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# AN UNEXPECTED SHORT TOOTH REPLACEMENT CYCLE PERIOD IN *MARESAURUS COCCAI* (PLESIOSAURIA; RHOMALEOSAURIDAE) FROM THE BAJOCIAN OF ARGENTINEAN PATAGONIA

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*Keywords*: Plesiosauria; Tooth replacement; Neuquen Basin; Argentina; Los Molles Formation; Bajocian; Jurassic.

*Abstract:* The Rhomaleosauridae were a clade of Jurassic plesiosaurians, characterized by triangular skulls, an elongated preorbital region, marked premaxillary-maxillary constriction, and intermediate body proportions that fall between pliosauromorphs and plesiosauromorphs. Despite recent progress in the study of dental replacement in plesiosaurians, the replacement features in rhomaleosaurids have not been studied yet. Here, the dental features of the rhomaleosaurid *Maresaurus coccai* Gasparini, 1997 are described and analyzed based on the holotype specimen. Regarding symmetry, it was determined that *M. coccai* shows symmetrical replacement in the maxillary-premaxillary and asymmetrical replacement in the dentary. Additionally, the tooth replacement cycle period (TRCP) of two alveoli was determined for the dental series, except for the anterior part of the left mandibular ramus, which presents an TRCP of three, an asymmetry considered here as teratology. This result indicates that the replacement cycle period (TRCP) of the two alveoli would correspond to a primitive character for Plesiosauria, displaying an increase of TRCP from two to three alveoli in taxa comparatively more derived within Pliosauridae.

## Introduction

Dental characteristics have been a key tool for the understanding of phylogeny and paleoecological aspects of vertebrates, as teeth are a source of phylogenetic characters and also show features strongly related to trophic habits (Massare 1987; Ciampaglio et al. 2005; Larson & Currie 2013; Gregory et al. 2016; Hastings & Hellmund 2017). The dentition of sauropterygians shows a wide variation in tooth morphology and other features associated with dentition, such as the ones related to replacement (Massare 1987; Rieppel 2001; Neenan et al. 2013; Sassoon et al. 2015; Kear et al. 2017). Despite this importance, the information related to some features, such as symmetry in tooth replacement and tooth replacement cycle period, is not well known

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for several plesiosaurians, even for species with well-preserved skull and dental material as it is the case of the rhomaleosaurid *Maresaurus coccai*.

Rhomaleosaurids are a group of plesiosaurians whose biochron extends between the Hettangian and Callovian stages (Sato & Wu 2008; Benson et al. 2012). Rhomaleosaurids are characterized by a large skull with a slightly elongated preorbital part of the skull and a more or less marked constriction in the maxillo-premaxillary suture, dorsomedial foramen in premaxilla and bowed mandible (Cruickshank 1994; Gasparini 1997; Sato & Wu 2008; Ketchum & Benson 2010). Rhomaleosaurids show a general intermediate morphotype between pliosauromorph and plesiosauromorph (O'Keefe 2002). *Maresaurus coccai* is a rhomaleosaurid from the Middle Jurassic (Bajocian) and, therefore, one of the youngest rhomaleosaurids worldwide, together with the Callovian *Borealonectes russelli* (Sato & Wu 2008) and indeterminate rhomaleosaurids from England and Russia (Gasparini 1997; Sato & Wu 2008; Benson et al. 2015).

The aim of this contribution is to characterize the dental replacement of *Maresaurus coccai* as well as its comparison with other plesiosaurians in order to improve our understanding of the distribution of tooth replacement among plesiosaurians.

**Anatomical abbreviations.** TRCP, tooth replacement cycle period.

**Institutional abbreviations.** MOZ, Museo Prof. Olsacher, Zapala, Neuquén, Argentina.; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, UK; DORCM, Dorset County Museum, Dorchester, UK; NHMUK, Natural History Museum, London, UK.

## Materials and Methods

The study is focused on the analysis of the skull and mandible of *Maresaurus coccai*, MOZ 4386 V. To study the internal anatomy, a CT scan of the holotype of *Maresaurus coccai* was performed using a Picker International, Inc., PQ 600 model. The CT scan has 1008 slices, each with a thickness of 0.8 mm and a matrix size of 512. For the visualization and segmentation of the tomography (focused on the reconstruction of functional and replacement teeth), the free software InVesalius 3.0 (Martins et al. 2007) was used, and the thresholding segmentation technique was applied. Regarding dental replacement cycles, the methodology and definitions of Sassoon et al. (2015) were followed. The tooth replacement cycle period (TRCP) is used here as the number of alveoli between two matching tooth development stages along a tooth arcade (Sassoon et al. 2015, Figure 1). Symmetry refers to a pattern of the disposition of the teeth at the same stage of development that appears in the corresponding alveoli on both sides of the sagittal plane. Finally, the term anisodonty is referred to a regional partitioning of tooth size, but without real variation in shape and robustness. In contrast, heterodonty, following Sassoon et. al. (2015), is defined as a regional division of size, shape, and robustness between the anterior and posterior teeth.

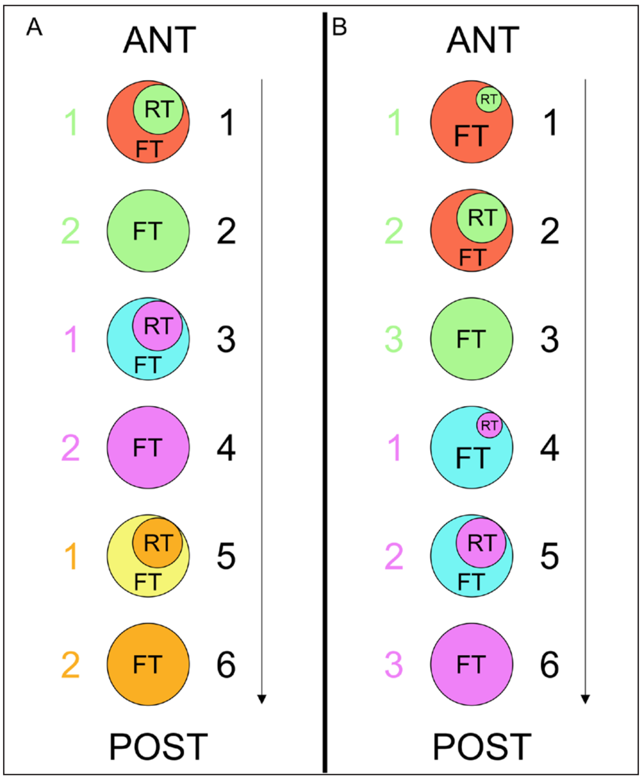


Fig. 1 - Schematic representation of two (A) and three (B) teeth TRCP. The colored numbers and circles symbolize the successive waves of tooth replacement. FT: functional tooth; RT: replacement tooth; ANT: anterior region; POST: posterior region.

