

RESEARCH ARTICLE

A Late Cretaceous dinosaur and crocodyliform faunal association–based on isolate teeth and osteoderms–at Cerro Fortaleza Formation (Campanian-Maastrichtian) type locality, Santa Cruz, Argentina

Ariana Paulina-Carabajal^{1*}, Francisco T. Barrios², Ariel H. Méndez³, Ignacio A. Cerda⁴, Yuong-Nam Lee^{5*}

1 Instituto de Investigaciones en Biodiversidad y Medioambiente (CONICET-Universidad Nacional del Comahue), San Carlos de Bariloche, Río Negro, Argentina, **2** Museo Provincial de Ciencias Naturales “Profesor Olsacher”, Zapala, Neuquén, Argentina, **3** Instituto Patagónico de Geología y Paleontología (CCT CONICET-CENPAT), Puerto Madryn, Chubut, Argentina, **4** Instituto de Investigación en Paleobiología y Geología (CONICET- Universidad Nacional de Río Negro), Museo Carlos Ameghino, Cipolletti, Río Negro, Argentina, **5** School of Earth and Environmental Sciences, Seoul National University, Seoul, Republic of Korea

* a.paulinacarabajal@conicet.gov.ar (APC); ynlee@snu.ac.kr (YNL)



OPEN ACCESS

Citation: Paulina-Carabajal A, Barrios FT, Méndez AH, Cerda IA, Lee Y-N (2021) A Late Cretaceous dinosaur and crocodyliform faunal association–based on isolate teeth and osteoderms–at Cerro Fortaleza Formation (Campanian-Maastrichtian) type locality, Santa Cruz, Argentina. PLoS ONE 16(9): e0256233. <https://doi.org/10.1371/journal.pone.0256233>

Editor: Max Cardoso Langer, Universidade de Sao Paulo, BRAZIL

Received: March 24, 2021

Accepted: August 2, 2021

Published: September 8, 2021

Copyright: © 2021 Paulina-Carabajal et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper.

Funding: Funding for this project was provided by Agencia Nacional de Promoción Científica y Tecnológica PICT 2015-0920 to AHM, and the National Science Foundation of Korea (NRF) grant funded by the Korean government (MEST) number 2019R1A6A1A10073437 to YNL.

Abstract

The Late Cretaceous dinosaur record in southern South America has been improved recently; particularly with findings from Chorrillo and Cerro Fortaleza formations, both bearing ankylosaur remains, a clade that was not previously recorded in the Austral Basin. The dinosaur fauna of the type locality of Cerro Fortaleza Formation is known from -and biased to- large-sized sauropod remains and a single described taxon, the titanosaur *Dreadnoughtus schrani*. Here, we report the taxonomic composition of a site preserving thirteen isolated teeth and several osteoderms belonging to three dinosaur clades (Abelisauridae, Titanosauria, and Nodosauridae), and at least one clade of notosuchian crocodyliforms (Peirosauridae). They come from sediments positioned at the mid-section of the Cerro Fortaleza Formation, which is Campanian-Maastrichtian in age, adding valuable information to the abundance and biodiversity of this Cretaceous ecosystem. Since non-titanosaur dinosaur bones are almost absent in the locality, the teeth presented here provide a window onto the archosaur biodiversity of the Late Cretaceous in southern Patagonia. The nodosaurid tooth and small armor ossicles represent the first record of ankylosaurs for this stratigraphic unit. The peirosaurid material also represents the most austral record of the clade in South America.

Competing interests: The authors have declared that no competing interests exist.

Introduction

The Cerro Fortaleza Formation (Campanian-Maastrichtian in age) crops out along the West and East margins of La Leona River, and south of Lago Viedma, Santa Cruz Province, Argentina (Fig 1). This formation is part of the Austral-Magallanes Basin, a sedimentary infill accumulated during the Late Cretaceous dominated by deep-marine and coastal deposits, located at the southern edge of the South American plate. The continental sedimentary succession within the basin, however, remains poorly known and different lithostratigraphic schemes entered the literature [1,2]. The type locality of Cerro Fortaleza Formation is exposed along the oriental margin of La Leona river at the homonymous hill (Cerro Fortaleza), where its largest exposure—approximately 400 m—is observed [1, and references therein]. The geology and stratigraphy of this area have been thoroughly studied along the last century, but the

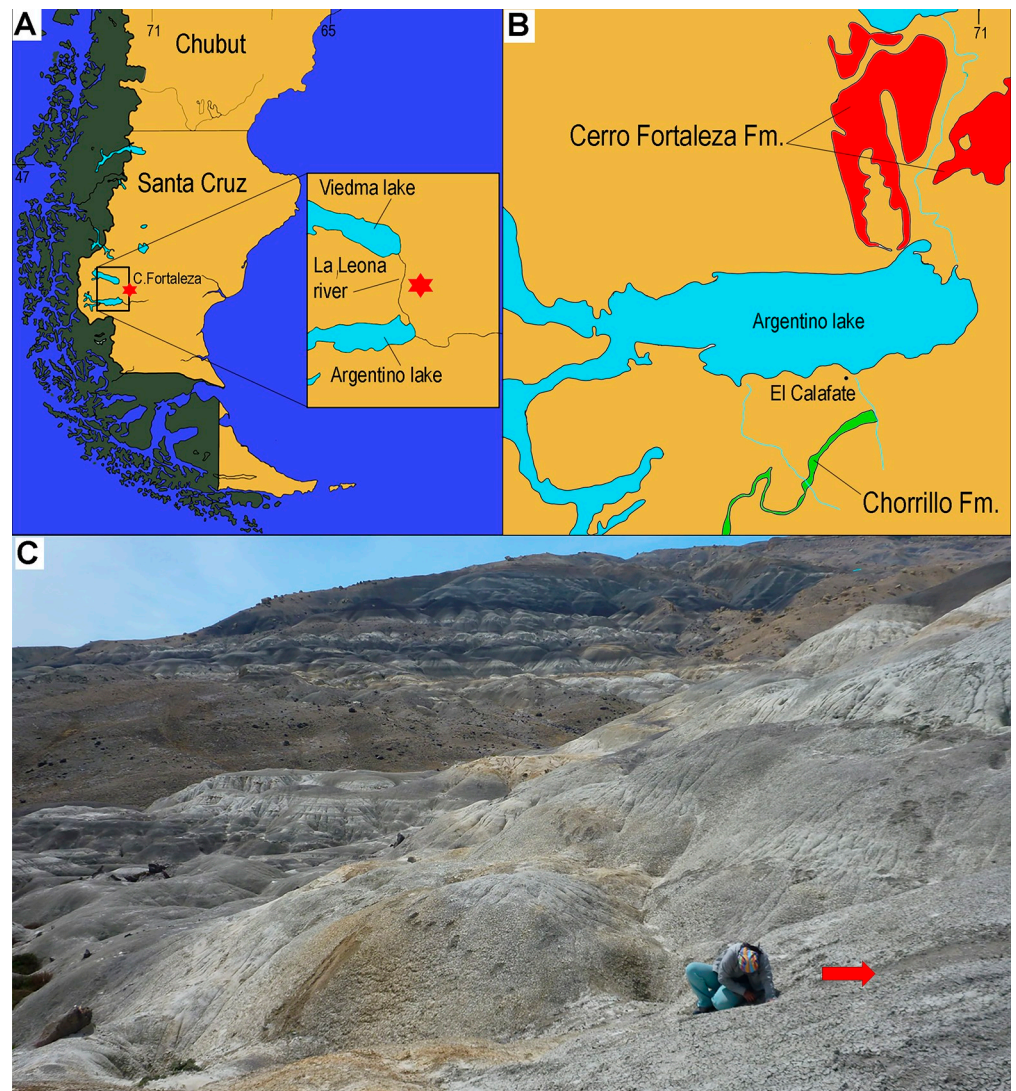


Fig 1. Location map showing the provenance of the teeth and osteoderms. Southern South America, with the Cerro Fortaleza type-locality indicated by the star (A). Region between Viedma and Argentino lakes showing the Cerro Fortaleza Formation (red color) outcropping at both sides of La Leona river. The Chorrillo Formation is indicated in green (B). Photography of the site, the red arrow indicates the level with teeth and osteoderms (C). B is based on [2,16].

<https://doi.org/10.1371/journal.pone.0256233.g001>

interpretations about the exposed rocks remain controversial [1–4]. For example, the Cerro Fortaleza locality and near areas were given contradicting ages in the literature (from Cenomanian to Campanian-Maastrichtian), and other formation names were proposed for this locality, such as “Mata Amarilla” (Cenomanian beds now considered to outcrop only at areas near Tres Lagos city), or “Pari Aike” [e.g. 3,5–8]. A recent sedimentological analysis [2] included the Cerro Fortaleza, La Anita, La Irene, and Chorrillo (another dinosaur-bearing unit [9,10]) formations as lithologically similar beds under the denomination “Uppermost Cretaceous Continental Deposits”. Regardless of their names, the dinosaur-bearing units were generally considered as Campanian-Maastrichtian [4,6,11–16].

The dinosaur taxa described for Cerro Fortaleza Formation include the theropods *Orkoraptor burkei* [6] and *Austrocheirus isasii* [12], the elasmarian ornithopod *Talenkauen santacruensis* [13], and the large-sized titanosaurs *Puertasaurus reuili* [14] and *Dreadnoughtus schrani* [11]. Whereas most taxa were found at the south of Lago Viedma, west of La Leona river, *D. schrani* is the only species found at Cerro Fortaleza locality up to date (Fig 1A and 1B). In this locality, the most commonly found dinosaur remains are biased to large-sized sauropod bones, as in other outcroppings of the Cerro Fortaleza Formation [15], and only an abelisaurid theropod metatarsus has been reported so far [17]. As for crocodyliforms, their record in the unit come from the area west of La Leona river and corresponds to an indeterminate scute [15].

During a fieldwork carried out in December 2016 at the Cerro Fortaleza locality, several isolate dinosaur and crocodyliform teeth were recovered from the Cerro Fortaleza Formation (Fig 1C). The sample presented here is not large, and most specimens consist of fractured and/or highly eroded dinosaur and crocodyliform teeth (MPM-PV-18805.1–14). However, the association observed in the sample is rich in terms of archosaur taxonomic diversity for the Austral Basin; particularly, peirosaurid teeth are reported here for the first time. Interestingly, the other highly diverse dinosaur-bearing unit in the basin, the Chorrillo Formation, located 160 km south from the Cerro Fortaleza locality, has been recently considered as late Campanian-early Maastrichtian based on its faunal content [9,10]. The correlation between the two formations is not clear, and there are differences in the faunas documented in the Chorrillo and the probably underlying Cerro Fortaleza formations. Both units generally share the same dinosaur clades [9,10], i.e., titanosaurs, theropods (abelisauroids, megaraptorids), elasmarian ornithopods, and ankylosaurs. Taxonomical differences are at generic level, and one group of non-avian dinosaurs—hadrosaurids—have been documented only in the Chorrillo Formation.

In this context, isolated teeth are key pieces of evidence to assess vertebrate paleo-ecological diversity [18]. Tooth measurements were first employed by Currie et al. [19], and Farlow et al. [20] for systematic identification of theropod teeth, and later authors followed or modified this method to document similar isolated remains [e.g. 21,22]. More recently, a number of workers have successfully used dinosaur tooth morphology for taxonomic purposes [18,22,23]. The aim of this study is to describe the morphology of the isolated dinosaur and crocodyliform teeth from a Late Cretaceous microremains site. The vertebrate fossils from the Cerro Fortaleza Formation, particularly the ankylosaur (probable nodosaurid) specimen, may help to increase our understanding about the vertebrate paleoecology, paleoenvironments, and possible biotic dispersal events during the Late Cretaceous from the southern latitudes.

