

TETRAPOD COPROLITES FROM THE CENOMANIAN BONE-BED OF NORTHEASTERN, BRAZIL

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Abstract—In the past few years, hundreds of vertebrate remains have been collected from an outcrop called Coringa flagstone, on Cajual Island, Maranhão state, where predominantly fluvial sediments of the Cenomanian (Alcântara Formation) were deposited in the São Luis Basin. The outcrop at Coringa flagstone corresponds to a 4-km-long exposure of a bone bed deposited in a near shore environment, subject to tidal currents containing numerous fossilized bones, teeth and stems of conifers and ferns. The fossil assemblage corresponds to a diverse dinosaur community with associated reptiles and fish. This paper describes and analyzes the preserved coprolites collected at this site. All of the identified coprolite categories (ovoid, conic, spiral and cylindrical), occur in different sizes and were formed under similar diagenetic conditions. Some of the specimens were processed to analyze the internal structure by petrographic slicing and x-ray fluorescence to explore the biotic interactions of the South America Cretaceous tetrapod community.

INTRODUCTION

The first record of coprolites in Brazil is from the beginning of the past century when Permian spiraled coprolites were found in São Paulo State (Ruedemann, 1929). However, more complete studies were only published at the end of the century - spiraled coprolites from the Permian of the Corumbataí Formation (Ragonha, 1987); bird coprolites from the Tertiary in the Tremembé Formation, in São Paulo state (Castro et al., 1988); and mammals deposits from the Quaternary in Rio Grande do Sul state (Kerber and Oliveira, 2008). There were also studies of coprolites from the Santa Maria Formation (Middle Triassic) which were associated with mammal-like reptiles (Souto, 2001), and the Adamantina Formation (Upper Cretaceous) of the Paraná Basin, also in the São Paulo state, associated with crocodylomorph nesting areas (Souto et al., 2005).

Currently, studies are currently ongoing in outcrops of the northern region of the territory, where coprolites occur associated in a Cretaceous (Cenomanian) bone bed. Those sediments pertain to the Alcântara Formation of the São Luis Basin, in the state of Maranhão (Fig. 1A). This occurrence is characterized by the presence of abundant coprolite and a variety of morphotypes, providing information about the interactions of this paleocommunity near the end of the Mesozoic Era.

GEOLOGICAL CONTEXT

The bone bed of the Laje do Cajual is on the coast of Maranhão. Outcrops here expose sedimentary sequences containing fossiliferous levels that in the Alcântara Formation. This region has been traditionally considered as part of the São Luis Basin (Corrêa Martins, 1997).

The concentration of fossil material in the Cretaceous deposits of the São Luis Basin is a consequence of both climate and intense subsidence that occurred in this region related to rifting, forming deposits of the Itapecuru Group which includes the Alcântara Formation (Rossetti et al., 2001). The Alcântara Formation is comprised of a sequence of layers deposited in an environment dominated by waves and tides, which are now exposed on cliffs, and extensively along the coast, in the region of the São Luis and the Alcântara (Truckenbrodt and Rossetti, 1997).

The analysis of pollen in outcrops on islands of the São Marcos Bay reveals a Cenomanian age, while the sequences of the more inland Itapecuru Group are considered as Albian age (Pedrão et al., 1993). The process of subsidence was most intense along the coastline, causing faster sediment accumulation and the formation of thicker deposits, com-

pared to inland Cretaceous sequences, coastal depositions continued until the early Cenomanian, while sediment accumulation inland ceased at the end of the Albian (Aranha et al., 1990, Rossetti et al., 2001) (Fig. 1B).

MATERIAL AND METHODS

Approximately eighty coprolites were collected at the Laje do Coringa locality on Cajual which is situated on the coast of Maranhão state. The coprolites are housed in Departamento de Geologia, of Universidade Federal do Rio de Janeiro, UFRJ-DG. The specimens were analyzed and described according to the criteria proposed by Thulborn (1991) and by Hunt et al. (1994). External morphological analysis included measurements and documentation of features considered indicative of a biologic origin.

