



BIOEROSION TRACE FOSSILS ON DINOSAUR BONES FROM THE LAGO COLHUÉ HUAPI FORMATION, UPPER CRETACEOUS OF CENTRAL PATAGONIA, ARGENTINA

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ABSTRACT – We describe for the first time in the Lago Colhué Huapi Formation (Coniacian–Maastrichtian), south Central Patagonia, Argentina, continental bioerosion traces on dinosaur remains. Specifically, six different morphotypes, showing also different morphologic patterns, were identified. The preliminary identification of the trace makers include: crocodyliform, possibly a peirosaurid notosuchian (morphotypes A and B), a theropod dinosaur (morphotype C), and the activity of arthropod pupation (morphotype D) and insects such as termites and dermestids (morphotypes E and F). This study increases our knowledge about the biodiversity registered to the moment in the Lago Colhué Huapi Formation and specifically for the “middle section” of this formation, probably Santonian–early Maastrichtian in age. These bioerosion traces support a warm climate with periods of semi-aridity or at least drier conditions as it was proposed for this interval of time in this section of the formation.

Keywords: bone modification, ichnofossils, Late Cretaceous.

RESUMO – Pela primeira vez foi descrito na Formação Lago Colhué Huapi (Coniaciano–Maastrichtiano), centro-sul da Patagônia, Argentina, vestígios de bioerosão continental em fragmentos de dinossauros. Foram identificados seis morfotipos distintos, os quais também apresentaram padrões morfológicos diferentes entre si. A identificação preliminar dos organismos produtores de erosão inclui: Crocodylifórmes, possivelmente um peirosauridae notosuchio (morfotipos A e B), um dinossauro terópode (morfotipo C), a pupação de artrópodes (morfotipo D) e atividades de insetos como cupins e dermestídeos (morfotipos E e F). Este estudo contribui para o conhecimento sobre a biodiversidade documentada até o momento na Formação Lago Colhué Huapi e especificamente para a “seção média” desta unidade, que provavelmente data do período Santoniano–Maastrichtiano inicial. Esses traços de bioerosão sustentam um clima quente com períodos de semiaridez ou pelo menos condições mais secas, como foi proposto para esse intervalo de tempo nesta seção da formação.

Palavras-chave: modificação óssea, icnofósseis, Cretáceo Superior.

INTRODUCTION

In the fossil record, the interaction among organisms from the same environment can be indirectly inferred through the taxonomic diversity, phylogenetic affinities and morphofunctional interpretations of the coexisting fossil fauna in the area. Thus, it also can be inferred based on the arrangement in the field of the remains of carnivorous and herbivorous organisms (Kowalewski, 2002). In addition, the

mechanical alteration produced by one organism on a remnant of another organism is direct evidence of interaction between predators and prey (Kowalewski, 2002; Filippi & Bellardini, 2021). Bioerosions are a specific type of taphonomic alterations caused by biological agents on consolidated surfaces of hard sediments such as rocks, leaflets, shells, wood or bones, among others (Neumann, 1966; Frey, 1973; Warne, 1975; Ozeki *et al.*, 2020). In particular, traces left on bones by biotic and trophic interaction between tetrapods and other invertebrate organisms are not frequent; however,

they are very useful for understanding biodiversity as well as they are evidence of trophic and paleoecological relationships that sometimes cannot be interpreted from the fossil record (Behrensmeyer, 1978; Tappen, 1994; Roberts *et al.*, 2007; Longrich & Ryan, 2010; Saneyoshi *et al.*, 2011; Belaústegui *et al.*, 2012; De Mendoza & Haidr, 2018; Paes Neto *et al.*, 2018; Augustin *et al.*, 2019, 2020; Benyoucef & Bouchemla, 2023).

Likewise, bioerosional marks have also been used to reconstruct the taphonomic history of bone accumulations (Jans, 2008; Bader *et al.*, 2009; Huchet, 2014; Talevi & Brezina, 2019). Different processes may be involved in bioerosion, depending on the type of activity of the biological agent on the substrate, which will generate different trace fossil designs (Höpner & Bertling, 2017; Talevi & Brezina, 2019). The importance of the study of bioerosion traces and their application in the reconstruction of marine paleoenvironments has been highlighted (*e.g.*, Rhoads, 1975; Wilson, 2007; Jamison-Todd *et al.*, 2023). Nevertheless, their application in continental paleoenvironments is less addressed (*e.g.*, Roberts *et al.*, 2007; de Valais *et al.*, 2012; Pirrone *et al.*, 2014a,b; Lucas, 2016; Freimuth & Varricchio, 2019).

In this context, bioerosion traces preserved in dinosaur bones have been described in detail in different sites around the world, including those made by insects on Triassic bones (*e.g.*, Leal *et al.*, 2002; Paes Neto *et al.*, 2016; Cunha *et al.*, 2024). Likewise, Jurassic traces related with predation of crocodiles in turtle and dinosaur bones (*e.g.*, Britt *et al.*, 2008; Bader *et al.*, 2009; Augustin *et al.*, 2020), whereas those from the Cretaceous are also described (*e.g.*, Longrich & Ryan 2010; Schwimmer & Harrell, 2010; Augustin *et al.*, 2019). Nevertheless, detailed studies of bioerosion traces on continental vertebrates are relatively less common, standing out the works of Fiorelli (2010), de Valais *et al.* (2012), Pirrone *et al.* (2014a,b), Gianechini & de Valais (2015), and Filippi & Bellardini (2021). However, in the Cretaceous continental environments of the Golfo San Jorge Basin, it is the first time that a study of this characteristic is performed, in other words, focusing only on bioerosion traces.

Therefore, the present work constitutes the first study of different fossil traces of bioerosion present in dinosaur bones found in an outcrop of the “middle section” of the Lago Colhué Huapi Formation (Coniacian–Maastrichtian); these stratigraphic levels, preliminarily assigned, to the Santonian–early Maastrichtian. This area is informally referred to as “Playa Kruger”. Furthermore, the analysis and identification of the bioerosion trace fossils in the dinosaur bones enhance our comprehension of the paleoecology and biodiversity of the youngest unit of the Chubut Group in the Golfo San Jorge Basin.

Institutional abbreviations. UNPSJB-PV, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia; Chubut; Argentina.

GEOLOGICAL SETTING

The Golfo San Jorge Basin is located in central Patagonia, Argentina, between latitudes 44°S and 47°S and meridians

65°W and 71°W. It is bordered to the south by the Deseado Massif region, to the north by the Cañadón Asfalto basin, to the west by the Andes Cordillera, and to the east by the oceanic shelf (Figure 1A–B). The origin of this basin is linked to the extensional stresses that caused the dismemberment of the Gondwana supercontinent and the origin of the Atlantic Ocean from the Upper Jurassic (Fitzgerald *et al.*, 1990; Figari *et al.*, 1999), while for other authors it corresponds to a synorogenic foreland basin (Gianni *et al.*, 2015; Navarrete *et al.*, 2015).