Materials and methods

A batch of 13 teeth and 9 osteoderms are under the collection number MPM-PV-18805, Museo Padre Molina (Río Gallegos, Santa Cruz, Argentina). The teeth (MPM-PV-18805.1–13) were found isolated, and all correspond to dinosaur and crocodyliform crowns missing the

Table 1. Cerro Fortaleza theropod and crocodyliform teeth measurements (in mm).

	CH	CBL	CBW	CBR	DC
Theropoda					
MPM-PV-18805.1	13+	9	4	0.44	11.5
Peirosaurid					
MPM-PV-18805.5	25.0	11.0	9.11	0.83	2.8
MPM-PV-18805.6	18.3	10.0	7.63	0.76	3.0
MPM-PV-18805.7	6.76	6.23	4.28	0.69	4.2
MPM-PV-18805.8	6.36	5.63	4.08	0.73	3.5
MPM-PV-18805.9	4.86	3.35**	3.61	-	4.0
MPM-PV-18805.10	3.66	4.42**	3.47	0.79**	4.8
MPM-PV-18805.11	6.17	5.64	4.19	0.74	3.4
MPM-PV-18805.12	8.76	-	5.19**	-	5.5
MPM-PV-18805.13	6.79**	5.09	4.45	0.87	5.5

Abbreviations: CBL, crown base length measured at the base of the crown from its mesialmost to distalmost extension (excluding the carinae); CBR, crown base ratio, numeral value derived from dividing CBW and CBL (= labiolingual compression); CBW, crown base width, labiolingual extension of the crown at its base; CH, crown height; DC, denticle density (per 5 mm in theropods; per 1 mm in crocodyliforms).

*at mid-crown.

**partial measurement.

<https://doi.org/10.1371/journal.pone.0256233.t001>

roots. The osteoderms (MPM-PV-18805.14–22) correspond to small sized ankylosaur interstitial ossicles. All the specimens were collected from the surface in an area not larger than 4 m² (GPS coordinates are -49.94°, -72.05°). The location of the site corresponds approximately to the mid-to-upper portions of the Cerro Fortaleza Formation type-section, interpreted as sediments deposited in fluvial-tidal environments [8,24,25].

The terminology used to describe the theropod teeth follows Hendrickx et al. [18,23], and the crocodile teeth follows Legasa et al. [26–28] and Ösi [29]. The following dental measurements and ratios (proposed by Smith et al. [21] and updated by Hendrickx et al [18]) were used in the descriptions (Table 1).

Histological thin sections from two dermal ossicles (MPM-PV-18805.19 and 18805.22) were prepared at the Carlos Ameghino Museum (Cipolletti, Río Negro Province, Argentina). The slices were prepared using standard methods outlined by Cerda et al. [30] and studied using a petrographic polarizing microscope (Leica DM 750P). The nomenclature and definitions of structures used in this study are derived from Francillon-Vieillot et al. [31] and Cerda et al. [32].

Geological settings. The sandstones and mudstones of Cerro Fortaleza Formation (maximum exposure of 390m) were deposited in paralic, fluvial, and fluvial-tidal environments [1]. This can explain the presence of fish scales in the sample, which may correspond to both freshwater or marine forms.

Fossil assemblage and taxonomic affinities

Theropod remains

Theropoda Marsh, 1881

Abelisauroida Bonaparte and Novas, 1985

Abelisauroida indet. MPM-Pv-18805.1 (Fig 2A–2C) is an incomplete ziphodont tooth (preserved length = 11 mm, if the crown was complete it could have reached 19–20 mm), missing the crown apex and the root. In lateral view, the crown is posteriorly curved, with slightly

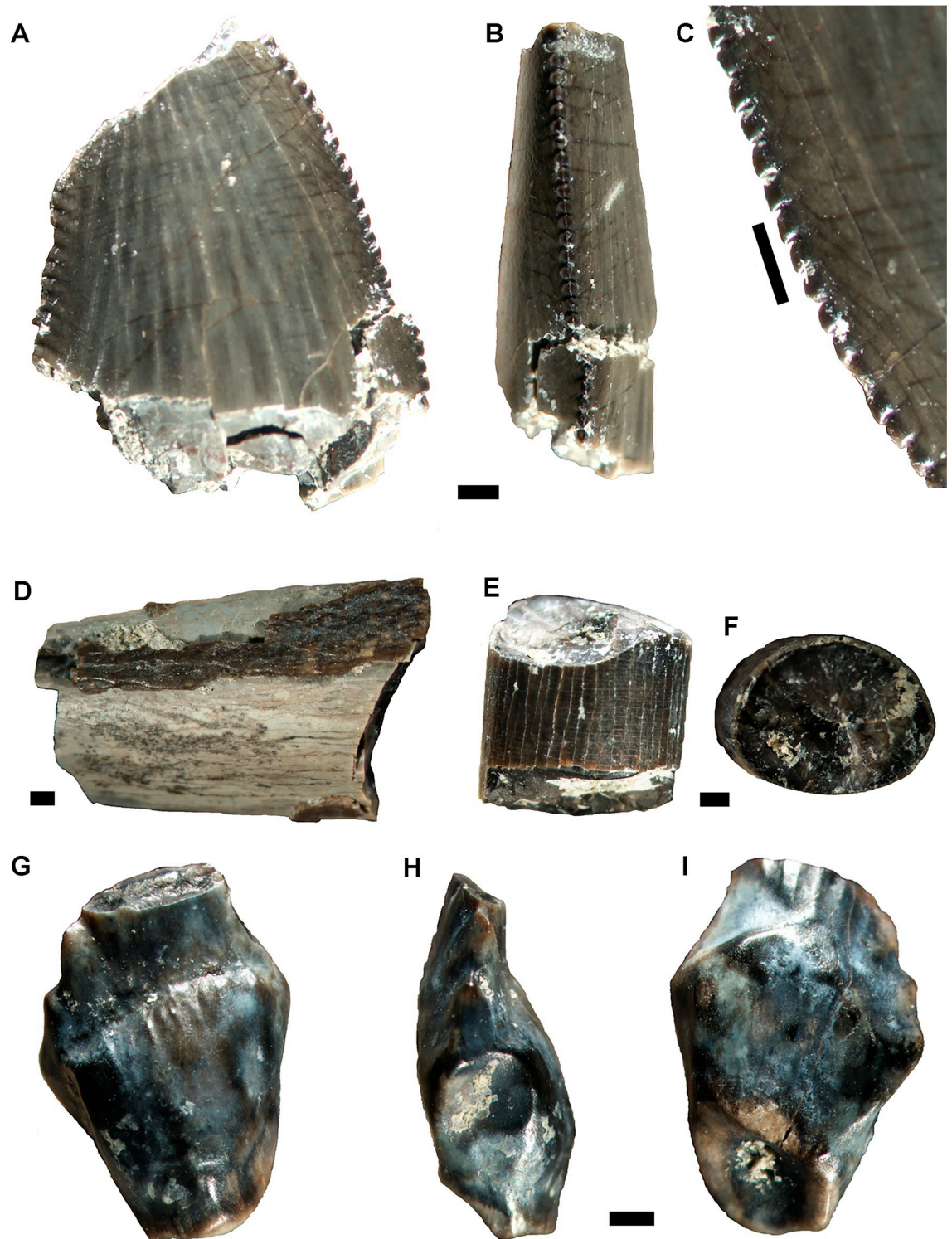


Fig 2. Dinosaur teeth. A-C, *Abelisauria* indet. (MPM-PV-18805.1), partial tooth in lingual or labial (A) and mesial (B) views; detail of mesial denticles (C). D, partial tooth (MPM-PV-18805.2) of a non-identified archosaur, preserving a patch of enamel showing a highly marked ornamentation. E-F, *Titanosauria* indet. (MPM-PV-18805.3), partial tooth. G-I, *Ankylosaur* (MPM-PV-18805.4) partial tooth in labial (G), distal (H) and lingual (I) views. Scale bars = 1 mm (except in A, B = 5mm).

<https://doi.org/10.1371/journal.pone.0256233.g002>

convex mesial and straighter distal margins. The tooth is strongly labio-lingually narrow (CBR = 0.44; labiolingual width is 44.4% of mesiodistal length), and the cross-section type is lenticular or D-shaped. In mesial/distal views, the serrated mesial and distal carinae are straight and centrally positioned on the crown (Fig 2A and 2B). The enamel is smooth (corresponds to the irregular type described by [18]). This irregular, smooth enamel texture is observed in abelisaurid teeth [18,22,33]. Denticles on the mesial carina have asymmetrical convex margins, are hooked and strongly apically recurved. They show separate narrow interdenticular spaces (interdenticular slit in [18]). Distal denticles are proximo-distally longer (proximodistally sub-rectangular denticles) than mesial denticles, and slightly apically oriented or chisel-like. Denticle density is approximately the same in both carinae, e.g., number of denticles per 5 mm at the mid-crown on the mesial carina is 11.5 (Fig 2C), and 11.3 on the distal carina (Table 1).

Abelisaurid tooth traits defined by Hendrickx and Mateus [22], and shared by MPM-Pv-1805.1 include an almost straight distal profile of the tooth, transversal and short marginal undulations on the crown, denticles with strongly developed interdenticular sulci, distal denticles with an apex pointing towards the tip (although the mesial denticles in MPM-Pv-1805.1 are markedly more hooked than in the abelisaurid described by Hendrickx et al [18]), a DSDI (denticle size density index) close to one, an irregular enamel texture, and the presence of apically pointed denticles on the distal carina. The CBR of this specimen (0.44) is similar to that of other abelisaurids (circa 0.5) described by Hendrickx and Mateus [22]. A ziphodont tooth, with a lenticular cross-section of the crown base, and carinae with hooked mesial denticles (although not as prominently hooked), and elongate distal denticles, is reminiscent of the morphotypes 1 and 2 described by Canale et al. [33], which have abelisaurid affinities.

Theropoda (?) indet. MPM-PV-18805.2 (Fig 2D) is a large, longitudinally fragmented and eroded tooth (preserved length: 16 mm; maximum diameter: 9.5 mm) preserving enamel patches attached to the dentine. Although its shape remains unknown, the enamel ornamentation is markedly different from that of other theropod or crocodile teeth. It shows an intricate pattern of markedly large rugosities and grooves (Fig 2D), clearly observed at plain sight. This ornamentation is largely similar to that described as “braided enamel texture” by Hendrickx et al. [18,23] in *Acrocanthosaurus*, and to that described as “veined enamel” in spinosaurids, although the enamel ornamentation is markedly smaller in the mentioned taxa. The owner of this large tooth from the Cerro Fortaleza locality remains unidentified.

Sauropod remains

Sauropoda Marsh, 1878

Eusauropoda Upchurch, 1998

Titanosauriformes Salgado et al., 1997

Titanosauria indet. MPM-PV-18805.3 is an isolate fragmented pencil-like (cylindrical) tooth (Fig 2E and 2F). The preserved fragment is only 9 mm long, and is sub-circular in cross section (largest diameter = 6.5 mm). The enamel is smooth, and there are no marked carinae, as observed in *Nigersaurus* and *Diplodocoidea* [34]. This fragmented tooth is very similar to those described for titanosaurids, which are generally cylindrical, with nearly parallel margins and lack denticles [e.g. 35]. The cross section varies from circular to elliptical, some being gently D-shaped [e.g. 36]. The large amount of titanosaurid bones present in the Cerro Fortaleza Formation suggests the tooth described here belongs to this clade. The slightly compressed section suggests the fragment corresponds to a distal portion of the crown.

