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Communication

Bioerosion Structures on Dinosaur Bones Probably Made by Multituberculate Mammals and Dermestid Beetles (Guichón Formation, Late Cretaceous of Uruguay)

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Abstract: We describe the first fossil traces from the skeletal remains of dinosaurs from Uruguay, from the Upper Cretaceous Guichón Formation. We describe the first biting/gnawing fossil traces reported for Uruguay, *Machichnus bohemicus* Mikulás et al., 2006, probably made by small tetrapods, such as multituberculate mammals. Moreover, traces likely made by sarcosaprophagous beetles, namely *Cubiculum* Roberts et al., 2007, cf. *Cubiculum*, and cf. *Osteocallis* Roberts et al., 2007, are described. The presence of *Cubiculum* and *Osteocallis* supports previously proposed depositional conditions in a warm and arid to semi-arid continental environment for the referred stratigraphical unit. All traces would indicate a certain period of subaerial exposure before the definitive burial of the bones.

Keywords: *Machichnus bohemicus*; *Cubiculum*; cf. *Osteocallis*; dinosaur bones; Cretaceous; Uruguay

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1. Introduction

The association between the skeletal remains of vertebrates and invertebrate traces has been reported for dinosaurs and other Mesozoic vertebrates (e.g., [1–11]), although several observations have been made in Cenozoic mammal bones as well (e.g., [12–17]). This type of association is even less common in bird fossil bones [18,19]. Biting and gnawing traces on bones are common in the fossil record and are significant for paleobiological studies [20].

Bioerosion is the modification of hard substrates by biological action [21].

Bioerosion traces usually provide important paleoecological information, and this is more useful if the recurrent patterns of the biological activity they represent are included in a clear nomenclature [22].

Comparatively, bioerosion traces in bone have been less studied than bioerosion traces in other substrates, and the ichnotaxonomic value of traces of bioerosion in bones, without taking into account the traces of vertebrate bites, has not been deeply studied yet [1,22]. Updated synopses of this matter can be found in Pirrone et al. [23], and Lucas [24]

Insect traces associated with dinosaur bones assigned to the ichnogenus *Cubiculum* Roberts et al., 2007, were first recorded in the Late Cretaceous of Madagascar and Utah [25]. Posteriorly, Pirrone et al. [6] described traces assigned to the same ichnogenus in Late Cretaceous dinosaurs from Argentina, as also did Xing et al. [5] in Middle Jurassic dinosaur bones from China. This ichnogenus was also described in association with Cenozoic mammal bones from Africa [16] and South America [17]. The ichnogenus *Machichnus*, in turn, was defined for Miocene bone remains of reptiles and mammals of the Czech

Republic [20], and was also reported in sauropod dinosaurs from the Late Jurassic of Colorado [26].

Herein, we describe the first occurrence of dinosaur remains associated with fossil bioerosion traces from Uruguay. It consists of a variety of traces in sauropod bones from the Upper Cretaceous Guichón Formation, which crops out in the northwestern part of the country (Figure 1). This finding allows making inferences about the environmental conditions during the deposition of this unit and the taphonomic processes involved.

