Cretaceous Research 56 (2015) 651–661

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Osteoderms of *Montealtosuchus arrudacamposi* (Crocodyliformes, Peirosauridae) from the Turonian-Santonian (Upper Cretaceous) of Bauru Basin, Brazil

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ARTICLE INFO

Article history:
Received 23 March 2015
Received in revised form
1 June 2015
Accepted in revised form 2 July 2015
Available online 30 July 2015

Keywords:
Osteoderms
Crocodyliformes
Montealtosuchus arrudacamposi
Peirosauridae
Brazil
Cretaceous

ABSTRACT

The skin of Crocodyliformes is characterized by osteoderms of various sizes and shapes. It plays roles in defence, thermoregulation, sexual attraction, calcium reserves, and locomotion. This study presents the morphometric characteristics of osteoderms preserved in the nuchal, dorsal, ventral and appendicular shield of *Montealtosuchus arrudacamposi*, a Peirosauridae crocodyliform from the Turonian-Santonian (Upper Cretaceous) of Adamantina Formation, Bauru Basin, Brazil. The results of the analysis show that its dermal shield had protective and thermoregulatory functions and a well-defined mechanical function allowing terrestrial locomotion and enabling good agility and capacity for movement.

1. Introduction

The Crocodyliformes are currently represented by 23 species belonging to three families: Crocodylidae, Gavialidae and Alligatoridae. Along with birds, they are the only living group of Archosauria, and they present a variety of important characteristics for the taxonomic interpretation of their species (Benton and Clark, 1988; Ross and Garnett, 1989). The distinction between families is based on the particularities of the bony skeleton, which mainly occur on the skull, the number and characteristics of the teeth, and the distribution of osteoderms on the skin (Richardson et al., 2002).

The osteoderms of archosaurs are also known as scales, dermal plates, or bone plates. These osteoderms are covered with a keratin shield and have various functions, including defence, thermoregulation, sexual attraction, calcium reserves and locomotion (Pough et al., 2004).

The osteoderms on both living and extinct species of Crocodilyformes are ornamented with grooves, depressions, tubercles and ridges on the superficial external portion (Hill, 2005). According to Buffrénil et al. (2014), observations and experimental data show that the bony ornamentation is created by bone reabsorption with a complex erosion process and subsequent remodelling. The result is an adjustment of the diameter and depth of the pits during the somatic growth period, thus causing permanent modification through extension, shrinkage, or complete filling of the grooves.

According to Milinkovitch et al. (2013), the osteoderms of the crocodyliform head differ from the postcranial osteoderms. The osteoderms of the head are apparently created by cracks caused by surface tension resulting from the rapid embryonic growth of jaw bones associated with the development of a keratin skin. The result is a mechanical stress that causes breaks in the surface of the skin, and the subsequent rearrangement of the skin to maintain the continuity of the tissue generates the diverse characteristics and random patterns of the crocodile skull scales.

By microscopic analysis of internal structures of the deep surface of the postcranial osteoderms of crocodyliforms *Itasuchus*

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http://dx.doi.org/10.1016/j.cretres.2015.07.002
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jesuinoi Price, 1955 and *Uberabasuchus terrificus* Carvalho et al., 2004, Marinho (2006) perceived that the deep surface of osteoderms on these Crocodyliformes has foramina and grooves.

In the Cretaceous deposits of the Bauru Basin, the osteoderms of Crocodilyformes are found in abundance due the large number of preserved individuals (Carvalho et al., 2004). The specimen of *Montealtosuchus arrudacamposi* Carvalho et al., 2007 (MPMA-16-0007/04), a crocodyliform from the Peirosauridae family, is important for the study of fossil osteoderms because this species is preserved with the nuchal, dorsal, ventral and appendicular shields. The holotype comes from the Bauru Basin, Bauru Group, Adamantina Formation, and is of Turonian-Santonian age (Dias-Brito et al., 2001; Carvalho et al., 2010). It has been found in the area of the city of Monte Alto in São Paulo State, Brazil.

This study presents a morphometric description of osteoderms of *M. arrudacamposi* in order to better understand their functions.

Institutional Abbreviations: CPPLIP: Paleontological Research Center Llewellyn Ivor Price (Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Peirópolis, Uberaba, Minas Gerais State). **DGM**: Geology and Mineralogy Division, National Bureau of Mineral Production (Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Rio de Janeiro). **FMNH**: The Field Museum, Chicago. **MPMA**: Paleontological Museum "Prof. Antonio Celso de Arruda Campos " (MPMA – Museu de Paleontogia de Monte Alto). **UA**: Université d'Antananarivo, Antananarivo, Madagascar.

2. Geological background

The osteoderms described herein belong to the holotype of *M. arrudacamposi*, a representative of Crocodyliformes from the Peirosauridae family, preserved in the Turonian-Santonian (Upper Cretaceous) strata of Bauru Group, Adamantina Formation, Bauru Basin (Carvalho et al., 2010), in the region of Monte Alto, São Paulo, Brazil.

The Bauru Basin is located in the south-central region of the South American Platform (Fernandes and Coimbra, 1996). The Adamantina Formation, located in the Bauru Basin, belongs to the Bauru Group (Paula e Silva et al., 2003). The Bauru Group is composed of terrestrial deposits, accumulated during the Late Cretaceous. It is mostly composed of alluvial (Marília Formation) and fluvial (Adamantina and Uberaba Formations) strata (Fernandes and Coimbra, 2000). According to Basilici et al., 2009, the Marília Formation was characterized during the Late Cretaceous by a semi-arid climate regime (in view of the preponderance of carbonates in paleosol horizons) and the environment of the Adamantina Formation was interpreted by Carvalho and Bertini (2000) as a hot climate with torrential rains and flashfloods (Fig. 1).

3. Materials and methods

The osteoderms analysed in this study belong to the axial and appendicular skeleton of *M. arrudacamposi*, specimen MPMA-16-

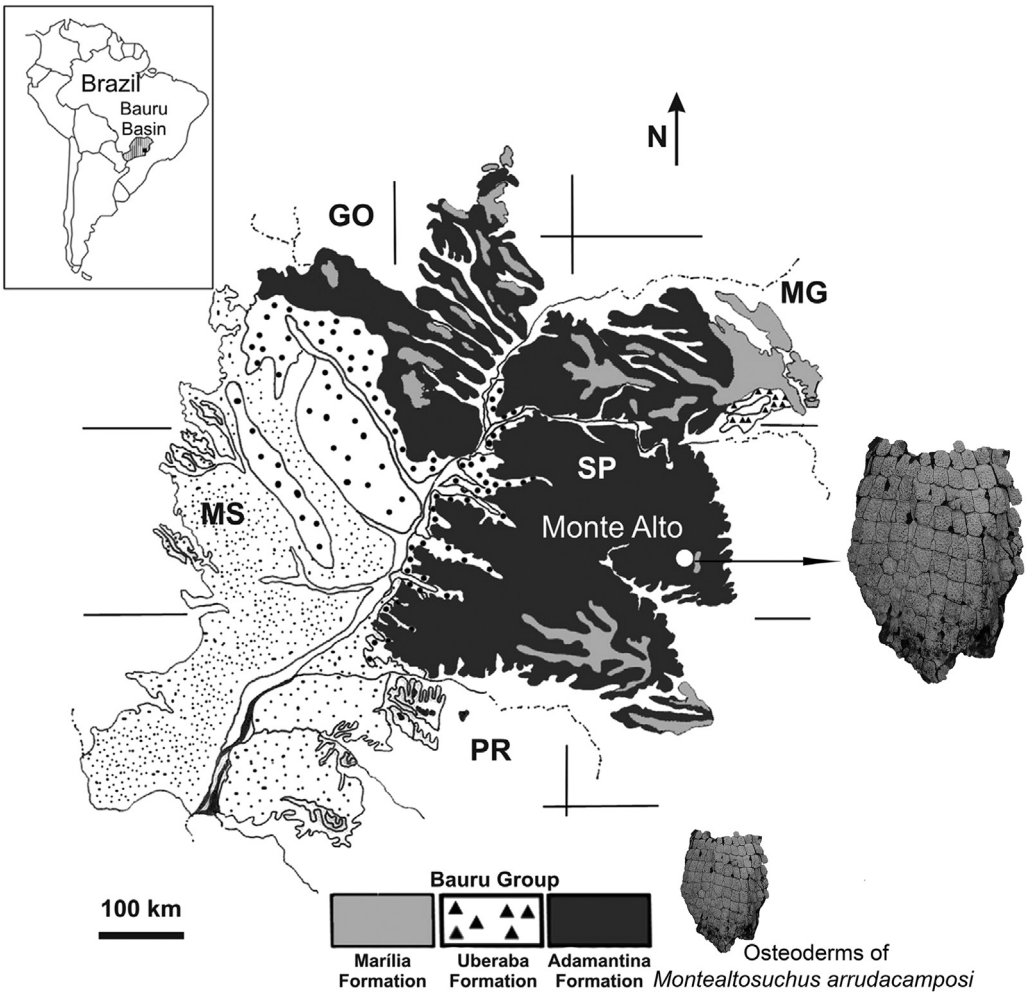

Fig. 1. Geological map of the Bauru Basin (modified from Fernandes and Coimbra, 1996).