The thin-section analysis technique was applied to radial and longitudinal cuts with 75 µm and 100 µm thickness and analyzed by an optical petrographic microscope (Carl Zeiss Axioplan 2) and microphotographs were taken a digital camera. The chemical analysis (Table 1) of the coprolites was made on powdered samples obtained by iron drill from 30 mm and 20 mm depth from both matrix and coprolites (Hirsch, 1979). The powders were analyzed by x-ray diffraction (Rigaku-miniflex) and x-ray fluorescence (Phillips PW-2400) to determinate mineral and elemental composition (Edwards, 1973).

Description of coprolites

Most of the coprolites are found free from sediment and associated with teeth and bones of vertebrates as well as plant stems. The coprolites have a massive structure and there are only rare complete specimens. Morphologically, they were classified in four groups: ovoid, conical, cylindrical and spiral (Figs. 2-3). The coprolite's surface features include terminal deformations, and surface grooves which resulted from the plastic consistency of these biological structures after they were excreted. The greatest width measured for each coprolite category was 8 to 12 cm in ovoid forms, 4 to 9 cm in cylindrical forms, 6 to 8 cm in spiral forms and 8 to 9 cm in the conical forms.

Taphonomic interpretations proposed by Holz (2003) suggests that this region, in the time when the Alcântara Formation was deposited, was dominated by a large transgressive event. A tidal complex in a coastal paleoenvironment retroacted towards the south-southwest and was subject to periodic transgressions and reworking by waves.