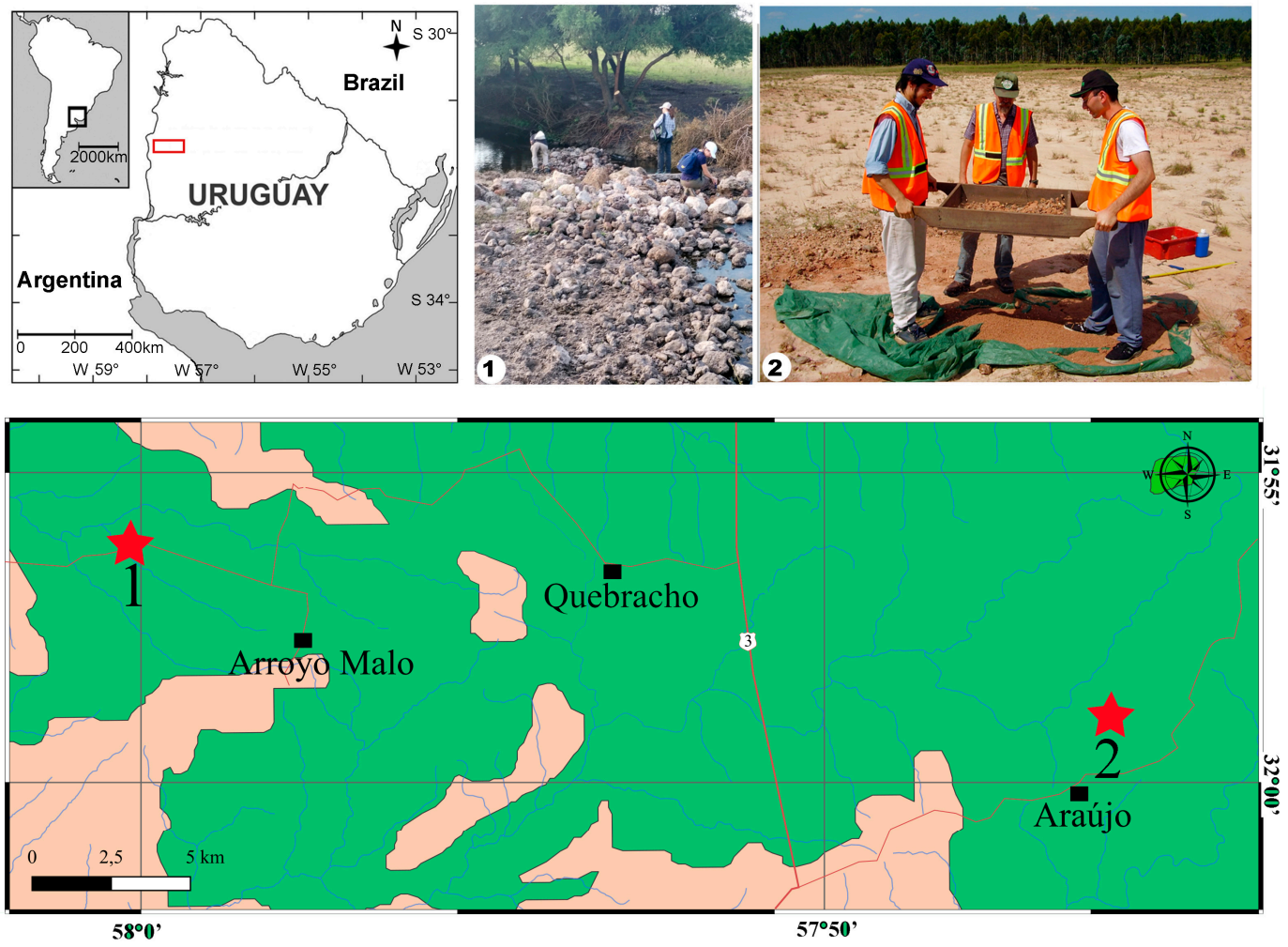

Figure 1. Map showing the two localities (1 and 2) with bioeroded dinosaur bones, and panoramic photos of them.

2. Materials and Methods

The studied material is stored in the fossil collection of the Facultad de Ciencias/UdelaR, Uruguay (FC-DPI-9924; 9925, and FC-DPV-1900; 3595).

The trace fossils found in the bones were analyzed with a stereomicroscope at different magnifications and, when necessary, some traces were cast with latex to better appreciate the internal structure.

The formal stratigraphy used in this work follows the rules and suggestions of the International Stratigraphic Guide [27] and the International Chronostratigraphic Chart [28].

The measurements were taken with manual calipers accurate to 0.01 mm and expressed in millimeters.

3. Geological Setting and Age

The Guichón Formation [29], equivalent to the "Guichón Sandstones" of Lambert [30] is a siliciclastic unit which crops out in the Paysandú and Río Negro departments, northwest Uruguay. It unconformably overlies thick Early Cretaceous basaltic flows (Arapey Formation, the Uruguayan equivalent of the Brazilian Serra Geral Formation) and is in turn unconformably overlain by the coarser Late Cretaceous deposits of the Mercedes Formation [29]. Following Goso & Perea [31], the Guichón Formation comprises pink-grayish to orange- and red-grayish, fine- to medium-grained sandstones, rich in quartz and feldspars, with an abundant (35%) argillaceous matrix (i.e., feldspathic wackes). These sandstones are interbedded with medium to fine conglomerates and thin, massive but scarce mudstones. The unit is interpreted as the deposition of SW-flowing proximal braided rivers, with local aeolian and/or aeolian reworked deposits (e.g., Meseta de Artigas, Paso Hervidero).

The two fossil-bearing localities are located in the Paysandú department, one near the Arroyo Malo Town and the other near Araújo Town (Figure 1). The first one corresponds to small outcrops alongside a secondary road. These pinkish and orange, fine- to medium-grained sandstones and orthoconglomerates, with massive structures and presence of rizolithes, sometimes showing intense local silicification, correspond to fluvial facies of the Guichón Formation. The second locality is a large gully, formed by the weathering and erosion of the typical orange sandstones of the lithological unit, which was first mentioned by Soto et al. [32,33].

