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A Mesozoic dino-feast: multiple teeth marks on a sauropod dinosaur bone from the Upper Cretaceous of Patagonia and evidence on theropod feeding behavior

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A MESOZOIC DINO-FEAST: MULTIPLE TEETH MARKS ON A SAUROPOD DINOSAUR BONE FROM THE UPPER CRETACEOUS OF PATAGONIA AND EVIDENCE ON THEROPOD FEEDING BEHAVIOR

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Abstract. Marks left by teeth on bones are evidence for inferring trophic interactions. In carnivorous dinosaurs, such evidence is rare in the fossil record. We present here the description of a fragment of sauropod appendicular bone, which exhibits teeth marks consistent with multiple trace makers. The specimen MPM-PV-19111 comes from Cretaceous rocks outcropping at Cerro Fortaleza locality (Cerro Fortaleza Formation, Campanian–Maastrichtian), Santa Cruz Province, Argentina. It preserves three faces, two bearing grooves, and a third bearing shallow pits. There are about 100 scars (we identified at least 99 grooves and 19 pits), with the grooves mainly oriented more or less perpendicular to the main axis of the bone. These grooves have a width ranging from 1 to 3.5 mm, and generally narrow distally. The pits and punctures are circular to subcircular and variable in diameter (1.5–4 mm). The feeding traces are attributable to theropod dinosaurs -abelisaurids and megaraptorids were recorded in the same formation- of mid to large body size, notosuchid crocodyliforms, and a possible indeterminate small mammal. The teeth marks are considered *post-mortem* based on the lack of healing on the surrounding bone. The high number of teeth marks suggests both repeated high-power bites in a restricted area (gnawing-like behavior?) and multiple producers, probably biting the bone at different moments since smaller-sized animals would intend to avoid the larger ones. This study aims to describe and interpret the possible origin of the bite marks preserved on this Cretaceous sauropod bone.

Key words. Teeth marks. Feeding marks. Trophic interaction. Gnaw. Cretaceous mammal.

Resumen. UN FESTÍN MESOZOICO: MÚLTIPLES MARCAS DE DIENTES EN UN HUESO DE DINOSAURIO SAURÓPODO DEL CRETÁCICO SUPERIOR DE PATAGONIA Y EVIDENCIAS SOBRE COMPORTAMIENTO DE ALIMENTACIÓN EN TERÓPODOS. Las marcas de dientes en los huesos son evidencias utilizadas para inferir interacciones tróficas. En los dinosaurios carnívoros, esta evidencia es rara en el registro fósil. Describimos aquí un fragmento de hueso apendicular de saurópodo que exhibe marcas de dientes consistentes con múltiples productores de trazas. El especimen MPM-PV-19111 proviene de rocas del Cretácico aflorantes en la localidad de Cerro Fortaleza (Formación Cerro Fortaleza, Campaniano–Maastrichtiano), Provincia de Santa Cruz, Argentina. Conserva tres caras, dos con surcos y una tercera con "*pits*" poco profundos. Hay aproximadamente 100 impresiones (identificamos al menos 99 surcos y unos 19 "*pits*"), con surcos más o menos perpendiculares al eje principal del hueso. Los surcos varían de 1 a 3,5 mm de ancho y generalmente se estrechan distalmente. Los *pits* son circulares a subcirculares y de diámetro variable (1,5–4,00 mm). Estas trazas de alimentación son atribuibles a dinosaurios terópodos -abelisáuridos y megaraptóridos se registraron en la formación- de tamaño mediano a grande, cocodrilos notosúquidos y un posible pequeño mamífero indeterminado. Las marcas se consideran *post-mortem* debido a la ausencia de cicatrización del hueso circundante. El elevado número de marcas de dientes indica tanto mordidas fuertes y repetidas en un área restringida (¿comportamiento similar al de roer?), como también múltiples productores que probablemente mordieron el hueso en diferentes momentos, ya que los animales de menor tamaño intentarían evitar a los más grandes durante el proceso. Este estudio tiene como objetivo describir e interpretar el posible origen de las marcas conservadas en el ejemplar.

Palabras clave. Marcas de dientes. Marcas de alimentación. Interacción trófica. Roer. Mamífero Cretácico.

BITE-RELATED MARKS or traces on bones are bioerosion that –potentially– evidence direct interactions between carnivorous animals and their food. These kinds of marks have been used for inferring inter- and intraspecific trophic interactions and behaviors in extinct animals, providing critical information about predator-prey relationships and different possible carnivore behaviors (*e.g.*, Avilla *et al.*, 2004; Pobiner, 2008; Bell & Currie, 2010; Longrich & Ryan, 2010; Schwimmer, 2010; Hone & Tanke, 2015; Brownstein, 2018; Pujos & Salas-Gismondi, 2020; Lei *et al.*, 2023). Although true predatory bite marks form when a predator catches and kills its prey, traces left *post-mortem* or during the feeding process by predators and scavengers are usually identified as "predatory traces" (Carpenter, 2013; Sadlok, 2022). In the case of the non-avian dinosaurs, bite marks (produced both pre and/or *post-mortem*) have been used to document and infer inter- and intraspecific interactions between several clades. These behaviors include non-predatory biting during fighting (in this case, the bones exhibit signs of healing, see Sadlok, 2022 and references therein) to diverse methods of feeding (*e.g.*, Erickson & Olson, 1996; Carpenter, 1998; Jacobsen, 1998; Chure *et al.*, 1998; Farlow & Holtz, 2001; Holtz, 2003, 2008; Carpenter *et al.*, 2005; Gignac *et al.*, 2010; Schwimmer, 2010; Hone *et al.*, 2018; Filippi & Bellardini, 2021; Brown *et al.*, 2021; Dalman & Lucas, 2021; Lei, *et al.*, 2023), including cases of cannibalism (Rogers *et al.*, 2003; Longrich *et al.*, 2010), and play behavior (Rothschild, 2014). In any way, predation and scavenging (facultative and/or obligated) have been the main strategies suggested for theropods in general, one event implying the killing of the food item and the other the consumption of remains of an item already dead, respectively (Holtz, 2003). However, determining from the fossil record (*i.e.*, bite marks) which event (predation or scavenging) is taking place faces its difficulties (Holtz, 2003; Lei *et al.*, 2023), as it is also difficult to assign trace makers for such bioerosion (Hone & Chure, 2018).