Ankylosaur remains

Thyreophora Nopcsa, 1915

Ankylosauria Osborn, 1923

Nodosauroida Marsh 1890

Nodosauridae indet. MPM-PV-18805.4 (Fig 2G–2I) is a single isolated tooth, consisting of a crown missing its apex and root. The crown is labio-lingually compressed, leaf-like tooth, with few denticles along the mesial and distal carinae. Its total preserved height is 8.5 mm, the maximum width at the base is 3.5 mm. The lingual and labial surfaces are smooth and swollen around the base. There is a cingulum on the lingual side similar to that observed in nodosaurids. The mesial and distal carinae bear a series of approximately 6 or 7 large and irregular in size denticles, although the complete number is unknown because the apex is eroded. There is a constriction just below the crown. The tooth lacks the outer enamel—a common condition in shed nodosaurid teeth from the Late Cretaceous of North America [e.g. 37]. Nodosaurid characters present in this tooth include a well-developed cingulum at the base of the crown [38], and the root constriction below the root-crown contact [39]. There are no clear wear marks along the faces of the crown as in ankylosaurids, and probably the wear pattern in MPM-PV-18805.4 was tooth-to-tooth only on the top of the crowns as in polacanthids and nodosaurids [39]. In ankylosaurids wear facets develop on the crown faces rather than apically across crowns [40]. Also, the presence of a cingulum is more common among nodosaurids than in ankylosaurids [41]. MPM-PV-18805.4 is highly similar to the teeth of *Antarctopelta oliveroi* [42].

Ankylosauria indet. MPM-PV-18805.14–22; small-sized isolated osteoderms (Fig 3). These specimens correspond to interstitial armor ossicles (ossicles that fill the interstitial spaces between larger osteoderms, particularly the ventral side and limbs [see 43–45]). In general terms, these ossicles resemble those reported for the Early Cretaceous Australian nodosaur *Kunbarrasaurus ieverisi*, which is considered a small sized ankylosaur, and for *Antarctopelta oliveroi*, which is a possible nodosaurid ankylosaur from Antarctica [46]. Their maximum diameter is approximately 6 mm. Different from other taxa (e.g. *Antarctopelta oliveroi*), the ossicles reported here are heterogeneous regarding their general morphology. Some are oblate spheroid-shaped elements, with a heptagonal contour in superficial view (Fig 3A–3C, 3I and 3J). Others are strongly narrow and tall, having a roughly rectangular outline (Fig 3F–3H and 3M–3P). The deep (= ventral, basal, or internal) surface can be identified by its particular texture, with straight fibers that cross orthogonally, giving a distinct, interwoven texture to the surface (Fig 3H and 3J). This surface bears 1 or 2 neurovascular foramina, which connect with canals internally as shown by fractures and thin sections (Fig 3E and 3W). These features are commonly recorded in the osteoderms deep surface of several other vertebrates, particularly in non-avian dinosaur ossicles [46–51]. The superficial (= dorsal or external) surface is rugose and exhibits several irregular depressions bounded by sharp ridges (Fig 3A, 3D and 3O). A similar pattern has been recorded in the superficial surface of *Antarctopelta oliveroi* ossicles [51].

Two of the interstitial ossicles have been sectioned for histological analysis. The sections were performed in a plane parallel to the superficial/deep axis. The elements are almost entirely composed of compact primary bone tissue, with some vascular spaces located in the inner core (i.e. medullary region) (Fig 4A and 4B). This bone tissue is mainly composed of closely packed bundles of mineralized collagen fibers (i.e. structural fibers), which exhibit a complex and highly ordered spatial organization. In this regard, three systems of fiber bundles are distinguished: one vertical (i.e., parallel to the superficial/deep axis) and two horizontals (i.e., perpendicular to the superficial/deep axis) (Fig 4C and 4D). The horizontal systems are arranged roughly perpendicular to one another. The horizontal bundles become more obliquely oriented toward the external surface in the marginal areas of the ossicles. The bundles located in the inner core are comparatively narrower than those observed in the deep,

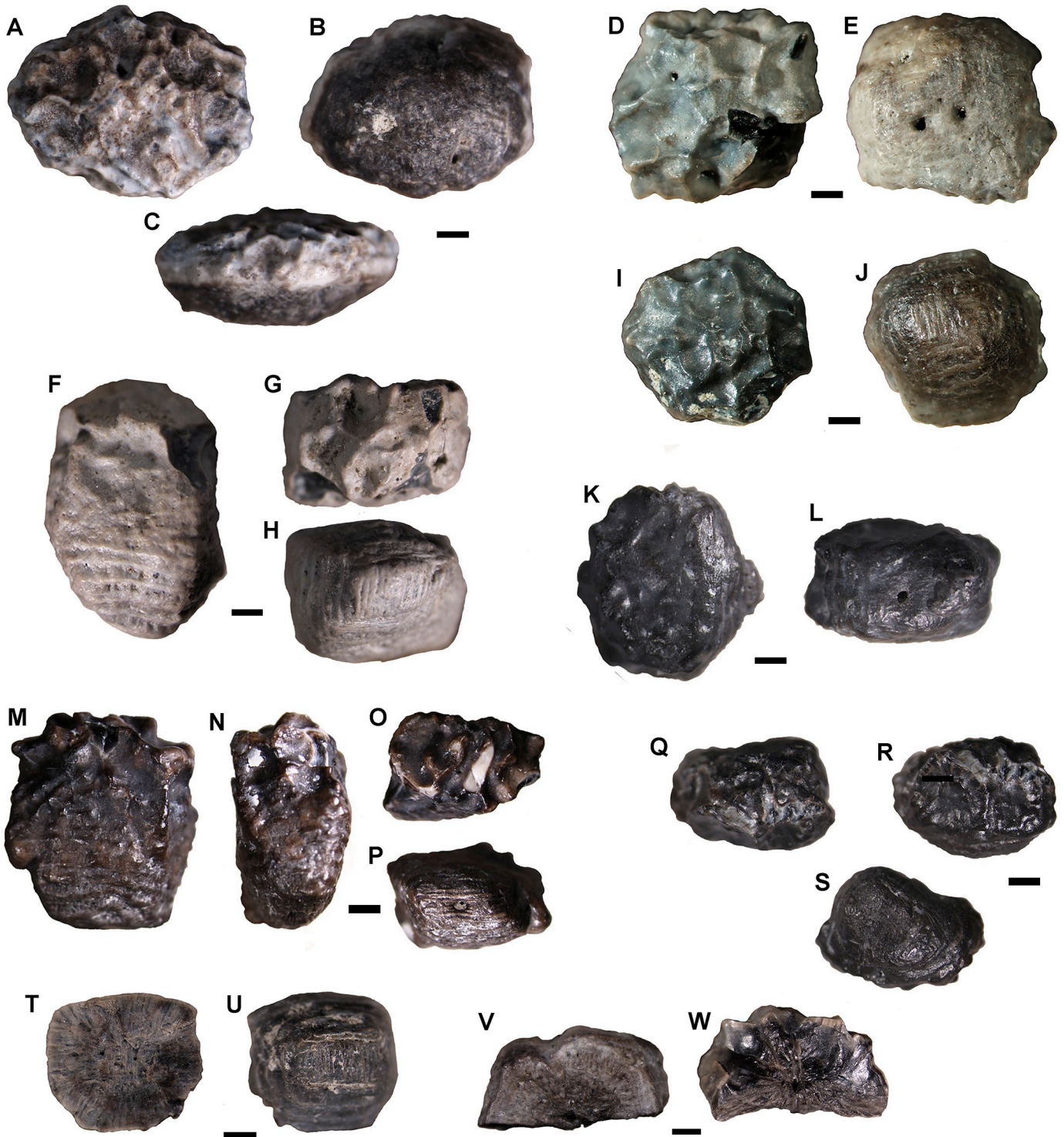


Fig 3. Ankylosaur interstitial ossicles (osteoderms) in superficial, internal and lateral views. MPM-PV-18805.14 (A-C), MPM-PV-18805.15 (D-E), MPM-PV-18805.16 (F-H), MPM-PV-18805.17 (I-J), MPM-PV-18805.18 (K-L), MPM-PV-18805.19 (M-P), MPM-PV-18805.20 (Q-S), MPM-PV-18805.21 (T-U), MPM-PV-18805.22 (V-W). Scale bars = 1mm.

<https://doi.org/10.1371/journal.pone.0256233.g003>

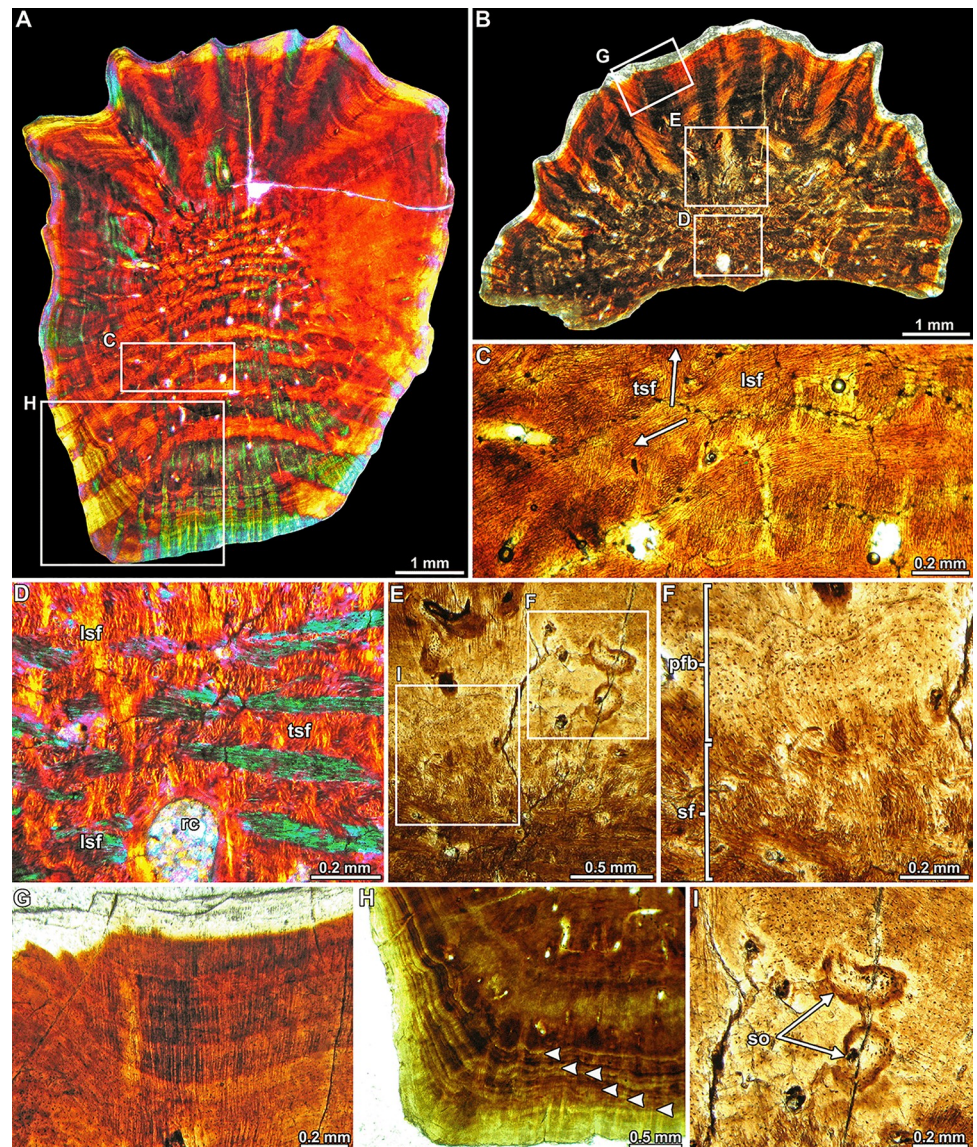


Fig 4. Bone histology of ankylosaur interstitial ossicles. (A-B) Complete sections of elements MPM-PV-18805.19 (A) and MPM-PV-18805.22 (B). In both images the superficial surface is oriented toward the top of the figure. The deep cortex of MPM-PV-18805.v-w is not preserved. The complex pattern of mineralized structural fiber bundles is clearly observed in the inner core and deep cortex of MPM-PV-18805.m-p. (C-D) Primary bone tissue composed by intercrossed bundles of mineralized structural fibers. White arrows in (C) signal the orientation of the fiber bundles. (E, F) General view (E) and detail (F) of the transition between the inner core (formed by structural fibers) and the external cortex (mostly formed by parallel fibered bone). (G) Detail of the outer cortex at the superficial portion of the ossicles. Note the profuse abundance of mineralized collagenous fibers. (H) Lines of arrested growth in the deep cortex (white arrowheads). (I) Detail of secondary osteons. Pictures have been taken under normal transmitted light (C, E-I), cross-polarized light (B) and cross-polarized light with a lambda filter (A and D). The epoxy resin layer that surrounds the elements in (A) and (B) has been digitally erased to enhance visibility. Abbreviations: lsf, longitudinally sectioned structural fiber bundles; rc, resorption cavity; so, secondary osteons.