### Tooth character reconstruction

The phylogenetic analysis is based on the data set of Benson and Druckenmiller (2014) and Serratos et al. (2017), modified by O'Gorman (2019) and O'Gorman et al. (2021) with the addition of the polycotylids from the data set of Fischer et al. (2018) and three characters and scoring

| Alveolus | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Diameter | 84 | 196 | 185 | 230 | 235 | 137 | 52 | 86 | 120 | 160 | 132 | 84 | 95 | 69 | 48 | 80 |

Tab. 1 - Relation between the alveolus number and each diameter in the dentary. Measurements of diameter, $mm^2$.

of Morgan and O'Keefe (2019) - for details see O'Gorman (2022, 2023). The scoring of *Nothosaurus rostellatus* (Shang, 2006) was added based on the descriptions of Shang et al. (2007) and Qinghua (2006). The complete data set comprises 126 OTUs and 290 characters compiled using Mesquite (Maddison & Maddison 2011) and is given as Supplementary Material 1.

The complete data set was analysed with the TNT 1.5 software package (Goloboff & Catalano 2016). Only Character 155 (modified by O'Gorman 2019) was considered ordered. The analyses were carried out using Tree New Technology (sectorial search, ratchet, drift, tree fusing with the default settings options) with 10,000 replicates. The MPTs obtained were then used as the starting point to perform TBR swapping. An ancestral states analysis of TRCP used the strict consensus tree topology and parsimony reconstructions in Mesquite version 3.61 (Maddison & Maddison 2019). Data scores are listed in Supplementary Material 1. States were defined as: '0' for TRCP = 2 and '1' for TRCP = 3.

## Systematic Paleontology

SAUROPTERYGIA Owen, 1860
**Plesiosauria** de Blainville, 1835
Rhomaleosauridae Kuhn, 1961
Genus *Maresaurus* Gasparini, 1997

***Maresaurus coccai*** Gasparini, 1997
Figs. 2, 4, 5 A-C, 6 A-B

**Holotype**: MOZ 4386 V. An articulated skull and mandible, atlas-axis complex and five anterior cervical vertebrae.

**Locality and horizon**: Chacaico Sur Locality, Neuquén Province, Argentina. Upper part of the Los Molles Formation, lower Bajocian beds (Fig. 3).

### Description

*Teeth characterization*. The holotype of *Maresaurus coccai* preserves five premaxillary teeth (right and left) and 19 (right) and 14 (left) maxillary teeth (Fig. 4). Therefore, the combined premaxilla and maxilla dental series has 24 teeth. The dentary conserved the entire dental series, with 24 teeth on both sides.

The teeth of *M. coccai* have an elongated cylindrical base topped by a protruding conical crown. The teeth have different characteristics depending on their position along the dental arch. The anterior teeth of the dentary are larger and more robust than the posterior teeth, which are smaller and have less curvature and a smoother texture (Figs. 5, 6). Thus, a clear regional differentiation regarded as heterodonty (sensu Sassoon et al. 2015) is observed (Table 1).

*Replacement*. The CT scan allows us to infer that during tooth ontogeny, the bone separating each functional alveolus and the replacement alveolus are progressively resorbed as the replacement tooth grows and moves labially, entering the functional alveolus. Fig. 7 shows the sequence of tomograms (A-E), illustrating the tooth replacement and the alveolar resorption in axial view. This follows the typical pattern of replacement in other plesiosaurians (Rieppel 2001).

Regarding the dental replacement cycles, the tooth dental series of the premaxilla shows a tooth replacement cycle period (TRCP) that comprises two alveoli on both sides of the dental arch and a symmetrical pattern of replacement (Fig. 8). It should be noted that the preservation of the upper teeth (premaxillary and maxillary teeth) is poor, so the TRCP was partially inferred considering the alveoli and replacement teeth (Fig. 8).

On the other hand, the TRCP in the anterior part of the mandible comprises two alveoli in the right mandibular ramus. In contrast, it consists of three alveoli in the left mandibular ramus (Fig. 9), generating an asymmetrical pattern (see Discussion). The posterior mandibular sector comprises a TRCP of two alveoli (Fig. 10).

In the anterior portion of the left mandibular ramus, four waves of dental replacement can be distinguished (represented by the colors: red, blue, yellow and orange, Fig. 9). The blue and orange


Fig. 2 - A-C - Holotype of *Maresaurus coccai* (MOZ 4386 V), skull and mandible in (A) lateral, (B) dorsal and (C) ventral views. Scale bar: 100 mm.

waves are complete with three teeth, but in the red and yellow waves only the second and third teeth are observed, since the first of them was most likely replaced by the third tooth of the blue and orange waves.

In the right mandibular ramus, two waves of dental replacement are individualized (represented by the colors: light blue and pink, Fig. 9). Both waves are complete with two teeth each. A third wave (the green one) in which the second tooth is lost and is represented by a dotted line, is also inferred.

## Discussion

*Teratology.* The holotype of *M. coccai* (MOZ 4386 V), as mentioned above, exhibits an asymmetric pattern of TRCP in the anterior part of the mandible (which we defined between the first and seventh alveolus, associated with a change in alveolar diameter), evidencing a TRCP of two alveoli in the right mandibular ramus, and three alveoli in the left mandibular ramus. Meanwhile, in the posterior teeth, a TRCP of two alveoli is continued in both mandibular rami.