Despite being paleobiologically interesting, dinosaur teeth traces remain today poorly studied in general due in part to the fact that there is a lower frequency of teeth marks in the fossil record of Mesozoic systems (*e.g.*, Fiorillo, 1991; Hone & Rauhut, 2010; Lei *et al.*, 2023). Early hypotheses associated the lack of record of teeth marks with the idea of largest theropods being primarily scavengers, meaning their dentition was not apt to hard tissue processing and, therefore, the resulting marks were accidental events of contact between the teeth and bones (see Holtz, 2003; Hone & Rauhut, 2010; Lei *et al.*, 2023). However, there is much uncertainty regarding the predatory or scavenging capabilities of most theropod taxa, and the truth is that little is known about their foraging ecology yet (see Carpenter, 1998, 2013; Holtz, 2003, 2008; Farlow & Holtz, 2001; Carpenter *et al.*, 2005; Dalman & Lucas, 2018; Drumheller *et al.*, 2020; Pahl & Ruedas, 2021; Kane *et al.*, 2016, 2023). Besides this, there is a greater chance that many theropod bite mark samples remain unnotified simply because they have been over-looked in the field and the fossil collections, recognized only by specialists actively searching for such evidence of behavior. Chure *et al.* (1998) also mentioned incomplete preparation or the earlier use of casting materials to fill imperfections, as causes of avoiding the detection of teeth marks, particularly the subtlest ones. Also, most of the mentioned reports are often focused on the northern hemisphere, whereas few concern southern hemisphere ecosystems (*e.g.*, Rogers *et al.*, 2003; de Valais *et al.*, 2012; Gianechini & de Valais, 2015; Filippi & Bellardini, 2021; Gomes da Costa Pereira *et al.*, 2022). From all mentioned here, reporting new findings is important (Hone *et al.*, 2012).

Here we report a fragment of a sauropod dinosaur bone from the Upper Cretaceous of Patagonia (Cerro Fortaleza Formation, Campanian–Maastrichtian) that exhibits an unusually high number of bioerosions interpreted as bite marks. In the bibliography, teeth marks are generally characterized as scratches and punctures produced by a single bite. Evidence of repeated biting on bones (in a restricted area) is rare except in tyrannosaurids (Hone & Watabe, 2010; Brown *et al.*, 2021; Dalman & Lucas, 2021). This report provides new data on the feeding style of coexisting dinosaurs during the end of the Cretaceous at southern Patagonia. Furthermore, we interpret that the bite marks were produced by multiple trace makers based on the morphological disparity observed in the sample of traces, representing probably diverse feeding strategies.

MATERIAL AND METHODS

The specimen MPM-PV-19111 was found isolated on the surface at the mid-section of the outcrops of the Cerro Fortaleza Formation (Campanian–Maastrichtian), at the Cerro Fortaleza locality, Santa Cruz Province, Argentina (Sickmann *et al*., 2018; Tettamanti *et al*., 2018), and collected with the permission of the Secretaría de Cultura de la Provincia de Santa Cruz during the 2016 fieldwork (Fig. 1).

The specimen is an indeterminate sauropod bone fragment measuring approximately 10.5 cm long and 8.5 cm wide preserving the surface cortex on three of the four sides. The shape and convexity of the fragment sides suggest it could belong to a section of the diaphysis of a relatively small and slender leg bone or the margins of a large plate-like bone (*e.g.*, pectoral or pelvic girdle margins) (Fig. 2). Despite its fragmentary condition, the surface of the bone is preserved without evidence of deformations, although there are signs of transportation and damage by weathering consistent with a long time of exposure of the fossil in a desertic climate. The bone structure (internally massive, with a dense sponge and cortical bone) is consistent with other large sauropod bones – titanosaurs are the most common taxa recorded in the formation-found in the same area (*e.g.*, Lacovara *et al*., 2014; Paulina-Carabajal *et al*., 2021). The bite traces were measured using a caliper to provide a range of sizes. Clay casts of the

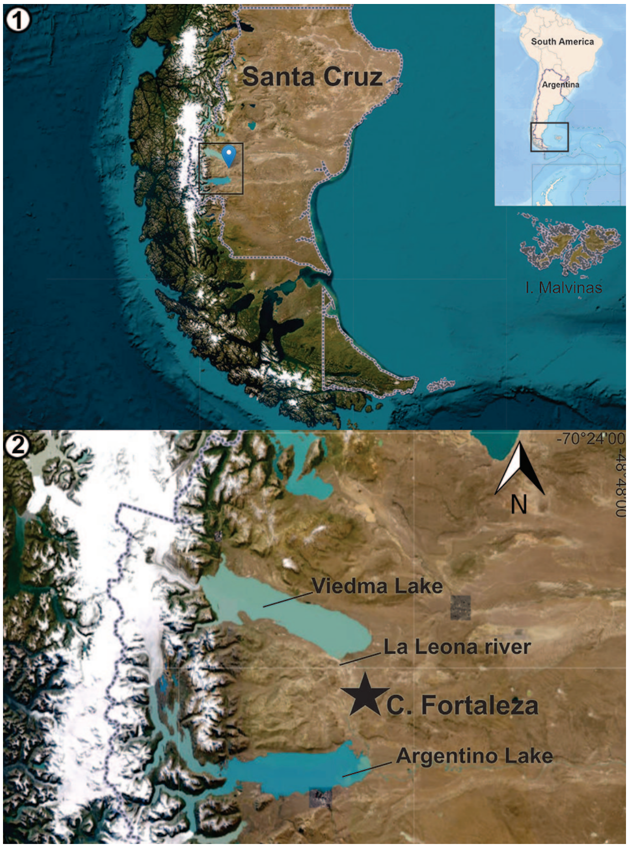

Figure 1. Location map. **1,** South America and a detail of southernmost Patagonia. **2,** Detail of Santa Cruz Province; the star indicates the locality of Cerro Fortaleza (Santa Cruz Province, Southern Patagonia, Argentina), showing the provenance of the specimen **MPM-PV-19111** and the two *in situ* specimens.