The age of the Guichón Formation has been a subject of debate. Goso & Perea (2003) [31] proposed a late Early Cretaceous age, mainly based on lithological similarities with the Aptian–Albian Migues Formation of the Santa Lucía Basin, southern Uruguay. However, the fossil content is more consistent with a Late Cretaceous age. The derived saltasauroid *Udelartitan celeste* plus cf. *Sphaerovum* eggshells imply a younger, late Late Cretaceous age [34]. This is also consistent with the U-Pb age obtained for the calcretization process for the overlying Mercedes Formation, which gives a Maastrichtian age [35]. However, the notosuchian *Uruguaysuchus aznarezi* [36] favors an early Late Cretaceous age (i.e., Cenomanian–Turonian, [37]). The issue remains open, and an indeterminate Late Cretaceous age for the unit is adopted herein.

4. Results

Systematic Ichnology

The following ichnotaxa were clearly identified in association with the dinosaur remains:

Ichnogenus *Machichnus* Mikulás et al., 2006

Type ichnospecies *Machichnus regularis* Mikulás et al., 2006

Machichnus bohemicus Mikulás et al., 2006 (Figure 2A)

Material. FC-DPI-9924, two groups of shallow, subparallel, convergent smooth bottom scratches, and three isolated similar scratches in a possible sauropod metacarpal fragment (Figure 2), associated with FC-DPI-9925 (see above).

Locality and stratigraphic level. Town of Arroyo Malo, near Quebracho, Paysandú department, Guichón Formation (Figure 1).

Description. There are three groups of scratches on one side of the bone. One forms a kind of "bouquet" or "crochet" of about 0.5 cm^2 in surface; the largest one, of about 1 cm^2 in surface area, shows parallel scratches; and close to them, three curved marks of ca. 0.5 cm long are isolated but not far from to each other (Figure 2).

Comments: The surface of the bone is smooth and shows little wear, which allowed the preservation of small, delicate traces such as *Machichnus bohemicus.* Such ichnospecies could be interpreted as a gnawing (rasping) trace. A similar interpretation can be applied to *Gnathichnus* Bromley, 1975. However, the grooves of *Machichnus* are oriented perpendicular

to the substrate edge and, as noted by Mikulás et al. [20], they primarily affect substrate edges, which is not the case for *Gnathichnus*.