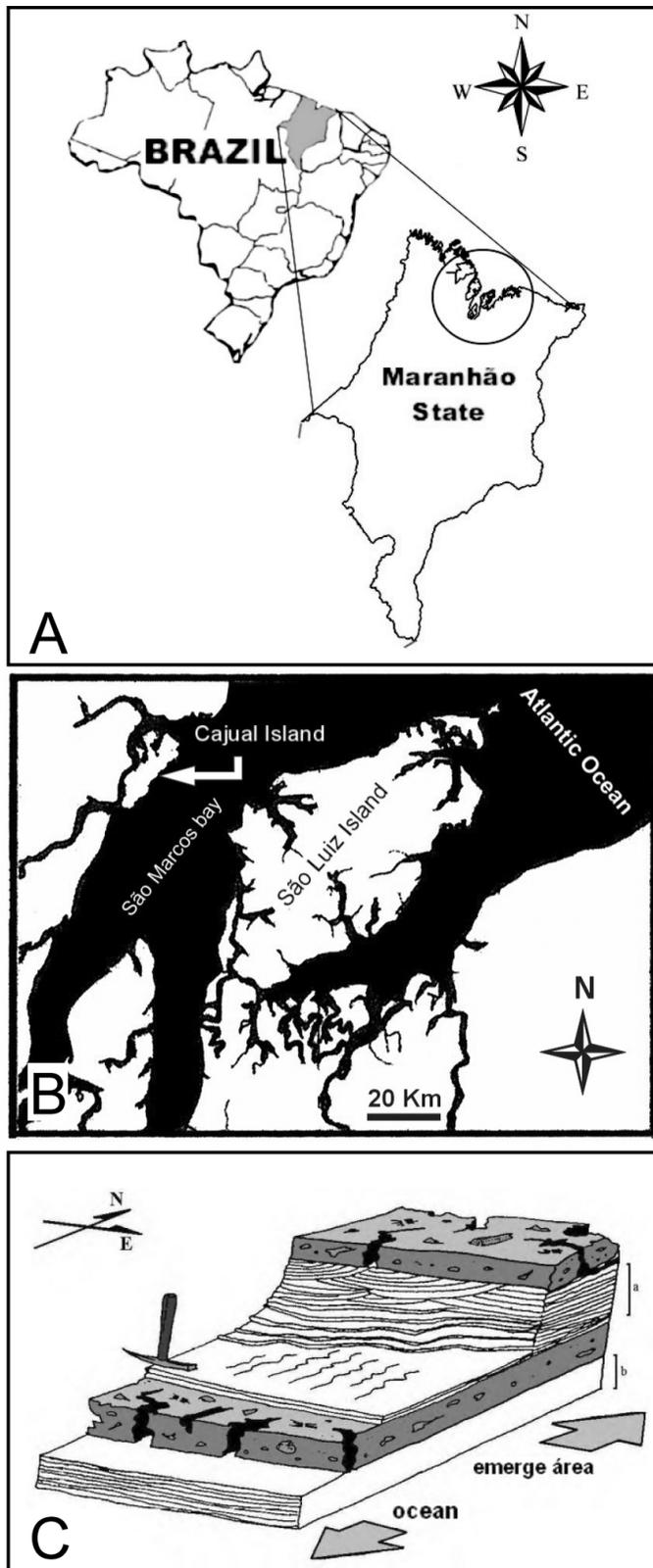


FIGURE 1. Location and context of study area. A-B, Location map of Maranhão State with enlarged to show the São Marcos Bay area and Cajual Island. C, The three dimensional layout of a section of the bone bed of Laje do Coringa, showing the two main conglomeratic levels, where most of the fossils are concentrated in (a) stratified sandstone and (b) interbedded shale and sandstone, (modified from Medeiros, 2001).

TABLE 1. The results of chemical composition (per cent) by x-ray fluorescence analysis of coprolites (C) and host sediment (hS) from the Alcantara Formation. C1, UFRJ-DG 28 IcV (cylindrical shape); C2, UFRJ-DG 222 IcV (ovoid shape); C3, UFRJ-DG 163 IcV (conical shape); C4, UFRJ-DG 227 IcV (cylindrical shape); C5, UFRJ-DG 142 IcV (spiral shape), LB: loss by burning.

Groups	C1	C2	C3	C4	C5	hS
Elements (%)						
SiO ₂	1.46	36.56	21.93	1.57	0.01	26.72
Al ₂ O ₃	0.01	0.47	4.36	0.36	0.01	0.01
Fe ₂ O ₃	13.63	2.52	2.61	14.76	1.62	38.18
MnO ₂	0.73	0.78	1.72	0.62	0.01	0.01
MgO	0.00	0.86	19.36	0.01	0.01	0.01
CaO	41.20	27.51	27.85	40.59	48.75	22.15
K ₂ O	0.00	0.01	1.24	0.01	0.01	0.00
P ₂ O ₅	34.72	21.81	0.00	31.95	38.45	0.01
SO ₃	1.83	1.99	0.54	2.55	4.39	1.32
SrO	0.12	0.01	0.01	0.01	0.20	0.01
L.B.	6.30	7.50	20.10	7.50	6.60	11.60