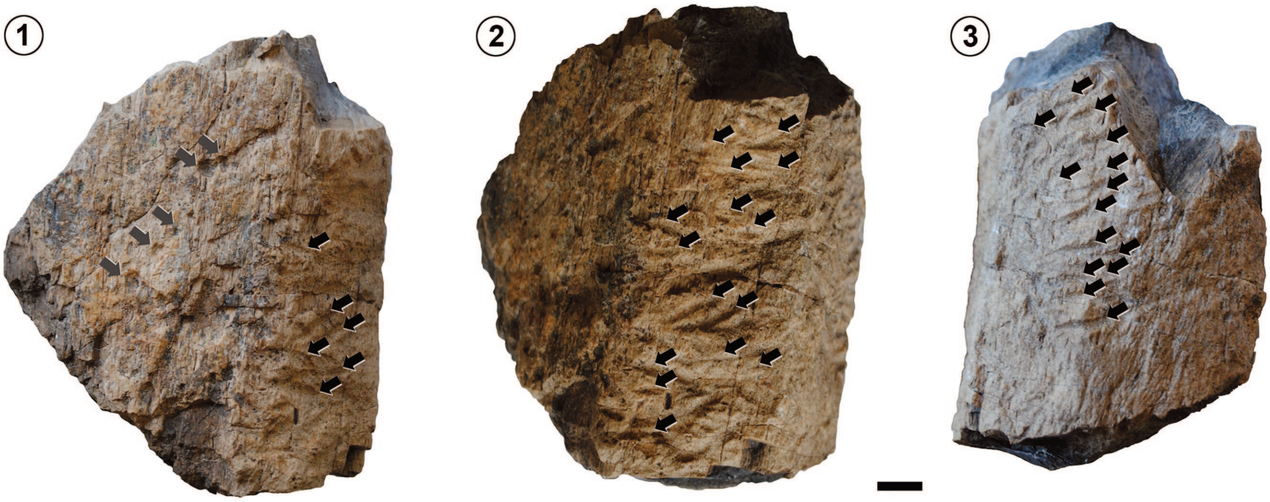

Figure 2. Fragment of the indeterminate sauropod bone **MPM-PV-19111** in three views. **1,** Surface "a"; **2,** surface "b"; **3,** surface "c". The arrows indicate grooves (black) and pits (grey). Scale bar= 10 mm.

three surfaces bearing traces were made to better visualize the tooth marks in positive relief (Figs. 3, 4). Photos -taken with a Nikon D300 camera- were used to create a PDF 3D model of the bone (Suppl. Inf. 1) and the clay cast (Suppl. Inf. 2) using the photogrammetry software Agisoft PhotoScan.

Following Pirrone *et al.* (2014) we understand the bioerosion traces in fossilized bones as biogenic structures that cut hard osseous tissue structures as the result of mechanical processes. We follow the nomenclature and definitions proposed by Hone and Watabe (2010) to refer to a series of theropod bite traces that many different research groups have recently used to identify and classify bite marks on dinosaur and other Mesozoic reptile bones (*e.g.*, Rivera-Sylva *et al.*, 2012; Robinson *et al.*, 2015; Drumheller *et al.*, 2020; Brown *et al.*, 2021). Furthermore, we identify different morphotypes but we do not applicate ichnotaxonomy to these fossil traces. The marks were

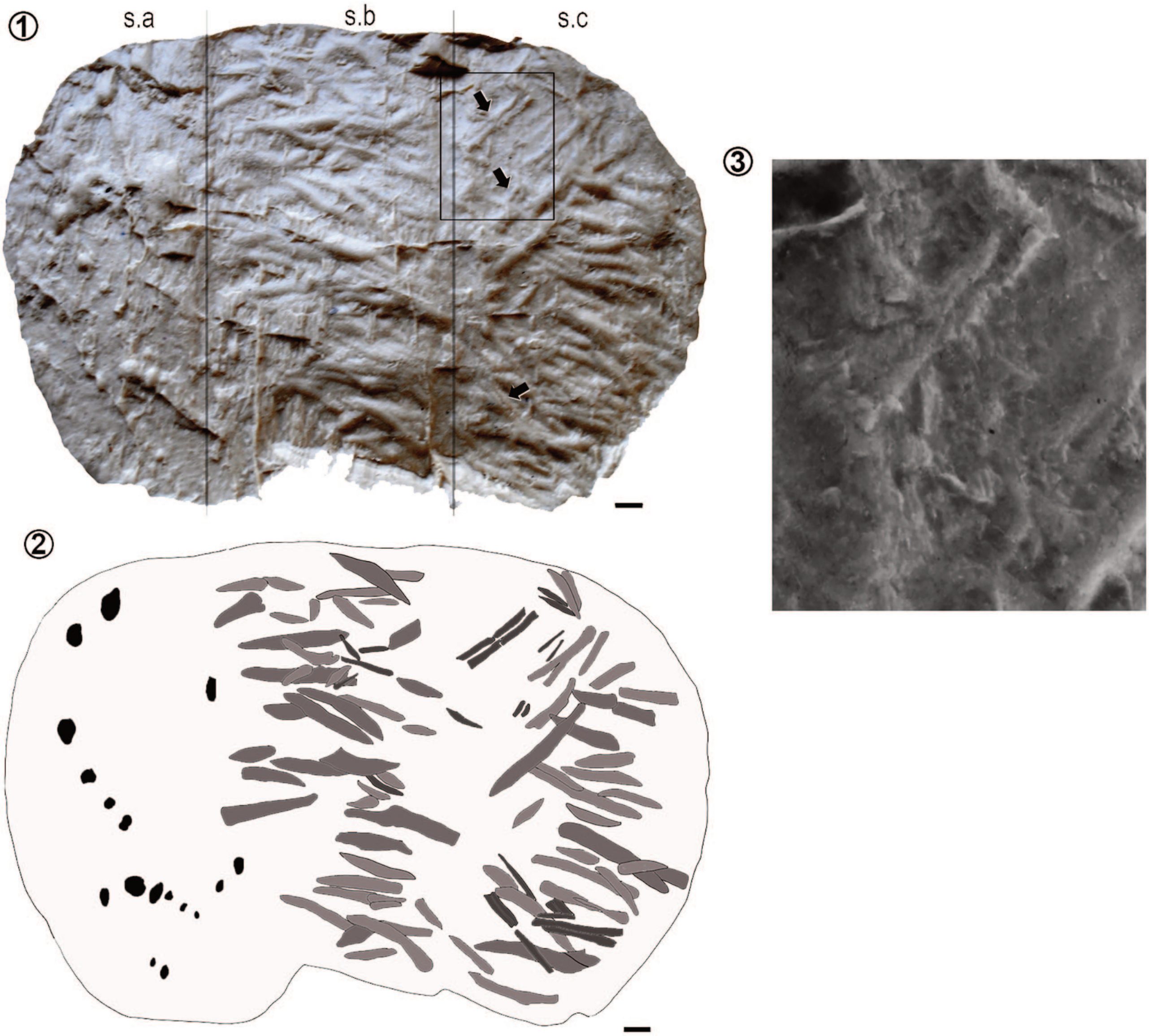

Figure 3. Bite marks in **MPM-PV-19111**. **1,** Clay cast of the three sides bearing traces, which are displayed in positive relief. The vertical lines indicate separation between sides; the box encloses the possible mammalian bite traces. **2,** Line drawing interpretation of the pits and grooves. The grooves are in different colors indicating similar sizes. **3,** detail of "mammalian-like" teeth marks. Abbreviations: **s.a,** surface "a"; **s.b,** surface "b"; **s.c,** suface "c". Scale bars= 5mm.

described and compared to published data on Mesozoic systems.