The Chubut Group (Lesta & Ferello, 1972) stands out in the sedimentary fill of the basin, which includes deposits of lacustrine and fluvial origin with the participation of volcanoclastic material (Umazano *et al.*, 2008, 2012; Paredes *et al.*, 2015, 2021, among others). The age of the Chubut Group varies, being Barremian for Hechem and Strelkov (2002) and Vallati (2013), while Allard *et al.* (2022) suggest an age of middle Albian, and De Sosa Tomas *et al.* (2023) early Albian. The age for the top of the Group is regarded as late Maastrichtian (Casal *et al.*, 2015; Vallati *et al.*, 2016, 2020). The Chubut Group is comprised of the Pozo D-129, Matasiete, Castillo, Bajo Barreal, Laguna Palacios and Lago Colhué Huapi formations (Figure 1C).

The bones that are the subject of this work were found in levels of the informally named “middle section” of the youngest unit of the Chubut Group, the Lago Colhué Huapi Formation (Coniacian–Maastrichtian, Casal *et al.*, 2015, 2016). Based on faunal content and stratigraphic relationships, the “middle section” levels exposed on the eastern shore of Lake Colhué Huapi and the cliff bordering it at Playa Kruger would correspond to the Santonian–early Maastrichtian (Figure 2). In times of high lake level, the shore is partially or entirely covered by water up to the edge of the cliff. On the other hand, in dry times, thick to medium-sized sandstones of a fluvial channel exhumed by the current erosive action of the aforementioned lake are exposed on the coast and where numerous fossil vertebrate remains are deposited (Casal *et al.*, 2016; Castaño *et al.*, 2019; Ibiricu *et al.*, 2020) (Figure 2).

MATERIAL AND METHODS

The trace fossils were identified in six ($n = 6$) of the 91 trace fossil remains studied ($n = 91$). Most of the bioerosion traces are present in isolated remains (UNPSJB-PV1036; 1037; 1045) that are housed in the “Paleontology Collection of the Universidad Nacional de la Patagonia San Juan Bosco (Repository of Scientific and Didactic Materials “Dr. Eduardo Musacchio”), Comodoro Rivadavia; Chubut; Argentina, under the acronym UNPSJB-PV. The rest of the materials bearing trace fossils are at the field (see Results and Discussion section). The identified traces were cleaned with soft brushes and acetone to remove all sediment.

The traces are currently grouped in six morphotypes (A to F), depending on the morphology of the traces. In addition, they were recorded in five different anatomical dinosaur bones from the appendicular and axial skeleton, all of which were preliminarily assigned to sauropod dinosaurs. We use the methodology proposed by Pirrone *et al.* (2014a) to describe

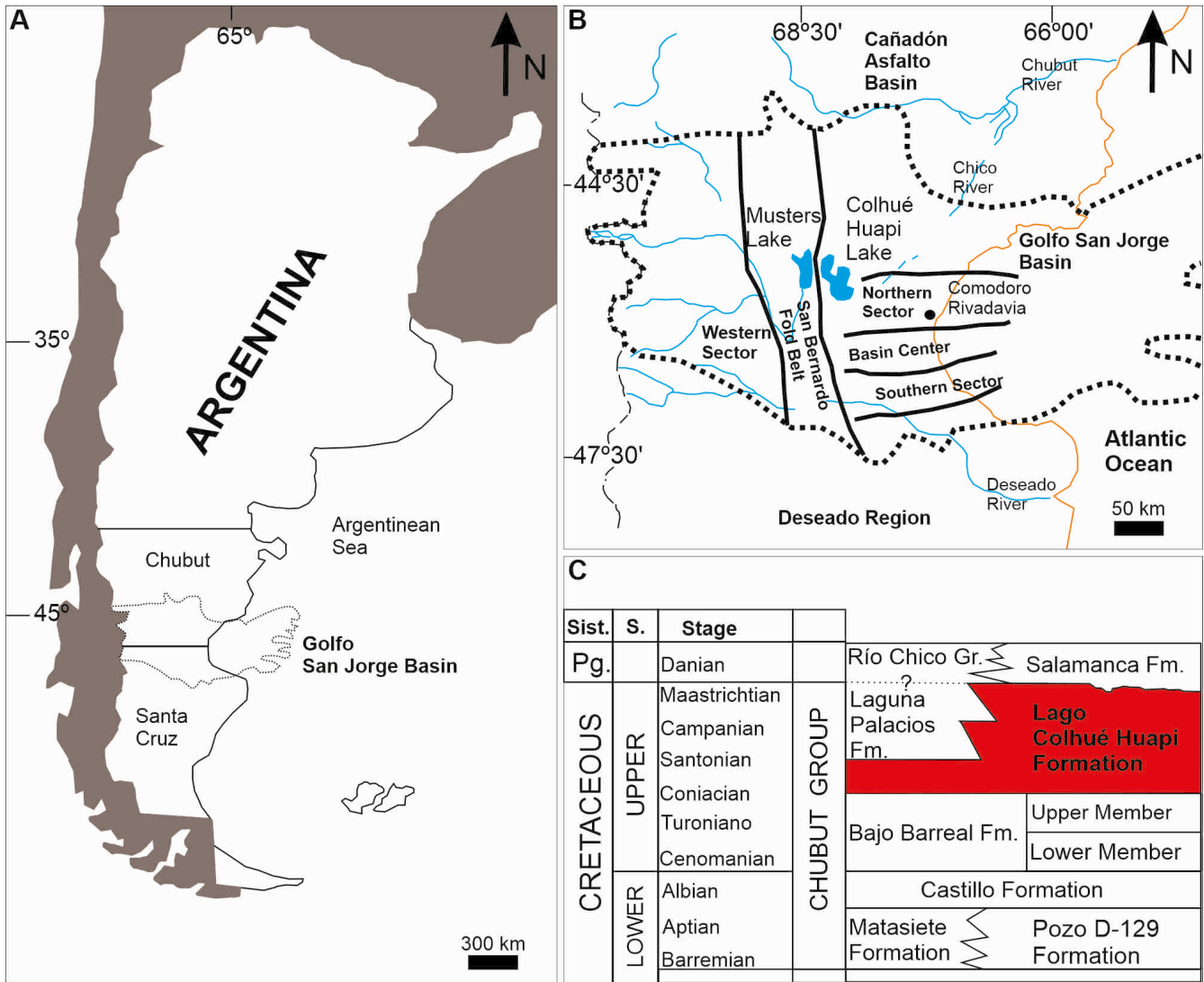


Figure 1. A, geographic location map of the Golfo San Jorge Basin, Argentina. B, structural context of the basin. The thick lines indicate the main structures of the basin (modified from Figari *et al.*, 1999). C, stratigraphic chart of the Chubut Group in the Golfo San Jorge Basin (modified from Casal *et al.*, 2015).

or characterize the shape, location, and orientation with respect to the axial axis of the fossil, size, and depth. Thus, we follow the same authors to classify the design of the trace fossils according to its morphology as grooves, striations, pits, perforations, tubes, chambers and canals. For tetrapod traces, the proposal of Schneider *et al.* (2022) was followed for trace fossil caused by carnivore bites, including pits, scores/striations, punctures, furrows and fracturing.

Trace fossil remains were photographed with a Nikon P900 24–2000 digital camera with a Raynox macro lens in normal view and under low angle lighting. Each trace’s length, width, and depth were measured using Stainless Hardened digital calipers. For traces with elliptical morphology, the largest and the minor diameters were measured perpendicularly. The description was performed using a Motic SMZ-168 binocular magnifier, 800x USB digital microscope and digital caliper. Measurements are taken in millimeters (mm).