0007/04 (Fig. 2) described by Carvalho et al. (2007). The osteoderm measurements were made according to the sagittal axis of *M. arrudacamposi* with a MAUb-CH Stainless calliper.

In the morphological description, the osteodermic coverage of this member of Crocodyliformes was sub-divided into a nuchal shield (osteoderms in the region of the cervical vertebrae), dorsal shield (thoracic vertebrae, lumbar and lateral), ventral shield (abdomen), and appendicular shield (osteoderms of the fore- and hind-limbs). This subdivision was used by Brazaits (1987) for dermal shields in living Crocodyliformes (Fig. 3). Hill (2014) used the same subdivision for dividing the osteoderms of *Simosuchus clarki* described by Buckley et al. (2000). The shape, the external ornamentation (external articular facet, tubercles, alveolar sculpture, keel position, grooves), and the deep ornamentation (grooves, foramina and deep articular facet) are described following the methodology of Marinho et al. (2006) (Fig. 4).

The osteoderms of *M. arrudacamposi* were compared with those of the other Crocodyliformes, such as *Peirosaurus tormini* Price, 1955, *Uberabasuchus terrificus*, Carvalho et al., 2004, *Simosuchus clarki*, Buckley et al., 2000, *Armadillosuchus arrudai*, Marinho and Carvalho, 2009 and *Baurusuchus albertoi*, Nascimento and Zaher, 2010.

4. Preservation

The remains of *Montealtosuchus* were found in association with fragments of the another skull, corresponding to the left side, and there are several other postcranial fragments of at least four other individuals that appear to belong to the same species. According to Carvalho et al. (2005), the occurrence of almost complete articulated skeletons suggests that these animals could dig large, deep burrows in soft substrates that allowed thermoregulation, like in living alligators.

The skull of the *Montealtosuchus* holotype was separated from the postcranial skeleton by taphonomical processes, probably due to water-currents as there are no signs of activity of predators or scavangers (e.g., bite marks) in the skeleton. However, the postcranial skeleton of the specimen shows a great degree of articulation. The cervical, thoracic and lumbar vertebrae have been preserved and articulated all along the sagittal axis. The appendicular skeleton has only the elements of the right side preserved and articulated.

In the dorsal view, some osteoderms and caudal vertebrae have been preserved and articulated on the claws, phalanges, metacarpals and carpals. The radius, ulna, humerus, scapula and left

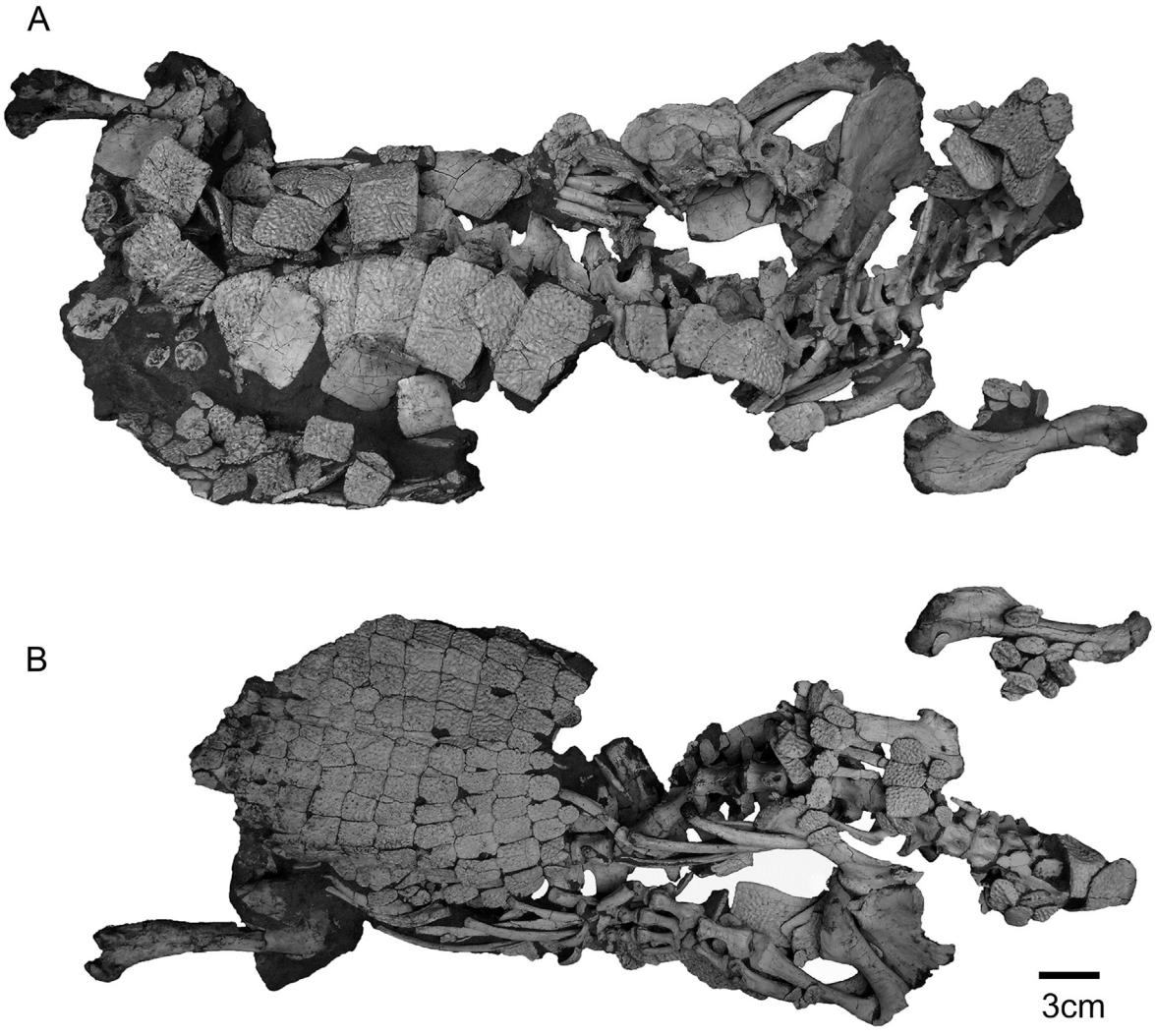

Fig. 2. Postcranial skeleton of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, dorsal view; B, ventral view, where the osteodermic elements can be observed.

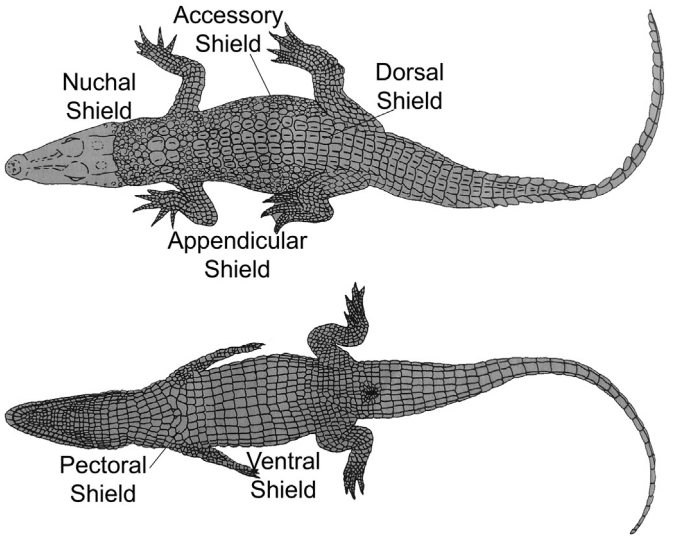

Fig. 3. Position of dermal shields in living Crocodyliformes (modified from Brazaits, 1987).

coracoid are also articulated. The right coracoid is in its original position, although it is disarticulated from the left humerus, and the latter is separated from the rest of the body. In the ventral view, some osteoderms of the appendicular shield are retained on the humerus. Regarding the hindlimbs, the right humerus is preserved, and in its dorsal portion there are some osteoderms of the appendicular shield. Osteoderms are also observed in the cervical, thoracic and lumbar dorsal and accessory shield. There are also some osteoderms of the gastral shield, which suffered post-mortem displacement.