Locality and Horizon. Austral Basin, Cerro Fortaleza Formation. Diverse fauna from different localities of the Cerro Fortaleza Fm. includes the sauropods *Dreadnoughtus schrani* Lacovara, Ibiricu, Lamanna, Poole, Schroeter, Ullmann, Voegele, Boles, Egerton, Harris, Martínez & Novas 2014 and *Puertasaurus reuili* Novas, Salgado, Calvo & Agnolin 2005, the theropods *Orkoraptor burkei* Novas, Ezcurra & Lecuona 2008a and *Austrocheirus isasii* Ezcurra, Agnolin & Novas, 2010, and the ornithopod *Talenkauen santacrucensis* Novas, Cambiaso & Ambrosio 2004. From the type locality, titanosaur, abelisaurid, megaraptorid, and ankylosaur remains were recovered (Lacovara *et al.*, 2014; Canale *et al.*, 2019; Paulina-Carabajal *et al.*, 2021).

Other described materials. Upper Cretaceous unpublished material used for comparisons includes two uncollected dinosaur bones with tooth marks from the Cerro Fortaleza locality and an incomplete dinosaur rib from the collections of the Museo de la Asociación Paleontológica Bariloche (MAP).

The two samples corresponding to large sauropod bones bearing single bite marks were photographed *in situ* at the Cerro Fortaleza locality during the 2023 fieldwork. The complete femur is located at the coordinates S 49° 56,543′ W 72° 03,446′, whereas the more fragmented bone is located at the coordinates S 49° 58,182′ W 72° 3,832′ (Fig. 5).

The specimen MAP-BAR-8011 corresponds to a saurischian fragmented rib from the Late Cretaceous of Rio Negro province (Allen Formation), bearing several bite marks (Fig. 6).

Institutional Abbreviations. MAP-BAR, Museo de la Asociación Paleontológica Bariloche, San Carlos de Bariloche, Argentina; **MPM-PV,** Museo Padre Molina, Río Gallegos, Argentina.

DESCRIPTION

The sauropod fragment -of an indeterminate bone- described here preserves three facets with cortical bone. The large number and overlapping of grooves prevent the exact count of the traces. The side identified as surface "a" exhibits about 17–19 shallow circular and sub-circular pits, whereas the remaining two sides (surfaces "b" and "c") bear up to 99 grooves (Figs. 2, 3). The traces are distinct singled and paired grooves (scores or drag marks), and shallow pits (affecting only the cortical bone), which are consistent with at least three distinct patterns (Fig. 4, Tab. 1).

In the described specimen, the grooves are elongated traces (*e.g.* this kind of traces may be produced by tooth dragging), and they do not break through the surface of the cortex (Hone & Watabe, 2010; Lei *et al.*, 2023). We counted up to 99 elongated traces, oriented more or less perpendicular (in angles range from 45–90 degrees) to the main axis of the bone (Figs. 2, 3; Tab. 1). The grooves are well distributed on two adjacent surfaces (identified as surfaces "b" and "c" in figure 3) of the bone. Most grooves seem to be primarily U-shaped in cross-section and are narrow at the ends. These grooves exhibit different morphologies (form and size) and patterns: single (small to large elongated marks), paired (small to large elongated and parallel marks that do not touch each other), and adjacent-paired (elongated marks contacting medially to each other) (Figs. 3, 4; Tab. 1).

The grooves are the most common marks, and we recognize three sizes (large, medium, and small) in terms of the length and width of the scores (Fig. 3.2). The most extensive marks are 3.5 mm wide and reach up to 20 mm long, representing approximately the 25% of the total sample. The mid-sized marks are about 1.5–2 mm wide and represent 50% of the sample, being the most common size. The smaller marks are about 1 mm wide and represent

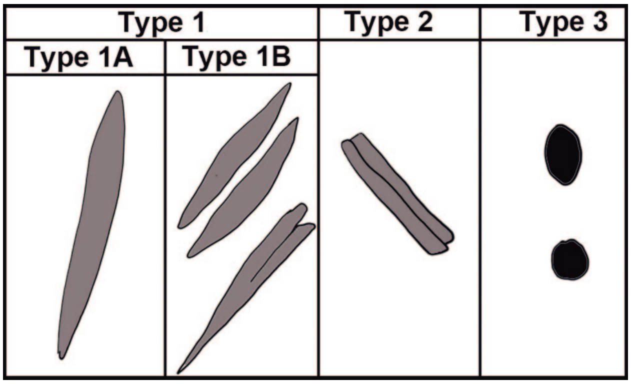

Figure 4. Illustration of the three trace morphotypes observed in **MPM-PV-19111**, as shown in figure 3.2. Not to scale.

TABLE 1 – Number and type of traces on the surfaces of the specimen MPM-PV-19111

	Surface "a"	Surface "b"	Surface "c"
Number of traces	17	~47	~52
Description	pits	grooves	grooves
Sizes			
Large (3 mm width)	-	17 (36%)	8 (15%)
Mid (2 mm width)	-	25 (53%)	26 (50%)
Small (1 mm width)	-	5 (10%)	18 (34%)
	-	1-5 mm diameter	
Morphotype	3	1a, 1b	1a, 1b, 2

Figure 5. Photographs of two *in situ* titanosaur sauropod bones with teeth marks, photographed at Cerro Fortaleza locality. Arrows indicate teeth marks. **1, 2,** Partial humerus with one slightly curved tooth mark; **2,** Detail of the tooth mark, with smaller arrows indicating possible serration marks; **3,** Fragment of indeterminate leg bone bearing a single tooth mark. Scale bar= 10 mm.

approximately 23% of the sample (Tab. 1). Among the small-sized marks, there is a set of paired and adjacent marks (Figs. 3.1, 4). These particular set of marks look similar to traces interpreted as made by mammalian incisive-like teeth and will be discussed below.

Most of the grooves are isolated marks, and the large number of traces partially obscures the anatomical information of many of them. However, it is possible to recognize that some equally sized traces (some large, some mid-sized and some small) run more or less parallel (*e.g.*, parallel grooves may result from dragging of two continuous teeth made them during a single bite event, Fig. 3.1). Also, although it is difficult to determinate a chronological order of the bites there is evidence of grooves overlapping other grooves. This could be indicating that different bites were made at different times -and possibly- by different trace makers (see discussion below).