<https://doi.org/10.1371/journal.pone.0256233.g004>

marginal, and superficial areas. The patterns of intercrossed bundles of structural fibers is distinct between the inner core and the deep cortex, being much more diffuse in the marginal cortex and almost inexistent in the superficial cortex. In this regard, there is an abrupt change

in the microstructure at the boundary between the medullary region and the inner portion of the superficial cortex. In this area, the well-defined pattern of intercrossed bundles of structural fibers abruptly changes to an avascular matrix formed by parallel fibered bone, which predominates in the superficial cortex (Fig 4E and 4F). Densely grouped mineralized collagenous fibers predominate in the superficial cortex (Fig 4G). The continuity between these fibers and the structural fiber bundles of the inner core is difficult to assess with confidence. A stratified pattern originated by the presence of cyclical growth marks (i.e., lines of arrested growth) is distinct in the outer portion of the superficial marginal and deep cortices (Fig 4H). Secondary remodeling is only evident for the presence of few resorption cavities and small Haversian systems scattered in the inner core and superficial cortex (Fig 4I).

Millimeter-sized ossicles are known in adult ankylosaurid specimens from the Late Cretaceous of North America [44] and in the nodosaurids *Kunbarrasaurus ieversi* [52,53], *Borealopelta markmitchelli* [54: Fig 1], and *Antarctopelta oliveroi* [46,51]. The oblate spheroid shape and size (approximately 6 mm in diameter) of the ossicles from the Cerro Fortaleza Formation are markedly similar to those described in *Kunbarrasaurus ieversi* by Molnar [52], including the dorsal superficial ornamentation formed by ridges and valleys (APC pers. obs.). A similar pattern has also been observed in the superficial surface of *Antarctopelta oliveroi* ossicles [51]. Regarding the histology of the Cerro Fortaleza Formation ossicles, it is strongly similar to that described for the ossicles of *Antarctopelta oliveroi* [46,51]. The only important difference is the predominance of parallel fibered bone in the specimens here analyzed.

Dermal ossicles possibly formed an extensive basement underlying the epidermal scales of ankylosaurs [44]. Unlike larger osteoderms, interstitial ossicles show no consistent differences among ankylosaur groups, at least among highly nested nodosaurids and ankylosaurids [50]. Thus, it is not possible to assign the specimens to a clade less inclusive than Ankylosauria. Despite its taxonomical uncertainties, this report not only increases the vertebrate diversity of the Cerro Fortaleza Formation, but also represents the first record of ankylosaur interstitial ossicles for South America.

Peirosaurid remains

Crocodyliformes Hay, 1930 (sensu Benton and Clark, 1988)

Mesoeucrocodylia Whetstone and Whybrow, 1983 (sensu Benton and Clark, 1988)

Notosuchia Gasparini, 1971 (sensu Sereno et al., 2001)

Peirosauridae Gasparini, 1982 (sensu Gasparini et al., 1991)

MPM-PV-18805.5–13 comprise nine tooth crowns missing the roots, some of them fragmented (Fig 5). All the teeth correspond to isolated “true” ziphodont teeth [sensu 27]. These are crowns in which the medio-distal diameter is larger than the labio-lingual, and with finely denticulated carinae. The carinae have a continuous series of true isomorphic denticles perpendicular to the margin of the tooth [sensu 55]. These denticles are isolated and separated by interdenticular grooves. The preserved teeth comprise crowns of conical, spatulate, and globose morphology [sensu 28].

The teeth are assigned to Peirosauridae based on their general morphology, which is reminiscent of that observed in other taxa [56–63] in having conical, spatulate and globular tooth crowns, with subcircular or oval cross section, slightly convex faces, finely serrated carinae, and a poorly marked constriction between the crown and the root [64,65] (Fig 5). In addition, peirosaurids are a frequent component of continental Cretaceous vertebrate faunas of southwestern Gondwana [63,66–68]. Within the sample of peirosaurid teeth, four morphotypes are recognized.

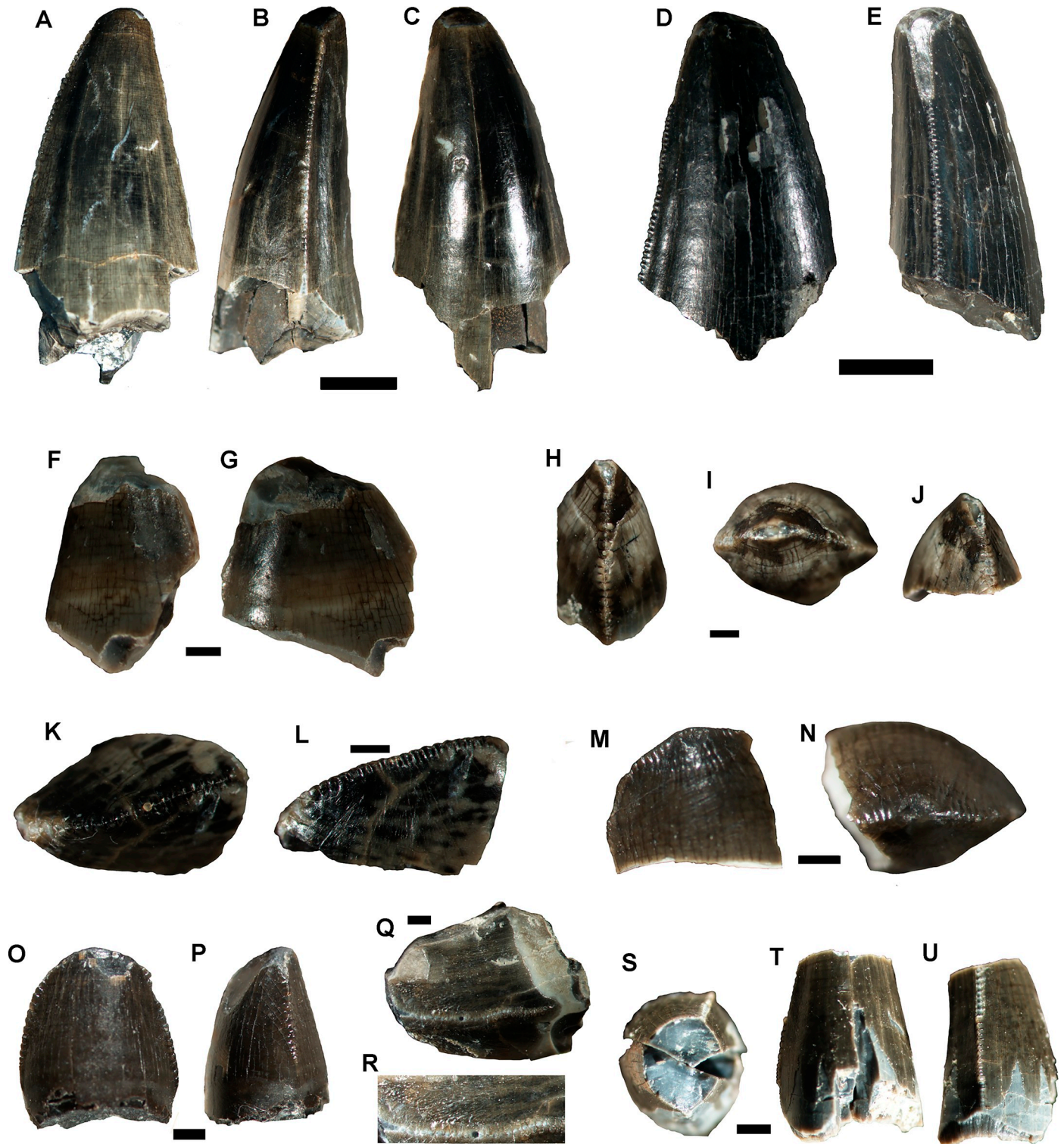


Fig 5. Peirosaurid teeth. MPM-PV-18805.5 complete crown in lingual (A), mesial (B) and labial (C) views. MPM-PV-18805.6 complete crown in labial (D) and distal (E) views. MPM-PV-18805.7 fragmented crown in mesial (F) and lingual (G) views. MPM-PV-18805.8 almost complete crown in mesial or distal (H), apical (I) and mesial or distal (J) views. MPM-PV-18805.9 fragmented crown in mesial or distal (K) and labial (L) views. MPM-PV-18805.10, fragmented crown in labial (M) and apical (N) views. MPM-PV-18805.11, complete crown in lingual (O) and mesial (P) views. MPM-PV-18805.12, fragmented crown in mesial or distal (Q) and detail of the denticles (R). MPM-PV-18805.13, crown missing the tip in apical (S), lingual (T) and distal (U) views. Scale bars (A-E) = 5 mm; (F-U) = 1 mm.

<https://doi.org/10.1371/journal.pone.0256233.g005>

Morphotype I. Morphotype I correspond to tall and conical crowns, with a subcircular cross-section. In the peirosaurid skull, this morphology is present in the anteriormost teeth (Fig 6).

MPM-PV-18805.5 (Fig 5A–5C) corresponds to a tooth with most of the crown preserved. It is conical (the base is subcircular in cross-section), apico-basally tall, with a slight constriction at the base, and well-marked mesial and distal carinae. The tooth has a slight lingual curvature distally, a labial face markedly convex, and a lingual face slightly concave. These faces are smooth and are separated by the medial and distal carinae, which bear small denticles. The lingual side of the crown bears a central convexity with a shallow groove mesially, adjacent to the denticulated mesial carina. The denticulated mesial and distal carinae extend from the base to the apex of the crown, with small denticles distributed regularly and similar in size and morphology. The denticles have an external rounded keel and are separated by interdenticular grooves. The apex of the crown has a semicircular wear facet, apical wear [sensu 69], slightly displaced to the mesiolabially side.