The bones had no mechanical preparation in order to avoid damage to the bone surface that may simulate bioerosional traces (Wiest *et al.*, 2018); therefore, we can discard the possibility of an artificial origin for the trace fossils analyzed.

RESULTS AND DISCUSSION

Morphotype A. This bioerosion trace is displayed in an incomplete appendicular bone (Figure 3A). This material was analyzed in situ, because it is in coarse sandstone matrix of a fluvial channel. The lower third of the shaft exhibits a well-marked groove associated with a perforation (Figure 3A–B). The groove is arranged perpendicular to the axial axis of the shaft. The groove has a length of 8 mm, a maximum width of 3.5 mm, and a depth of 2 mm (Figure 3C). It begins with a sharp edge and ends in a perforation that has a subcircular

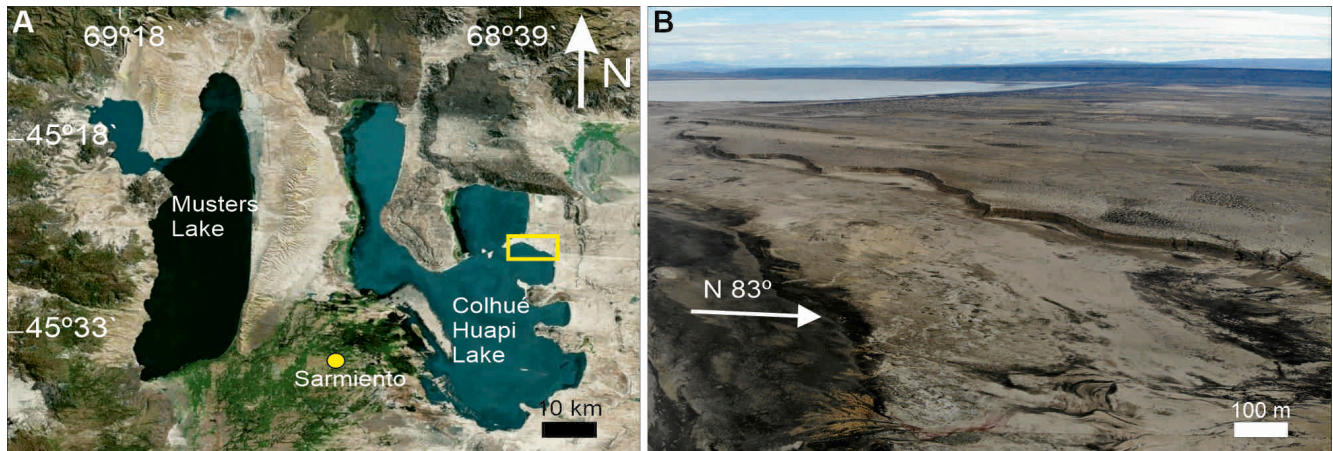


Figure 2. **A**, image from Landsat/Copernicus 2018; Google Earth, accessed December 2021. The yellow rectangle indicates the study area. **B**, view to the north of the study area showing the sandstones of a fluvial channel of the Lago Colhué Huapi Formation exposed in the dry lakebed and where the fossils were found, in the background the cliffs with strata of the same unit.

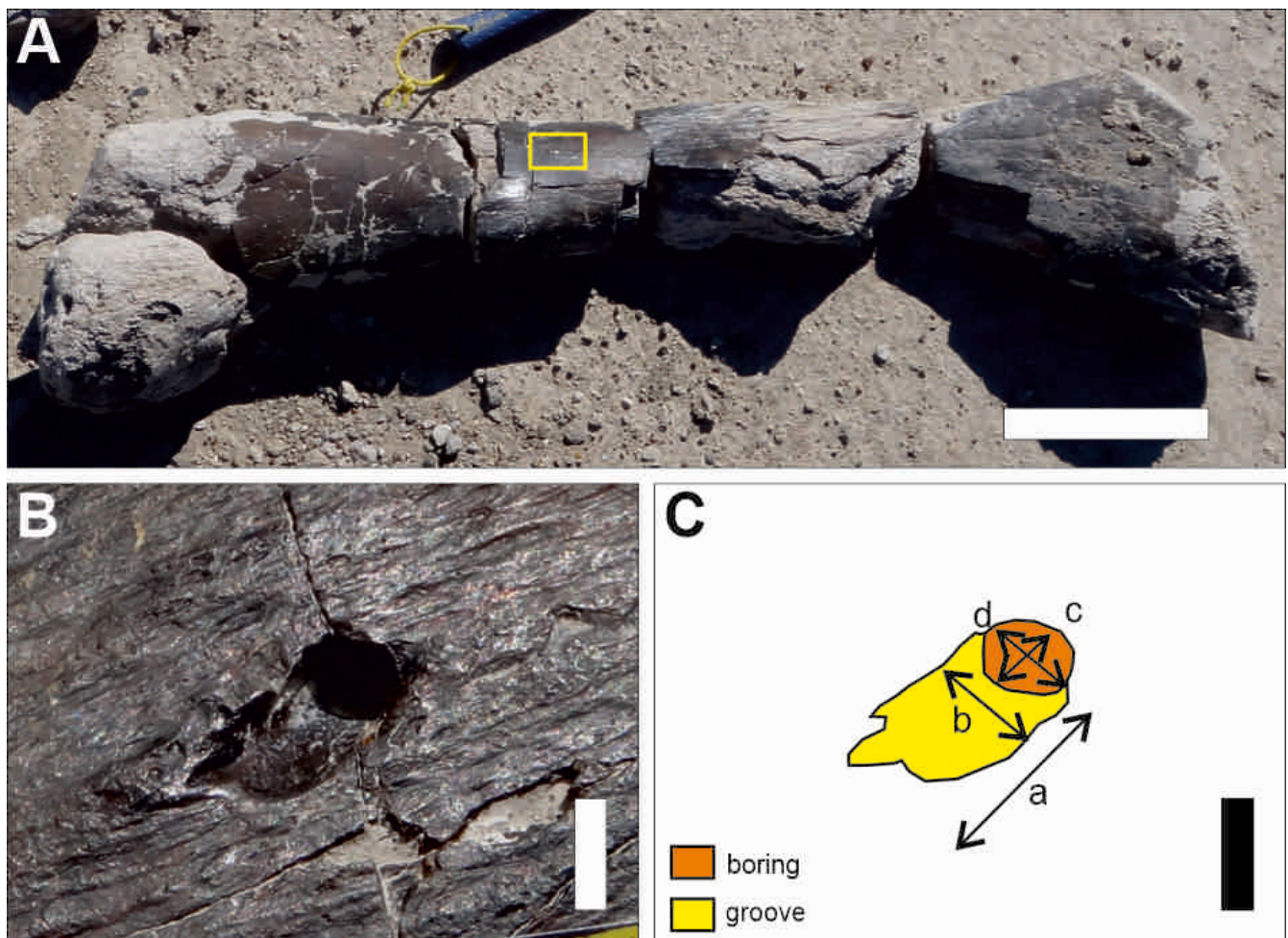


Figure 3. **A**, incomplete appendicular bone, probably of a titanosaur sauropod. Yellow rectangle indicates location of bioerosion marks. **B**, detail of morphotype A. **C**, schematic of morphotype A showing perforation and sulcus dimensions. a: length of sulcus, b: width of sulcus, c: minor diameter of perforation, d: major diameter of perforation. Scale bars: A = 15 cm; B–C = 3 mm.

to elliptical cross-section, with a major diameter of 2.5 mm, a minor diameter of 2 mm, and depth of 5 mm (Figure 3C).