A particular set of drag marks corresponds to markedly small and shallow adjacent-paired grooves. Although only one pair is clearly observed (Fig. 3.1), there are other three or four marks sharing this morphology. These paired and adjacent marks (we interpreted here each groove corresponding to a single tooth) are in two sizes. The larger ones are 1.4 mm width grooves (the paired grooves are then 3 mm wide), and the smaller ones are 1 mm width grooves.

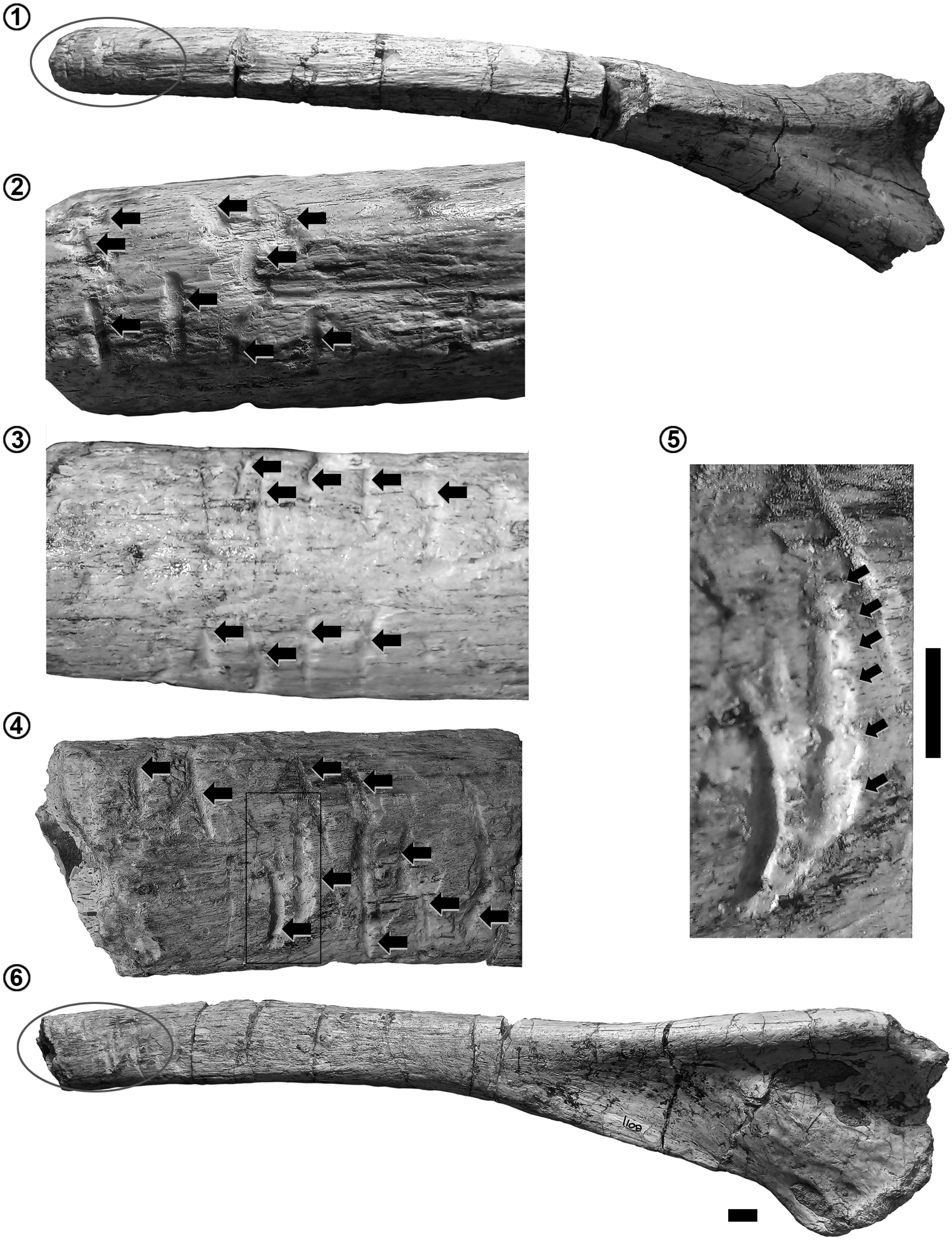

Figure 6. Photographs of the saurischian dinosaur (titanosaurid?) rib **MAP-BAR-8011** showing several bite marks on the shaft. **1, 6**, Proximal section of a rib in dorsal (1) and ventral (6) views. **2–5,** Details of bite marks in dorsal (2), lateral (3), and ventral (4,5) views. **5,** Detail of a tooth mark with festooned margins. Scale bars= 10 mm.

Finally, pits and punctures are all on the same side of the bone (identified as surface "a"). They are shallow and circular and subcircular in shape, and variable in diameter from 1.5 to 4.5 mm (Figs. 2A, 3B).

Classification of the bite marks

The grooves and pits were classified into three morphotypes based on size and shape (Fig. 4).

Type 1. Corresponds to grooves or furrows, arranged individually or in pairs.

Type 1A corresponds to single and elongated grooves, generally with parallel margins, which taper at the ends. We interpreted them as drag marks, as the serrated, laterally compressed teeth of theropods carve into the bone, with gouges with U to V-shaped sections that taper at either end. This size-independent morphotype includes 1–3 mm wide and up to 20 mm long scores, that we classified in large, medium and small (Figs. 3, 4). The smaller teeth marks are 1 mm wide and up to 16 mm long (Fig. 3, Tab. 1). Although we cannot discard that larger animals may produce smaller marks depending on the angle of contact between teeth and substrate, and bite pressures, the markedly smaller size -and consistency of the width along its length- of these grooves compared to the ones described above suggests that small-sized animals made these marks. The sole bite marks reported for the two *in situ* titanosaur bones at the Cerro Fortaleza locality correspond to type 1A (Fig. 5).

Type 1B corresponds to paired parallel or subparallel grooves interpreted as marks left by two consecutive teeth during the same bite (in other words, belonging to the same cluster of marks). In the specimen MPM-PV-19111, there are a few sets of paired scores, 1.5–2.3 mm wide, some with a tapering or merged end (Fig. 3.1). In the specimen MAP-BAR-8011 there are short and parallel groves in two sides of the rib interpreted as marks left by opposed jaws, which also fit into this morphotype (Fig. 6.3).