A group of nuchal osteoderms shifted to the ventral part of *Montealtosuchus* body, where it is also possible to observe at least 10 ribs. The osteoderms of the pectoral shield are articulated and connect the right and left coracoids to the gastral shield. They are well preserved, displaced from the sagittal axis and the right portion of the animal, and vary in shape and size.

5. Morphometric description of osteoderms

The holotype of *M. arrudacamposi* presents osteoderms that are organized in different dermal shields preserved along the axial and appendicular skeleton. The excellent preservation of these osteoderms allowed a detailed analysis of the characteristics presented in these bone structures.

5.1. Nuchal shield

The osteoderms of the nuchal shield of *Montealtosuchus arrudacamposi* were stacked together. These have been brought together, approximately one under the other, with the dorsal surfaces still directed dorsally, near the cervical vertebrae. Altogether, 11 entire plates and one fragmented plate were available for study (Fig. 5).

In general, the osteoderms of this shield are ornamented on the external surface with shallow excavations and deep grooves surrounded by a net of tubercles. The anterior articular facet is well evidenced and has little ornamentation, becoming more flattened toward the anterior margin of the facet. As in the dorsal shield, the deep surface (ventral) is flattened and has several foramina that penetrate perpendicularly on the surface. The marked grooves are also evident in these dermal plates.

Four of these osteoderms are D-shaped with a maximum length of 39 mm and approximately the same width, which is 35 mm. The articular facet can be distinguished from the rest of the external surface by a slight step. They have a keel in the medial region with a caudal-medial orientation. It is convex when viewed in the axial plane with an angle of approximately 90°.

Three of the 11 cervicals preserved in the nuchal shield measure approximately 30 mm long by 40 mm wide (rectangular). The keel originates in the medial region of these osteoderms and follows with tangential orientation caudolaterally to the right on one of the plates and to the left on the other two plates. The anterior articular facets of these osteoderms have a slight wave. In axial view, they are convex with an angle of approximately 130°.

Four other osteoderms from this cluster are rectangular. Two of these are approximately 30 mm long and 45 mm wide, while the remaining two osteoderms represent the longest in this set, measuring 30 mm long by 50 mm wide. In axial view, these are convex with an angle of approximately 130°. The keels are oriented tangentially and in a caudomedial direction and are shorter than those present in D-shaped osteoderms. In the anterior articular facets a slight bulge is present in its anterior edges.

Additionally, two small dermal plates are found in this cluster. They are standing over a D-shaped osteoderm, which likely was based on the occipital region of this Crocodyliformes. One of the plates is fully preserved, oval and small (13 mm long and 10 mm wide). It has small round excavations surrounded by small tubercles. The other is fragmented in the anterior portion and measures 20 mm wide. The ornamentation of the surface portion of this plate has small excavations and tubercles. There are vertebrae articulated to each other along the sagittal axis. In the dorsal view, we observed osteoderms of the nuchal shield on one small keel in the external surface. These osteoderms are almost flat in axial view.

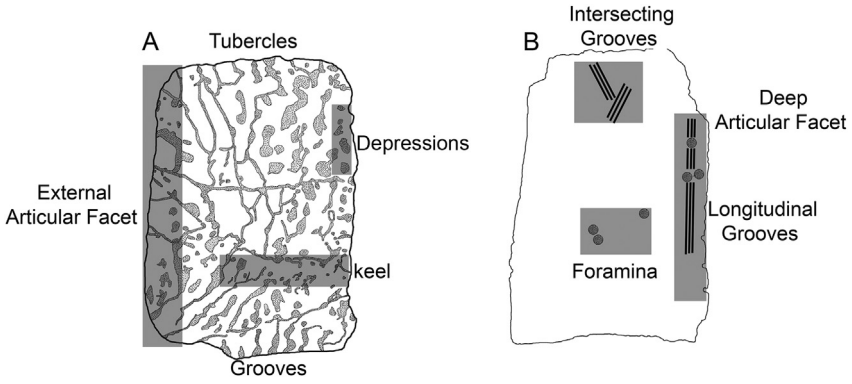

Fig. 4. Morphological parameters used in the osteoderms analysis. A, external surface; B, deep surface (based on Marinho et al., 2006).

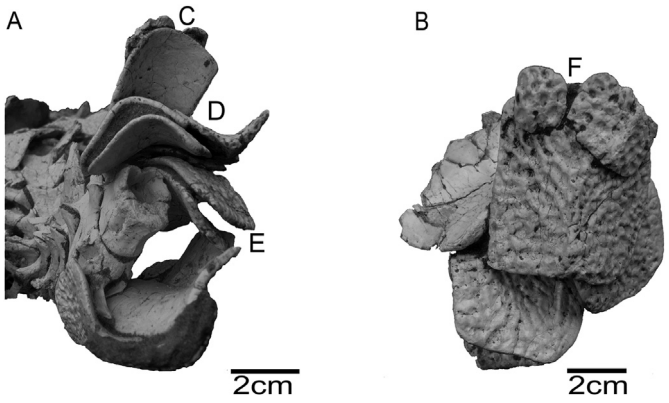

Fig. 5. Nuchal shield of *Montealtosuchus arrudacamposi* associated with cervical vertebrae (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, front view; B, dorsal view; C and F, two small dermal plates over a D-shaped osteoderm; D, osteoderms post-occipital; E, possible osteoderms from the nuchal rosetta.

5.2. Dorsal shield

The dorsal shield in *M. arrudacamposi* is represented by osteoderms from the thoracic and lumbar regions. It corresponds to a row of parasagittal osteoderms on each side, forming a double paravertebral shield, segmented in the sagittal line along the vertebral column of the Crocodilyformes (Fig. 6A).

At least 24 osteoderms were preserved on this shield. Five are shown to overlap parasagittally to the neural spine of the lumbar vertebrae. The posterior articular facets, on the deep articular surface, are overlaid above the anterior articular facets in the external surface portion of the osteoderm (Fig. 6B).

In general, the anterior articular facet of the dorsal osteoderms is smoothly ornamented and slightly raised, becoming wavy in

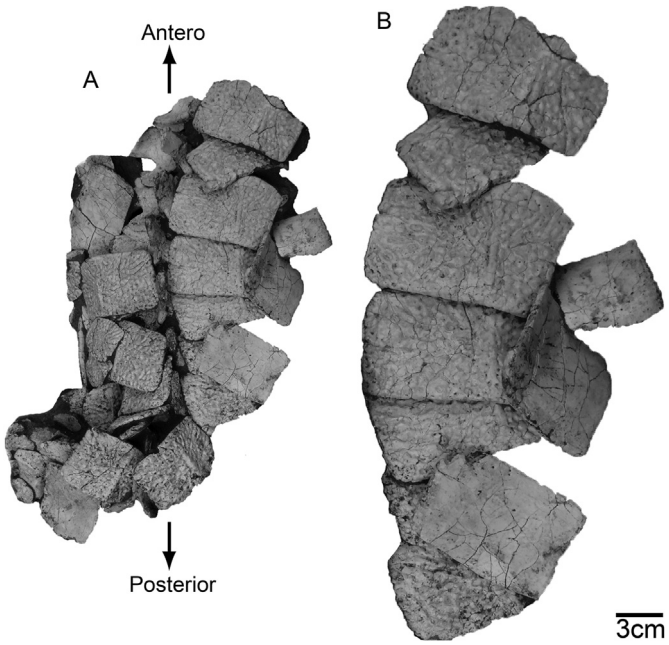

Fig. 6. Dorsal shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, osteoderms from the thoracic and lumbar region associated with dorsal vertebrae; B, detail of some imbricated osteoderms.

preserved osteoderms from the thoracic region, which are contiguous to the vertebrae in this region. Some more proximal left thoracic osteoderms moved from the original position and were fossilized with the deep surface facing upward. The plates are rectangular and slightly round on the edges, measuring approximately 35 mm long and 53 mm wide in the lumbar region. The plates become longer (29 mm) toward the chest and narrower (40 mm) toward the ribs.

