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Armadillosuchus arrudai (Sphagesauridae, Crocodyliformes), Adamantina Formation (Turonian – Santonian), Bauru Basin, southeastern Brazil: Dental development aspects

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A B S T R A C T

Armadillosuchus arrudai, an extinct crocodyliform, has a complex pattern of tooth replacement. Replacement of functional teeth followed an alternating numerical and directional wave from posterior to anterior. Notably, the presence of an initial fossa in some teeth indicated root resorption and facilitated the development of tooth replacement. These aspects suggest a coordinated tooth replacement process, enabling the animal to maintain functional dentition. This study provides insights into the unique dental dynamics of *Armadillosuchus arrudai*, highlighting its lifelong polyphyodonty and the meaning of alternating replacement patterns. Microtomography allowed the comprehension of these intricate tooth replacement processes.

1. Introduction

Armadillosuchus arrudai Marinho and Carvalho, 2009 is a sphagesaurid crocodyliform with peculiar characteristics, particularly regarding its dentition, which proves to be the most striking feature of the group (Kuhn, 1968; Marinho and Carvalho, 2009). Aspects such as the oblique position of the teeth, tuberculated keels, and triangular crowns commonly appear in the group, along with heterodonty (Pol, 2003; Marinho and Carvalho, 2009). These characteristics were observed in *Sphagesaurus huenei* Price, 1950, *Caipirasuchus montealtensis* (Andrade and Bertini, 2008), *Caipirasuchus paulistanus* Iori and Carvalho, 2011, *Armadillosuchus arrudai* Marinho and Carvalho, 2009 and *Caryonosuchus pricei* Kellner et al., 2011. Based on these characteristics with the observation of dental wear in the group, it can be concluded that there is a food processing behavior through chewing (Pol, 2003; Andrade and Bertini, 2008; Marinho and Carvalho, 2009, Ösi, 2014). Chewing is possible by the masticatory apparatus, heterodonty, and dental occlusion, which are not commonly observed in most crocodyliform clades. These features have been compared in the literature to mechanisms used by mammals for chewing food (Ösi, 2014), in which tooth replacement occurs twice during life and is referred to as diphyodoncy (Cabreira et al., 2022).

However, in Crocodyliformes, tooth replacement takes place continuously throughout life, a condition known as polyphyodonty (Edmund, 1960; Leblanc et al., 2017). According to Edmund (1960), many groups of reptiles are polyphyodonts and exhibit a pattern of dental replacement that progresses from posterior to anterior, with alternating numerical replacement. Older teeth have thicker walls and show advanced replacement within their pulp cavities,

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whereas newly established teeth have thinner walls and no replacements. Edmund (1960) also describes the development of a shallow pit in the lingual root wall of the old tooth, formed through resorption of the tooth base, which allows the entry of the replacement tooth into the pulp chamber. In a more advanced stage, this pit becomes wider and eventually perforates the pulp cavity, merging with the tooth bases. Additionally, replacement teeth are generally larger than functional teeth. A similar pattern as described above was observed by Marinho and Carvalho (2013) in the teeth of *Gondwanasuchus scabrosus*, which demonstrated a wave of dental replacements with alternating numerical and posterior-to-anterior direction, as described by Edmund (1960). This study aims to describe the tooth replacement mechanism and its structures in *Armadillosuchus arrudai* using microtomography, aiming to contribute to a deeper understanding of the biology of this group.

1.1. Geological setting

The Bauru Basin covers an area of approximately 370,000 km^2 with a maximum thickness of 300 m of sedimentary rock. The basin occurs in the central São Paulo, northeastern Mato Grosso do Sul, southeastern Mato Grosso, southern Goiás and western Minas Gerais states (Fig. 1). Its basement is the Serra Geral Formation basalts, upon which continental sedimentation occurred, consisting very fine sandstones, notably in the Araçatuba and Adamantina formations, transitioning to fine and medium sandstones in the intermediate portions of the Adamantina and Uberaba formations. The upper portion is composed of medium to coarse sandstones with conglomerate levels of the Marília and Serra da Galga formations (Batezelli, 2007; Soares et al., 2020).

The fossil analyzed in this study was found in the Adamantina Formation, located in General Salgado, São Paulo State. It is the lithostratigraphic unit with the largest distribution area in the Bauru Basin (Batezelli, 2007; Ladeira, 2016; Menegazzo et al., 2016). The formation consists of fine to coarse-grained reddish sandstones, intercalated with reddish siltstones and mudstones and some conglomerate levels. These sediments were deposited in shallow fluvial systems, where fossils were primarily accumulated in alluvial plains during flooding events (Goldberg and Garcia, 2000; Carvalho et al., 2010; Carvalho et al., 2011). Isotopic studies and micropaleontology indicate a chronostratigraphic assignment between the Turonian and Santonian stages (Dias-Brito et al., 2001).

2. Materials and methods

The fossil of Armadillosuchus arrudai, is housed in the collection of the Departamento de Geologia at the Universidade Federal do Rio de Janeiro (UFRJ), under the code number UFRJ DG 380-R. In order to obtain high-resolution images for observing the internal tooth morphology, it was used a microtomograph located at the Centro de Documentação da Biodiversidade (CDB) in the Faculdade de Filosofia, Ciências e Letras at the Universidade de São Paulo (USP), Ribeirão Preto campus, São Paulo State. Micro-CT scanning was conducted using a GE Phoenix v|tome|x S240 scanner with 800−900 projections, skipping 1, averaging 2−3, exposure time of 200−333 ms, voltage of 90 kV, current of 180 uA, voxel size of 60−80 μm (μm) and a 0.5 mm copper filter. The obtained images allowed the observation of adjacent teeth close to eruption and the identification of possible structures such as the next-generation tooth, the functional tooth, the thickness of tooth walls, and initial fossae.