MPM-PV-18805.6 (Fig 5D and 5E) is a conical tooth preserving an almost complete crown. It is apico-basally tall and with no constriction at the base, which is subcircular to oval in cross-section. The tooth has a slight lingual curvature, with the labial face strongly convex, and the lingual face slightly concave to straight. Both surfaces are smooth. The labial side bears a shallow groove distally, adjacent to the denticulated carina, and well-marked in the base. The carinae on the mesial and distal edges are serrated with marked denticles. These denticles are small, isomorphic, and regularly distributed, with an external rounded keel and separated by interdenticular grooves. The crown has an apical wear facet extended over the distal carina (apico-carinal wear).

MPM-PV-18805.13 (Fig 5S–5U) is a partially preserved conical, and apico-basally tall crown with a circular base in cross-section. The labial face is strongly convex, and the lingual face is slightly concave. They lack the grooves adjacent to the carina mesially and distally. Both faces are smooth and are separated by well-marked serrated carinae (the mesial carina is better preserved). The denticles are small, individual, and separated by interdenticular grooves. The denticle size varies at the base of the mesial carina, where small denticles intercalate sets of one or two larger ones. Denticle external keels are rounded.

Morphotype II. Morphotype II corresponds to low and sub-globose conical crowns, sub-circular in cross-section, with well-defined constriction between crown and root. In the peirosaurid skull, this morphology is present in anteriormost teeth (Fig 6).

MPM-PV-18805.7 (Fig 5F and 5G) is a fragmented crown, missing most of the apex and basal region. It is possible, however, to determine that it is an apico-basally low crown with conical outline, slightly curved distally. The distal carina has poorly preserved small denticles.

MPM-PV-18805.11 (Fig 5O and 5P) is an almost complete apico-basally low crown, slightly conical and globose, with labial face strongly convex and lingual face slightly convex to straight. Both faces are smooth, separated by well-marked and serrated carinae, and lack the grooves mesially and distally adjacent to the carina. The denticles of the carina are small, distributed regularly, and have well-defined interdenticular grooves. The denticles at the base and the apex are smaller. The external keel of the denticles is apically curved, with interdenticular grooves slightly curve ventrally towards the central region of the crown. The base of the crown is subcircular in cross-section, and has a constriction (which is more marked mesio-distally) that separates the crown from the root. The crown has an elliptical apical wear facet that extends on the labial face.

Morphotype III. Morphotype III corresponds to low, labio-lingually compressed crowns, which are oval in cross-section, and have a spatulate outline in lateral view. In the peirosaurid skull, this morphology is present in post-caniniform teeth (Fig 6).

MPM-PV-18805.9 (Fig 5K and 5L) represents half of an apico-basally low and spatulate crown, slightly labiolingually compressed, and oval in cross-section at the base. The labial face is convex and the lingual face is slightly straight, both separated by serrated carinae and lacking grooves adjacent to the carina. The denticles are smaller at the base, regularly distributed and separated by marked interdenticular grooves. The external keel of the denticles is rounded. This crown lacks wear facets.

MPM-PV-18805.10 (Fig 5M and 5N) is a fragmented apico-basally low crown, spatulate in lateral view, and labiolingually compressed. There is a constriction between crown and root, well-marked mesiodistally. The labial face is convex and the lingual face is slightly concave, both separated by well-marked and serrated carinae. The apex has apico-basally extending striations on the labial and lingual faces. The denticles in both carinae are individual (separated by well-defined interdenticular grooves), similar in size, and regularly distributed. The apical interdenticular grooves match the distribution of the above mentioned striations. The external keel of the denticles is rounded. This crown lacks wear facets.

MPM-PV-18805.12 (Fig 5Q and 5R) is a partially preserved apico-basally low and spatulate crown, missing the apex. The base is sub-oval in cross-section. The labial face is convex and the lingual face is slightly concave. Both faces are separated by poorly marked and badly preserved serrated carinae. Labial and lingual faces have irregular apico-basally striations that converge in the carinae, but lacks marginal grooves. The denticles are small and individual, separated from one another by an interdenticular groove. The denticles are regularly distributed, and their sizes vary along the length of the carina; small denticles are intercalated between two larger denticles. Near the base, the preserved (mesial or distal?) carina has a slightly apicobasal undulation, with a small convexity towards the lingual face. This convexity bears relatively larger denticles, whereas the denticles are smaller near the base. On the labial and lingual faces, there are small striations mostly concentrated at the apical region, which are not related to the denticles nor with the interdenticular grooves. The external keel of the denticles is rounded.

Morphotype IV. Morphotype IV corresponds to low and globose crowns, molariform type, which are subcircular in cross-section. In the peirosaurid skull, this morphology is present in posteriormost teeth (Fig 6).

MPM-PV-18805.8 (Fig 5H–5J) is an almost complete, apico-basally low crown, globose, and sub-circular in cross-section. Labial and lingual faces are convex and separated by a

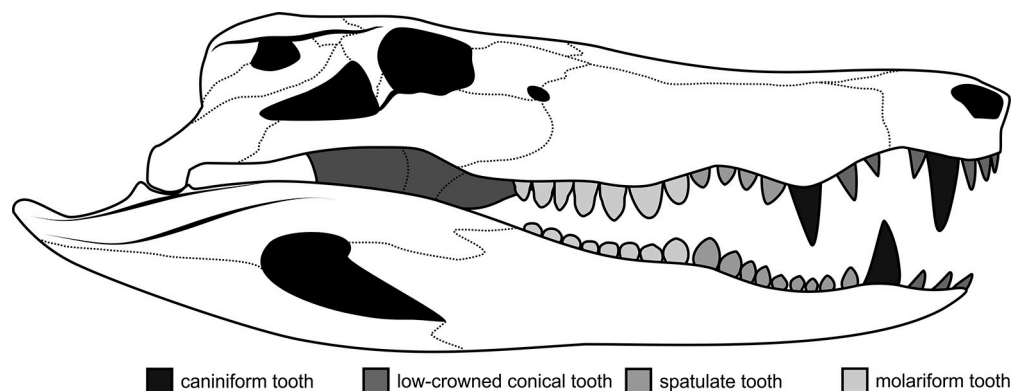


Fig 6. Scheme of a peirosaurid skull showing heterodont teeth and the probable location of morphotypes I to IV. Abbreviations: 1, caniniform tooth; 2, low-crowned conical tooth; 3, spatulate tooth; 4, molariform tooth.

<https://doi.org/10.1371/journal.pone.0256233.g006>

well-defined and serrated carina. Both faces have small apicobasal striations, well-marked apically. The lingual and labial faces bear a central convexity bordered by a pair of mesial and distal subtle grooves. The denticles are regularly distributed, with smaller elements both apically and basally. Each individual denticle has a rounded external keel, separated from one another by marked interdenticular grooves. In this crown, a small apical wear is present.

Discussion

Cretaceous archosaurian record of Cerro Fortaleza Formation

Isolated teeth are commonly found in Mesozoic rocks, the tetrapod faunas of which were dominated by polyphyodont taxa that continually replaced their functional dentitions [21 and references therein]. In many fossil bearing beds, dinosaur and crocodyliform teeth are more common than other well preserved skeletal remains [e.g. 70]. This responds in part to the large number of teeth on their jaws, and also to the fact that most dinosaurs and crocodyliforms had an almost continual supply of teeth that could be shed into the local environment [e.g. 19,21,27,71–74]. However, until now, this was not the case of the Cerro Fortaleza Formation, where isolated teeth are scarce. The identification of the teeth from the micro-remains site studied here, allowed to determine the presence of certain taxa (such as theropod and ankylosaur—probably nodosaur—dinosaurs and peirosaurid crocodyliforms), whose skeletal remains are not yet recorded. The faunal assemblage of dinosaurs is, in part, taxonomically similar to that recently recovered in the Chorrillo Formation [9,10], which is dominated by ornithischians.

The only reports of theropods in the Cerro Fortaleza Formation correspond to the megaraptorid *Orkoraptor burkei* (“Pari Aike” Formation in [6], found in rocks outcropping south Lago Viedma), and the probable [see 75] abelisauroid *Austrocheirus isasii* [12], although only the former has preserved teeth. The theropod tooth MPM-PV-18805.1 from the Cerro Fortaleza locality differs in shape from those of *Orkoraptor burkei* (the crowns of which have a 8-shaped cross section and a curved distal margin) and, more importantly, in the presence of a serrated mesial carina (not serrated in *Orkoraptor burkei*). Remains assignable to Megaraptoridae, Abelisauroidae, and Unenlagiidae were found in the Chorrillo Formation [9], although only one tooth was described (MACN-Pv 19066) and assigned to a megaraptorid. Furthermore, the only record of theropod remains from the Cerro Fortaleza locality corresponds to a partial abelisauroid metatarsus reported recently [17]. Altogether, this suggests that the new tooth probably corresponds to the clade, supporting the presence of mid to large-sized abelisauroids in the Late Cretaceous of southern Patagonia. As for the sauropods, titanosaur remains are commonly found in the Cerro Fortaleza Formation, including *Puertasaurus reuili* [14] and *Dreadnoughtus schrani* [11], which are among the largest-sized sauropods, together with *Nulloitan glaciensis* from the Chorrillo Formation [9]. The fragmented specimen described here, is a pencil-like tooth with a subcylindrical crown (at least at the preserved section of the tooth), smooth enamel and lacking carinae, all traits observed in the Diplodocoidea [e.g. 76], rebbachisaurids, and highly nested titanosauriforms [77, and references therein]. The lack of the apical region of the tooth described here prevents further comparisons at this point.

The ornithischian record from Cerro Fortaleza Formation is restricted to the elasmarian ornithopod *Talenkauen santacrucensis* [13] and the ankylosaur remains described here from the type locality. From the Chorrillo Formation, the ornithischian fauna includes hadrosaurian remains, the elasmarian ornithopod *Isasicursor santacrucensis*, and an indeterminate ankylosaur. The later constitutes the southernmost record of the clade in South America and together with the specimen from Cerro Fortaleza confirm a geographical link with the ankylosaur record from Antarctica. The ankylosaur fossil record remains scarce in South America, and to

date comes only from rocks of Campanian-Maastrichtian age. This is true for other Gondwanan areas, although better preserved specimens have been recovered in Antarctica and Australia [42,53,78]. In Argentina, there are no skull remains of ankylosaurs so far, and the most complete specimen corresponds to the Antarctic taxon *Antarctopelta oliveroi* [42]. The tooth recovered from the Cerro Fortaleza locality probably belongs to a nodosaurid ankylosaur, the same probable affinity of the other specimens collected in Argentina. The first record of ankylosaur remains in the country corresponds to a femur, large osteoderms, and one tooth from the Allen Formation (Campanian-Maastrichtian), northern Patagonia [79,80]. Later, large-sized armor osteoderms were recovered from the Puerto Yeruá Formation (Late Cretaceous?) in Entre Ríos Province [81], La Colonia Formation (Campanian-Maastrichtian) in Chubut Province [82], and more recently from the Allen Formation (Campanian-Maastrichtian), Río Negro Province [83] and the Chorrillo Formation, Santa Cruz Province (Rozadilla et al 2021). None of the above-mentioned materials correspond to small-sized ossicles as those from Cerro Fortaleza Formation. Millimeter-sized ossicles are known in adult ankylosaurid specimens from the Late Cretaceous of North America [44], and in the nodosaurids *Kunbarrasaurus ieveri* [52,53] and *Borealopelta markmitchelli* [54, Fig 1]. However, the osteoderm histological analysis is insufficient to discriminate between ankylosaur families.

The ankylosaur *Antarctopelta oliveroi* [42] was found in the James Ross Island -Antarctic Peninsula- in rocks of Campanian age. At that time, the Antarctic Peninsula was connected to South America, allowing faunistic interchange between both continents, with the nodosaurids probably arriving to South America around the late Campanian, through Central America [e.g. 10,81]. The dinosaur assemblages including ankylosaur remains from Chorrillo [9,10] and Cerro Fortaleza formations are the first records filling the gap between Antarctica and North Patagonia, supporting an ankylosaurid common fauna.