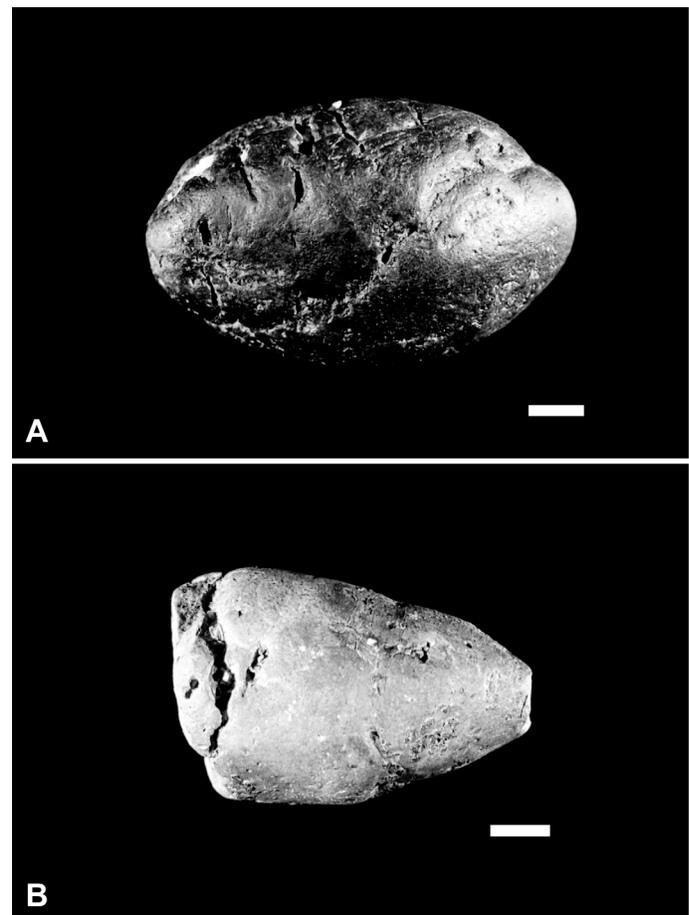


FIGURE 2. Coprolites from the Coringa flagstone, Cajual Island, with A, ovoid and B, conical morphology. Scale bar equals 1 cm.

The fossil material would include parautochthonous and allochthonous elements, from fluvial deposits eroded during cycles of base level reduction. During these events the deposits exposed above this level would be eroded and their contents transported by river currents and, deposited close to the coastline. During transgressions, such deposits would be reworked by wave action, and begin to integrate transitional horizons and shallow marine deposits (Medeiros, 2001; Medeiros and Schultz, 2001).

The coprolites found in Laje do Coringa occur in conglomeratic lenses deposited between layers of fine sandstones, where clasts of different sizes and fossilized remains of plants (fragments of stems) and

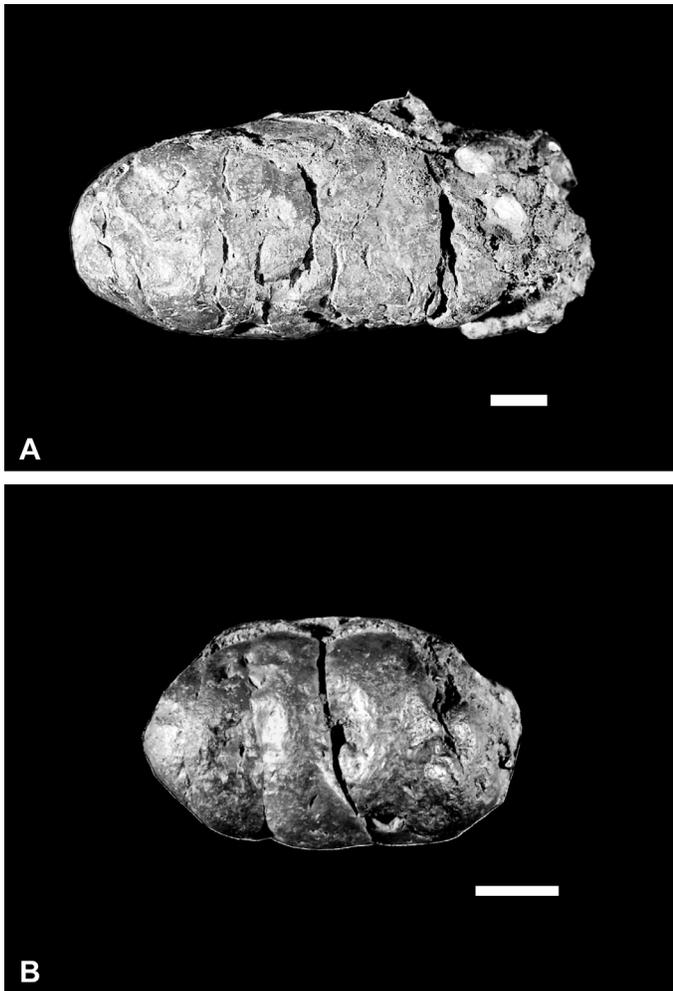


FIGURE 3. Coprolites from the Coringa flagstone, Cajual Island, with **A**, cylindrical and **B**, spiral morphology. Scale equals 1 cm.