The images were processed using the software AVIZO 7, a high-tech software available on major platforms such as Linux, Windows, and MacOS. With this software, it was possible to select

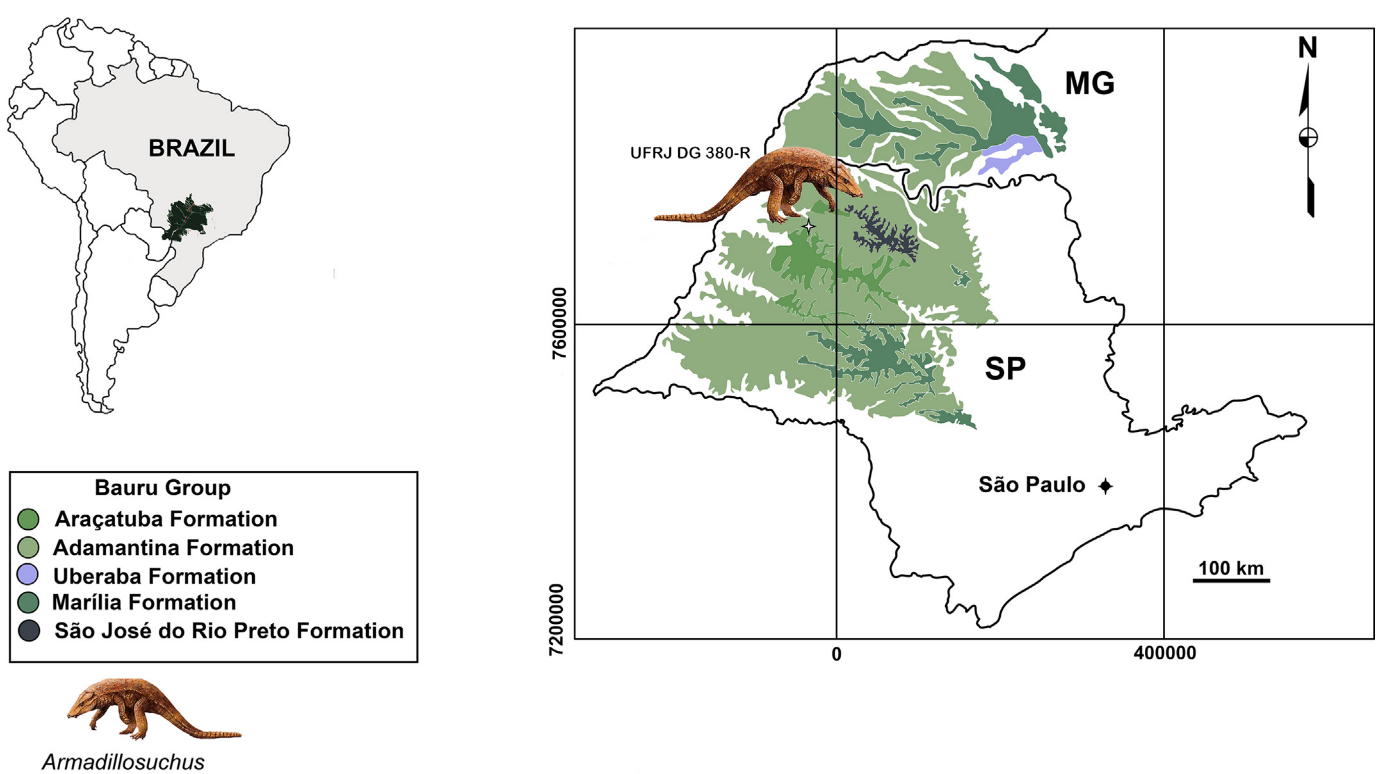

Fig. 1. Bauru Basin in São Paulo and Triângulo Mineiro region of Minas Gerais State, Brazil. Marked with a star symbol is the location where the fossil of *Armadillosuchus arrudai* was found in the municipality of General Salgado, São Paulo State (modified from Martinelli et al., 2018).

areas, segment each layer of the teeth, and create a three-dimensional image for better interpretation. Models were obtained after selecting the anatomical structures, enabling the interpretation, description, and comparison of tooth replacement.

To assess the degree of development of the replacement teeth, a parameter was adopted that evaluates the completeness of the teeth within the alveoli. This degree of development is measured by the percentage of completeness of the replacement teeth, and specific margins were established for each degree of development. An advanced degree of development is considered when 90 %–100 % of the replacement tooth is preserved. A moderate degree of development is considered when 50 %–89 % of the replacement tooth is preserved, and a low degree of development is considered when 1 %–49 % of the replacement tooth is preserved.

3. Results

The functional teeth are well-preserved, with the exception of the missing tooth 9 in the right maxilla (Rm6), tooth 1 of the left premaxilla (Lpm1), as well as teeth 8 (Lm5) and 9 (Lm6) of the left maxilla. Overall, all teeth show some level of replacement. The premaxilla and right maxilla exhibit fine preservation of the next-generation teeth, allowing for the observation of the replacement pattern.

There is a wave of replacement that closely resembles the pattern described by Edmund (1960) for other reptiles and even for extant Crocodyliformes. This wave occurs on the maxilla in a posterior to anterior direction, with odd teeth alternating their replacement with even teeth.