On the external surface portion, the osteoderms are ornamented with excavations and marked grooves, delimited by a net of tubercles. In one-third of the surface portion of the dorsal osteoderms there is a keel oriented tangentially caudolateral (Fig. 7A–F).

The deep surface of the dorsal osteoderms is flat and smoothly concave. Several foramina are spread throughout this area, mainly in the central region, and penetrate the surface perpendicularly. Some marks may represent grooves along the entire surface of the osteoderm. In some osteoderms, a pattern of intersecting grooves is evident near the lateral edges, as on the anterior articular facet; however, these grooves are longitudinal. In most distal osteoderms, the grooves are evident in the medial longitudinal direction (Fig. 7G–J).

5.3. Accessory shield (lateral osteoderms)

On the medial left side of the vertebral column, adjacent to the dorsal osteoderms, there are six displaced osteoderms that might compose a shield of lateral osteoderms. These osteoderms are D-shaped and approximately 26 mm long and 23 mm wide. The surface of osteoderms is ornamented with grooves surrounded by tubercles and present a keel with a small bulge posteriorly on the back portion of the right surface, extending right to the medial-side of the plate (Fig. 8).

5.4. Gastral (ventral) shield

The gastral (ventral) shield preserved in *M. arrudacamposi* consists of a set of osteoderms with different shapes and sizes. They are well-preserved, and mostly articulated, except for a few osteoderms from the right portion. In order to preserve the gastral shield, it was decided to keep intact the rock matrix that surrounds it, making the description of the features preserved on the internal surface impossible (Fig. 9).

Eight wedge-shaped osteoderms, 10–20 mm long, determine the sagittal axis of this dermal shield. The ornamentation in the surface is formed by shallow grooves surrounded by a net surface of tubercles (Fig. 10B).

Most osteoderms are located in the medial portion of the shield. They are arranged in transverse rows and are of rectangular and pentagonal shapes. The rectangular osteoderms are maximally 20 mm long and become ovoid and smaller in both the proximal and distal directions. They are paired side by side with no evidence of overlapping and have no keel. This shield presents at least six parasagittal rows on each side, as well as 11 transverse lines (Fig. 10A, C).

From the 6th transverse line starts a new parasagittal row on each lateral of the shield with five osteoderms. Like other osteoderms that form this set, they are irregular and measure approximately 10 mm; some are rectangular and others are slightly oval, presenting shallow and round excavations separated by small ridges.

The intercalated osteoderms are the smallest in this gastral shield. Approximately 14 were preserved, 5 mm–10 mm long. The osteoderms are ornamented on the external surface, but the ornamentation is subdued. Some osteoderms are round and arranged between the osteoderms of the sagittal plane and their

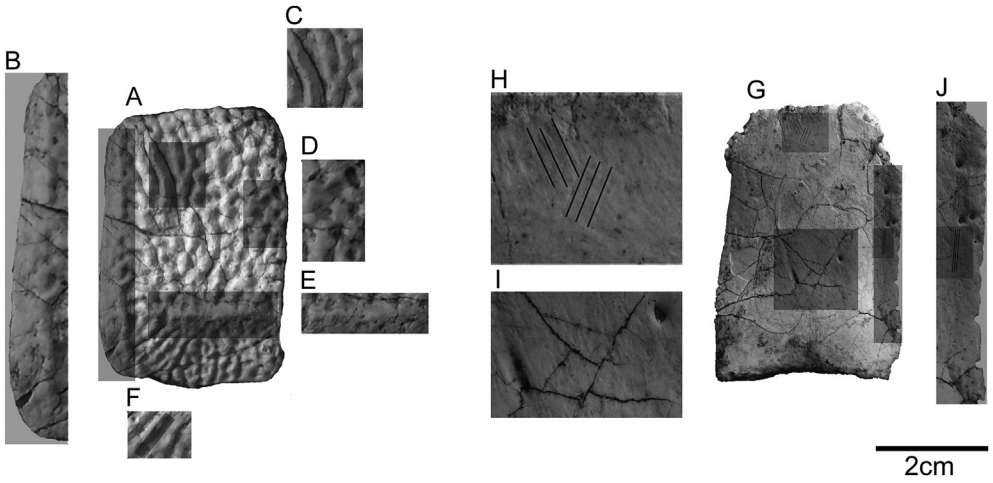

Fig. 7. Details of osteoderms of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, external surface; B, external articular facet; C, tubercles; D, depression; E, keel; F, grooves; G, deep surface; H, intersecting grooves; I, foramina; J, deep articular facet with foramina and longitudinal grooves.

adjacent plates, while the other intercalated osteoderms, which lie primarily between the rectangular gastral osteoderms, have an ellipsoidal shape (Fig. 11B, C).

5.5. Pectoral shield

The osteoderms preserved in the pectoral region of *M. arrudacamposi* present the same characteristics as the osteoderms from the gastral shield. The pectoral osteoderms are ornamented with round shallow excavations with small tubercles on the surface and are separated by intersections, resembling the threads of a woven textile. Keels are not present on the external surface (Fig. 12). In total, 13 pectoral osteoderms were preserved, seven in the anterior portion and six posteriorly in the ventral part of the coracoid bones. Seven of these osteoderms are oval, and three have a more rectangular shape. Six osteoderms form a bridge that posterolaterally connects the right and left coracoids. These six osteoderms are all oval and small in size, approximately 17 mm long and 12 mm wide (Fig. 12B).

It is likely that the osteoderms in the anterolateral position also formed a bridge between the coracoid bones; however, this cannot be confirmed because only four osteoderms are preserved in this region. A section of one of the anterolateral osteoderms is found in the left anterolateral portion of the right coracoid and is oval (Fig. 12C). The other three osteoderms are rectangular with round smooth edges and are at most 20 mm long and 15 mm wide. These were preserved toward the anterolateral region of the left coracoid in the ventral portion of the first thoracic vertebra. The three smallest osteoderms of the set are ovoid, and one of these is also positioned on the first thoracic vertebra, while the remaining osteoderms are in the left ventral proximal-lateral portion of the right coracoid.

5.6. Appendicular shield

The appendicular osteoderms of the fore- and hindlimbs preserved in *M. arrudacamposi* are predominantly elliptical, with the superficial portion ornamented with shallow grooves surrounded by tubercles. The osteoderms have a relatively high medial keel when compared to the keels present in the dorsal shield, which occupies the entire length of the osteoderm. The deep surface of these osteoderms is flat with multiple foramina randomly distributed (Fig. 13B, C).

The osteoderms preserved in the forelimbs do not exceed 20 mm in length and 13 mm in width. Fourteen osteoderms were preserved in the left humerus. Twelve are disordered in the medial-ventral region, one in the right anterolateral portion, and one in the left proximal region of the humerus. Three whole osteoderms and one fragmented osteoderm were preserved in the medial-ventral portion of the radius and the left ulna (Fig. 13A).

One osteoderm associated with the left scapula was preserved and may belong to the group of scapular scales. Another osteoderm

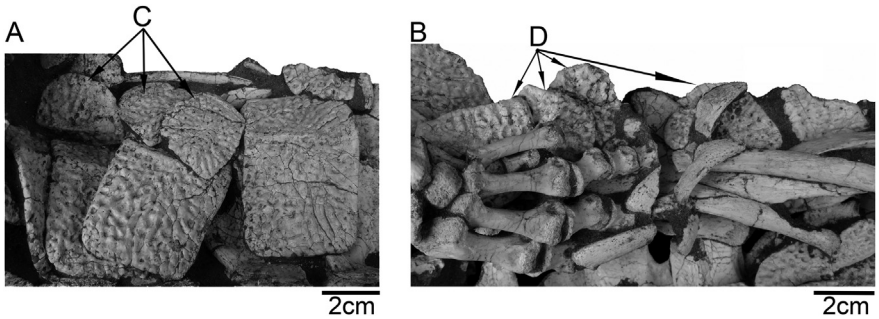

Fig. 8. Accessory shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, B, accessory shield (lateral osteoderms); C, lateral contiguous to dorsal osteoderms; D, lateral osteoderms in the cervical region.