Serrated ziphodont teeth are common within Crocodyliformes [e.g. 27,84,85]. In the Late Cretaceous of Argentina, such teeth have been recorded in Baurusuchidae [86,87] and Peirosauridae [88], the latter being the most common and diverse crocodyliforms during this period [e.g. 62,87,89–92]. In addition, baurusuchid teeth are strongly compressed labiolaterally and distally recurved [e.g. 93], unlike those of peirosaurids. The peirosaurid teeth presented here exhibit heterodonty, and correspond to the most austral record of the clade so far. The previous record of peirosaurids in southern Patagonia include *Colhuehuapisuchus lunai* from Chubut Province [63], although none of the teeth described here exhibit autapomorphies of this taxon. This suggests the presence of at least two different taxa in Southern Patagonia. More comprehensive explorations, and more complete crocodyliform specimens from the Cerro Fortaleza locality and Formation will shed some light on our understanding of the diversity of the clade at these latitudes.

Considering the morphological variation observed along the tooth row (i.e., anterior teeth have conical, tall, and circular cross-sectional crowns, whereas posterior teeth have low, spatulate and globose crowns, which are oval to circular in cross-section) in extant and many extinct crocodyliform taxa [27–29] four morphotypes were identified. Morphotype I corresponds to an anterior caniniform tooth, morphotype II corresponds to low conical teeth anteriorly positioned, morphotype III corresponds to a tooth of an intermediate position, and morphotype IV correspond to molariform teeth, i.e., the type of tooth most posteriorly positioned in the peirosaurid jaws (Fig 6). Strikingly, the denticle morphology observed in MPM-PV-18805.11 (Fig 5O and 5P), corresponding to the morphotype II, is recognized in some teeth of the African peirosaurid *Hamadasuchus rebouli* [27], but not in South American taxa. This suggests that MPM-PV-18805.11 belongs to a taxon with more affinities with African than South American peirosaurids.

Implications of the faunal association

One of the first steps in studying interactions among extinct organisms and their environments is identifying the taxa that comprised the ecosystem [21]. Dinosaur associations of ankylosaur, ornithopod, theropod, and sauropod remains have been reported globally, based on bones [e.g. 94] or tracks [e.g. 95,96]. In Patagonia in particular, the dinosaur taxonomic richness of some Cretaceous stratigraphic units and sites is considered high [e.g. 97,98]. However, in southern Patagonia, only the Chorrillo and Cerro Fortaleza formations recorded ankylosaur remains [10], and only the later peirosaurid remains. The micro-remains site at Cerro Fortaleza indicates the coeval association of titanosaur sauropods, abelisaurid theropods, ankylosaurs (probably nodosaurids), ornithopods, and peirosaurids. The peirosaurid crocodyli-form teeth represent 75% of the sample, suggesting a predominance of crocodyli-forms over dinosaurs, which is congruent with the rise of notosuchian diversity during the Late Cretaceous [99]. This statement however, should be supported by taphonomical analyses or further findings in the area. The coexistence of different species of large reptiles is possible if they occupy different niches, reducing the competition for resources [100]. In terms of other taxonomical components of the ecosystem, the previously reported non-dinosaur fauna of the Cerro Fortaleza locality is diverse, including fishes and turtles. The studied flora in this area indicates a high predominance (75:25) of gymnosperms over angiosperms, and interestingly, these fossil woods also provided evidence for seasonal growth regimens in the region, based on growth rings [4]. This supports a pronounced seasonality caused by rainfall patterns based on sedimentological analyses [8]. Furthermore, the presence of *Zamuneria amyla* (Cycadales) in the Cerro Fortaleza locality indicates humid and warm climate, as extant cycads grow in tropical to subtropical areas [101].

Among the ankylosaur remains from both the Chorrillo and Cerro Fortaleza formations, particularly the tooth recovered from the later exhibits nodosaurian traits. Interestingly, nodosaurids are found with high frequency in coastal environments. It has been suggested that either this group inhabited a broader range of paleo-environments than ankylosaurids, or even that nodosaurids alone preferred such environments [102,103, contra 104]. In congruence with these hypothesis, the Cerro Fortaleza Formation is characterized by lithified fluvial sands, overbank mud deposits, and paleosols deposited in fluvial, fluvial-palustrine, and coastal plain environments from the northeastern margin of the Austral Basin [1,16,4]. In turn, the continental Chorrillo Formation is part of a rock succession that conforms a late Campanian-early Maastrichtian regressive episode, characterized by braided and meandering fluvial deposits [2,9].

Both, Chorrillo and Cerro Fortaleza formations share a faunal association with a dinosaur diversity composed by large sauropods, abelisaurid and megaraptorid theropods, ornithopods, and ankylosaurs. Differences in faunal composition rely on the hadrosaurids recovered only in Chorrillo Formation, and peirosaurids recorded only in Cerro Fortaleza Formation. So far, this supports both the Campanian (approximately 72 My [16]) and Maastrichtian [16] ages proposed for Cerro Fortaleza Formation that probably correlates with the lower section of the Chorrillo Formation (Campanian-Maastrichtian in age) [10]. However, further discoveries are necessary to better understand the correlation between these two formations.

In this panorama, although it is more likely that the deposition of teeth found in the site at Cerro Fortaleza locality was an attritional event, the data provided by this micro-remains site indicates that at least titanosaur sauropods, abelisaurid and megaraptorid theropods, elasmarian ornithopods, nodosaurid ankylosaurs, and a variate number of crocodyli-form taxa were part of the same late Cretaceous ecosystem. This paleoenvironment, as indicated by the fossil record, sedimentology, and paleoclimate interpretations for the area, was characterized by a



Fig 7. Paleambiental reconstruction of Cerro Fortaleza locality (Cerro Fortaleza Formation) showing the coeval dinosaurs and peirosaurid notosuchians described in the present study (and right below is *Zamuneria*). Illustration by J. González.

<https://doi.org/10.1371/journal.pone.0256233.g007>

meandering fluvial system converging with a shore landscape, associated with a subtropical forest (Fig 7).

Conclusions

Here, we report the faunal taxonomic composition of a micro-remains site at Cerro Fortaleza locality (Cerro Fortaleza Formation, Campanian-Maastrichtian) based on isolated teeth and osteoderms, providing insights into the paleobiodiversity of a Late Cretaceous ecosystem in South America. Although scarce, the tooth sample from Cerro Fortaleza locality is taxonomically rich, representing different dinosaur and crocodyliform clades that probably cohabitated the same bioma during the Late Cretaceous. This report enriches the faunal knowledge in a site where other kind of skeletal remains poorly represent these clades (except for the sauropods), or were not previously reported. The archosaur taxonomic composition of the Cerro Fortaleza Formation includes Titanosauria, Theropoda (Abelisauridae and Megaraptoridae), Ornithischia (Ornithopoda and Ankylosauria), and notosuchian crocodyliforms (Peirosauridae), with the later representing the predominant archosaurs in the studied sample. The peirosaurid teeth from Cerro Fortaleza locality are the first recorded at this latitude. The ankylosaur specimens from Cerro Fortaleza and Chorrillo formations, indicate that this group of

dinosaurs reached an austral distribution at least since the late Campanian, filling the gap in the fossil record between Antarctica and central-northern Patagonia.

Acknowledgments

We would like to thank the owners of the Estancia La Flora (Santa Cruz Province) Juan José Maglio and his son Pablo Maglio, for allowing doing fieldwork in their land and helping us provide the use of facilities at the site, and to Secretaría de Cultura de la Provincia de Santa Cruz (through Carla Almazán) that provided the corresponding permits to carry out the fieldwork and further studies. We also thank Magalí Cárdenas (MACN) and Mariela Fernández (INIBIOMA) for their help collecting the specimens. Kenneth Carpenter kindly helped with the identification of the ankylosaur tooth. We thank the work made by the editor, Max Langer, and the reviewers Agustín Martinelli and an anonymous reviewer, who largely improved the first version of this manuscript with their comments.

Author Contributions

Conceptualization: Ariana Paulina-Carabajal.

Funding acquisition: Ariel H. Méndez, Yuong-Nam Lee.

Investigation: Ariana Paulina-Carabajal, Francisco T. Barrios.

Visualization: Ariana Paulina-Carabajal, Francisco T. Barrios, Ignacio A. Cerda.

Writing – original draft: Ariana Paulina-Carabajal, Francisco T. Barrios, Ariel H. Méndez, Ignacio A. Cerda, Yuong-Nam Lee.

References

1. Marensi SA, Casadío S, Santillana SN. Estratigrafía y sedimentología de las unidades del Cretácico superior-Paleógeno aflorantes en la margen sureste del lago Viedma, provincia de Santa Cruz, Argentina. *Rev Asoc Geol Argent.* 2003; 58 (3): 403–416.
2. TETTAMANTI C, MOYANO PAZ D, VARELA AN, TINEO DE, GÓMEZ-PERAL LE, POIRÉ DGet al. Sedimentology and fluvial styles of the Uppermost Cretaceous Continental Deposits of the Austral-Magallanes Basin, Patagonia, Argentina. *Lat Am J Sedimentol Basin Anal.* 2018; 25(2): 149–168.
3. Egerton VM. The Geology, Paleontology and Paleoecology of the Cerro Fortaleza Formation, Patagonia (Argentina), Department of Biology. PhD Thesis, Drexel University. 2011. Available from <https://core.ac.uk/download/pdf/190335754.pdf>.
4. Egerton V, Williams CJ, Lacovara KJ. A new Late Cretaceous (late Campanian to early Maastrichtian) wood flora from southern Patagonia. *Palaeogeogr Palaeoclimatol Palaeoecol.* 2016; 441: 305–315.
5. Riccardi AC, Roleri EO. Cordillera Patagónica Austral. In: Turner JC, editor. Segundo Simposio de Geología Regional Argentina; 1980. pp. 1163–1306.
6. Novas FE, Ezcurra MD, Lecuona A. *Orkoraptor burkei* nov. Gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cret Res.* 2008; 29: 468–480.
7. Varela AN, Poiré DG, Martín T, Gerdes A, Gelfo JN, Hoffmann S. U-b zircon constraints on the age of the Cretaceous Mata Amarilla Formation, southern Patagonia, Argentina: its relationship with the evolution of the Austral Basin. *Andean Geol.* 2012; 39: 359–379.
8. Varela AN, Veiga GD, Poiré DG. Sequence stratigraphic analysis of Cenomanian greenhouse palaeosols: a case study from southern Patagonia, Argentina. *Sediment Geol.* 2012. 271–272: 67–82.
9. NOVAS FE, AGNOIN FL, ROZADILLA S, ARANCIAGA-ROLANDO A, BRISSON-EGLI F, MOTTA MJet al. Paleontological discoveries in the Chorrillo Formation (upper Campanian-lower Maastrichtian, Upper Cretaceous), Santa Cruz Province, Patagonia, Argentina. *Rev Mus Argent Cienc Nat.* 2019; 21 (2): 217–293.
10. ROZADILLA F, AGNOLÍN F, MANABE M, TSUIHIJI T, NOVAS FE. Ornithischian remains from the Chorrillo Formation (Upper Cretaceous), southern Patagonia, Argentina, and their implications on ornithischian paleobiogeography in the Southern Hemisphere. *Cret Res.* 2021; 125: 104881.