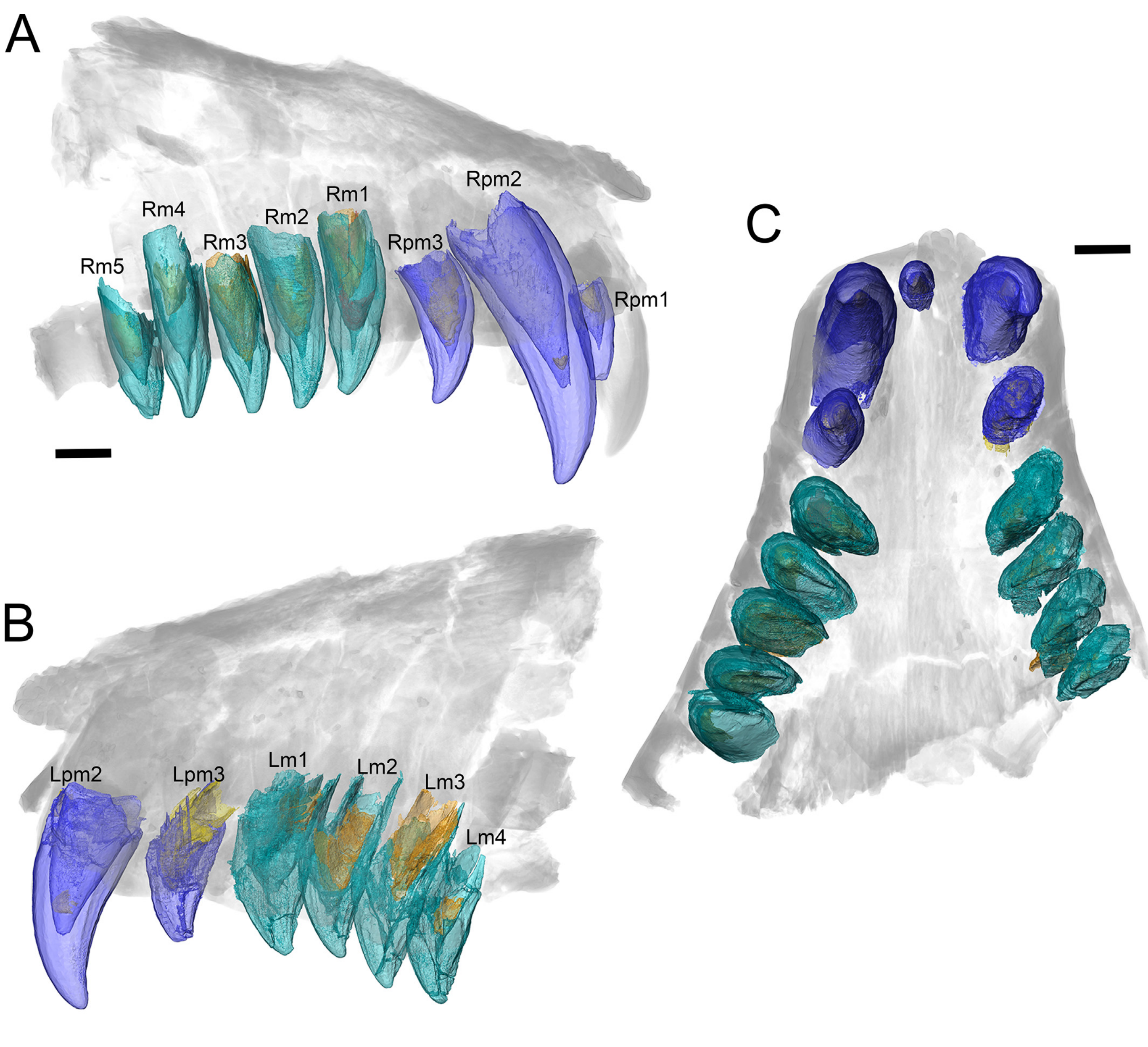

Fig. 2. Maxilla of *Armadillosuchus arrudai* UFRJ DG 380-R. A, right lateral view; B, left lateral view, and C, ventral view. Rpm1, Rpm2, and Rpm3 are the premaxillary right alveoli, and Rm1, Rm2, Rm3, Rm4, and Rm5 are the right maxillary alveoli, while Lpm2 and Lpm3 are the left premaxillary alveoli, and Lm1, Lm2, Lm3, and Lm4 the left maxillary alveoli. Scale bar with 1 cm.

3.1. Description of functional series

The right and left premaxilla (Fig. 2) present all functional teeth are well-preserved, except for tooth 1 of the left premaxilla, which is missing, and tooth 3 (Lpm3), which is highly fragmented. The crowns are conical and concave distally, positioned parallel to the central axis of the skull exhibiting non-carinated crowns and a circular cross-sectional shape. The enamel on the crowns displays vertical ridges from the cervix region to the apex, a characteristic typically observed in other sphagesaurids (Pol, 2003; Andrade and Bertini, 2008; Ösi, 2014), more pronounced on the lingual side.

The first tooth of the right premaxilla (Rpm1) is the smallest among all and shows slight wear at the crown apex. The second teeth of the premaxilla (Rpm2 and Lpm2) are the largests among all teeth analyzed, with a more pronounced inclination distally towards the crown apex, showing no indications of dental wear. The third teeth of the premaxilla (Rpm3 and Lpm3) are intermediate size compared to the first and second teeth of the premaxilla. Exceptionally, the right premaxillary tooth (Rpm3) exhibits a constriction in the cervix in the mesial direction, unlike the others lacking such a structure. Additionally, its apex has the most pronounced curvature towards the distal side among the three described teeth, adopting a hook-like shape. The equivalent tooth in the left premaxilla (Lpm3) shows slight wear at its apex.