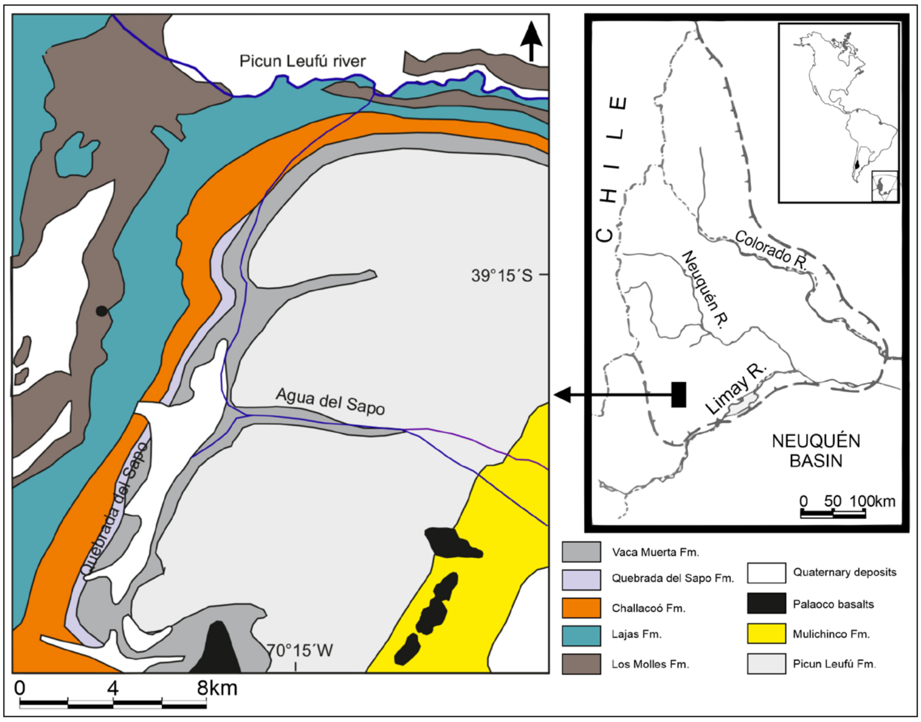


Fig. 3 - Locality and horizon (Los Molles Formation, 170-168 Ma) where MOZ 4386 V (*Maresaurus coccai*) was found. Chacaico Sur Locality, Zapala, Neuquén Province, Argentina.

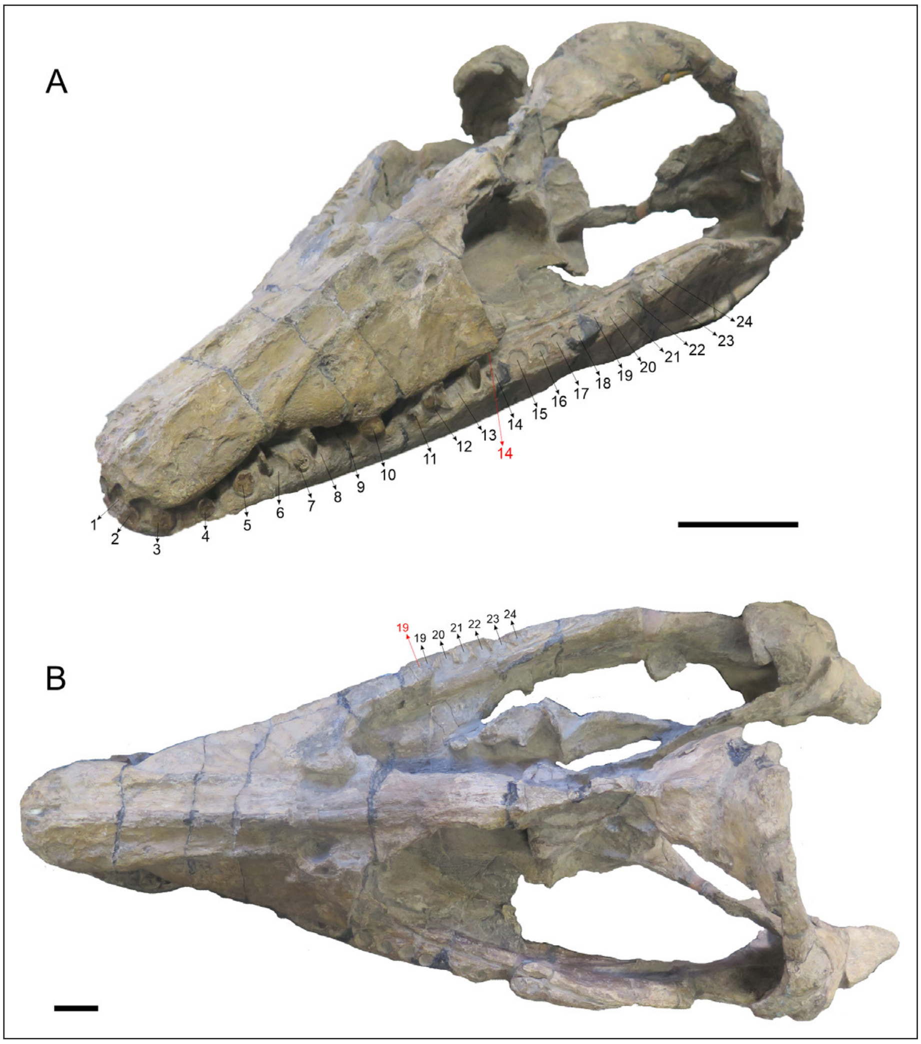


Fig. 4 - A, B - *Maresaurus coccai* cranium and mandible alveoli (A) mandible and (B) maxillary. Mandible, red arrow and numbers; maxilla, black arrows and numbers. Scale bar: 150 mm.