animals (disarticulated bones) are associated. The coprolites are found dissociated, independent of their size and shape, with other fossilized elements which were eroded by tidal action, with attached matrix. The preservation of whole coprolites is rare, and most specimens present several breaks with polished surfaces and mineral impregnation. However, some of them present evidence of plastic consistency, such as curved ends, grooves, and organic structures, for example in one specimen (UFRJ-DG 154-IcV) where scales appear attached to the surface (Fig. 4A).

The coprolites analyzed here underwent permineralization by iron oxide which confers a solid consistency. However, in some spiral specimens the loss of internal structure was observed, leaving only the outer layer preserved (Fig. 4B).

DISCUSSION

The analyses by x-ray diffraction and laminar sections reveal that the coprolites suffered partial replacement by goethite, characterized by the presence of botrioidal crystals of iron and quartz grains that fill the spaces with the coprolite matrix with the formation of a thin secondary outer layer of limonite as a result of a chemical reaction with sea water.

In transverse cuts made along the major axis of coprolites, it showed two distinct consistencies of the coprolite's matrix, one is more compact and hard and other is more friable and porous (Fig. 4C-D). Thin sections reveal the presence of organic inclusions such as the fish scales (UFRJ-DG 255-IcV and UFRJ-DG 278-IcV) with rhomboidal shape and a maxi-

mum size of six mm in length. The fish scales are orientated in different planes and, appear to be fragmented with variation in shape, volume and original size, and the angle of position due to random insertion in the matrix of the coprolites. The structure of the scales reveals the presence of layers of ganoin, osteocytes, channels and Williamson and Sharpey's fibers (Fig. 5A-B).

A plant structure preserved in thin cut of on specimen (UFRJ-DG 265 IcV) represents a fragment of stem tissue with longitudinal cells with a secreting duct very similar to the one described for the specimens of the genus *Paradoxopteris* (Mussa et al., 2000) a kind of fern common in regions of estuarine environment (Fig. 5C).

The analysis of the isolated ostracod in an ovoid coprolite considered ingested accidentally during the feeding process in similar occurrence as described by Bradley (1946), Sohn and Chatterjee (1979) and Tverdokhlebova (1986), in which the ostracodes found within the coprolites were interpreted to have been produced by a terrestrial vertebrate (Fig. 5D).

The chemical composition of the coprolites obtained by x-ray fluorescence showed in ovoid and conical forms relatively larger amounts of calcium (27%) and silica (21% to 36%), whereas in cylindrical and spiral coprolites the concentrations of the elements phosphorus (<30%) and calcium (<40%) were higher. This distribution is probably related to metabolism process and suggests that herbivorous/omnivorous animals eliminated the ovoid or conical feces, while the spiral and cylindrical forms are associated with carnivorous producers. The spiral forms are probably formed by chondrichthyans and the cylindrical coprolites by other reptile groups.

The relationship between cylindrical coprolites and carnivorous producers has been attributed to metabolism in that these animals have a rapid as processing of fecal material during the digestive process (Bartlett et al., 1998). Considering the fossil assemblage preserved at this outcrop (Elias et al., 2005) the potential producers of these coprolites are *Spinosaurus*, a kind of dinosaur with jaw structure adapted to fishing (Kellner and Campos, 1996) and *Sarcosuchus imperator*, a giant crocodyliform, which lived in coastal regions and brackish waters and was adapted to feed on large fishes and other reptiles (Serenio et al., 2001).

The coprolites present the same biostratigraphic features as those for other fossil materials found in the outcrop, such as breaks, rounding and scaling. In some samples of coprolites a spiral structure is complete, although with hollow center, indicating that these have been produced and preserved on site and then the calcium phosphate was removed by durophagous organisms.