Type 2. This type corresponds to paired adjacent small grooves (there is no space between them), not tapering distally, and slightly more "chisel"-like (Figs. 3, 4). It is preserved in the specimen MPM-PV-19111. The traces are long and straight and each mark has the same width (approximately 1 mm) along its entire length. The better-preserved example corresponds to two adjacent grooves 16 mm long, which exhibit a slight interruption halfway (*e.g.*, traces indicated inside the box in Figure 3.1), which suggests they are opposed pairs.

Type 3. This morphotype corresponds to rounded and oval pits or punctures (Fig. 4). The pits and punctures are circular to subcircular, and variable in diameter from 1.5–4 mm. Some pits dispose aleatorily, whereas is possible to identify two arcuate alignments of pits formed by 3 small pits in a straight line followed by 3 larger pits disposed in a curve (Fig. 3.2).

DISCUSSION

Although the teeth marks on fossil bones directly indicate an interaction between them, interpreting the behavior behind such marks is more difficult. Ethological categories and ichnotaxa have been only recently proposed (Sadlok, 2022), but are not discussed here. We identified approximately 100 distinct teeth marks (between drag marks and pits) preserved on the specimen MPM-PV-19111 in a 30 x 20 cm restricted surface and distributed over three sides of a fragment of possible leg bone. All these traces are interpreted as teeth marks and are considered *post-mortem* because there is no evidence of healing in the surrounding bone (Rivera-Sylva *et al.*, 2012). Due to the fragmentary nature of the bone, it is not possible to determine if these marks resulted from predatory and/or scavenging events. However, the large number of traces could be indicating that they were produced after the death of the animal, and that the body spent some time of sub-aerial exposure (Gianechini & de Valais, 2015). This sauropod bone (and its surrounding meat) was probably a high economy element in terms of carcass nutrient availability (see Drumheller *et al.*, 2020), and it seems to have been used by carnivorous individuals of various sizes. Thus, these trace fossils are interpreted as the result of scavenging activities.

The parallel alignment of the grooves on the specimen MPM-PV-19111 -regardless of their size- suggests they may have resulted from successive teeth making contact with the bone surface during single bites. Furthermore, the marks are in general oriented more or less perpendicular to the main axis of the bone, and upper and lower jaw teeth may have participated, leaving marks on two of the surfaces of the bone. As described for other specimens, since the teeth marks are relatively deep and narrow, they were probably made by the laterally compressed dentary and maxillary teeth rather than the more incisiform premaxillary teeth. Furthermore, the inclination of the grooves of types 1A and 1B with respect to the main axis of the bone (they are not perfectly perpendicular) may suggest that they were made by the maxillary teeth moving laterally. Other authors have suggested how tightly packed premaxillary teeth of large theropods would also be expected to have left a series of closely spaced scores (Longrich & Ryan, 2010).

Regarding the circular pits, crocodyliform bite marks on vertebrate remains are well-represented throughout the Mesozoic and are another credible source of bite marks on larger terrestrial bones (*e.g.*, Schwimmer, 2010; Brownstein, 2018 and references therein). The subconical teeth of crocodyliforms produce shallower score marks or deep pits where the tooth punctures the bone (Avilla *et al.*, 2004; Njau & Blumenshine, 2006; Longrich & Ryan, 2010). It must be borne in mind, however, that sizeable-sized puncture marks were also attributable to theropods (Erickson & Olson, 1996; Avilla *et al.*, 2004).

Although there are records of gnawing-like behavior in theropods, published samples of bones have a limited number of marks (12–20), and were considered as the result of both single or multiple bites (*e.g.*, Chure *et al.*, 1998; Brown *et al.*, 2021). Moreover, in reports of bones with several marks, the latter are generally attributed to a single event of scavenging by one animal. The specimen MPM-PV-19111 reported here is thought to have been bitten by several individuals at different moments after the death of the animal.

Identification of trace maker

Determining whether the teeth or bite marks on a fossil bone result from predatory behavior (using teeth as killing weapons) or scavenging behavior (record of *post-mortem* feeding) is always difficult (Holtz, 2003). However, it is also difficult to determine the identity of the trace makers based only on the morphology of the traces. For example, the collapse of the bone surface indicates particularly strong bites (Lei *et al.*, 2023 and references therein). Still, the traces described here are interpreted as drag marks related to a gnawing-like behavior in the larger producers. The trace maker body size can be hypothesized from parallel traces left by a teeth row during a single bite (as in the hadrosaur rib MAP-BAR-8011) because the distance separating each mark reflects the spacing between the teeth. However, identifying coetaneous teeth marks in the MPM-PV-19111 is only possible with further statistical analyses. In this bone, the largest marks are around 3 mm wide and up to 20 mm long. Scores of similar sizes (about 3 mm wide) were described in sauropod bones where the trace maker was identified as a mid-to-large sized theropod (*e.g.*, tyrannosaurids, Brown *et al.*, 2021). Based on these estimates, the larger bite marks described in this study were made possibly by a large-bodied theropod, probably more than 4 m long. The mid-sized tooth marks are about 1.5–2 mm wide, and up to 20 mm long (Fig. 3.2, Tab. 1). Scores within this width range have been adjudicated to mid-to-large sized theropods (*e.g.*, Gignac *et al.*, 2010; Brown *et al.*, 2021), the larger ones being probably up to 3–4 m long animals. However, we must keep in mind that large and medium-sized marks could be both produced by large size animals, resulting from different teeth angle contacts with the bone, or different bite pressures, among others.

Cerro Fortaleza locality (MPM-PV-19111 and *in situ* specimens) trace makers. Based on the sizes and morphologies of the teeth marks on the specimen MPM-PV-19111, we interpret that more than one trace maker was involved in the feeding event of a sole carcass. These traces were produced by compressed and conical teeth. The animals with ziphodont dentition recorded so far from the Cerro Fortaleza Formation are theropod dinosaurs and notosuchian crocodyliforms. Regarding the age and provenance of the fossils under study, three groups of animals could have created the different sets of bite marks in the specimen MPM-PV-19111 and correspond to abelisaurid and megaraptorid theropods, peirosaurids, and possibly mammals (*e.g.*, Novas *et al.*, 2008a; Ezcurra *et al.*, 2010; Novas *et al.*, 2019; Paulina-Carabajal *et al.*, 2021).

The elongated grooves in the specimen MPM-PV-19111 are mostly parallel, a typical morphology associated with theropod bite marks (*e.g.*, Longrich & Ryan, 2010). Meanwhile, the smaller paired and adjacent (with no median space between them) marks may represent mammalian bite marks, and we consider the slight interruption observed in the traces as consistent with a bite mark left by anterior opposing teeth (*e.g.*, upper and lower incisors). Small sized mammals were not recovered yet from Cerro Fortaleza Formation, but from other Cretaceous formations of the same basin (see below).