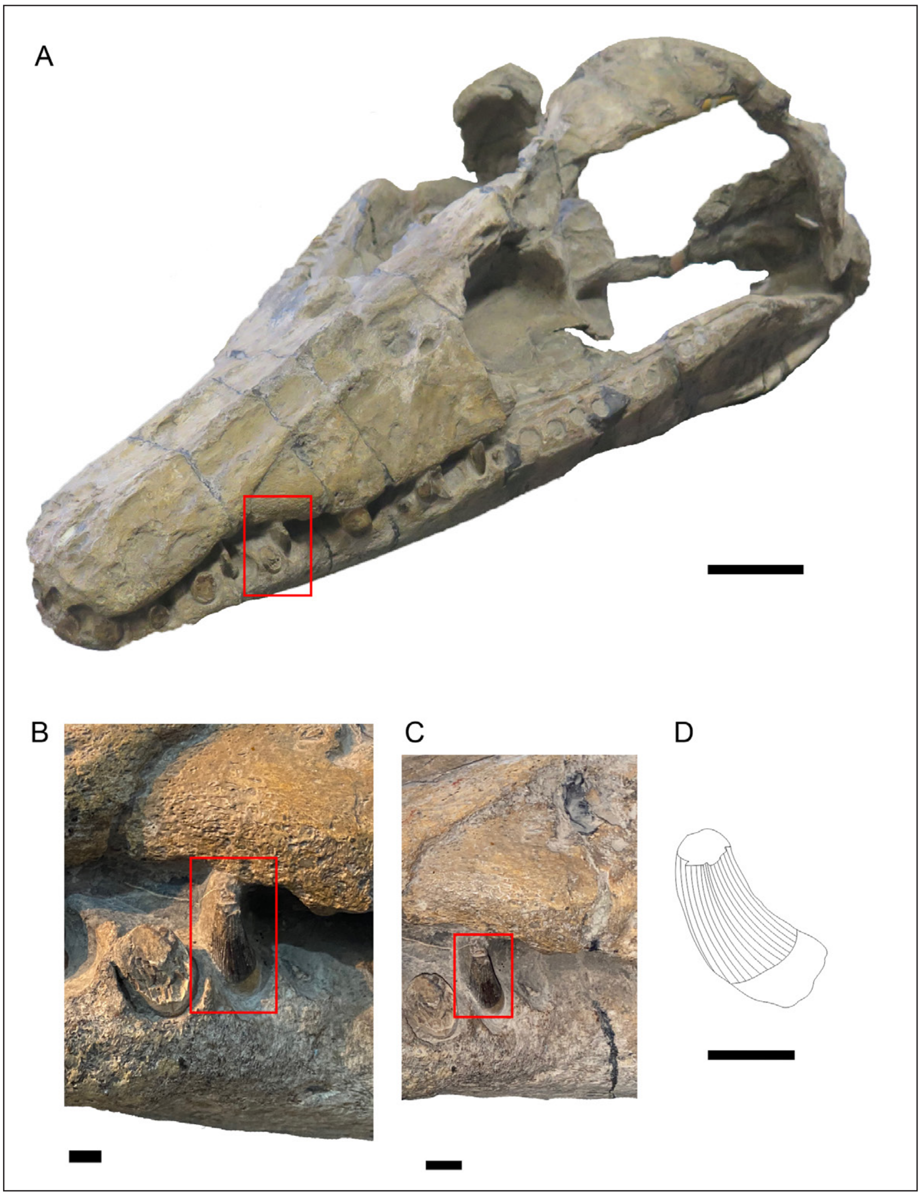


Fig. 5 - Anterior teeth morphology of *Maresaurus coccai.* (A, B, C), photos and (D) schematic illustration of seventh mandibular tooth in lateral view Scale bar A: 100 mm; B – C – D: 10 mm.

Given this observation and the fact that the TRCP of the other sectors of dental arches (premaxilla-maxilla and posterior mandibular) is two alveoli, it is highly probable that this asymmetry is a teratologic condition.

| Taxon | Anterior part of left mandibular ramus TRCP | Anterior part of right mandibular ramus TRCP | Premaxilla (left) TRCP | Premaxilla (right) TRCP |
|---|---|---|---|---|
| ***Maresaurus coccai*** | 3”* | 2* | 2 | 2 |
| *Thalassiodracon hawkinsii* | 2** | 2** | 2 | 2 |
| *Peloneustes philarchus* | 3** | 3** | 3 | 3 |
| *Pliosaurus westburyensis*; *P. kevani*; *P. carpenteri* | 3** | 3** | 3 | 3 |

Tab. 2 - Comparison of TRCP (tooth replacement cycle period) between plesiosaurian taxa. Data of *Thalassiodracon hawkinsii* (CAMSM J.46986), *Peloneustes philarchus* (NHMUK R8574), *Pliosaurus westburyensis* (BRSMG Cc332); *P. kevani* (DORCM G.13,675); *P. carpenteri* (BRSMG Cd6172) taken from Sassoon et al. 2015. (“) refers to the teratology (see Discussion); (*) refers to the anterior region comprised between the first and seventh alveolus and (**) between the first and sixteenth alveolus.

*Comparative replacement features.* The TRCP and replacement symmetry show a wide variation within Sauropterygia. Placodontians (basal clade Sauropterygia) show a symmetric replacement of both the maxillary and palatal teeth (Pommery et al. 2021). By comparison, *Nothosaurus rostellatus* presents a differentiated asymmetric replacement pattern (short cycle of two-teeth) in the premaxilla. The mandible shows an asymmetric pattern of replacement in the symphyseal area, as in the premaxilla (Shang 2007). Unfortunately, available data from the maxilla (MX) are scarce, but the caniniform present a symmetric replacement.