Identification of the trace maker. Morphologically similar traces were interpreted by Drumheller & Brochu (2014) and Drumheller *et al.* (2014) as crocodyliform bite marks. Likewise, other authors have studied traces produced by this group of reptiles in the fossil record as well as in actualistic experiments (Njau & Blumenschine, 2006; Noto *et al.*, 2012; Boyd *et al.*, 2013; Njau & Gilbert, 2016). In particular, that of Njau & Gilbert (2016), based on actualistic feeding monitoring, supports that those marks with this morphology indicates lateral movements of the crocodyliform skull while maintaining a toothed grip.

Among the numerous experimental studies about actualistic tooth marks generated by carnivore animals, Massigoge *et al.* (2014, see fig. 2) attribute similarly patterned marks to pampas fox (*Lycalopex gymnocercus*) and wildcat (*Leopardus geoffroyi*). Orihuela *et al.* (2016, see fig. 12), recognized traces with a similar design in zooarchaeological remains attributed to canid carnivores. Likewise, authors of this work (GAC and LMI) observed marks with the same pattern on the pelvis of a Patagonian ñandú (*Rhea pennata*) caused by the action of a puma (*Puma concolor*) (Figure 4), which is the main predator in Patagonia (Kaufmann *et al.*, 2016; Marchionni *et al.*, 2020). Consequently, the design of this morphotype suggests predation, with a strong initial pressure where the teeth are driven into the bone, breaking bone tissue and perforating it.

In this context, and based on the morphology of the perforation present in the bone of the Lago Colhué Huapi Formation, and the fossil record of these levels, it is considered that the producer of this bioerosion trace would most likely correspond to a crocodyliform. In this regard, Castaño *et al.* (2019) and Alvarez *et al.* (2023) documented the finding of isolated crocodyliform teeth in “Playa Kruger”, while in possibly equivalent stratigraphic levels Lamanna *et al.* (2019) described the peirosaurid *Colhuehuapisuchus lunai*. However, it cannot be ruled out that the producer was a theropod dinosaur, taking into account that the premaxillary

teeth show a subcircular cross-section (Casal *et al.*, 2009) as those marks recovered in the appendicular bone. In these stratigraphic levels, Alvarez *et al.* (2023) described an isolated abelisaurid tooth supporting that this group of theropods as possible producers as well.

Morphotype B. As in the case of the previous morphotype, the bone carrying of the morphotype B was in situ included in a coarse fluvial sandstone matrix; therefore, it was also analyzed directly at the field. The bone is identified as a probable incomplete ulna of a titanosaur sauropod (Figure 5A). On the surface of the diaphysis, there are two holes separated from each other by a distance of 130 mm. Thus, they are aligned with respect to the axial axis of the bone (Figure 5A). The holes are subcircular in shape and the measurements are (left to right): 10 mm in major diameter and 8 mm in minor diameter, and 8 mm in major diameter and 6 mm in minor diameter respectively (see Figure 5B). The depth of each hole is greater towards the medial margin of the bone reaching 9 mm. The holes gradually decrease towards the opposite sector, showing wedge geometry.

Identification of the trace maker. The elliptical morphology of the orifices is consistent with marks described and interpreted as the action of crocodyliform bites on vertebrates (*e.g.*, Schwimmer, 2002; Boyd *et al.*, 2013; Csiki *et al.*, 2010; Schwimmer & Harrell, 2010; Fiorelli, 2010). The present morphology would be diagnostic of the distal conical teeth of these predators, which tend to create subcircular orifices as a result of the compressive force (Njau & Gilbert, 2016). The separation between the two perforations supports a relatively large maker. In addition, the measurements of the holes and the distance between both perforations are in average to that recovered in the tooth and alveolus of Crocodyliformes (see Boyd *et al.*, 2013). Likewise, mentions of bite marks produced by large crocodiles on dinosaur remains are frequent (*e.g.*, Schwimmer, 2002; Rivera-Sylva *et al.*, 2009; Schwimmer & Harrell, 2010; Backwell *et al.*, 2012, among others). Therefore, the morphotype B is attributed to a crocodyliform, probably belonging to the Peirosauridae, already registered

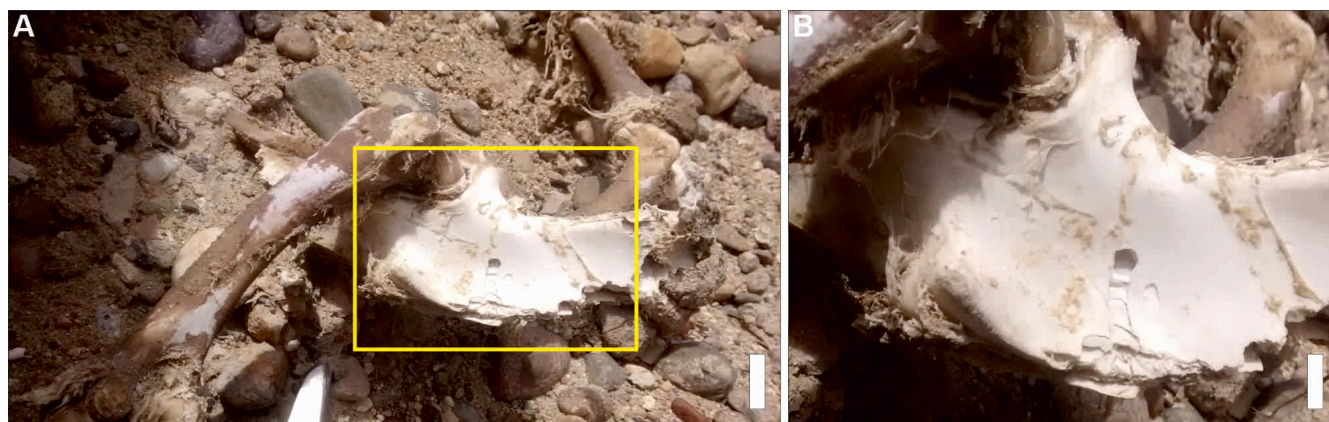


Figure 4. A, articulated pelvis and hind limb of *Rhea pennata* (ñandú patagónico) where the yellow rectangle indicates a bioerosion trace on the left ilium. B, detail view of the actual bioerosion trace consisting of hollow and groove and produced, probably, by *Puma concolor* (puma) and showing a design similar to morphotype A. Scale bars: A = 5mm; B = 2 mm.

in this formation in equivalent stratigraphic levels (Lamanna *et al.*, 2019).

Morphotype C. This morphotype is displayed in an incomplete, probably distal caudal vertebra (UNPSJB-PV 1037) of a titanosaur sauropod (Figure 6A). The vertebra exhibits two straight well marked grooves (=G1 and G2; Figure 6B–C). G1 is located on the posterior third of the left lateroventral face and it is obliquely oriented (Figure 6A, C). On the other hand, the G2 is arranged vertically on the

posterior edge of the right lateral face (Figure 4B, E). In G1 the maximum length is 27 mm, whereas the maximum width is 5 mm at the center, and 4 mm depth in the center while at the ends it does not exceed 2 mm of depth (Figure 6D). G2 has a total length of 50 mm, whereas the maximum width and depth are 5 mm and 10 mm respectively (Figure 6F).