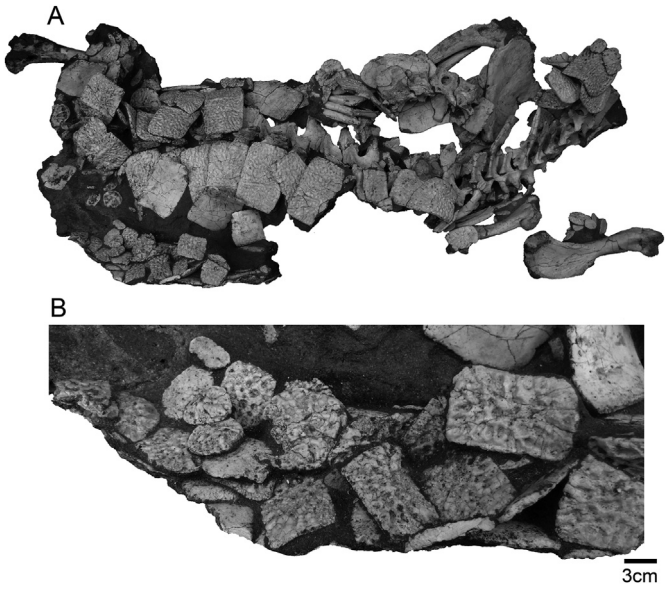

Fig. 9. Gastral shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, dorsal view of the postcranial; B, detail of some osteoderms facing the internal part of this set.

with the same shape is isolated near the ventral surface of the left humerus; however, this osteoderm is fragmented and is at most 20 mm long and 19 mm wide. These two osteoderms are fan shaped. In the superficial portion, there are grooves, tubercles and a small posteromedial keel oriented posterolaterally to the right of the osteoderm.

Regarding the hind limbs of *M. arrudacamposi*, only the left femur was preserved. However, three preserved osteoderms remained associated with this bone. They are elliptical and have a maximum length of 20 mm and a width of 17 mm and are positioned in the left medial-lateral proximal dorsal region (Fig. 14).

6. Discussion

The gastral shield was the best preserved dermal shield in the postcranial region of *M. arrudacamposi* with regard to the organization of osteoderms, despite its displacement outside the sagittal axis. We observed a distinct convexity in this set due to the morphology of the animal's abdomen. In crocodilians, the different osteoderms that compose the gastral shield form a large armour in the ventral portion. In *M. arrudacamposi*, it appears that this shield was displaced toward the right lateral part of the abdomen.

Further evidence that indicates a displacement of the gastral shield is the disarticulation of some osteoderms from the right portion of the set. It appears that a short distance transport probably forced the breakdown of these osteoderms, as they had shifted to the internal part of the set (Fig. 9B).

In the dermal shield description of a crocodyliform *Simosuchus clarki*, Hill (2014) characterizes the gastral shield with multiple large osteoderms of rectangular shape with round edges and is arranged in three horizontal lines. However, there is a smaller osteoderm on each side of the more medial pair of osteoderms in parasagittal lines, equal in anteroposterior length but narrower in the mediolateral dimension when compared to the main osteoderms. Some alternated osteoderms settle randomly between the rectangular osteoderms. These have irregular shapes, and a pattern may exist in which a larger osteoderm may be notched to accommodate an irregularly shaped intercalary osteoderm within what would otherwise be its rectangular outline. As in *Simosuchus*, the shield of *M. arrudacamposi* is also composed mainly of rectangular osteoderms with round corners. However, in *M. arrudacamposi* each osteoderm has a maximum length of 20 mm, the osteoderms are arranged in a minimum of 11 transverse rows, and the presence of a sagittal row comprising dermal plates in wedge shape separates the more medial pair of osteoderms. As in *Simosuchus*, the intersecting osteoderms are randomly distributed throughout the shield. They are irregular in shape and occupy part of the larger osteoderms.

The dorsal shield of *M. arrudacamposi* is well-preserved with respect to the orientation of osteoderms. Some were preserved imbricated, allowing for the correct understanding of the articulation of this shield along the back of this representative of Crocodyliformes.

The dermal plates of the dorsal shield are the largest found in the specimen and present a well-defined ornamentation in the external surface portion that is different from the more subdued ornament present on the osteoderms in the ventral shield. The dorsal dermal plates of *Montealtosuchus* present some different characteristics when compared with the dorsal shield osteoderms of other Crocodyliformes from the Peirosauridae family.

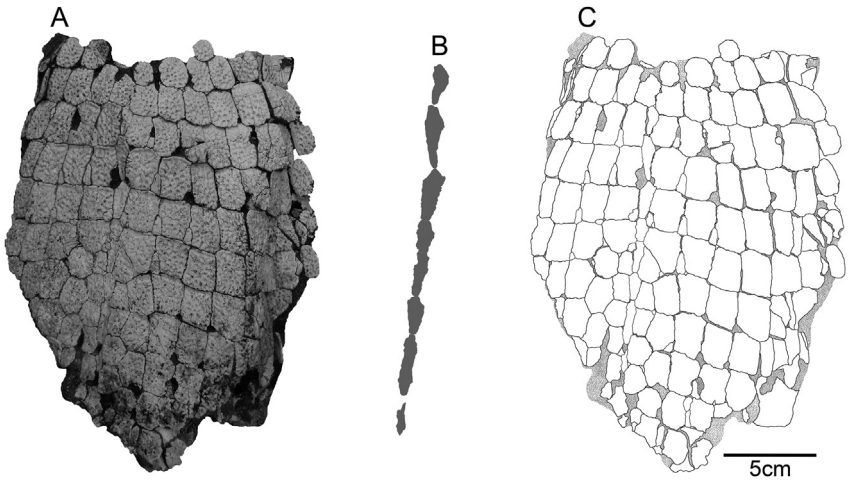

Fig. 10. Gastral shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, arrangement of osteoderms forming the gastral shield; B, schematic drawing of wedge shaped osteoderms (the sagittal axis of the shield); C, schematic drawing of gastral shield.

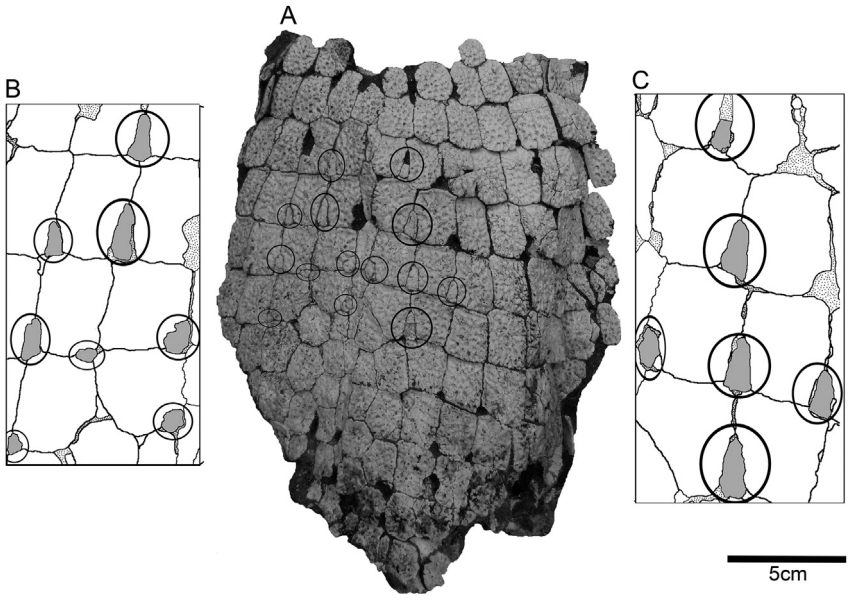

Fig. 11. Gastral shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, general view of the arrangement of intercalated osteoderms; B, schematic drawing of the intercalated osteoderms to the right of the sagittal line; C, schematic drawing of the intercalated osteoderms to the left of the sagittal line.