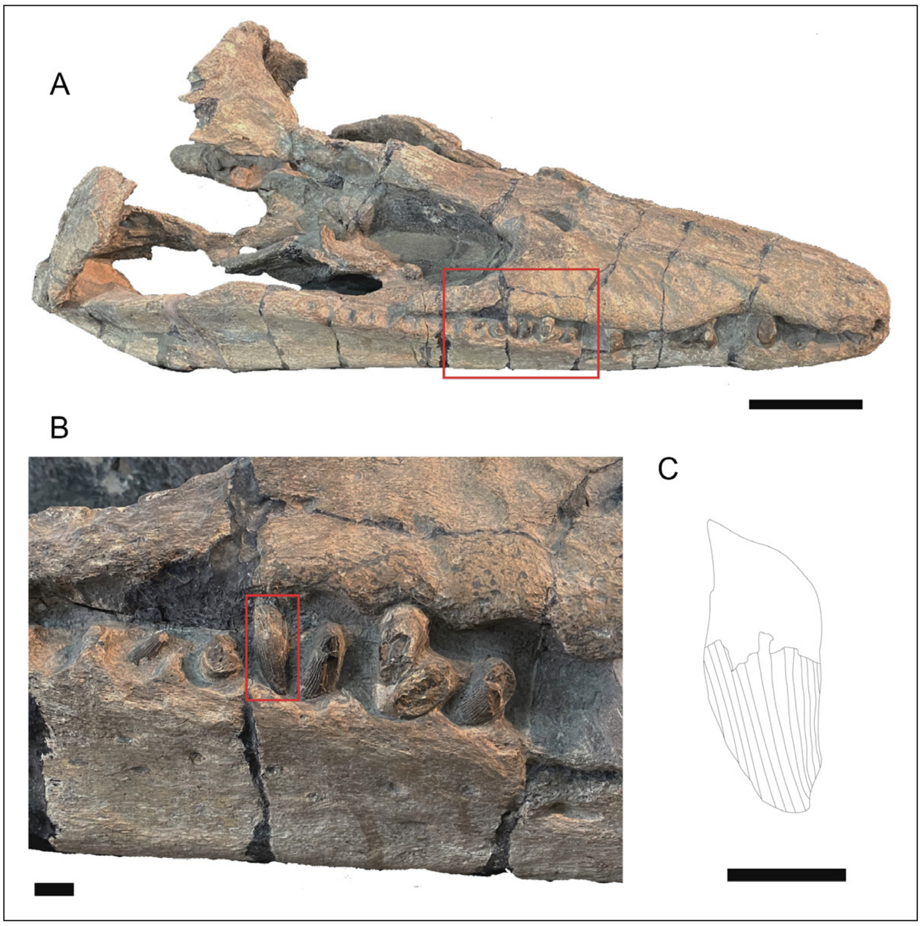


Fig. 6 - Posterior teeth morphology of *Maresaurus coccai.* (A – B), photography and (C) schematic illustration of sixteenth maxillary tooth. Scale bar A: 100 mm; B – C: 10 mm.

Focusing on the TRCP of plesiosaurians (Table 2), *T. hawkinsii* shows a TRCP (sensu Sassoon et al. 2015) of two alveoli along the entire dental series, while the derived pliosaurids *P. philarchus, Pliosaurus westburyensis*, *P. kevani* and *P. carpenteri* show a TRCP of three alveoli in the anterior part of mandibular dental series (Sassoon et al. 2015). However, in both *Peloneustes* and *Pliosaurus,* there is a change beyond alveoli 16th in TRCP and symmetry (Sassoon et al. 2015). The cycles seem to cluster more closely, and the TRCP decreases to two alveoli, but the replacement remains symmetric in the upper jaw and changes to asymmetric in the mandible. This differs from *Maresaurus coccai*, which presents a TRCP of two alveoli in the right mandibular ramus and in the premaxilla. Conversely, in the lower jaw, *Maresaurus*

| Taxon | Anterior dentary teeth TRCP | Posterior dentary teeth TRCP | Symmetry of anterior teeth dentary / premaxilla | Symmetry of posterior teeth dentary / premaxilla |
|---|---|---|---|---|
| ***Maresaurus coccai*** | 2/3” | 2* | Asymmetric/Symmetric | Symmetric/ Symmetric |
| *T. hawkinsii* | 2 | 2** | Symmetric/ Symmetric | Symmetric/ Symmetric |
| *Peloneustes philarchus* | 3 | 2** | Symmetric/ Symmetric | Asymmetric/Symmetric |
| *Pliosaurus westburyensis*; *P. kevani*; *P. carpenteri* | 3 | 2** | Symmetric/ Symmetric | Asymmetric/Symmetric |

Tab. 3 - Comparison of TRCP (tooth replacement cycle period) and symmetry between plesiosaurian taxa. Data of *Thalassiodracon hawkinsii* (CAMSM J.46986), *Peloneustes philarchus* (NHMUK R8574), *Pliosaurus westburyensis* (BRSMG Cc332); *P. kevani* (DORCM G.13,675); P. carpenteri (BRSMG Cd6172) taken from Sassoon et al., 2015. (”) refers to the teratology (see Discussion); (*) refers to the posterior region starting from the seventh alveolus and (**) from the sixteenth alveolus.

| Taxon | Age (geologic time) | Teeth cross section | Teeth morphology |
|---|---|---|---|
| ***Maresaurus coccai*** | Early Bajocian | circular to subcircular | Backward-curved teeth. The ridges do not branch dichotomously and have a compact distribution; the pattern corresponds to an alternation between a successively shorter and a longer ridge. |
| *Thalassiodracon hawkinsii* | Rhaetian – Hettangian | suboval | The teeth are thin, weakly curved, with apico-basally oriented ridges, with some of them extending to the apex of the crown. |
| *Peloneustes philarchus* | Callovian | subcircular | Distally recurved, conical. With enamel adorned with longitudinal ridges extended over half the apico-basal enamel height. It presents a greater spacing of the ridges on the convex mesial surface. |
| *Pliosaurus westburyensis*; *P. kevani*; *P. carpenteri* | Late Kimmeridgian | trihedral or subtrihedral | Curved, conical teeth with flattened (to extremely flattened) labial surfaces. Thick ridges oriented in an apico-basal direction. There are no ridges on the mesial surface, which is flattened. |

Tab.4 - Comparison of dental morphology and cross section between plesiosaurian taxa. Modified from Sassoon et al. 2015.