Identification of the trace maker. Its origin would respond to the sliding of the teeth due to occlusion of the mouth simultaneously with the gradual increase in pressure,

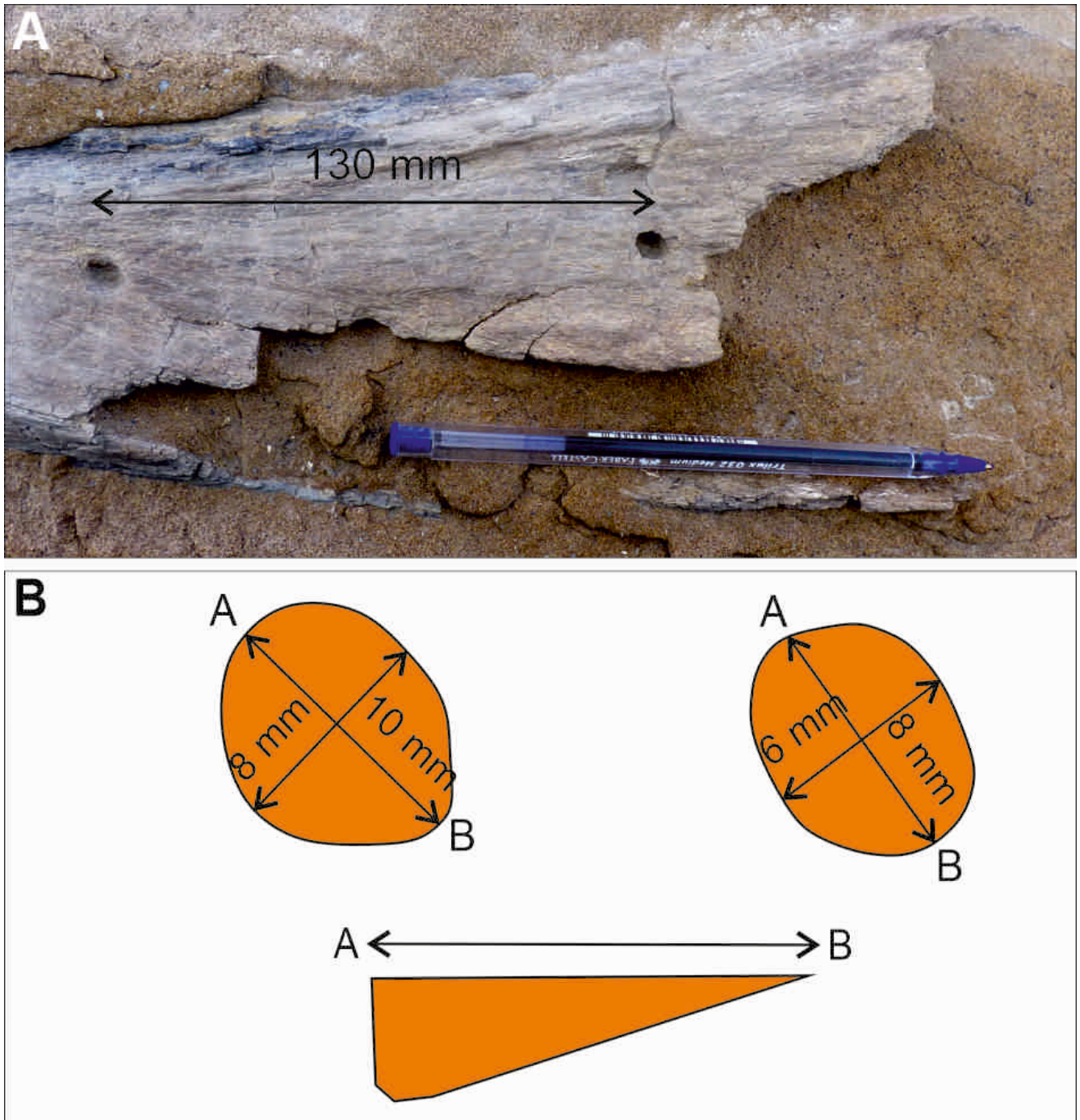


Figure 5. A, a probable incomplete ulna of titanosaur sauropod found in situ, showing three morphotype B. B, schematic of morphotype B showing the dimensions of the 2 holes and the design of the x-y cross section a-b of the hole.

generating an ever-deeper groove in the bone. According to Gangloff & Fiorillo (2010), parallel, straight or curved grooves, more or less deep and ending in a V-shape, are characteristic morphologies of a bite caused by theropod dinosaur premaxillary teeth. The laterally compressed shape of theropod teeth tends to create deeper V-shaped marks in cross section, as opposed to the more conical crocodyliform teeth which leave U-shaped marks transversely (Noto *et al.*, 2012). Similar marks attributed to theropods have been

documented in the fossil record on remains of sauropods (Bader *et al.*, 2009, fig. 10) and hadrosaurids (Rivera-Sylva *et al.*, 2012, fig. 1D), among others. Recently, Filippi & Bellardini (2021, fig. 3) reported deep parallel grooves in sauropod vertebral remains from the Santonian of the Bajo de la Carpa Formation and they are attributed to the action of a theropod dinosaur. Therefore, the asymmetry presented by the groove in a transversal direction in relation to the arrangement of the muscle fibers and the acute-angled ending in “V”