According to Marinho et al. (2006), the dorsal osteoderms of *Peirosaurus tormini* (MGD-433-R) and *Uberabasuchus terrificus* (CPPLIP-630) are rectangular in shape, and the dorsal plates of *Uberabasuchus* are thicker than the dorsal plates of *Peirosaurus*. The articular surface facet of *Peirosaurus* is short and is shallower than the ornamental piercings. In *Uberabasuchus*, this facet is short and shallow. Another difference presented by Marinho et al. (2006) is the external surface ornamentation of the osteoderm. In *Peirosaurus*, we find a format of deep, oval and circular excavations, while in *Uberabasuchus*, the ornamentation is homogeneous and consists of shallow, circular pits, with two or three occasionally uniting to form a channel. The *Peirosaurus* and the *Uberabasuchus* osteoderms present a keel, which is centrally located on the osteoderms. The dorsal shield osteoderms of *M. arrudacamposi* are rectangular, similar to those in the above mentioned peirosaurids; however, the thickness and ornamental pattern is similar to the external surface of *Uberabasuchus terrificus*. In *M. arrudacamposi*, the articular surface facet overlies the entire length of the anterior portion of the osteoderm. This facet is shallow in the osteoderms from the lumbar region, and forms a slight step between the facet and the rest of the ornamented surface of plates positioned in the thoracic region. The keel described in *Peirosaurus* and *Uberasuchus* is also present in the dorsal osteoderms of *M. arrudacamposi*. However, the keel is high and is located proximate to the side of these plates.

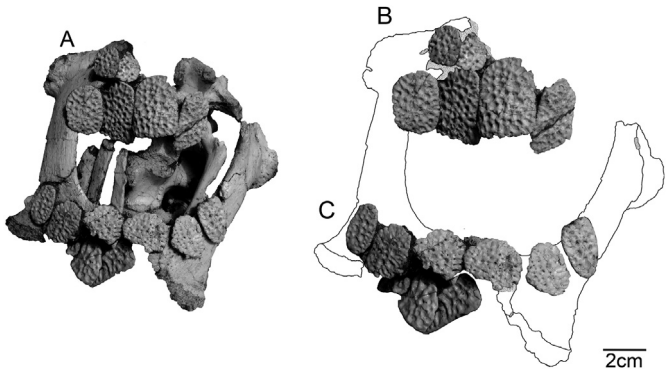

Fig. 12. Pectoral shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, general view of osteoderms associated with vertebrae, ribs and coracoids; B, osteoderms present in anterolateral position of coracoids; C, pectoral osteoderms preserved posteriorly associated in the ventral part of coracoid bones.

Another representative of Crocodyliformes that has a well-preserved dorsal shield is *Simosuchus clarki*. According to Hill (2014), the dorsal shield osteoderms of *Simosuchus* have quadrilateral shapes. The shield is paravertebral open with osteoderms arranged in two pairs of parasagittal lines (tetraserial). These osteoderms have no sharp keel, are sagittally segmented, and have a lateral accessory dermal plate. A transverse row of dorsal osteoderms has six osteoderms in each side, showing that several parasagittal accessory rows of osteoderms are incorporated in the dorsal shield.

The external surface portions of the osteoderms of the paravertebral shield are ornamented with gentle grooves and low ridges extending peripherally from the geometric centre and giving a radial appearance. The keel is slightly separated by tangential grooves toward the medial and lateral regions of the osteoderm. The anterior articular facet is sparsely ornamented, with shallow grooves.

The dorsal shield of *Simosuchus* differs from the dorsal shield of *M. arrudacamposi*. The dorsal osteoderms of *Simosuchus* are quadrilateral, while those of *Montealtosuchus* are rectangular. The paravertebral shield of *Montealtosuchus* is not as open as that of *Simosuchus* because the shield presents a relatively sharp caudal-medially oriented curve in the keel located in the lateral region of the external surface of the osteoderms. In *Simosuchus*, the dorsal armour is arranged in two pairs of paravertebral lines, while in *M. arrudacamposi*, it is arranged in a double line.

The accessory shield of *Simosuchus* is incorporated into the dorsal shield, forming a transverse row of six osteoderms on each side. In *M. arrudacamposi*, the lateral osteoderms are disarticulated but are very close to the dorsal paravertebral osteoderms, which

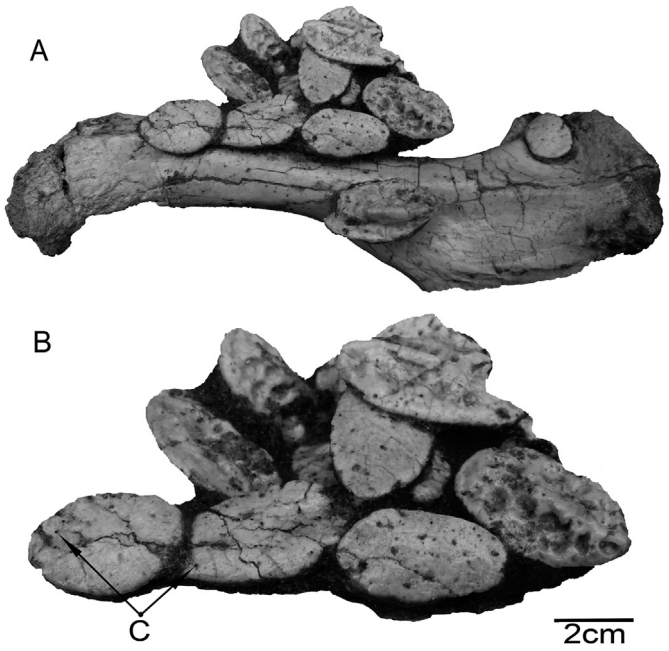

Fig. 13. Appendicular shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, preserved osteoderms associated with left humerus; B, schematic drawing showing the characteristics of the external surface of osteoderms; C, view of the deep surface with some foramina in detail.

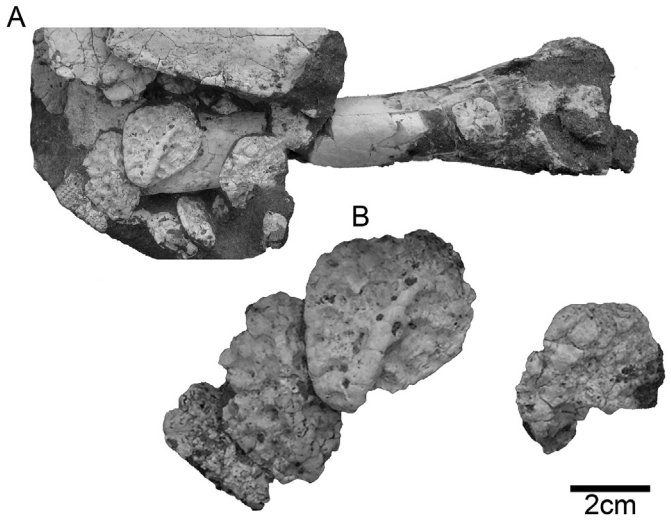

Fig. 14. Appendicular shield of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, preserved osteoderms associated with left femur; B, detail of osteoderms preserved in the left femur.

may suggest the existence of at least one parasagittal line of lateral osteoderms.

The ornamentation of the dorsal shield osteoderms of *Montealtosuchus* is strongly evident of deep round grooves, in some parts forming channels surrounded by tubercles, while in *Simosuchus*, it is characterized by gentle grooves and low ridges.

The presence of one double line of paravertebral osteoderms in *M. arrudacamposi* characterizes this shield as closed (Salisbury and Frey, 2001), and almost completely involves the epaxial muscles of this representative of Crocodyliformes. This characteristic is present in basal Crocodyliformes, such as *Protosuchus, Orthosuchus*, and *Hesperosuchus* (Colbert and Mook, 1951; Ross and Mayer, 1983; Clark et al., 2000).

The dorsal osteoderms are also preserved in some specimens of Baurusuchidae. They are arranged in a double row that articulates craniocaudal with little imbrication in the dorsoventral axis of the vertebrae neural spines that form the back of this animal. The dorsal and ventral surfaces have an intercalated micro-texture with a mesh of structural fibres (Vasconcellos, 2006; Nascimento and Zaher, 2010; Araújo-Júnior and Marinho, 2013).