The secondary changes are associated to bioerosion features produced by the action of marine invertebrates on the surface including elliptical patterns made by crustaceans and drill holes made by polychaete worms.

CONCLUSIONS

The taphonomic evidence from coprolites analyzed in Laje do Cajual indicates two distinct biostratigraphic episodes: first was transport of alluvial origin where the fossil elements were concentrated with lithoclasts and second, erosion and transport to the coastline and later deposition, whilst subjected to the continuous abrasive tide action and predation by marine organisms.

The coprolites are impregnated by iron oxide principally in the form of goethite but also with the formation of an outer coating of limonite which, in most bioclasts, forms a continuous layer. However, in those coprolites where the internal structure was exposed the calcium phosphate was removed by the recent action of marine organisms, leaving only the outer casing. This condition was only seen in spiral-shaped coprolites. This diagenetic phenomenon was also seen in cross section, and may also be related to the diet of the producer. Continental producers with intakes of compounds rich in calcium, phosphate and silica may

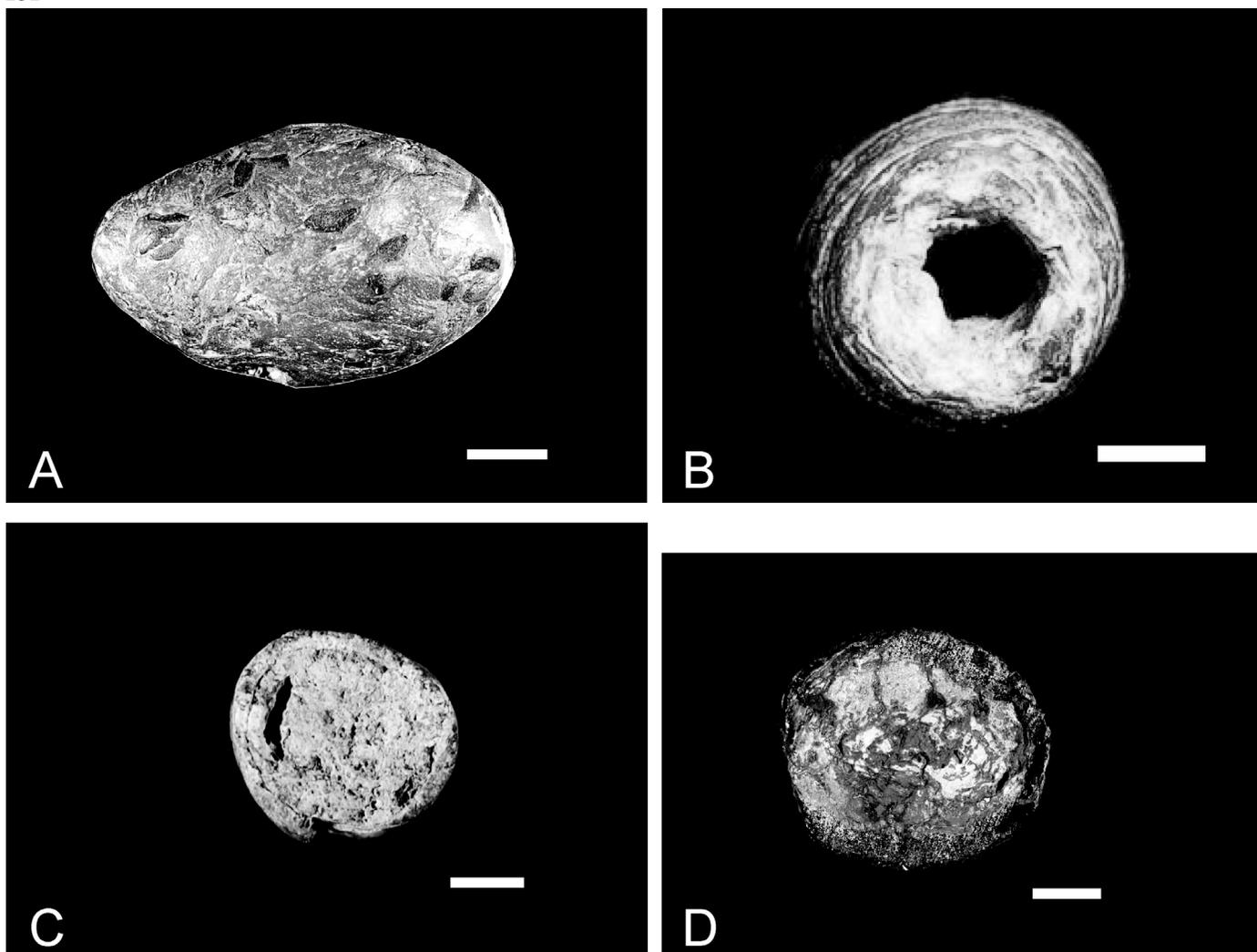


FIGURE 4. Details of coprolites. **A**, Scales attached (dark lozenges) to the surface of specimen UFRJ-DG 154 IcV. **B**, Central cavity due matrix remotion by bioerosive agents in specimen UFRJ-DG241 IcV. **C**, Transverse section of specimen UFRJ-DG 142 IcV with friable matrix. **D**, Transverse section of specimen (UFRJ-DG 267 IcV) with solid matrix. Scale bar equals 1 cm.

confer more rigidity to the coprolites, while the producers with a diet in calcium and magnesium would cause a coprolite with a less hard structure.

The coprolites with an ovoid morphology exhibit grooves and relatively have a greater length and thickness and an elevated amount of silica and calcium. These features suggest strongly the presence of herbivorous tetrapods and, are very similar to those described in coprolites of herbivorous reptiles like dinosaurs (Thulborn, 1991; Rodriguez et al., 1998).