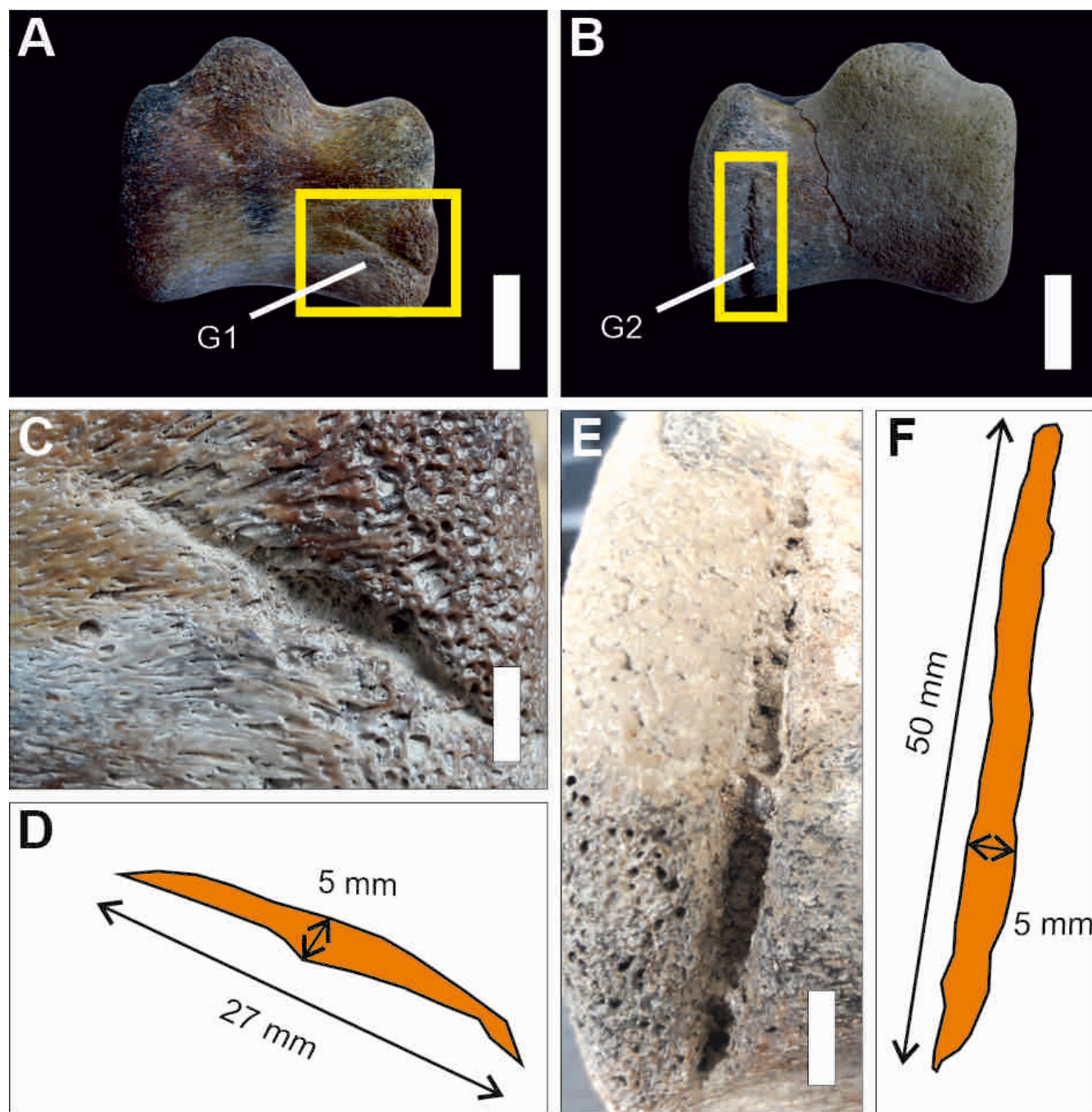


Figure 6. Probable distal caudal vertebra of a titanosaur sauropod (UNPSJB-PV 1037). **A**, left lateral view; **B**, right lateral view. The yellow rectangles indicate the location of the G1 and G2 grooves of morphotype C. **C**, detail view of the bioerosion trace formed by groove G1. **D**, schematic of groove G1. **E**, detail view of the bioerosion trace formed by groove G2. **F**, schematic of groove G2. Scale bars: A–B = 3 cm; C, E = 5 mm.

shaped, support the action of a theropod dinosaur. The marks are on the lateroventral aspect of the distal caudal centrum, near to the posterior articular surface an unusual bite site for a predator (Fiorillo, 1991; Pobiner, 2008; Filippi & Bellardini, 2021); therefore, it is most likely to the action of a scavenger. Finally, according to Drumheller *et al.* (2020) theropod tooth marks on the surface of bones are not frequently recovered in the fossil record, which may indicate that these organisms select for feeding soft tissues such as muscle or viscera, instead of bone tissue. In turn, this suggests that these traces in bones would be mainly accidental during feeding (Hone & Rauhut, 2010).

Morphotype D. The morphotype is exhibited in a probable distal caudal vertebra of a titanosaur sauropod (UNPSJB-PV 1036; Figure 7A). The marks, two sub-longitudinal grooves (G1 and G2), are in the anterior articular surface of the centrum, placed on the top portion of the articular surface (Figure 7B). The sinusoidal G1 shows a maximum length and of 30 mm and 2 mm respectively, whereas its maximum width is 3 mm. On the other hand, G2 displays a total length of 50 mm and maximum depth and width of 2 mm and 4 mm respectively (Figure 7C). The surface of both grooves is smooth, with no scratch marks or other visible alternations.

Identification of the trace maker. Traces on bones attributed to arthropods, specifically to insects, are relatively rare in both the fossil and modern records (Martin & West, 1995; West & Martin, 2002; West & Hasiotis, 2007). Nevertheless, this kind of alterations on fossil bones has been reported from the middle and late Triassic, late Jurassic, Cretaceous, Paleogene, and Neogene (Bader *et al.*, 2009; Cunha *et al.*, 2024). In this regard, Britt *et al.* (2008, fig. 2) recorded a series of grooves in a sauropod vertebra, interpreted as a product of dermestid action. On the other hand, Xing *et al.* (2015, fig. 3) reported alterations in dinosaur bones from the Middle Jurassic of China, represented by smooth grooves and interpreted as a product of the activity of terrestrial invertebrates. Huchet (2014, fig. 3) described smooth grooves in human bones, showing similar size to those currently herein described. The traces exhibited in UNPSJB-PV 1036 show similarities in their morphology, size, and design to those documented by

Britt *et al.* (2008) and Xing *et al.* (2015). The high diversity of arthropods makes the assignation of one of its members difficult, even though laboratory tests try to approximate it (Huchet, 2014; Backwell *et al.*, 2012; Parkinson, 2022). In this context, it is preliminarily interpreted that these traces may be the result of invertebrate activity, possibly arthropods.

Morphotype E and morphotype F. Both morphotypes are placed in a titanosaur left ulna (UNPSJB-PV 1045; Figure 8A). These biorosional traces are situated in different places of the ulna shaft. The morphotype E, is observed in the lateral surface of the diaphysis ventrally to the scar radial face (Figure 8A). This morphotype consists of depressions ornamented with overlapping of small grooves up to 2 mm length and irregularly arranged. In order to analyze this morphotype, we divide it in three zones depending on the characteristics of the grooves (Figure 8B–D). Zone 1 exhibited three shallow depressions ornamented with grooves with slight centripetal tendency (Figure 8B), whereas the grooves that ornament the depression which are located in zone 2 show a higher density. In addition, they are overlapping, although more randomly arranged (Figure 8C). On the other hand, the grooves of zone 3 are more centripetally positioned (Figure 8D). The remainder morphotype F is recognized on the posterior surface at the distal end of the ulna diaphysis (Figure 9A). As the morphotype E, the grooves are overlapping, but they display a zigzag pattern (Figure 9B–C). Individually, each groove has an average length of 5 mm, and the set of marks are subperpendicular to the axial axis of the fossil remains.

Identification of the trace maker. Similar morphologies as those seen in the morphotype E have been described in sauropod (Britt *et al.*, 2008), theropod (Gianechini & de Valais, 2015) and in an indeterminate dinosaur (Augustin *et al.*, 2019, 2020) remains. In particular, Augustin *et al.* (2020, fig. 2) interpreted these type of trace fossils as marks produced by termite activity. This type of producers starts with several grooves relatively shallow and as they move generate a central depression that is deeper. A similar activity or morphologic pattern was also described by Backwell *et al.* (2012, figs. 3 and 5) in actualist essays.