Importantly, the osteoderms of the back of Baurusuchidae and those of *Montealtosuchus* differ in their arrangement. In baurusuchids, the osteoderms are located at the apex of neural spines, whereas in the peirosaurid *Montealtosuchus*, the osteoderms are closer to the basal portion of the vertebrae neural spines.

Another member of Crocodyliformes, namely *Armadillosuchus*, also has an interesting dermal shield. The osteoderms of the nuchal, dorsal and accessory shield have been preserved in this specimen. The dorsal shield is formed by rectangular and decorated osteoderms with round excavations. They are imbricated and arranged in a double row associated with the accessory shield. The osteoderms are arranged in several rows composed of lateral osteoderms (Marinho and Carvalho, 2009).

The dorsal shield of *Montealtosuchus* is also formed by a double row of osteoderms but differs from the dorsal shield of *Armadilosuchus*, primarily with respect to the number of accessory osteoderms. In *Montealtosuchus* the accessory osteoderms appear to be arranged in a single row.

The nuchal shield of *Armadillosuchus* differs from the nuchal shields found in Crocodyliformes described in this study (*Simosuchus* and *Montealtosuchus*). According to Marinho and Carvalho (2009), the nuchal shield of *Armadillosuchus* is composed of many hexagonal osteoderms that are firmly attached to the skull by articulated lateral sutures. The entire perimeter of the shield is convex, allowing for independent articulation for the skull and the posterior portion of the dermal armour. The shield is hard, and the posterior edge is ornamented with parallel horizontal grooves.

The osteoderms of the nuchal shield of *M. arrudacamposi* are the most convex in axial view when compared to other osteoderms of this animal. The nuchal osteoderms were likely displaced before they were preserved, resulting in the formation of a cluster of osteoderms.

It can be inferred that four more rectangular osteoderms from this set would likely be settled in a more posterior portion of the shield when the shield was in its original position in the living animal. Together, these osteoderms could form a single plate, which in current crocodiles is known as a nuchal rosette (Richardson et al., 2002) (Fig. 5B).

The remaining osteoderms of this cluster – three rectangular and four D-shaped osteoderms – could establish a set of post-occipital scales or a line of scales positioned in front of the nuchal rosette and immediately behind the head (Richardson et al., 2002) (Fig. 5A).

Marinho et al. (2006) do not report osteoderms of the nuchal shield in their description of the osteoderms of *Peirosaurus tormini* and *Uberabasuchus terrificus*. However, Hill (2014) reports the existence of the shield in *Simosuchus clarki*, inferring that the osteoderms of this set do not have the convex characteristic in axial view to completely cover the epaxial muscles of the neck. The deep surfaces of the nuchal osteoderms of *Simosuchus* are flattened and slightly depressed below the keel. The texture of the deep surface is smoother than the external surfaces with some visible structural fibre bundles intersecting each other like the threads of a woven textile. The surface is pierced by small foramina.

The characteristics of nuchal osteoderms of *M. arrudacamposi* differ from those of the nuchal shield of *Simosuchus*. The nuchal shield osteoderms of *M. arrudacamposi* present a large convexity in axial view that could cover the epaxial muscles of the neck. The deep surface of osteoderms present similar characteristics to those of *Simosuchus*, namely, the presence of small foramina and structural fibre marks. The structural fibre marks are characteristics of archosaur osteoderms and were also observed by Scheyer and Sander (2004) in the osteoderms of ankylosaurid dinosaurs.

The pectoral osteoderms of *M. arrudacamposi* follow the same ornamentation pattern of the external surface described in the ventral shield, and the scales are varied in size and shape. There are no reports of the preservation of pectoral osteoderms in *Peirosaurus tormini* or in *Uberabasuchus terrificus*.

In *Simosuchus*, the osteoderms that are preserved in the pectoral region are located below the posterior margin of the coracoid bones. According to Hill (2014), these all have the form of an irregular discoid polygon and closely contact the adjacent osteoderms. The surface ornamentation of the pectoral osteoderms matches the pattern observed in gastral osteoderms.

Based on the location, morphology and ornamentation, these dermal elements may represent a contiguous anterior extension of the gastral shield. A significant gap, however, separates the osteoderms of the gastral shield of *Simosuchus*. The pectoral dermal shield of *M. arrudacamposi* most resembles that of *Simosuchus* with regard to the organization of osteoderms. However, six osteoderms form a bridge-like feature that links the right and left coracoid posterolaterally. These are not positioned immediately below the coracoids as in *Simosuchus* but are located in its ventral posterior portion.

The remaining seven osteoderms in the shield are housed in the anterior portion between the coracoids and likely formed a bridge between these bones. The greatest similarity between the pectoral shield of *M. arrudacamposi* and *Simusuchus clarki* is the presence of a gap separating the osteoderms of the pectoral region from the gastral region (Fig. 15).

The osteoderms of the appendicular skeleton of *M. arrudacamposi* are very similar to those of *Simosuchus clarki*, which presents many well-developed appendicular osteoderms associated with both fore- and hindlimb bones. All of the osteoderms are elliptical to lenticular in shape and have a keel oriented along the axis that divides the surface of the osteoderm into two equal portions. In axial view, these osteoderms have a very high keel.

Studies of postcranial osteoderms of *Montealtosuchus* allow for an understanding of the living habits of peirosaurids. The crocodyliform *Montealtosuchus* had a light armour, which allowed for terrestrial habits. This conclusion can be drawn from the arrangement of dermal shield osteoderms associated with the reduced number of osteoderm lines in the dorsal shield and the disarticulation of accessory osteoderms.

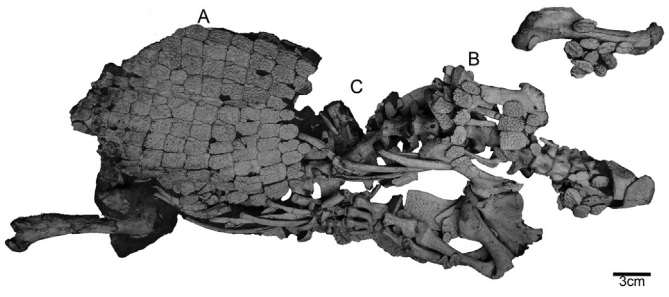

Fig. 15. Ventral view of *Montealtosuchus arrudacamposi* (specimen MPMA-16-0007/04 from the Turonian-Santonian Adamantina Formation, Brazil). A, general view of the arrangement of osteoderms that form the gastral shield; B, region where the pectoral osteoderms were preserved; C, gap that separates the osteoderms of the gastral region from the pectoral region.

The present study supports results of Price (1955), Carvalho et al. (2004, 2007), which analysed the peirosaurids cranial osteology. Moreover, Vasconcellos (2006), Vasconcellos and Carvalho (2006) and Nascimento and Zaher (2010) analysed the postcranial structures of Crocodyliformes *Uberabasuchus terrificus* and *Baurusuchus albertoi*, respectively. It was determined that these animals had a cursorial locomotion pattern. Vasconcellos (2006) stated that a particular structure between the femur and the ileum, as well as the imbrication of dorsal osteoderms, enabled *Uberabasuchus* to attain a more high-walking posture and ease of movement.

Marinho (2006) pointed to the small thickness of the dermal plates of peirosaurids *Peirosaurus tormini* and *Uberabasuchus terrificus*. He concluded that this characteristic allowed for the maintenance of body temperature and a greater flexibility during locomotion. As the thickness of *Montealtosuchus* osteoderms is similar to the peirosaurids studied by Marinho (2006), we suggest that this interpretation is also suitable for *Montealtosuchus*.

7. Conclusions

The present study of the dermal shield of *M. arrudacamposi* supports the results of the osteoderm analysis in *Uberabasuchus terrificus*, showing that this set of dermal plates had a well-defined mechanical function and also served for protection and thermoregulation.

The morphometric analysis indicates that the dermal shield that covered the entire postcranial region of *Montealtosuchus* provided a light armour, allowing for a more high-walking posture (semi-improved or semi-erect posture) of this animal in terrestrial habits.

With regard to the protection provided by the dermal shields, available evidence suggests that the arrangement of plates along the body of *M. arrudacamposi* would not have prevented a direct attack by large predators. However, poorly targeted attacks by smaller predators could have been less likely to cause damage due to the presence of this light armour.