The sizes of the larger teeth marks, as well as the diameters of the punctures, are consistent with tooth marks left by medium to large theropods and crocodyliforms. Given the poor range of possible trace maker candidates (carnivorous taxa) registered in the same site and geological formation as MPM-PV-19111 and the two isolate *in situ* specimens (Fig. 5.1–2)- this may be quite accurate. Therefore, the trace marker responsible for the teeth marks of types 1A and 1B can be narrowed down to relatively few numbers of mid-to-large theropod taxa. From the Cerro Fortaleza Formation, the megaraptorid theropod *Orkoraptor* (Novas *et al.*, 2008a) and the uncertain affinities theropod *Austrocheirus* (Ezcurra *et al.*, 2010) are known, whereas from the same formation and locality, remains of abelisaurid theropods were reported (Canale *et al.*, 2019; Paulina-Carabajal *et al.*, 2021). These two groups of relatively large-sized theropods -abelisaurids and megaraptorids- were at the top of the food chain during the Upper Cretaceous in South America and were the most likely producers of most of the bite marks.

Regarding the circular and subcircular pits, similar marks in dinosaur bones have been associated with both dinosaurs and particularly with crocodyliform bite marks (*e.g.*, Njau & Blumenschine, 2006; Boyd *et al.*, 2013). Cretaceous crocodyliforms are assumed to be capable of killing and eating a variety of dinosaurs (Boyd *et al.*, 2013). As mentioned above, the bite marks of crocodylians leave characteristic deep, circular to subcircular punctures (*e.g.*, Njau & Blumesnchine 2006; Noto *et al.*, 2012; Boyd *et al.*, 2013; Botfalvai *et al.*, 2014; Drumheller & Brochu, 2014; Brown *et al.*, 2021), which are highly similar to those identified in MPM-PV-19111 as “type 3” teeth marks. Various notosuchian teeth morphologies have been reported from the Cerro Fortaleza Formation, including some large caniniform serrated teeth (Paulina-Carabajal *et al.*, 2021). Furthermore, the alignment of the small and large consecutive pits in a curved disposition may represent a single bite mark. In this case, left by a lateral teeth row formed by larger anterior (caniniform) teeth and smaller (molar-like teeth) posterior teeth (Fig. 3.2). The size of this gauge falls within the range of snout size of known South American peirosaurids.

We interpreted here marks observed in MPM-PV-19111 identified as type 2 as possibly produced by anterior incisive-like teeth of a small-sized mammal. The longest set of marks is 16 mm long and has a deeper impression at each end (Fig. 3.1), which reminds the set of bite marks described for mammals in a dinosaur bone in North America (Longrich & Ryan, 2010). The marks in the specimen MPM-PV-19111, however, are shallower and longer than the latter. Unfortunately, the preservation of the bone does not allow further analysis. Scavenging on small dinosaurs by both large (*e.g.*, Hu *et al.*, 2005) and small (*e.g.*, Longrich & Ryan, 2010) Cretaceous mammals has been reported. There is no record of mammals at the Cerro Fortaleza Formation yet. However, the record of Mesozoic mammals in rocks of similar age (Campanian–Maastrichtian) in the Austral-Magallanes Basin of Argentina and Chile includes so far multituberculates, meridiolestids, dryolestids, and large therians (Bonaparte, 1990; Chornogubsky, 2011; Chimento, 2016, 2024; Novas *et al.*, 2019; Goin *et al.*, 2020; Martinelli *et al.*, 2021). While multituberculates have cranial and dental anatomy reminiscent of rodents, meridiolestidans are morphologically diverse and considered insectivores, herbivores, and omnivores. The teeth marks in the specimen MPM-PV-19111 are more consistent with incisive-like teeth, and therefore, we suggest that a multituberculate was a probable trace maker. However, tooth marks produced by the paired upper and lower canines of a eutherian or a marsupial cannot be discarded.

MAP-BAR-8011 rib trace maker. Ribs are high-economy skeletal elements (see Drumheller *et al.*, 2020). The rib MAP-BAR-8011 belongs to an adult-subadult saurischian dinosaur (Fig. 6). Since both theropod and titanosaurian ribs exhibit a high level of pneumaticity in the proximal area of the ribs, it is not possible to identify it further. However, it probably belongs to the latter. The shaft is covered by teeth marks consistent with the use of upper and lower jaws. Measurements of the paired grooves, 2–4 depending on the side, are equally separated by 5–7 mm from each other, a distance that represents the separation between the tip of the teeth. There are deeper and more superficial bites, as in the vertebra described by Filippi & Bellardini (2021), suggesting repeated bites involving different regions of the tooth row. Mid-to-large bodied ziphodont theropod taxa also from Allen Formation include the abelisaurids *Abelisaurus comahuensis* Bonaparte & Novas, 1985 (known only by its head), *Niebla antiqua* Aranciaga Rolando, Cerroni, Garcia-Marsa, Agnolin, Motta, Rozadilla, Brisson Egli & Novas 2020 (4.5 m long), *Quilmesaurus curriei* Coria, 2001 (4–5 m long; Grillo & Delcourt, 2016) and the unenlagiid *Austroraptor cabazai* Novas, Pol, Canale, Porfiri & Calvo 2008b (about 6 m long; Novas *et al.*, 2008b). Abelisaurids are among the most common theropods in the Allen Formation, and the sizes of the known taxa match the size of the rib trace makers.

One of the drag marks exhibits a strange morphology. One side is deeper and straight, whereas the other is more surficial and festooned. The festooned margin consists of 6 half-moon marks that we interpret as chipped-off material that probably resulted from the combination of the presence of serration denticles and the kinetics (pressure and inclination) of the teeth, as hypothesized by Sadlok (2022: figs. 2.9–12). Serrated teeth have been demonstrated to create un-striated bite marks in general (D'Amore & Blumenschine, 2009). If present, the striations left by the denticles are small parallel lines (within the groove or over the surface of the bone), and it is, in theory, possible to identify the trace maker using the spacing left by them. The festooned mark in the rib MAP-BAR-8011 is different and represents valuable anatomical data to support the future identification of the trace maker (Fig. 6.5).