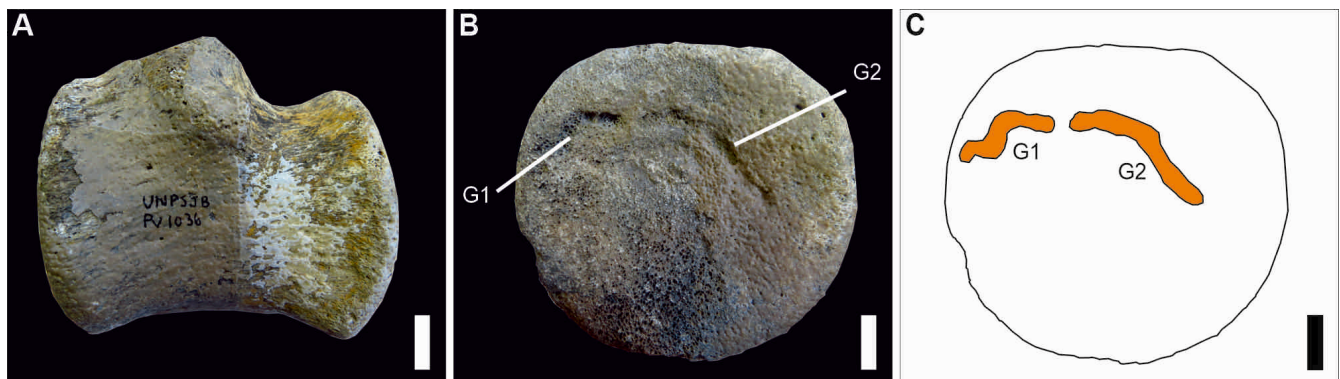


Figure 7. A, probable distal caudal vertebra of titanosaur sauropod (UNPSJB-PV 1036) in left lateral view. B, posterior view of vertebra UNPSJB-PV 1036. The yellow rectangle indicates the location of the G1 and G2 grooves of morphotype D. C, schematic of the posterior articular face of vertebra UNPSJB-PV 1036 and grooves G1 and G2. Scale bars = 3 cm.

On the other hand, Britt *et al.* (2008, fig. 1f) described a series of marks in the ornithomimid *Camptosaurus* similar in morphology, design and size to those seen in UNPSJB-PV 1045. They attributed these traces to the action of dermestid jaws. Gianechini & de Valais (2015), suggest that similar bioerosion trace fossils observed in a theropod could have been produced either by termites or dermestids. Pomi & Tonni (2011, fig. 2) reported the presence of traces assigned to the activity of insects in fossil remains of mammals from the Late Pleistocene, including a series of grooves forming a star-shaped depression. In this context, although the bioerosion traces recovered in the morphotype E are also similar in size and morphology with the grooves described by Augustin *et al.* (2019, 2020); however, it is challenging to attribute reliably

to the activity of termite; therefore, we consider that the trace markers were product of, in a broader context, the activity of insects. However, several actualistic works documented the degree of modification on the surfaces of the bones caused for the activity of modern insects, including dermestids, tenebrionids, clerids and termites (Watson & Abbey, 1986; Fernández-Jalvo & Monfort, 2008; Backwell *et al.*, 2012, 2021; Holden *et al.*, 2013; Zanetti *et al.*, 2014, 2015; Solari *et al.*, 2019; Charabidzé *et al.*, 2022; Fernández *et al.*, 2022). However, the assignment of the insect producing the fossil traces on bones seems to be difficult to ascertain (Huchet, 2014; Xing *et al.*, 2015). In part, this is because in nature a significant diversity of insects and other invertebrates act on the remains of dead organisms, altering the bone surface

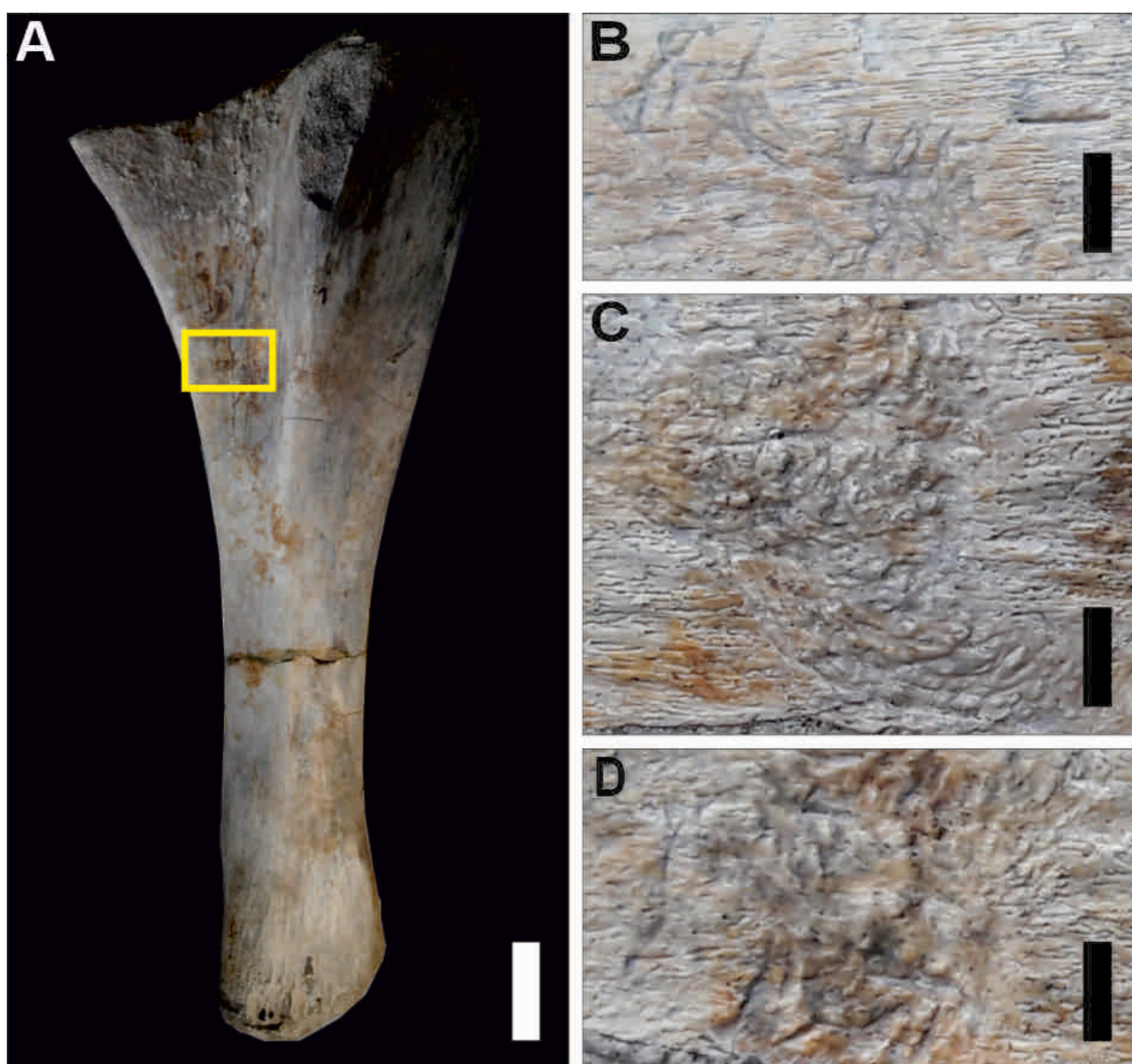


Figure 8. A, left ulna of a titanosaur sauropod (UNPSJB-PV 1045) in lateral view. The yellow rectangle indicates the location of the bioerosion traces corresponding to the E morphotype. B–D, detail of three recognized groove groups. Scale bars: A = 10 cm; B–D = 5 mm.

