveacrinid genera further suggests that these structures may represent a symplesiomorphic feature of the family, with important implications for the early evolution and subsequent diversification of the Roveacrinidae (Hess 2015).

In *S. reticulatus*, the sub-basal balls appear to be irregularly distributed, contrasting with the radially symmetrical arrangement reported in other roveacrinid taxa. The most likely cause of this is taphonomic, with post mortem decay of soft internal tissues resulting in displacement of internal structures. Differential preservation, partial dissolution, or subtle diagenetic modification may influence the appearance of internal skeletal features and diagenetic overprint may obscure or mimic primary morphological traits (Smith 1990; Gorzelak et al. 2016). Therefore, caution is required when distinguishing primary biological structures from taphonomic artifacts. Given that these features are internal and rarely accessible through conventional preservation, micro-CT imaging is essential to distinguish primary biological patterns from taphonomic artifacts (Rahman and Zamora 2023; Gorzelak et al. 2025).

There has been some speculation about possible buoyancy control mechanisms in roveacrinids. Schneider (1989, 1995) argued that the ontogenetic development of an aboral (basal) cavity in roveacrinids could have provided space for gases or fluids, reducing the specific gravity of the animal. He further suggested that movement of gases or fluids between the radial and basal cavities might have permitted vertical movement. However, Hess (2015) has pointed out the presence of gases in the lower (basal) chamber would have had the effect of inverting the crinoid, such that the arms would hang down and the aboral pole was uppermost, which is highly improbable. In this context, it is possible that the sub-basal balls may have functioned as a form of ballast. Such a mechanism would be particularly advantageous for the pelagic or weakly nektonic roveacrinids, as even small concentrations of mass in the cup could contribute to stabilizing body orientation and improving hydrodynamic control in the water column. Functional interpretations linking internal mass distribution to stability and buoyancy have been proposed for other echinoderms and pelagic organisms, emphasizing the biomechanical importance of internal skeletal architecture (Ausich and Botjer 1982; Hess et al. 1999; Seilacher and Hauf 2004; Baumiller 2008;).

Although direct evidence for the original soft-tissue composition of the sub-basal balls is not preserved, their recurrent presence across multiple roveacrinid genera supports the interpretation that they represent biologically meaningful structures rather than random skeletal features (Gale 2016, 2023). Future studies integrating micro-CT data from a broader taxonomic and stratigraphic range will be crucial to further test these functional hypotheses and to clarify the evolutionary significance of sub-basal balls within Roveacrinidae.

Finally, this study highlights the importance of the X-ray computed microtomography as a non-destructive tool for investigating internal skeletal features in microcrinoids. By revealing internal structures that are otherwise inaccessible, micro-CT provides new opportunities to explore functional morphology, phylogenetic characters, and evolutionary trends in fossil echinoderms (Gorzelak 2018).

Conclusions

This study demonstrates the utility of X-ray computed microtomography for the detailed analysis of fossils from the Roveacrinidae family, revealing the internal and three-dimensional presence of sub-basal balls in an additional genus of the family. Furthermore, the discovery of these structures in another genus raises the question of their distribution across other genera in the family, which may have implications for the phylogeny of the order Roveacrinida. Micro-CT proves to be an essential tool for advancing the understanding of the morphological and evolutionary characteristics of fossil groups, and further studies will be needed to explore their presence in other genera of the family.

Authors' contributions

BPP, lead author, conceptualization, investigation, data curation, formal analysis, writing—original draft, visualization; ASG, formal analysis; writing—review and editing; ACM, micro-CT data acquisition; imaging; methodology; LDM, writing—review and editing; MABSF, 3D modelling, 3D printing; BVG, SBF, writing—review and editing; GF, project administration, supervision, funding acquisition, conceptualization, resources, writing—review and editing.

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