The dental series of the right maxilla (Fig. 2A and C) consists of six teeth, with the last tooth missing. Overall, the teeth are well-preserved, clearly demonstrating the heterodonty characteristic of the group (Andrade and Bertini, 2008; Lecuona and Pol, 2008; Martinelli et al., 2018), allowing differentiation between incisiform, caniniform, and molariform teeth. The teeth generally share a similar shape and size, with tuberculate and obliquely oriented carinae, presenting a drop-shaped cross-section as observed in other sphagesaurids. There is a notable constriction at the cervix region in all teeth, and the enamel shows vertical striations from the base to the apex, more pronounced on the labial side, akin to the premaxillary teeth. Notably, there isn't significant dental wear observed on the crowns.

Unlike the right maxilla, the teeth of the left maxilla (Fig. 2B and C) are not well-preserved due to extensive fragmentation and the absence of teeth 5 and 6. Despite the poor preservation and absence, it's evident that the morphology follows the same pattern

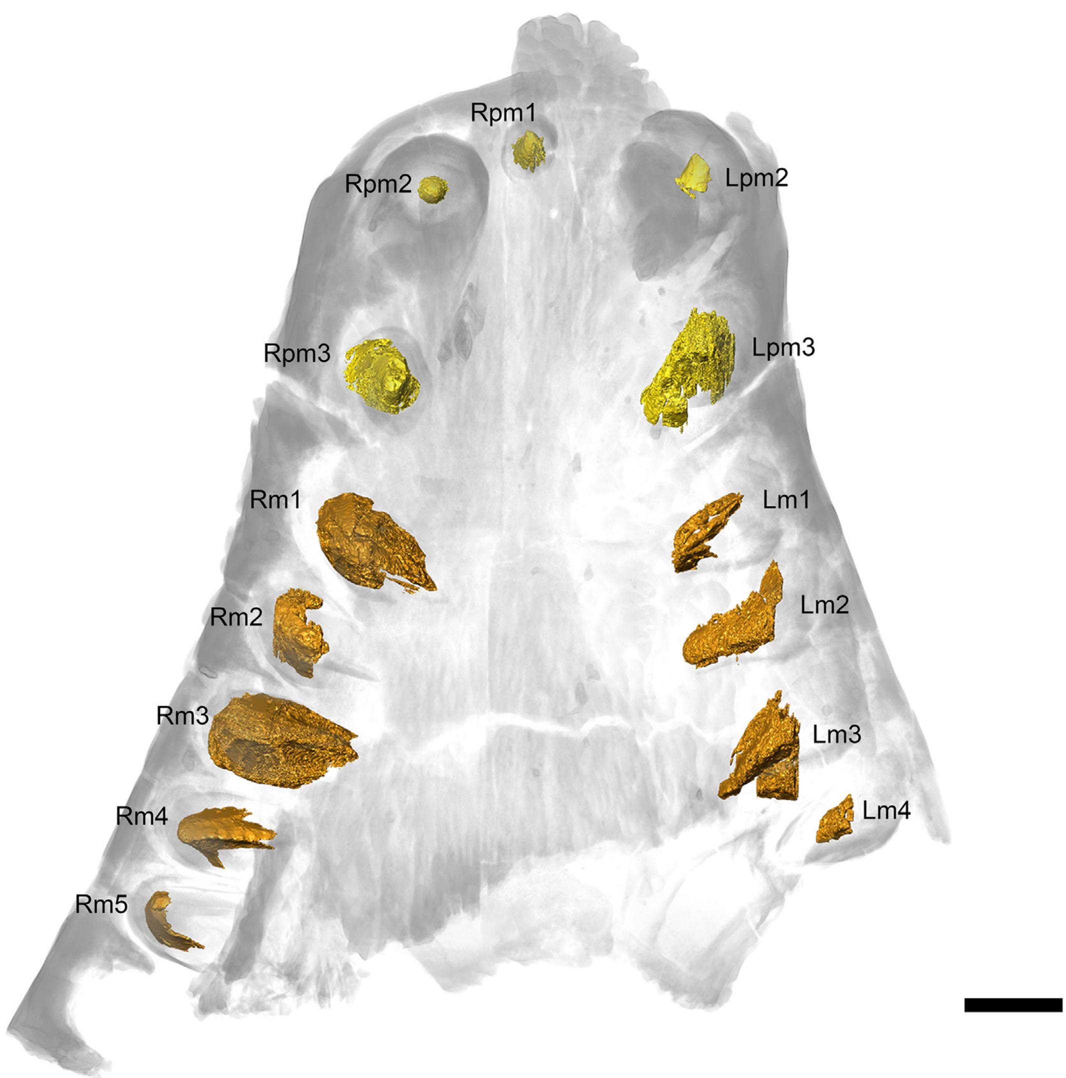

Fig. 3. Replacement teeth in ventral view of the maxilla of *Armadillosuchus arrudai*, UFRJ DG 380-R. Rpm1, Rpm2, and Rpm3 are the premaxillary right alveoli, and Rm1, Rm2, Rm3, Rm4, and Rm5 are the right maxillary alveoli, while Lpm2 and Lpm3 represent the left premaxillary alveoli, and Lm1, Lm2, Lm3, and Lm4, the left maxillary alveoli. Scale bar with 1 cm.

as described for the right maxilla, presenting a typical "sphagesauriform" dentition (Iori and Carvalho, 2018).

3.2. Right premaxilla and maxilla

In the odd series of the substitution teeth (Figs. 3 and 4), from posterior to anterior, teeth 7 (Rm4), 5 (Rm2), and 3 (Rpm3) show a moderate degree of development, with a preservation level between 50 % and 89 %. This indicates that their replacements were not recent and had undergone some progress. Tooth 1 (Rpm1) in this series displays the lowest degree of development, with less than 50 % preservation, suggesting a more recent replacement.