Thermoregulation was the most important function of the dermal shield in *M. arrudacamposi*. Living in a hot and arid environment, and in a regime of extreme temperature ranges, the plates served to radiate heat away from the animal, keeping the internal temperature of the body closer to the temperature at the surface. This mechanism is similar to that found in modern crocodile species.

The arrangement of dermal shield osteoderms of *Montealtosuchus* in association with the reduced number of lines of the dorsal shield and the arrangement of lateral osteoderms without joints indicate that this crocodyliform had a light armour. Combining the present results with the former studies of cranial and postcranial structures of peirosaurids and baurusuchids, we conclude that this member of Crocodyliformes was capable of an agile terrestrial locomotion.

Acknowledgements

We thank to the crew of Museu de Paleontologia “Prof. Antonio Celso Arruda Campos”, Antônio Celso de Arruda Campos (*in memoriam*), Cledinei A. Francisco, Fabiano Vidoi Iori, Deverson da Silva (Pepi), Paulo Gilberto da Rocha Tavares, José Augusto Bugarelli, Angélica Fernandes and Hellen Tavares, for the help in the field and laboratory work. This study was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ).

References

Araújo-Júnior, H.I., Marinho, T.S., 2013. Taphonomy of a *Baurusuchus* (Crocodyliformes, Baurusuchidae) from the Adamantina formation (Upper Cretaceous, Bauru Basin), Brazil: Implications for preservational modes, time resolution and paleoecology. Journal of South American Earth Sciences 47, 90–99.

Basilici, G., Dal Bo, P., Ladeira, B.F.S., 2009. Climate-induced sediment-palaeosol cycles in a Late Cretaceous dry aeolian sand sheet: Marília Formation (NW Bauru Basin, Brazil). Sedimentology 56, 1876–1904.

Benton, M.J., Clark, J.M., 1988. Archeosaur phylogeny and the relationships of the Crocodylia. In: Benton, M.J. (Ed.), The Phylogeny and Classification of Tetrapods, v.1: Amphibians, Reptiles, Birds, pp. 295–338. Systematics Association Special 35A.

Brazaits, P., 1987. In: Ross, C.A., Garnett, S. (Eds.), Identification of Crocodilian Skins and Products. In: Wildlife Management: Crocodiles and Alligators. Weldon Owen, p. 373.

Buckley, G.A., Brochu, C.A., Krause, D.W., Pol, D., 2000. A pugnosed crocodyliform from the Late Cretaceous of Madagascar. Nature 405, 941–944.

Buffrénil, V., de Clarac, F., Fau, M., Martin, S., Martin, B., Pellé, E., Laurin, M., 2014. Differentiation and growth of bone ornamentation in vertebrates: a comparative histological stud among the Crocodylomorpha. Journal of Morphology 276, 1–21.

Clark, J.M., Sues, H.D., Berman, D.S., 2000. A new specimen of Hesperosuchus agilis from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. Journal of Vertebrate Paleontology 2, 683–704.

Carvalho, I.S., Bertini, R.J., 2000. Contexto geológico dos notossúquios (Crocodylomorpha) cretácicos do Brasil. Revista Geologia Colombiana, Colômbia.

Carvalho, I.S., Ribeiro, L.C.B., Avilla, L.S., 2004. Uberabasuchus terrificus sp. nov. a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. Gondwana Research 7 (4), 975–1002.

Carvalho, I.S., Campos, A.C.A., Nobre, P.H., 2005. Baurusuchus salgadoensis, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. Gondwana Research 8 (1), 11–30.

Carvalho, I.S., Vasconcellos, F.M., Tavares, S.A.S., 2007. Montealtosuchus arrudacamposi, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. Zootaxa 1607, 35–46.

Carvalho, I.S., Gasparini, Z.B., Salgado, L., Vasconcellos, F.M., Marinho, T.S., 2010. Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 252–262.

Colbert, E.H., Mook, C.C., 1951. The ancestral crocodilian Protosuchus. Bulletin of the American Museum of Natural History 97, 143–182.

Dias-Brito, D., Musachio, E.A., Castro, J.C., Maranhão, M.S.S., Suárez, J.M., Rodrigues, R., 2001. Grupo Bauru: uma unidade continental do Cretáceo no Brasil–concepções baseadas em dados micropaleontológicos, isótopos e estratigráficos. Revue Paléobiologique 20 (1), 245–304.

Fernandes, L.A., Coimbra, A.M., 1996. A Bacia Bauru (Cretáceo Superior, Brasil). Anais da Academia Brasileira de Ciências 68 (2), 195–205.

Fernandes, L.A., Coimbra, A.M., 2000. Revisão estratigráfica da parte oriental da Bacia Bauru (Neocretáceo). Revista Brasileira de Geociências 30, 717–728.

Hill, R.V., 2005. Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. Systematic Biology 54, 530–547.

Hill, R.V., 2014. Osteoderms of simosuchus clarki (Crocodyliformes: Notosuchia) from the late cretaceous of Madagascar. Journal of Vertebrate Paleontology 30 (s1), 154–176.

Marinho, T.S., 2006. Osteodermos de crocodilomorfos e dinossauros da Bacia Bauru (Cretáceo Superior). Universidade Federal do Rio de Janeiro, p. 56 (MSc. thesis).

Marinho, T.S., Ribeiro, L.C.B., Carvalho, I.S., 2006. Morfologia de osteodermos de Crocodilomorfos do sítio paleontológico de Peirópolis (Bacia Bauru, Cretáceo Superior). Anuário do Instituto de Geociências 29 (2), 44–53.

Marinho, T.S., Carvalho, I.S., 2009. An armadillo-like sphagesaurid crocodylifom from the Late Cretaceous of Brazil. Journal of South American Earth Sciences 27, 36–41.

Milinkovitch, M.C., Manukyan, L., Debry, A., Di-Poï, N., Martin, S., Singh, D., Lambert, D., Zwicker, M., 2013. Crocodile head scales are not developmental units but emerge from physical cracking. Science 339, 78–81.

Nascimento, P.M., Zaher, H., 2010. A new Baurusuchidae from the Upper Cretaceous of Brazil. Papeis Avulsos de Zoologia 50 (21), 323–361.

Paula e Silva, F., 2003. Geologia de superficie e hidroestratigrafia do Grupo Bauru no Estado de São Paulo. Universidade do Estado de São Paulo, p. 166 (D.Sc thesis).

Pough, F.H., Andrews, R.M., Cadle, J.E., Crump, M.L., Savitzky, A.H., Wells, K.D., 2004. Herpetology. Pearson Prentice Hall, p. 726.

Price, L.I., 1955. Novos crocodilídeos dos arenitos da série Bauru. Cretáceo do Estado de Minas Gerais. Anais da Academia Brasileira de Ciências 27, 487–498.

Richardson, K.C., Webb, G.J.W., Manolis, S.C., 2002. Crocodiles: Inside Out. A Guide to the Crocodilians and Their Functional Morphology. Surrey Beatty & Sons, p. 172.

Ross, C.A., Garnett, S., 1989. Crocodiles and Alligators. Facts On File, p. 240.

Ross, F.D., Mayer, G.C., 1983. On the dorsal armor of the Crocodilia. In: Rhodin, A.G.J., Miyata, K. (Eds.), Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, pp. 305–331.

Salisbury, S., Frey, E., 2001. A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodilians. In: Grigg, G.C., Seebacher, F., Franklin, C.E. (Eds.), Crocodilian Biology and Evolution. Surrey Beatty & Sons, pp. 85–134.

Scheyer, T.M., Sander, P.M., 2004. Histology of ankylosaur osteoderms: implications for systematics and function. Journal of Vertebrate Paleontology 24 (4), 874–893.

Vasconcellos, F.M., 2006. Descrição do pós-crânio de Uberabasuchus terrificus Carvalho, Ribeiro & Avilla, 2004 (Crocodyliformes, Peirosauridae) do Cretáceo Superior da Bacia Bauru: Inferências morfofuncionais e paleoautoecológicas. Universidade Federal do Rio de Janeiro, p. 174 (MSc. thesis).

Vasconcellos, F.M., Carvalho, I.S., 2006. Condicionante etológico na tafonomia de Uberabasuchus terrificus (Crocodyliformes, Peirosauridae) da Bacia Bauru (Cretáceo Superior). Geociências 25 (2), 225–230.