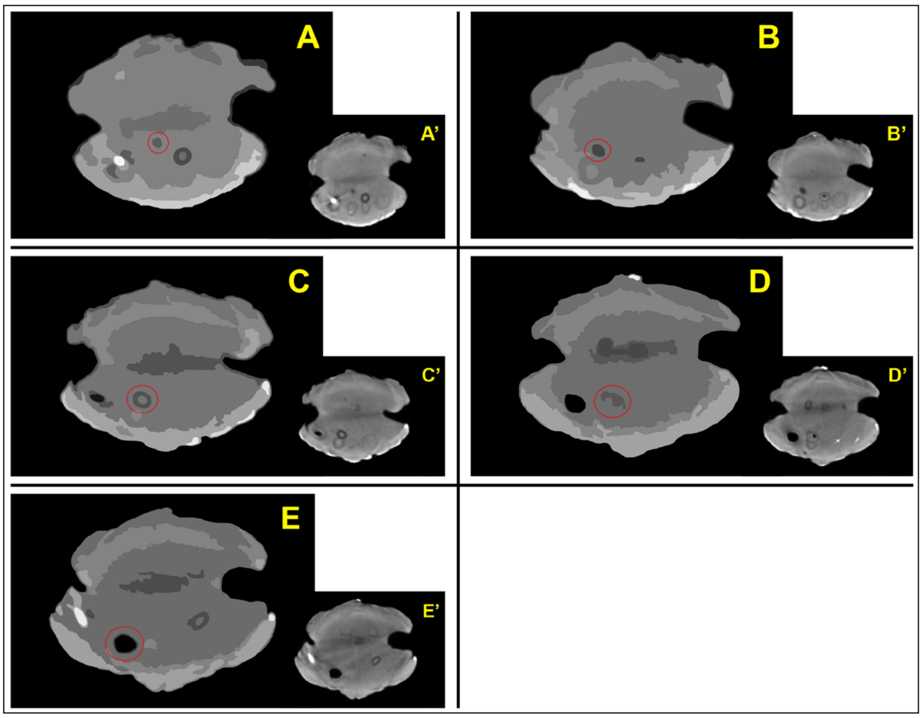


Fig. 7 - Sequence of tooth replacement and resorption of alveoli of *Maresaurus coccai*. A-E - (schematic illustration); A'-E' - (tomograms). The red circle indicates the replacement of the alveolus and tooth, showing an increase in alveolar/dental diameter. Transversal view.

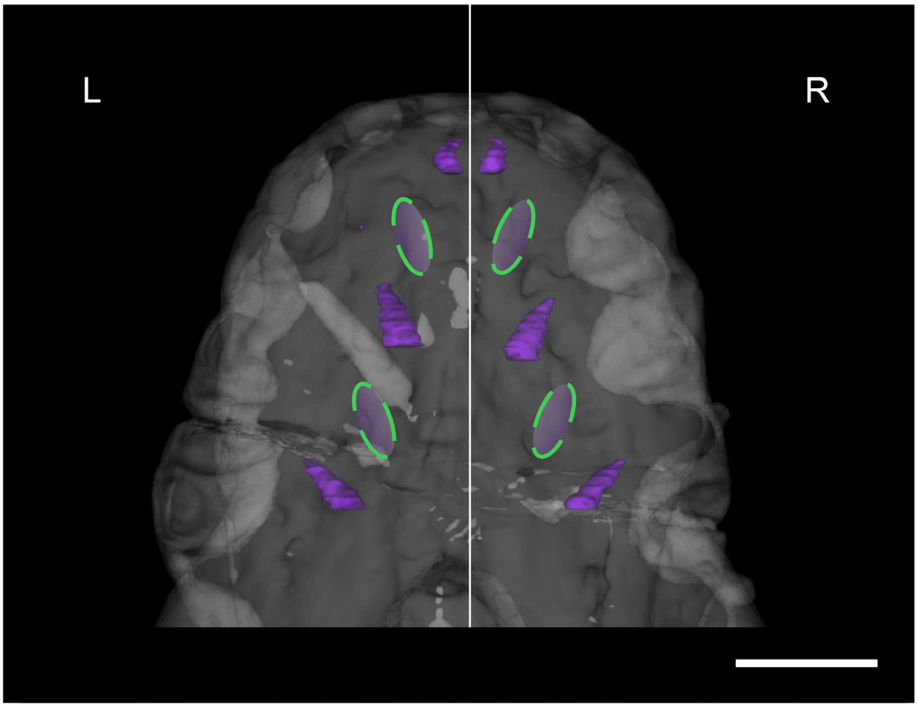


Fig. 8 - Dorsal view of TRCP (two teeth) in the premaxilla of *Maresaurus coccai*. Circles correspond to the space of replacement teeth formation (not formed yet),which complete the replacement cycle of two teeth. L: left; R: right. Scale bar: 30 mm.

*coccai* has a TRCP of two alveoli on the right mandibular ramus and a TRCP of three alveoli on the left mandibular ramus. In the posterior alveoli, the tooth replacement cycle of two alveoli (both branches) is continuous. Comparing tooth replacement between taxa (Table 3), the pattern observed in *M. coccai* is more similar to the observed in the basal *Thalassiodracon hawkinsii* than those derived from pliosaurids.

In addition to the comparison in dental replacement, there are several differences in the morphology and cross section of the teeth (Table 4).

Regarding the characteristics of the dentitions, *T. hawkinsii* shows anisodonty, i.e., a regional partition in the size of the teeth, but without real variation in shape and robustness. In contrast, *Peloneustes sp.*, *Pliosaurus* spp., and *M. coccai* stand out for presenting a marked heterodonty, recognizing