On the other hand, in the even series, tooth 8 (Rm5) exhibits a low degree of development, with less than 50 % preservation. Among all the analyzed teeth, replacement tooth 6 (Rm3) displays the highest degree of replacement development. It not only shows an advanced stage of the next-generation tooth but also demonstrates a reduction in the size of the root of the functional tooth, indicating the process of resorption. This resorption process likely begins with structures referred to as fossae by Edmund (1960). However, in *Armadillosuchus arrudai*, these fossae are not present in the lingual position but rather in the distal and mesial portions of the teeth. Along with the reduction in root length, there is a decrease in the thickness of the wall, creating space for the base of the next-generation tooth. Furthermore, tooth 4 (Rm1) exhibits an advanced replacement tooth, while tooth 2 (Rpm2) shows a replacement in a less developed stage, suggesting that it may have been the last tooth to be replaced in this series.

3.3. Left premaxilla and maxilla

In the left region of the substitution teeth (Figs. 3 and 5), the odd series in a posterior-to-anterior direction presents replacement tooth 7 (Lm4) with a low degree of development, followed by teeth 5 (Lm2) with a moderate degree of development, ranging between 50 % and 89 % completion, and tooth 3 (Lpm3) with an advanced degree of development, with over 90 % completion. Notably, replacement tooth 3 (Lpm3) displays an anteriorly directed apex inclination, almost leading to fusion between the replacement tooth and the functional tooth.

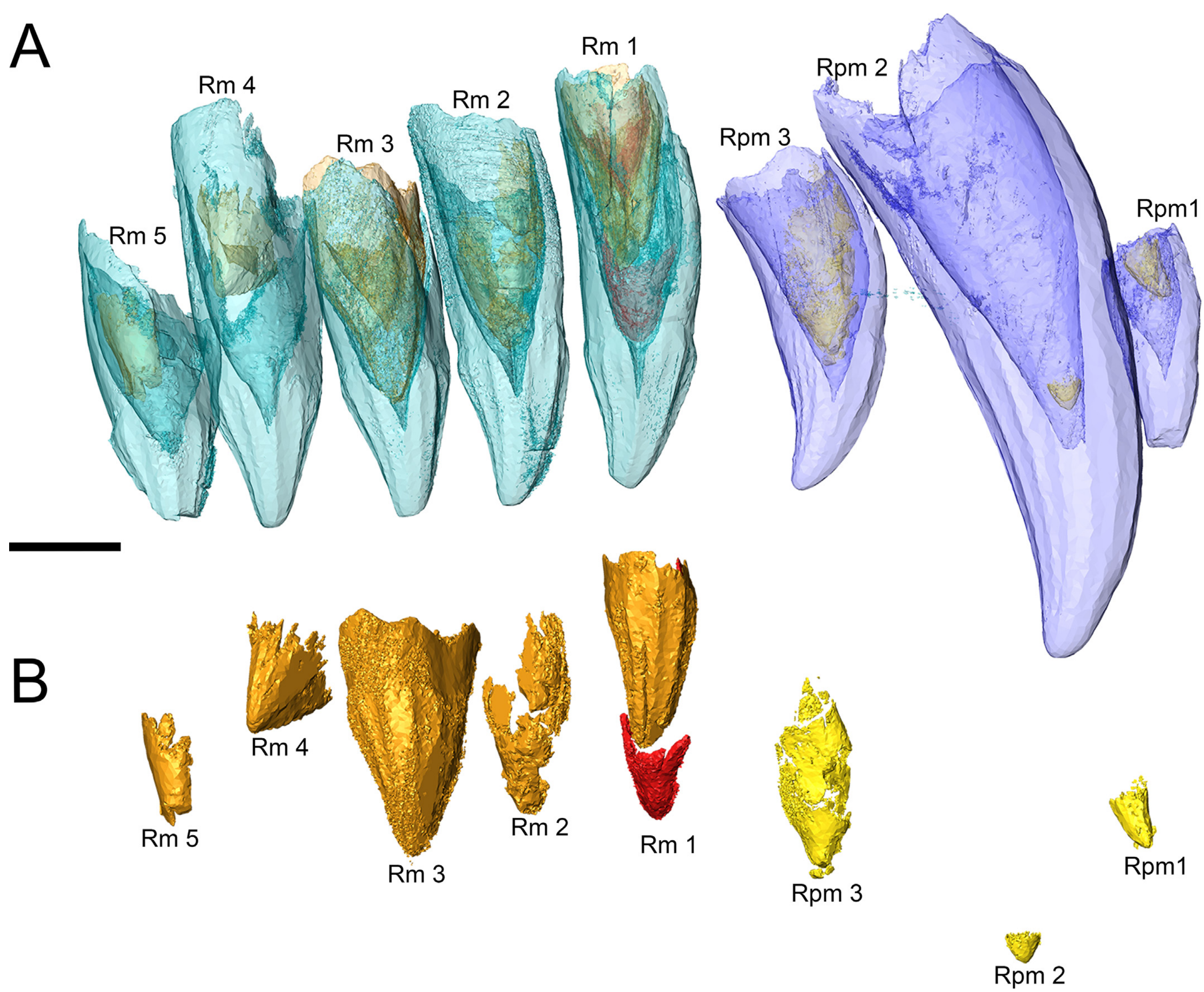

Fig. 4. Functional teeth of the right maxilla indicated by A, and B, replacement teeth. Rpm1, Rpm2, and Rpm3 are the right premaxillary teeth, and Rm1, Rm2, Rm3, Rm4, and Rm5 the right maxillary teeth. Scale bar with 1 cm.