Implications for behavior

The feeding behavior of carnivorous theropod dinosaurs has been largely surveyed. However, some aspects, such as the utilization or exploitation of bones by theropods (*e.g.*, preference of a particular kind of prey or a particular part of the skeleton of a prey, osteophagy, etc.), have been less explored (*e.g.*, Fiorillo, 1991; Chure *et al.*, 1998; Jacobsen, 1998; Hone & Rauhut, 2010). Also, these studies require the analysis of larger samples of bones with teeth marks from the same geological formation to introduce some clues on the dinosaur interactions in the studied ecosystems. In particular, the literature has little information regarding gnawing-like behavior in theropods (*e.g.*, Chure *et al.*, 1998; Brown *et al.*, 2021). The bite marks on different surfaces of the specimen MPM-PV-19111 may represent marks left by the upper and lower jaws during single and consecutive bites, showing strong evidence of what seems to be a repeated and localized biting behavior. This hypothesis is supported by the high number of identified teeth marks of different sizes (Tab. 1), plus the presence of grooves that overlap other -older- grooves, evidencing a chronological sequence of bites (separated by minutes or hours). The angle between the traces on both surfaces and the main axis of the bone suggests an oblique position of the snout of the trace marker (using probably maxillary teeth). A similar pattern with a high number of marks occurring in a restricted area has been previously suggested as a rare "gnawing-like behavior" among theropods (Brown, *et al.*, 2021). However, the number of marks in the specimen MPM-PV-19111 greatly exceeds any other published record in Argentina (*e.g.*, Gianechini & de Valais, 2015; Filippi & Bellardini, 2021).

As mentioned, grooves overlap other grooves, indicating that different bites were made at different times. Although it is difficult to identify a chronological order for all the bites, many of the mid-sized scores always overlap the large-sized scores, and some of the smaller scores overlap the mid-sized and large-sized scores, supporting our hypothesis of several individuals feeding along different times. The high number of tooth marks present in MPM-PV-19111 suggests two non-mutually exclusive scenarios: on one hand, a possible gnawing-like behavior for at least one of the trace makers; on another hand, a possible situation in which several trace makers of different sizes scavenged on the same carcass piece probably along a long period of time. In the former case, it could be a rare situation since the record of tooth marks in other bones at the same locality corresponds to isolated grooves, the most common trace in general (Fig. 5). On the contrary, if the latter is true, it is not possible however, to determine if the biting occurred at the same time or not. Different moments of the day seem to be the most probable situation since smaller animals (juveniles of one species or smaller specimens of different species) would intend to avoid encounters with the larger (adult) individuals while eating. In any case, we interpret for the specimen MPM-PV-19111 a series of scavenging events based on the morphology pattern and disposition of the different observed traces. In turn, the size of the gauges also indicates that different trace makers were involved, supporting the above-mentioned idea of multiple trace makers and biting events.

The beautifully preserved rib MAP-BAR-8011 from the Upper Cretaceous of Río Negro represents an example of a single bone bearing several marks (types 1A and 1B), attributed to a single producer during a sole feeding event (Fig. 6). In this rib, the biting marks correspond to parallel grooves perpendicular to the main axis and occur on three sides of the rib. The teeth marks are similar in morphology and exhibit a constant separation between each other, a pattern that is consistent with a single set of two or three teeth (possibly anterior or lateral premaxillary teeth) touching the bone at the same time. The high percentage of parallel drags suggests that the trace maker defleshed the carcass, moving the head backward, a pattern common among large theropods (Lei *et al.*, 2023 and references therein). The high number of marks represents another example of gnawing-like behavior for a Cretaceous theropod. Furthermore, this bone preserves an exquisite mark bearing a festooned side that we interpret as denticle-related. A final comment has to be made on the high pneumaticity observed in the head of the rib MAP-BAR-8011. Such degree of pneumaticity is observed in theropods and is also diagnostic of titanosaurids and has been reported in other groups of sauropods (*e.g.*, King *et al.*, 2024 and references therein). Although it is more probable that the rib belongs to an herbivorous dinosaur, there is a slight possibility that it belongs to a theropod dinosaur, in which case, the bite marks would represent a case of cannibalism.

Implications on social behavior? Unfortunately, social behavior related to feeding adaptations cannot be observed in fossils and it is only inferred (*e.g.*, Evans, 1983; Tanke & Currie, 1998; Avilla *et al.*, 2004). The different sizes of the bite marks indicate different-sized trace makers, although these differences could be taxonomic or ontogenetic related (Robinson *et al.*, 2015). Regarding the timing, most of the largest grooves were made first since medium and small-sized impressions overlap the largest ones. It supports the hypothesis that smaller animals feed after larger ones. The sharing of a carcass is something already proposed by other authors (*e.g.*, Paik *et al.*, 2011; Robinson *et al.*, 2015).

Highly tooth-marked bones probably result during capturing, dismembering, or scavenging (Njau & Blumenshine, 2006; Pujos & Salas-Grimoldi, 2020 and references therein). The marked size variability in the grooves and pits under study suggests several possible scenarios. However, we mention three (and considering that we do not know if, within the same species, there were hierarchies at the moment of feeding): a) gnawing-like behavior, (b) adult and young of the same species were feeding at the same time producing synchronic large and smaller marks, or (c) different sized species were feeding on the same carcass but during different moments to avoid competition. An actualistic comparison would be the African Savannah, where lions hunt prey, and many different scavengers (including hyenas, vultures, and smaller carnivorans) wait nearby until they can eat the leftovers. Moreover, some of these mammal and bird scavengers are nocturnal, as could have been the case of the Cretaceous mammals (*e.g.*, Maor *et al.*, 2017 and references therein). A fourth scenario would relate to the biostratinomic history of the fossil bone, considering the transportation of the carcass.

CONCLUSIONS

The fragment of sauropod bone presents evidence of teeth marks consistent with scavenging by at least three different groups of animals, including theropods, notosuchians, and possibly mammals. The teeth marks indicate that a certain number of large and small carnivores -of different ontogenetic stages or different species- shared a sauropod carcass. The feeding traces are attributed to mid- to large- sized theropod dinosaurs, probably megaraptorids and abelisaurids, crocodyliforms (peirosaurid notosuchians), and small mammals (undetermined, possibly a multituberculate?). We suggest that those animals feed from this sauropod carcass during different moments of the day to avoid direct competition. It is not possible to determine the chronology of the biting events, but it is probably unlikely that large, medium, and small trace makers (from the same species or not) scavenge the same carcass more or less at the same time. Theropods of different species would have waited for their turn, as did the mammals, which were probably more active during the darker hours of the day.

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SUPPLEMENTARY INFORMATION

Supplementary information for this article can be found online following these links:

Supplementary Information 1:
https://archive.org/details/512_20242612_SM1PaulinaCarabajaletal

Supplementary Information 2:
https://archive.org/details/512_20241216_SM2_PaulinaCarabajaletal

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