The abundance of large spiral coprolites of different sizes and with inclusions of scales suggests the presence of adult fishes with a carnivorous diet. As noted by Fange and Grove (1979), there is a strong relationship between the spiral folds of coprolites with fish groups such as chondrichthyans, dipnoans and sarcopterygians because of the presence of the spiral valve in the intestinal tract in these taxa. In the examples reviewed here there are cross-sectional spiral folds similar to those produced by chondrichthyans and in this case they probably represent Hybodont sharks whose teeth are present in this outcrop and which were widely distributed during the Mesozoic (Maisey et al., 2004).

In the cross-sections a peripheral thin layer surrounding the coprolites mass indicates fecal mucus which is preserved due to differentiation in the diagenetic process. This mucus, which enveloped the fecal mass when it was expelled, contributed significantly in the differentia-

tion and preservation of the coprolites, due to iron oxide that was precipitated on the boundaries of the layers, as has been observed in other biogenic structures (e.g. tracks and burrows) favoring its preservation as a result of the presence of compounds secreted by the organism itself (Mendes, 1988).

The scales analyzed inside and outside the coprolites are attributed to *Lepidotes*, abundant in fossiliferous sites of Cenomanian age from the northeastern coast of Brazil (Dutra and Malabarba, 2001, Carvalho and Silva, 1992). The scales were observed in coprolites with a coiled cylindrical morphology, indicating that these fish suffered predation, possibly by primitive Hybodont sharks and carnivorous reptiles represented in this fossil assemblage by *Spinosaurus* sp. and *Sarcosuchus imperator*.

The quantity and variety of coprolites at this location demonstrates that the community had significant biodiversity, and undoubtedly the amount of fecal material that was eliminated is much larger than what was preserved. This is consistent with the diverse variety of fossil taxa known from this locality and confirms the presence of a community composed of diverse trophic levels in this region during the Cenomanian.