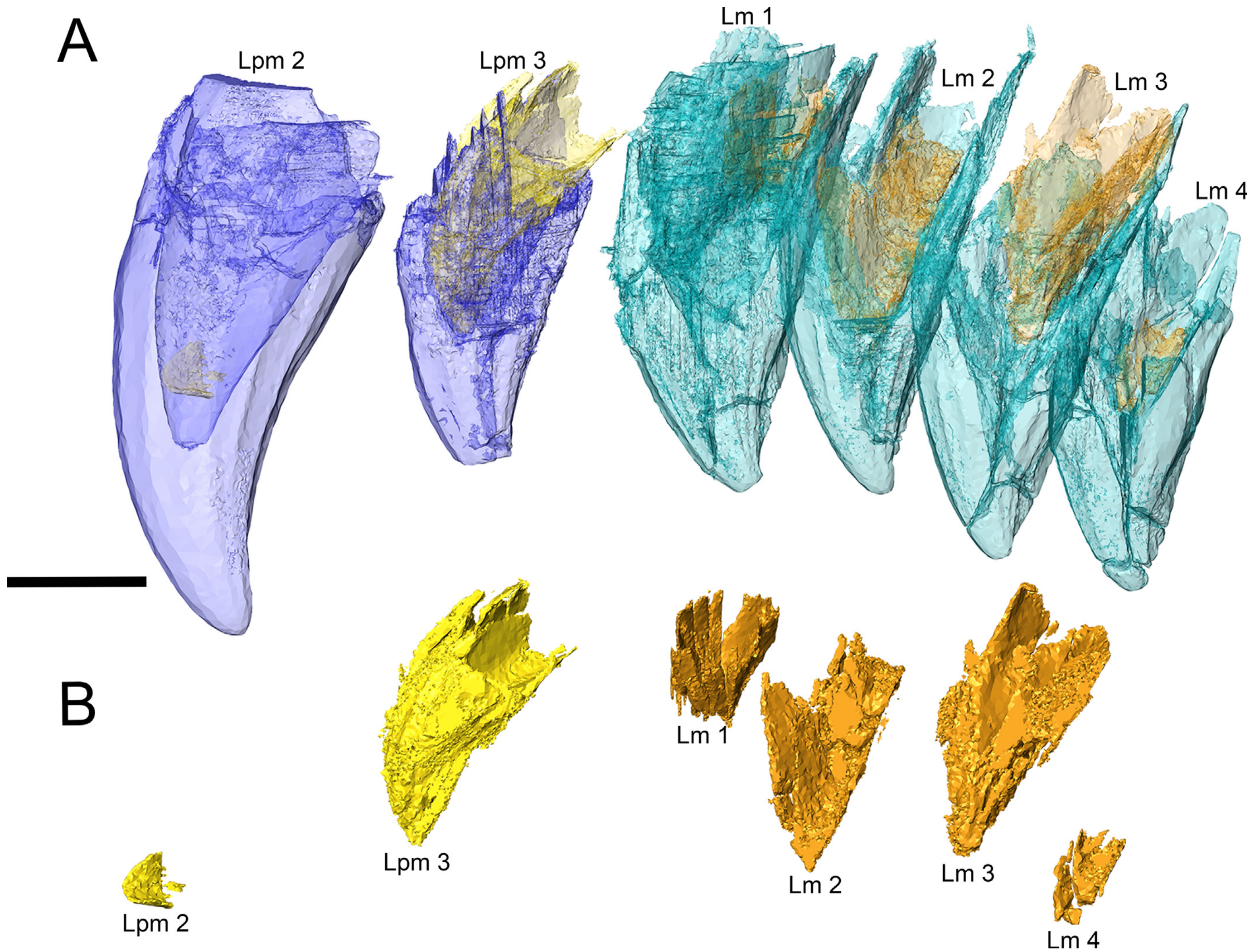

Fig. 5. A, functional teeth of the left maxilla; B, replacement teeth. Lpm2 and Lpm3 are the left premaxillary teeth, and Lm1, Lm2, Lm3, and Lm4 the left maxillary teeth. Scale bar with 1 cm.

In the even series, tooth 6 (Lm3) shows a moderate degree of development, followed by teeth 4 (Lm1) and 2 (Lpm2) with a low degree of completion. Teeth 1 (Lpm1), 8 (Lm5), and 9 (Lm6) are absent.

The high degree of development observed in replacement tooth 3 (Lpm3) suggests it would be the next tooth to be replaced. However, unlike tooth 6 (Lm3) in the right maxilla, the root of this tooth is not preserved, preventing verification of the presence of initial fossae. The low degree of development seen in replacements 2 (Lpm2), 4 (Lm1), and 7 (Lm4) suggests they were more recently replaced.

4. Discussion

It is possible to estimate the amount of time required for complete teeth formation and their replacement rates by using the von Ebner lines observed in various vertebrate groups, specifically in archosaurs, since dentin has a daily deposition (Erickson, 1996). In hadrosaurs and other herbivorous dinosaur groups, the formation of dental batteries probably occurred due to the slow dentine deposition process in contrast to rapid wear process, leading to the development of many replacement teeth (Erickson, 1996). According to Ricart et al. (2021), adult herbivorous archosaurs taxa exhibit thicker von Ebner lines, while typical carnivorous archosaurs taxa show thinner lines. Ricart et al. (2021) also notes that, among archosaurs, Notosuchia displays thicker von Ebner lines, indicating a high dentine deposition rate, yet with a thinner layer of dental enamel and significant dental replacement due to wear process caused by chewing abrasion.