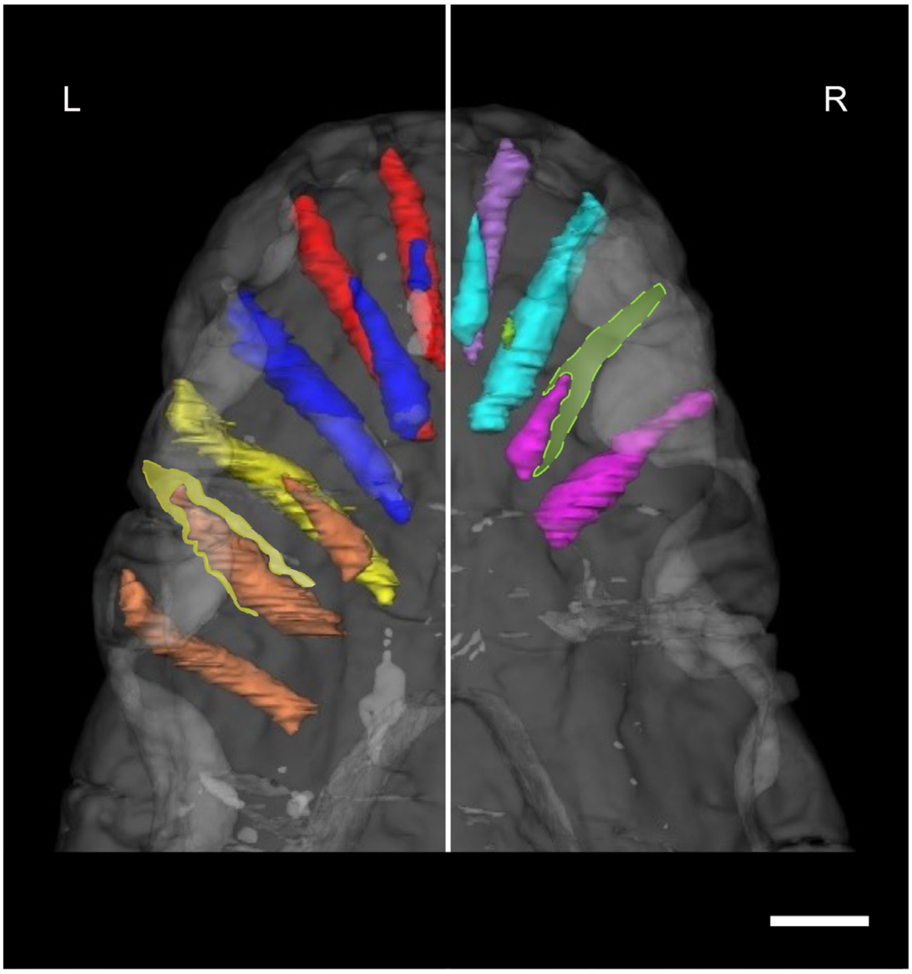


Fig. 9 - Dorsal view of the waves of both mandibular rami dental replacements differentiated by colors, evidencing an asymmetric pattern in *Maresaurus coccai*. L: left; R: right. Scale bar: 20 mm.

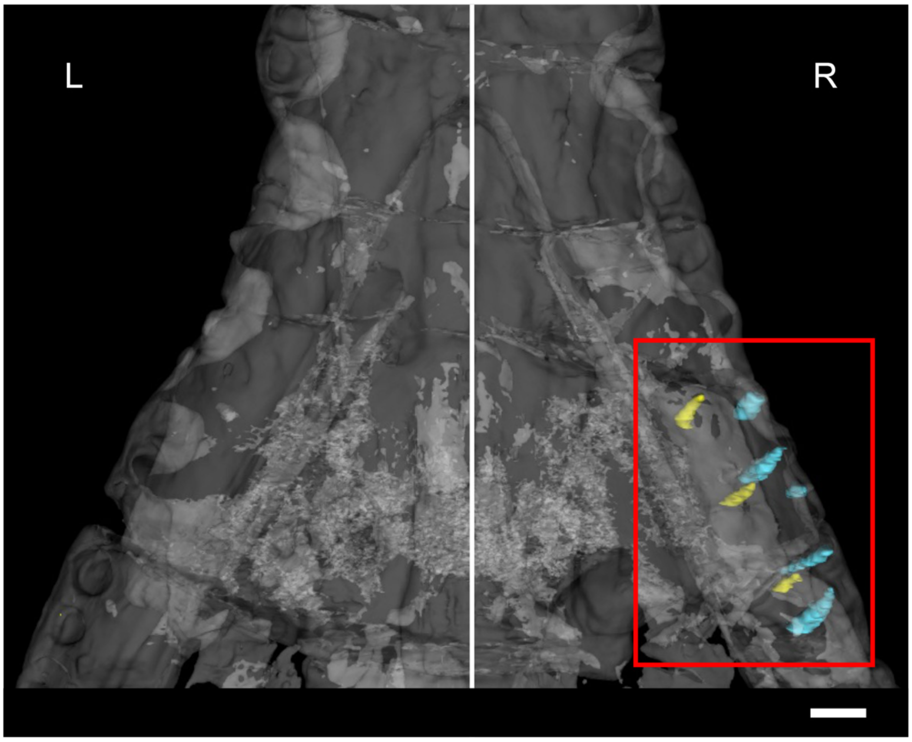


Fig. 10 - Dorsal view of the mandible (with detail on the posterior region) of *Maresaurus coccai*, where a TRCP of two teeth differentiated by colors (yellow for the replacement teeth and light blue for functional teeth) is observed. L: left; R: right. Scale bar: 20 mm.