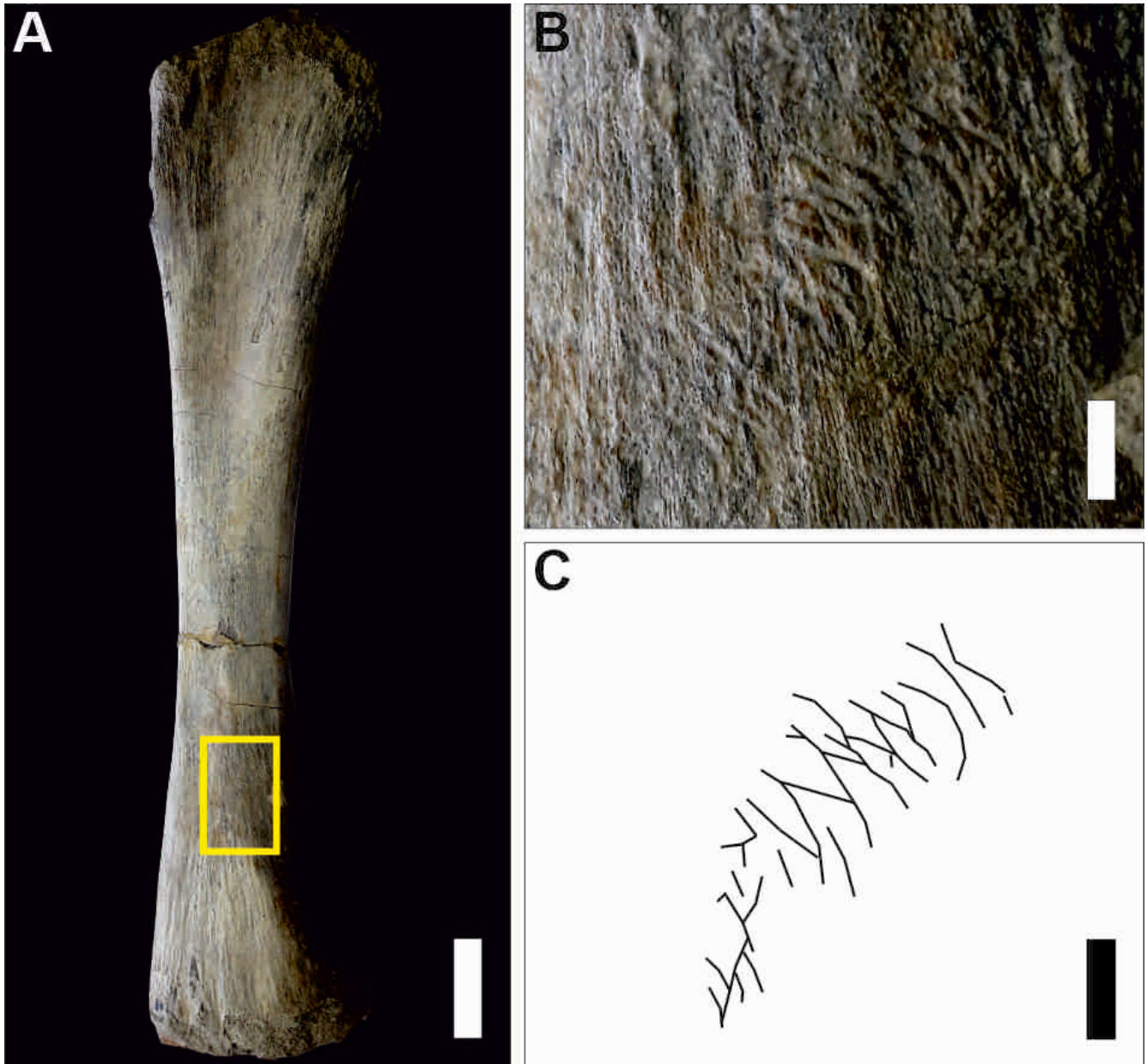


Figure 9. A, left ulna of a titanosaur sauropod (UNPSJB-PV 1045) in posterior view. The yellow rectangle indicates the location of the bioerosion traces corresponding to morphotype F. B, detail of bioerosion traces. C, schematic of the traces showing a zigzag pattern. Scale bars: A = 10 cm; B–D = 5 mm.

(Balek, 2002; Backwell *et al.*, 2021; Fernández *et al.*, 2022). Likewise, similar traces can be produced by different trace makers; therefore, it is difficult to identify the producer unequivocally.

Morphotype F, as mentioned above, exhibits a trail of groove pattern of traces. It is morphologically very similar to the trace *Osteocallis mandibulus*, being arched and apparently paired as described by Cunha *et al.* (2024) in Triassic rhynchosaurid remains. This type of groove arrangement and design was also documented by Britt *et al.* (2008, fig. 1h) in the ornithomimid *Camptosaurus*. They attributed it to the action of dermestid opposing jaw marks. In addition, similar traces were assigned to the activity of dermestid beetles or termites (Paes Neto *et al.*, 2016, fig. 6c). According to Britt

et al. (2008), whereas the carcass dries out, dermestids often infest it in a late stage of decomposition. The presence of dermestids traces may indicate subaerial exposure time of the bones in a dry environment before burial (Rogers, 1992; Li *et al.*, 2016; Paes Neto *et al.*, 2016; Perea *et al.*, 2020; Augustin *et al.*, 2021; Cruzado-Caballero *et al.*, 2021, among others).

These warm conditions, with periods of semi-aridity or at least drier, were identified in the Santonian–early Maastrichtian levels of the Lago Colhué Huapi Formation, where the bones analyzed here were recovered (Allard & Casal, 2013; Casal *et al.*, 2015, 2019). In this context, the morphotype F exposed on the titanosaur ulna is preliminarily associated with the action of dermestids.

CONCLUSIONS

This study presents, for the first time, evidence of traces of fossils in dinosaur bones from the Late Cretaceous of central Patagonia, in the Lago Colhué Huapi Formation at the locality informally called “Playa Kruger”, (Santonian–early Maastrichtian in age). The morphology of bioerosion trace fossils is varied and cannot be directly assigned to a specific taxon; however, it can be attributed to determined animal groups. In this context, we identified six different morphotypes recorded on the bones of titanosaur sauropod dinosaurs from the axial and appendicular skeleton. The morphotypes A and B based on its characteristics are attributed to the predatory action of crocodyliforms. In particular, due to the fossil record in the area, it is probably a member of the Peirosauridae. The morphology of the morphotype C suggests that it was generated during the scavenging of a theropod dinosaur. On the other hand, the rest of the morphotypes are related to the activity of invertebrates. In particular, the morphotype D represent most likely the pupation chambers of scavenging arthropods, whereas the morphotypes E and F may have been produced, probably, by the activity of osteophagic insects such as termites and dermestids, respectively. Although a detailed taphonomic study is in progress, the trace maker related to osteophagy marks herein identified, besides increase the biodiversity for the record of the formation, supports the paleoenvironmental condition inferred in the “middle section” of the Lago Colhué Huapi Formation (*i.e.*, warm conditions with periods of semi-aridity or at least drier). Finally, the identification of the bioerosion trace fossils on the dinosaurs bones represent an important data about the paleoecologic interaction among the taxa and/or group involved.

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