Ricart et al. (2021) further mentions that the von Ebner line formation rate within the Sphagesauridae group resembles the extant crocodyliforms, which is higher compared to other archosaurs. Thus, Navarro et al. (2022) analyzed the daily dentine growth data of Notosuchia, specifically of *Notosuchus terrestris* Woodward, 1896, and found a closer resemblance to Baurusuchidae, showing reduced deposition rates in this species compared to other Notosuchia. By gathering this with phylogenetic data, Navarro et al. (2022) demonstrated that the low dental growth rates found in *N. terrestris* might correspond to a plesiomorphic condition within the crocodyliform group. In contrast, Sphagesauridae and *Mariliasuchus amarali* Carvalho and Bertini, 1999, which have higher growth rates, present a more derived condition within the group. Navarro et al. (2022) even suggests the possibility that the ancestors of Notosuchia had higher growth rates, making the condition of Sphagesauridae and *M. amarali* plesiomorphic, while *Notosuchus terrestris* represents a regression.

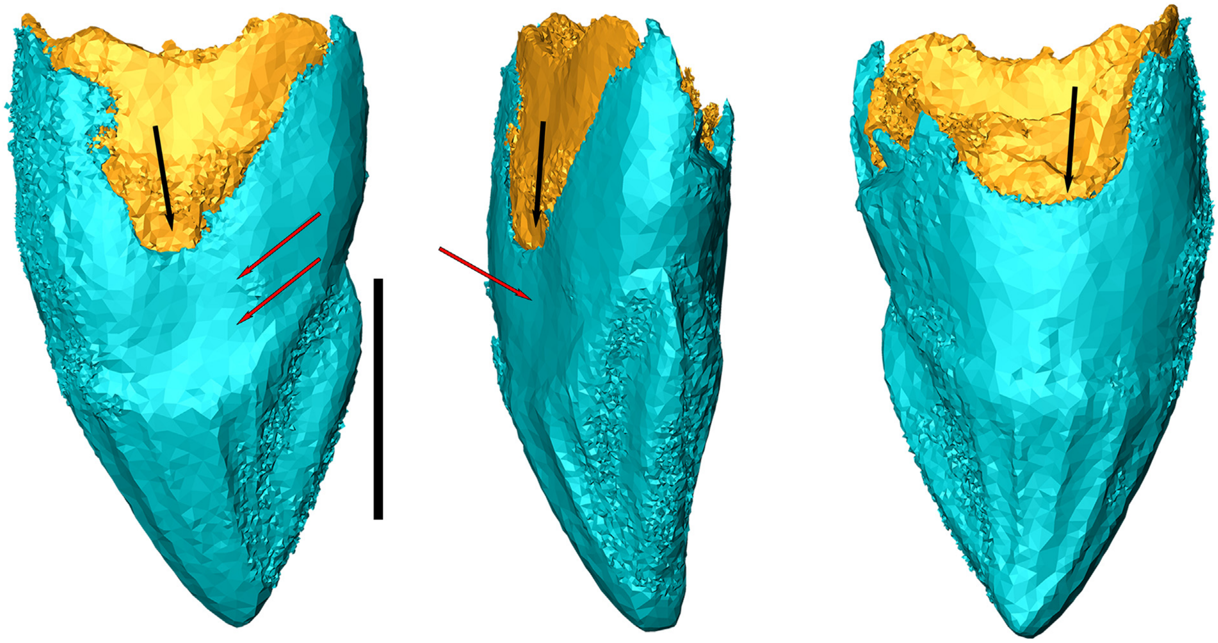

Fig. 6. Tooth 3 of the right maxilla (Rm3). The black arrows indicate the formation of the initial fossa responsible for the reduction of the functional tooth wall, making way for the root of the replacement tooth. The red arrows indicate a region that has a depression, called groove, which would be responsible for the beginning of the pit. Functional tooth in cyan and replacement tooth in orange. Scale bar with 1 cm.

Therefore, *A. arrudai* displays replacements at various stages and in all maxillary teeth on both sides, supporting Ricart et al. (2021) information that Sphagesauridae possesses a high dental replacement rate among crocodyliforms.

The region of the left premaxilla and maxilla is not well preserved, making it challenging to interpret what was the actual tooth root and what was merely sediment. Conversely, it was possible to observe all the tooth shapes in the region of the right premaxilla and maxilla. As described, all the teeth showed dental replacements at some level, and due to the advanced ontogenetic development of the specimen, it is possible to interpret that it would be polyphyodonty.

The degree of development of the replacement teeth showed a substitution wave that closely resembles the one described in other reptiles by Edmund (1960) for. They occur in a numerical alternation between odd and even teeth and in a posterior-to-anterior direction. This was observed due to the alternation in the development of replacement teeth, with the odd-numbered teeth located more posteriorly and the even numbered teeth located more anteriorly, indicating a possible alternation of replacements between them. In general, the functional teeth, except those in the premaxillae, showed very similar sizes, which are not good markers to predict the next replacements. As observed by Ösi (2014), fully erupted functional teeth may exhibit varying degrees of dental wear, thus serving as a good indicator of tooth age. Current extant Crocodyliformes have large, recently replaced young teeth and small, old teeth (Edmund, 1960). The lower degree of development of the replacement teeth indicates a recent substitution, while more advanced degrees indicate a closer timing to the replacement. This substitution wave shows that the teeth were not replaced randomly, allowing the animal to avoid losing many teeth at once. According to Ricart et al. (2021), due to their high rate of dental wear caused by the food maceration process, herbivorous animals tend to have thinner dental enamel and a high rate of dental replacement, which is clearly observed in *Armadillosuchs arrudai*, as even in advanced ontogenetic stages. All replacement teeth show some degree of development, indicating that the dental replacement mechanism was continuously active.

In addition to the alternation of teeth within the equivalent numerical series for replacements, the same occurred across different series. In other words, odd and even teeth were replaced in an inverse manner, where the odd-numbered teeth closer to the anterior region were being replaced, while the even-numbered teeth were replacing those closer to the posterior region, and so on alternately until the animal's death.