11. Lacovara KJ, Lamanna MC, Ibiricu LM, Poole JC, Schroeter ER, Ullmann V, et al. Gigantic, exceptionally complete titanosaur sauropod dinosaur from southern Patagonia, Argentina. *Sci Rep*. 2014; <https://doi.org/10.1038/srep06196> PMID: 25186586
12. Ezcurra MD, Agnolín FL, Novas FE. An abelisauroid dinosaur with a non-atrophied manus from the Late Cretaceous Pari Aike Formation of Southern Patagonia. *Zootaxa*. 2010; 2450: 1–25.
13. Novas FE, Cambiaso AV, Ambrosio A. A new basal iguanodontian (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia. *Ameghiniana*. 2004; 41 (1): 75–82.
14. Novas FE, Salgado L, Calvo J, Agnolín F. Giant titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia. *Rev Mus Argent Cienc Nat*. 2005; 7 (1): 37–41.
15. Novas F, Bellosi E, Ambrosio A. Los “Estratos con Dinosaurios” del lago Viedma y río La Leona (Cretácico, Santa Cruz): Sedimentología y contenido fosilífero. In: Cabaleri N, Cingolani CA, Linares E, López de Luchi MG, Osters HA, Panarello HO, editors. *Actas del XV Congreso Geológico Argentino*; 2002. Artículo N° 315, 7 pp.
16. SICKMAN ZT, SCHWARTZ TM, GRAHAM SA. Refining stratigraphy and tectonic history using detrital zircon maximum depositional age: an example from the Cerro Fortaleza Formation, Austral Basin, southern Patagonia. *Basin Res*. 2018; 30(4): 708–729.
17. Canale J, Paulina-Carabajal A, Mendez A, Lee Y-N. New Abelisauroida (Theropoda, Ceratosauria) remains from Cerro Fortaleza (Cerro Fortaleza Formation), Santa Cruz Province, Argentina. *PE-APA*. 2018, 19 (1): R6 <https://doi.org/10.5710/PEAPA.15.04.2019.296>
18. Hendrickx C, Mateus O, Araújo R. A proposed terminology of theropod teeth (Dinosauria, Saurischia). *J Vert Paleontol*. 2015; 35(5): e982797.
19. Currie PJ, Rigby Jr, JK Sloan RE. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter K, Currie PJ, editors. *Dinosaur Systematics: Approaches and Perspectives*. Cambridge: Cambridge University Press; 1990. pp. 107–125.
20. Farlow JO, Brinkman DL, Abler WL, Currie PJ. Size, shape and serration density of theropod dinosaur lateral teeth. *Mod Geol*. 1991; 16:161–198.
21. Smith JB, Vann DR, Dodson P. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *Anat Rec*. 2005; 285A: 699–736. <https://doi.org/10.1002/ar.a.20206> PMID: 15986487
22. Hendrickx C, Mateus O. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa*. 2014; 3759:1–74. <https://doi.org/10.11646/zootaxa.3759.1.1> PMID: 24869965
23. Hendrickx C, Mateus O, Araújo R, Choiniere J. The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. *Palaeontol Electronica*. 2019; 22.3.74 1–110 <https://doi.org/10.26879/820>.
24. VARELA AN. Tectonic control of accommodation space and sediment supply within the Mata Amarilla Formation (lower Upper Cretaceous) Patagonia, Argentina. *Sedimentology* 2015; 62: 867–869.
25. VARELA A, RICHIANO S, POIRÉ DG. Tsunami vs storm origin for Shell bed deposits in a lagoon environment: an example from the Upper Cretaceous of Southern Patagonia, Argentina. *Lat Am J Sedimentol Basin Anal*. 2011; 18: 63–85.
26. Legasa O, Buscalioni AD, Gasparini Z. The serrated teeth of *Sebecus* and the iberocretanian crocodile, a morphological and ultrastructural comparison. *Studia Geologica Salmanticensia*. 1994; 29: 127–144.
27. Prasad GVR, de Broin FL. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Ann de Paléontol*. 2002; 88: 19–71.
28. Frey E, Monninger S. Lost in action—the isolated crocodylian teeth from Enspel and their interpretive value. *Palaeodivers Palaeoenviro*. 2010; 90: 65–81.
29. ŐSI A. The evolution of jaw mechanism and dental function in heterodont crocodyliforms. *Hist Biol*. 2013; 26: 279–414.
30. Cerda IA, Pereyra ME, Garrone M, Ponce D, Navarro TG, González Ret et al. A basic guide for sampling and preparation of extant and fossil bones for histological studies. *PE-APA*. 2020; 20: 15–28.
31. Francillon-Vieillot H, de Buffrenil V, Castanet J, Geraudie J, Meunier FJ, Sire JY et al. 1990. Microstructure and mineralization of vertebrate skeletal tissues: In: CARTER JG, editor. *Skeletal Biomineralization Patterns, Processes and Evolutionary Trends*. New York: Van Nostrand Reinhold. pp. 471–548.
32. Cerda IA, García RA, Powell JE, López O. Morphology, microanatomy and histology of titanosaur (Dinosauria, Sauropoda) osteoderms from the Upper Cretaceous of Patagonia. *J Vertebr Paleontol*. 2015; 35: e905791

33. Canale JI, Apesteguía S, Gallina PA, Gianechini FA, Haluza A. The oldest theropods from the Neuquén Basin: Predatory dinosaur diversity from the Bajada Colorada Formation (Lower Cretaceous: Berriasian-Valanginian), Neuquén, Argentina. *Cret Res.* 2017; 71: 63–78.
34. Canudo JI, Filippi L, Salgado L, Garrido A, Cerda I, García Ret al. Dientes de terópodos asociados con una carcasa de saurópodo en el Cretácico Superior (Formación Plottier) de Rincón de los Sauces (Patagonia, Argentina). *Actas de las IV Jornadas Internacionales sobre Paleontología de dinosaurios y su entorno*, Burgos, 2008; pp. 321–330.
35. García RA, Salgado L, Fernández MS, Cerda IA, Paulina-Carabajal A, Otero A et al. Paleobiology of titanosaurs: Reproduction, development, histology, pneumaticity, locomotion and neuroanatomy from the South American fossil record. *Ameghiniana.* 2015; 52 (1): 29–68.
36. Wilson JA, Sereno PC. Early evolution and higher-level phylogeny of sauropod dinosaurs. *J Vert Paleontol, Memoir.* 1998; 5: 1–68.
37. CARPENTER K, BREITHAUPT B. Latest Cretaceous occurrence of nodosaurid ankylosaurs (Dinosauria, Ornithischia) in Western North America and the gradual extinction of the dinosaurs, *Journal of Vertebrate Paleontology*, 1986; 6:3, 251–257.
38. COOMBS WP. Teeth and taxonomy in ankylosaurs. In: CARPENTER K, CURRIE PJ, editors. *Dinosaur Systematics: Perspectives and Approaches*. New York: Cambridge University Press; 1990. pp. 269–279.
39. CARPENTER K. Ankylosaurs. In: Bret-Surman MK, Holtz TR, Farlow JO editors. *The Complete Dinosaur*, Bloomington: Indiana University Press. 2012, pp. 505–525.
40. CARPENTER K. Redescription of *Ankylosaurus magniventris* Brown 1908 (Ankylosauridae) from the upper Cretaceous of the Western Interior of North America. *Can J. Earth Sci.* 2004; 41: 961–986.
41. Blows W, Honeysett K. New teeth of nodosaurid ankylosaurs from the Lower Cretaceous of Southern England. *Acta Palaeont Pol.* 2014; 59(4): 835–841.
42. Salgado L, Gasparini Z. Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). *Geodiversitas*, 2006; 28(1): 119–135.
43. Arbour VM, Lech-Hernes NL, Guldberg TE, Hurum JH, Currie PJ. An ankylosaurid dinosaur from Mongolia with in situ armour and keratinous scale impressions. *Acta Palaeont Pol.* 2013; 58: 55–64.
44. Arbour VM, Burns ME, Bell PR, Currie PJ. Epidermal and dermal integumentary structures of ankylosaurian dinosaurs. *J Morph.* 2014; 275: 39–50. <https://doi.org/10.1002/jmor.20194> PMID: 24105904
45. KIRKLAND JI, ALCALÁ L, LOEWEN MA, ESPÍLEZ E, MAMPEL L, WIERSMA JP. The Basal Nodosaurid Ankylosaur *Europelta carbonensis* n. gen., n. sp. from the Lower Cretaceous (Lower Albian) Escucha Formation of Northeastern Spain. *PLoS ONE.* 2013; 8(12): e80405. <https://doi.org/10.1371/journal.pone.0080405> PMID: 24312471
46. Ricqlès A de, Pereda Suberbiola X, Gasparini Z, Olivero E. Histology of the dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antarctica. *PE-APA.* 2001; 7: 171–174.
47. Dodson P, Krause DW, Forster CA, Sampson SD, Ravoavy F. Titanosaurid (Sauropoda) osteoderms from the Late Cretaceous of Madagascar. *J Vert Paleontol.* 1998; 18: 563–568.
48. D’Emic MD, Wilson JA, Chatterjee S. The titanosaur (Dinosauria: Sauropoda) osteoderm record: review and first definitive specimen from India. *J Vertebr Paleontol.* 2009; 29:165–177.
49. Cerda IA, Powell JE. Dermal armor histology of *Saltasaurus loricatus*, an Upper Cretaceous sauropod dinosaur from Northwest Argentina. *Acta Palaeontol Pol.* 2010; 55:389–398.
50. Burns ME, Vavrek MJ. Probable ankylosaur ossicles from the Middle Cenomanian Dunvegan Formation of Northwestern Alberta, Canada. 2014. *PLoS ONE* 9(5): e96075. <https://doi.org/10.1371/journal.pone.0096075> PMID: 24816807
51. Cerda IA, Gasparini Z, Coria RA, Salgado L, Reguero M, Ponce et al. Paleobiological inferences for the Antarctic dinosaur *Antarctopelta oliveroi* (Ornithischia: Ankylosauria) based on bone histology of the holotype. *Cretac Res.* 2019; 103:104171.
52. MOLNAR RE. Armour of the small ankylosaur *Minmi*. In: Carpenter K, editor. *The Armored Dinosaurs*. Bloomington: Indiana University Press; 2001. pp. 341–362.
53. Leahey LG, Molnar RE, Carpenter K, Witmer LM, Salisbury SW. Cranial osteology of the ankylosaurian dinosaur formerly known as *Minmi* sp. (Ornithischia: Thyreophora) from the Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia. *PeerJ.* 2015; 3: e1475. <https://doi.org/10.7717/peerj.1475> PMID: 26664806
54. BROWN CM. An exceptionally preserved armored dinosaur reveals the morphology and allometry of osteoderms and their horny epidermal coverings. 2017. *PeerJ* 5:e4066. <https://doi.org/10.7717/peerj.4066> PMID: 29201564