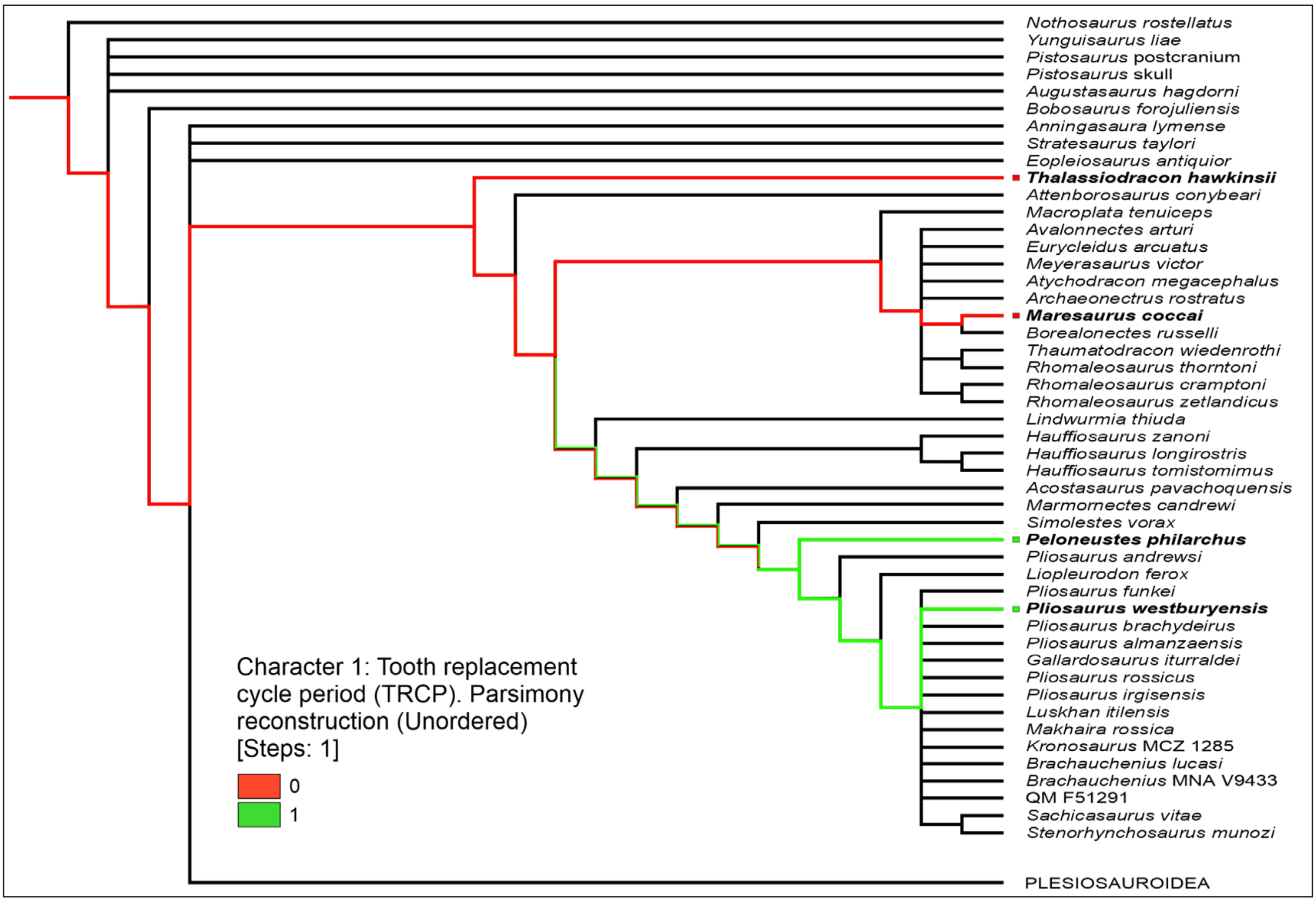


Fig. 11 - Phylogeny of Sauropterygia, focused on Plesiosauria (Pliosauroidea), with optimization of tooth replacement cycle.

a regional division of size, shape, and robustness between anterior and posterior teeth.

*Phylogenetic interpretation*. According to the description of the replacement cycles previously made (see Table 2), the reconstruction of the ancestral state of the character TRCP in the anterior part of the mandible is given in Fig. 11. The results show that the primitive character state is the presence of a short TRCP (two alveoli) in Plesiosauria. Hence, a TRCP of two alveoli in *Maresaurus coccai* indicates that the primitive character state of *Thalassiodracon* is also shared with at least some rhomaleosaurids. The question of the basal condition of TRCP in nothosaurids mandible is hard to assess. However, the presence of TRCP of two alveoli in the premaxilla *Nothosaurus rostellatus* could be interpreted as evidence of the same condition in the mandible. If this is the case, then the conclusion of this discussion achieves higher support. As for derived pliosaurids, the change of a TRCP from two to three alveoli in the anterior part of the mandibular series in *Peloneustes* sp. and *Pliosaurus* spp. analyzed by Sassoon et al. (2005) represents a marked change. In summary, some conclusions can be extracted from the ancestral character state reconstruction analyses. First, the TRCP of two alveoli is probably the plesiomorphic condition for the most inclusive clade that comprises *Thalassiodracon hawkinsii* and *Pliosaurus* spp., which includes all pliosaurids and rhomaleosaurids. Second, the new result indicates that the TRCP is not fully correlated with skull size as a TRCP of two alveoli is present in species with a small skull, such as those of *Thalassiodracon hawkinsii* and species with a relatively large skull, such as *Maresaurus coccai*. The only marked change occurs in species of the genera *Peloneustes* and *Pliosaurus*. Finally, the TRCP of three alveoli is recovered as synapomorphy of a derived clade of pliosaurids.

*Paleoecology*. Returning to the notion of symmetric or asymmetric dental replacement, one or another condition would have consequences on the hunting habits of plesiosaurians. Although this concept and others related to dental replacement were addressed in previous works (Shang 2007; Sassoon et al. 2015; Kear et al. 2017; Pommery et al. 2021), it is necessary to mention certain possible paleoecological aspects. The asymmetric replacement between the left and right rami of the lower jaw (excluding the previous teratological interpretation) would have a sustained explanation based on the availability of functional teeth at the time of hunting in each part of the dental series. The lag in dental turnover would have allowed the animal to catch the prey, perforating it with the anterior teeth, using the right or left teeth interchangeably since, naturally, there would be functional pieces on one side or the other.

On the other hand, a symmetrical replacement would mean that the animal would lose its teeth in the same sector, especially the premaxillae, in both branches of the jaw at the same time. Naturally (not considering external factors), the teeth are replaced when new pieces are developed below the functional ones.

Finally, assuming that the asymmetric replacement of the mandibular teeth was teratological in the holotype of *Maresaurus coccai*, it should not be taken for granted that the replacement will occur at the same time in both upper and lower dental series and, therefore, the hunting capacity would be impaired or diminished. Hence, since the replacement does not happen simultaneously, the continuous presence of functional perforating teeth is always inferred.

## Conclusions

To conclude and highlight certain specific aspects mentioned previously, the following stand out:

The holotype of *Maresaurus coccai* presents an asymmetrical tooth replacement in the anterior region of the mandible due to teratology. Without considering previous teratology, *M. coccai* has a TRCP of two alveoli.

The TRCP of three alveoli is identified as a possible derived feature of a derived clade of pliosaurids, which include *Peloneustes* and *Pliosaurus*. The TRCP value seems to be uncorrelated with skull length.

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