Tooth 6 (Rm3) of the right maxilla exhibits the highest degree of development among all the teeth, allowing us to observe a structure known as the initial fossa (Fig. 6). Located at the base of the tooth in the distal and mesial regions, this structure increases in size as the replacement tooth develops and is likely caused by the resorption of the root to make way for the new tooth. As it grows, the base of the replacement tooth takes the place of the functional tooth, establishing the begin of tooth replacement. Some other teeth at lower stages of development were observed with a kind of groove in the same region where the fossae emerge (Fig. 6). This may indicate that the formation of these structures begins through this groove, where the wall of the tooth base becomes increasingly thinner due to resorption until it eventually disappears, making room for the new tooth.

Exceptionally, tooth 4 of the right maxilla (Rm1), which has a replacement tooth in a medium stage of development, presents two additional replacements (Fig. 7), one located between the functional tooth and the more advanced replacement, and the other located below that same replacement. This fact was interpreted as a replacement that was generated but did not occur. Therefore, these existing layers would be resorbed by the replacement tooth at a more advanced stage. This explains the existence of similar structures in other teeth, such as teeth 1 and 2 (Rpm1, Rpm2), although without the replacement at more advanced stages as observed in tooth 4 (Rm1).

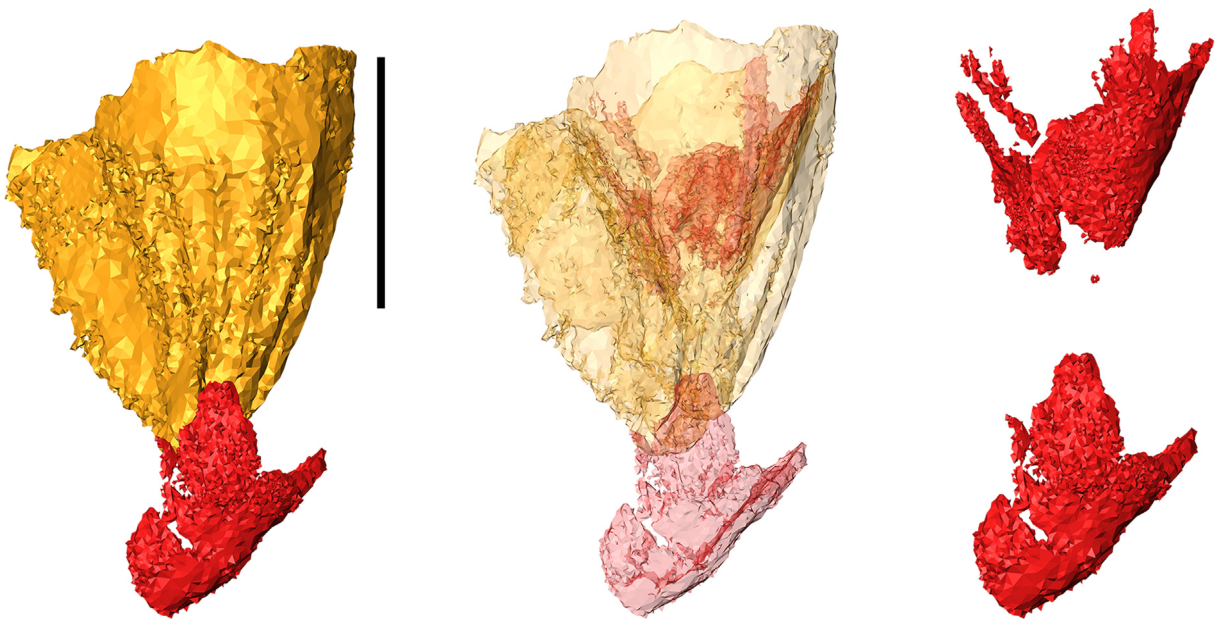

Fig. 7. Replacement tooth 1 of the right maxilla (Rm1) is shown in yellow, presenting two additional replacements in red, probably unsuccessful replacements that were reabsorbed. Scale bar with 1 cm.

5. Conclusion

Armadillosuchus arrudai exhibits a type of polyphyodont replacement, indicating that it likely replaced its teeth continuously throughout its life. However, there is a specific pattern of replacement involving numerical alternation and a posterior-to-anterior direction between odd-numbered and even-numbered teeth. This pattern ensures that the animal did not lose too many teeth simultaneously, which would hinder its predation and feeding abilities.

Teeth in more advanced stages of replacement display a structure known as initial fossa, located beneath the replacement tooth and between the replacement tooth and the functional tooth which indicates the resorption of the base by the replacement tooth. These fossae allow the base of the replacement tooth to gradually increase in size until it takes the place of the functional tooth's base, completing the replacement cycle.

The presence of structures between the functional tooth and the replacement tooth suggests that some replacements were not fully completed and were reabsorbed by the subsequent generation of replacements.

Finally, further studies that dive deeper into the von Ebner lines in conjunction with data from replacement tooth reconstructions could provide a better understanding of tooth replacement and feeding habits within this group. This would offer valuable insights about the ecology and functionality of those structures.

CRediT authorship contribution statement

Bruno de Tolvo Borsoni: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Ismar de Souza Carvalho:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Resources, Validation, Writing – review & editing. **Thiago da Silva Marinho:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Bruno de Tolvo Borsoni reports financial support was provided by Coordination of Higher Education Personnel Improvement. Ismar de souza Carvalho reports financial support was provided by National Council for Scientific and Technological Development. Ismar de Souza Carvalho reports financial support was provided by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro.

Data availability

Data will be made available on request.

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