55. Young MT, Steel L, Brusatte SL, Foffa D, Lepage Y. Tooth serration morphologies in the genus *Machimosaurus* (Crocodylomorpha, Thalattosuchia) from the Late Jurassic of Europe. *Roy Soc Open Sci*. 2014; 1: 140269. <https://doi.org/10.1098/rsos.140269> PMID: 26064563
56. Gasparini Z, Chiappe LM, Fernández M. A new senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodylian. *J Vert Paleontol*. 1991; 11 (3): 316–333.
57. BUFFETAUT E. A new crocodylian from the Cretaceous of southern Morocco. *C. R. Acad. Sci*. 1994; 319: 1563–1568.
58. Carvalho IS, Ribeiro LC, Ávila L. *Uberabasuchus terrificus* sp. nov. a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous) Brazil. *Gondwana Res*. 2004; 7: 975–1002.
59. Carvalho IS, Vasconcelos FM, Tavares SAS. *Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. *Zootaxa* 2007; 1607: 35–46.
60. Barrios F, Paulina-Carabajal A, Bona P. A new peirosaurid (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Patagonia, Argentina. *Ameghiniana*. 2015; 53: 14–25.
61. Lio G, Agnolín FL, Juárez Valieri R, Filippi L, Rosales D. A new peirosaurid (Crocodyliformes) from the Late Cretaceous (Turonian–Coniacian) of Patagonia, Argentina. *Hist Biol*. 2015; 28: 835–841.
62. Coria RA, Ortega F, Arcucci AB, Currie PJ. A new and complete peirosaurid (Crocodyliformes, Notosuchia) from Sierra Barrosa (Santonian, Upper Cretaceous) of the Neuquén Basin, Argentina. *Cret Res*. 2019; 95: 86–105.
63. Lamanna MC, Casal GA, Ibiricu LM, Martínez RDF. A new peirosaurid crocodyliform from the Upper Cretaceous Lago Colhué Huapi Formation of Central Patagonia, Argentina. *Ann Carnegie Mus*. 2019; 85 (3): 193–211.
64. GASPARINI Z. Una nueva familia de cocodrilos zifodontes cretácicos de América del Sur. V° Congreso Latinoamericano de Geología, Actas. 1982; 4: 317–329.
65. Larsson HCE, Sues H-D. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zool J Linnean Soc*. 2007; 149: 533–567.
66. TURNER AH. Crocodyliform biogeography during the Cretaceous: evidence of Gondwana vicariance from biogeographical analysis. *Proc Roy Soc Lond, B*. 2004; 271: 2003–2009. <https://doi.org/10.1098/rspb.2004.2840> PMID: 15451689
67. Candeiro CR, Martinelli AG. Paleogeographical and chronostratigraphical distribution of mesoeucrocodylian species from the Upper Cretaceous beds from Bauru (Brazil) and Neuquén (Argentina) Groups, southern South America. *J South Amer Earth Sci*. 2006; 22: 116–129.
68. Ibrahim N, Sereno PC, Varricchio DJ, Martill DM, Duthieil DB, Unwin DM, et al. Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. *ZooKeys*. 2020; 928: 1–216. <https://doi.org/10.3897/zookeys.928.47517> PMID: 32362741
69. Young MT, Brusatte SL, Beatty BL, Andrade MB, Desojo JB. Tooth-on tooth interlocking occlusion suggests macrophagy in the Mesozoic marine crocodylomorph *Dakosaurus*. *Anat Rec*. 2012; 295 (7): 1147–1158. <https://doi.org/10.1002/ar.22491> PMID: 22577071
70. Filippi L, Martinelli AG, Garrido AC. Una nueva asociación de dientes de vertebrados para la Formación Bajo de la Carpa (Santoniense, Cretácico Superior) en Rincón de los Sauces, Neuquén, Argentina. *Spanish J Palaentol*. 2015; 30 (2): 223–238.
71. ERICKSON GM. Daily deposition of dentine in juvenile *Alligator* and assessment of tooth replacement rates using incremental line counts. *J Morphol*. 1996; 228: 189–194. [https://doi.org/10.1002/\(SICI\)1097-4687\(199605\)228:2<189::AID-JMOR7>3.0.CO;2-0](https://doi.org/10.1002/(SICI)1097-4687(199605)228:2<189::AID-JMOR7>3.0.CO;2-0) PMID: 29852586
72. Larsson HCE, Sidor CA. Unusual crocodyliform teeth from the Late Cretaceous (Cenomanian) of southeastern Morocco. *J Vert Paleontol*. 1999; 19 (2): 398–401.
73. CANUDO JI. Una mirada de dentista: Los dientes de los dinosaurios saurópodos. *Asociación Paleontológica Aragonesa*, 2002; 32: 12–24.
74. D’Emic MD, Whitlock JA, Smith KM, Fisher DC, Wilson JA. Evolution of high tooth replacement rates in sauropod dinosaurs. *PLoS ONE*. 2013; 8(7): e69235. <https://doi.org/10.1371/journal.pone.0069235> PMID: 23874921
75. RAUHUT OWM. A reappraisal of a putative record of abelisauroid theropod dinosaur from the Middle Jurassic of England. *Proc Geol Assoc*. 2012; 123(5) 779–786.
76. Mocho P, Royo-Torres R, Mlafaia E, Escaso F, Ortega F. Sauropod tooth morphotypes from the Upper Jurassic of the Lusitanian Basin (Portugal). *Pap Palaeontol*. 2017; 3(2): 559–595.

77. Holwerda FM, Díez Díaz V, Blanco A, Montie R, Reumer JWF. Late Cretaceous sauropod tooth morphotypes may provide supporting evidence for faunal connections between North Africa and Southern Europe. *PeerJ*. 2018; 6:e5925. <https://doi.org/10.7717/peerj.5925> PMID: 30473934
78. MOLNAR RE. Preliminary report of a new ankylosaur from the Early Cretaceous of Queensland, Australia. *Mem Queensl Mus*. 1996; 39: 653–668.
79. Salgado L, Coria A. First evidence of an ankylosaur (Dinosauria, Ornithischia) in South America. *Ameghiniana*. 1996; 33: 367–371.
80. Coria RA, Salgado L. South American Ankylosaurs. In: Carpenter K, editor. *The Armored Dinosaurs*. Indiana University Press; 2001. pp. 159–168.
81. De Valais S, Apesteguía S, Udrizar Sauthier D. Nuevas evidencias de dinosaurios de la Formación Puerto Yerúa (Cretácico), Provincia de Entre Ríos, Argentina. *Ameghiniana*. 2002; 40: 507–511.
82. Gasparini Z, Sterli J, Parras A, O’Gorman JP, Salgado L, Varela J, et al. Late Cretaceous reptilian biota of the La Colonia Formation, central Patagonia, Argentina: Occurrences, preservation and paleoenvironments. *Cret Res*. 2015; 54: 154–168.
83. Murray A, Riguetti F, Rozadilla S. New ankylosaur (Thyreophora, ornithischia) remains from the Upper Cretaceous of Patagonia. *J S Am Earth Sci*. 2019; 96:102320.
84. Ősi A, Rabi M, Makádi L. An enigmatic crocodyliform tooth from the bauxites of western Hungary suggests hidden mesoeucrocodylian diversity in the Early Cretaceous European archipelago. *PeerJ*. 2015; 3: e1160. <https://doi.org/10.7717/peerj.1160> PMID: 26339542
85. Dal Sasso C, Pasini G, Fleury G, Maganuco S. *Razanandrongobe sakalavae*, a gigantic mesoeucrocodylian from the Middle Jurassic of Madagascar, is a oldest known notosuchian. *PeerJ*. 2017; 5: e3481. <https://doi.org/10.7717/peerj.3481> PMID: 28690926
86. WOODWARD AS. On two Mesozoic crocodylians *Notosuchus* (genus novum) and *Cynodontosuchus* (genus novum) from the red sandstone of the territory of Neuquén (Argentine Republic). *Anal Mus La Plata*. 1896; 6: 1–20.
87. Martinelli AG, Pais DF. A new baurusuchid crocodyliform (Archosauria) from the Late Cretaceous of Patagonia (Argentina). *C R Palevol*. 2008; 7(6): 371–381.
88. Martinelli AG, Sertich JJW, Garrido AC, Pradeiro AM. A new peirosaurid from the Upper Cretaceous of Argentina: implications for specimens referred to *Peirosaurus torminni* Price (Crocodyliformes: Peirosauridae). *Cret Res*. 2012; 37: 191–200.
89. Pol D, Gasparini Z. 2007. Crocodyliformes. In: Gasparini Z, Salgado L, Coria RA, editors. *Patagonian Mesozoic Reptiles*. Bloomington: Indiana University Press; 2007. pp. 116–142.
90. Leardi JM, Pol D. The first crocodyliform from the Chubut Group (Chubut Province, Argentina) and its phylogenetic position within basal Mesoeucrocodylia. *Cret Res*. 2009; 30: 1376–1386.
91. Filippi L, Barrios F, Garrido AC. A new peirosaurid from the Bajo de la Carpa Formation (Upper Cretaceous, Santonian) of Cerro Overo, Neuquén, Argentina. *Cret Res*. 2018; 83: 75–83.
92. Leardi JM, Pol D, Gasparini Z. New Patagonian baurusuchids (Crocodylomorpha; Notosuchia) from the Bajo de la Carpa Formation (Upper Cretaceous; Neuquén, Argentina): new evidence of the early sebecosuchian diversification in Gondwana. *C R Palevol*. 2018; 17 (8): 504–521.
93. Riff D, Kellner AWA. On the dentition of *Baurusuchus pachecoi* Price (Crocodyliformes, Metasuchia) from the Upper Cretaceous of Brazil. *Bol Mus Nac, Geol*. 2001; 59: 1–15.
94. Torices A, Currie PJ, Canudo JI, Pereda-Suberbiola X. Theropod dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain. *Acta Palaeontol Pol*. 2013; 60: 611–626.
95. Niedźwiedzki G, Pienskowski G. A dinosaur track association from the Early Jurassic deltaic deposits of Podole near Opatów, Poland. *Geological Q*. 2004; 48(4):333–338.
96. Petti FM, Porchetti SD, Sacchi E, Nicosia U. A new purported ankylosaur trackway in the Lower Cretaceous (lower Aptian) shallow-marine carbonate deposits of Puglia, southern Italy. *Cret Res*. 2010; 31:546–552.
97. Calvo JO, Porfiri JD, González-Riga BJ, Kellner AWA. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *An Acad Bras. Cienc*. 2007; 79 (3): 529–541. <https://doi.org/10.1590/s0001-37652007000300013> PMID: 17768539
98. Ibiricu LM, Casal GA, Martínez RD, Avarez BN, PoropaT ST. New materials and an overview of Cretaceous vertebrates from the Chubut Group of the Golfo San Jorge Basin, central Patagonia, Argentina. *J South Am Earth Sci*. 2020; 98: 102460.
99. Pol D, Leardi JM. Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. In: FERNÁNDEZ M, HERRERA Y, editors. *Reptiles Extintos. Volumen en Homenaje a Zulma Gasparini*. PE-APA. 2015; 15(1):172–186.

100. Lyson TR, Longrich NR. Spatial niche partitioning in dinosaurs from the latest cretaceous (Maastrichtian) of North America. *Proc Royal Soc B*. 2010; 278 (1709). <https://doi.org/10.1098/rspb.2010.1444> PMID: 20943689
101. Martínez LCA, Iglesias A, Artabe AE, Varela A, Apesteguía S. A new Encephalartea trunk (Cycadales) from the Cretaceous of Patagonia (Mata Amarilla Formation, Austral Basin), Argentina. *Cret Res*. 2017; 72: 81–94.
102. Coombs W Jr, Deméré TA. A Late Cretaceous nodosaurid ankylosaur (Dinosauria: Ornithischia) from marine sediments of coastal California. *J Paleontol*. 1996; 70: 311–326.
103. Butler RJ, Barrett PM. Palaeoenvironmental controls on the distribution of Cretaceous herbivorous dinosaurs. *Naturwissenschaften*. 2008; 95: 1027–1032. <https://doi.org/10.1007/s00114-008-0417-5> PMID: 18581087
104. Arbour V, Zanno L, Gates TA. Ankylosaurian dinosaur palaeoenvironmental associations were influenced by extirpation, sea-level fluctuation, and geodispersal. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2016; 449: 289–299.