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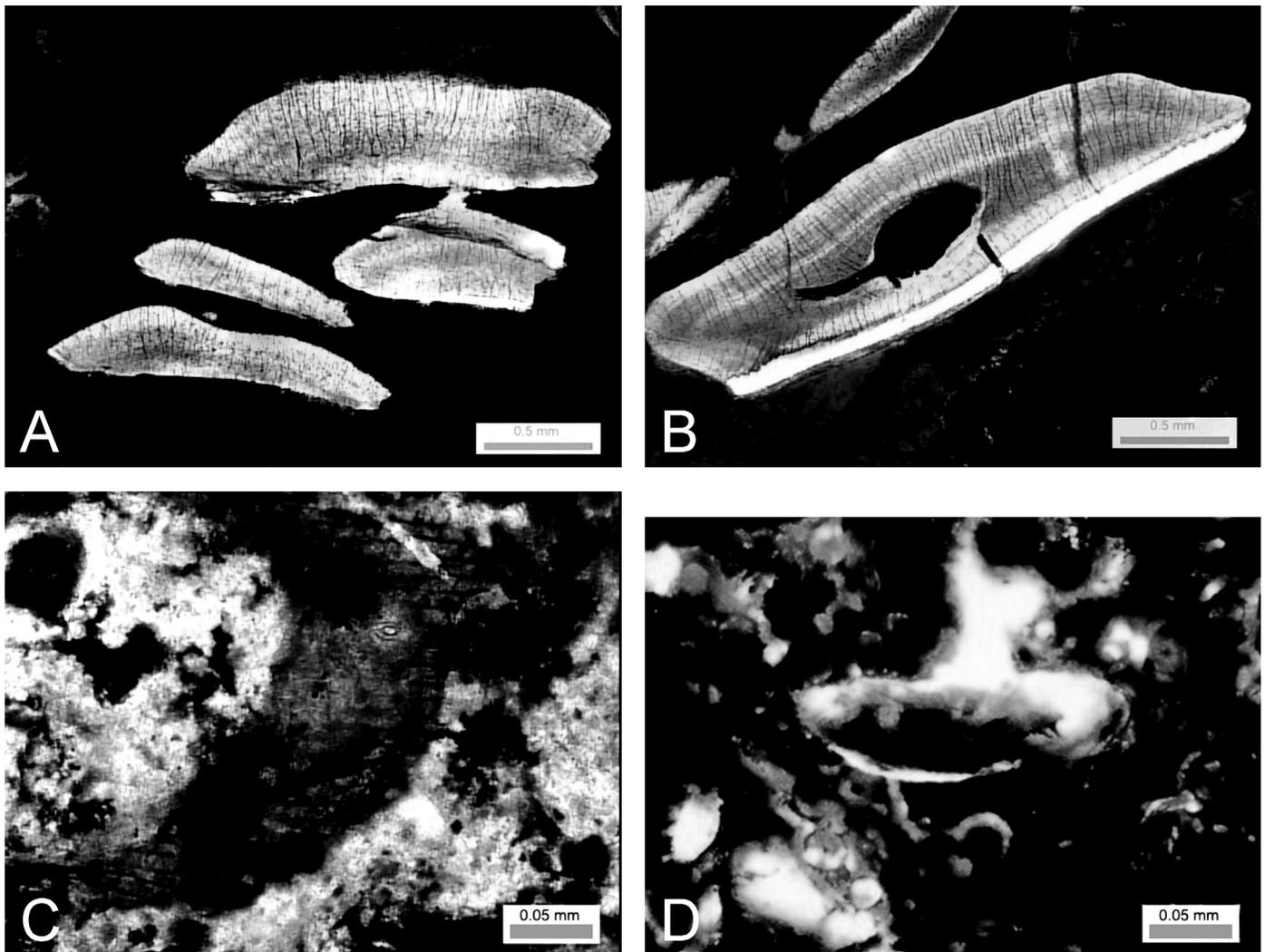


FIGURE 5. Lamina cuts of coprolites from São Luis basin with organic inclusions. **A**, Agglomerated scales. **B**, Scale from specimen UFRJ-DG-263 IcV. **C**, Plant fragment in specimen UFRJ-DG 265 IcV. **D**, Ostracod inside specimen UFRJ-DG 262 IcV.

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