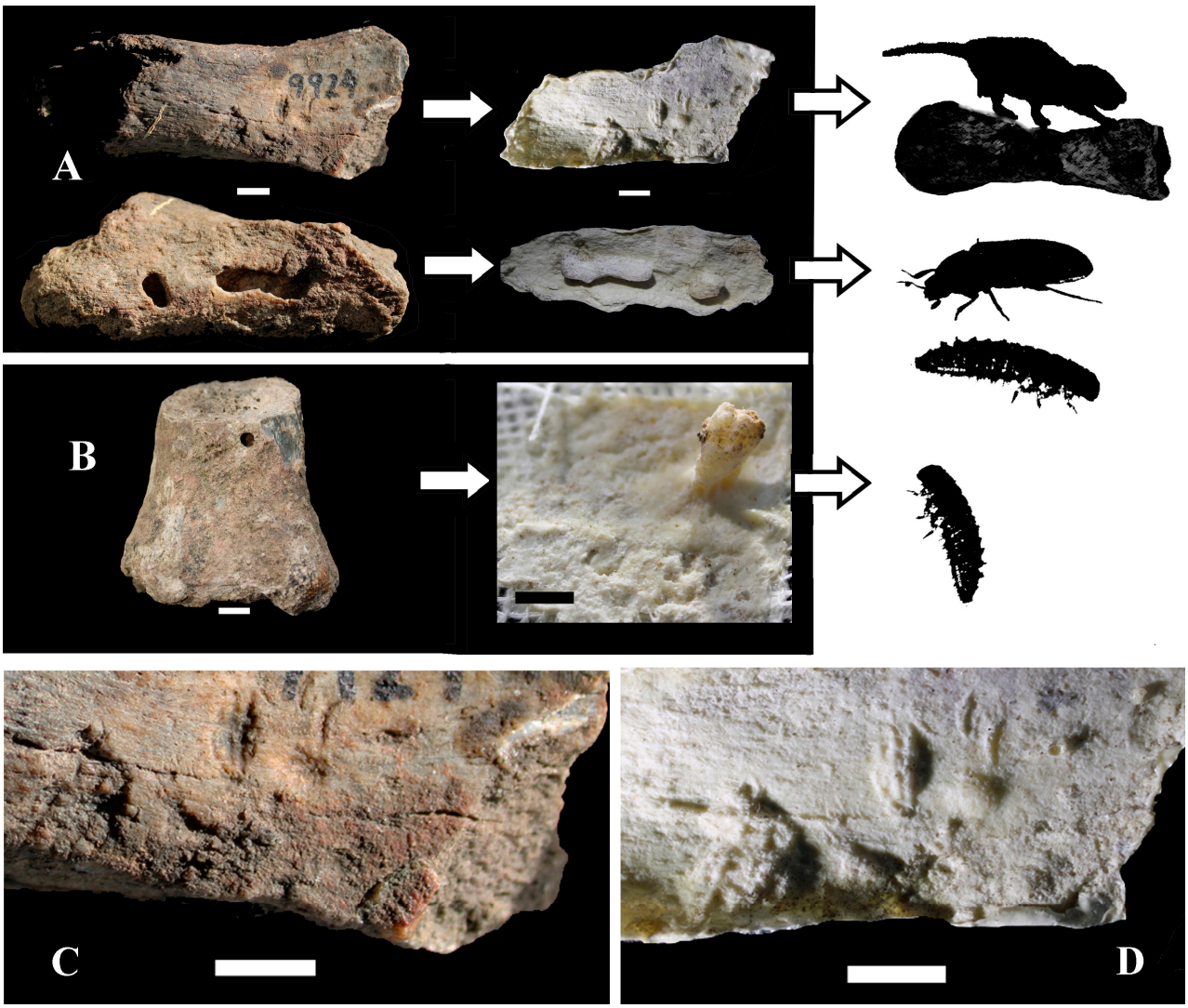

Figure 2. Above: (**A**) probable metatacarpal fragment of sauropod (FCDPI-9924) showing *Machichnus bohemicus* and *Cubiculum* isp. traces, and (**B**) caudal vertebral centrum of cf. *Udelartitan celeste* (FC.DPI-9925) with *Cubiculum* isp. In the center, corresponding latex casts of the bioerosion structures; on the right, probable interpretations of the tracemakers. Below: (**C**,**D**) part of Figure (**A**) enlarged to see details of *Machichnus bohemicus* and its corresponding cast. Scale bars 1 cm in all cases.

Scratches of the described morphology of *M. bohemicus* most likely occur during the feeding activity on soft tissues surrounding the bones [20]).

Ichnogenus *Cubiculum* Roberts et al., 2007.

Type ichnospecies *Cubiculum ornatum* Roberts et al., 2007, emended by Höpner & Bertling [22].

Cubiculum isp. (Figure 2A)

Material: FC-DPI-9924, two chambers in a possible sauropod metacarpal fragment. FC-DPI-9925 and a small boring in the proximal portion of a caudal vertebral centrum of cf. *Udelartitan celeste.*

Locality and stratigraphic level. Town of Arroyo Malo, near Quebracho, Paysandú department, Guichón Formation, Upper Cretaceous of Uruguay (Figure 1)

Description. Ovoid or ellipsoid excavations with chamber general morphology, moderately deep (between 4 and 8 mm), with a rounded base. One of them is approximately 30 mm long and 10 mm wide, and the other is approximately 14 mm long and 7 mm wide (Figure 2A). A small boring (5 mm diameter) with marked concavities on the flanks and bottom, and constriction of walls in the upper area (Figure 2B). Absence of internal scratches (bioglyphs).

Locality and stratigraphic level. Town of Arroyo Malo, near Quebracho, Paysandú department, Guichón Formation (Figure 1).

Description. A small (5 mm diameter) ball-shaped boring with marked concavities on the flanks and bottom, and constriction of walls in the upper area. Absence of internal scratches (bioglyphs).

cf. *Cubiculum* isp. (Figures 3 and 4).

Material. FC-DPV-3595, on the condyle of the third caudal centrum of *Udelartitan celeste* Soto et al., 2024. FC-DPV-1900, metacarpal referred to *Udelartitan celeste*.

Locality and stratigraphic level: Town of Araújo, near Quebracho, Paysandú department, Guichón Formation (Figure 1).

Description. The third caudal centrum shows two chamber-shaped perforations on the condyle surface. These have very irregular bottom surfaces, perhaps due to the highly spongy bone being used as a substrate (Figure 3). The metacarpal shows a small circular boring (about 5 mm diameter and 3 mm depth), probably a bore-probe, and near it an elongate convex structure that we interpret as the mineral filling of a chamber (Figure 4).

Ichnogenus *Osteocallis* Roberts et al., 2007.

cf. *Osteocallis* isp. (Figure 5). *Material.* FC-DPV-3595, on the condyle of the first caudal centrum and the cotyle of the second caudal centrum of *Udelartitan celeste*.

Figure 3. Condyle of the second caudal vertebra centrum of the holotype of *Udelartitan celeste* (FC-DPV-3595) showing bioerosion structures tentatively identified as cf. *Cubiculum* isp. Latex cast on the right. Scale bars 3 cm.

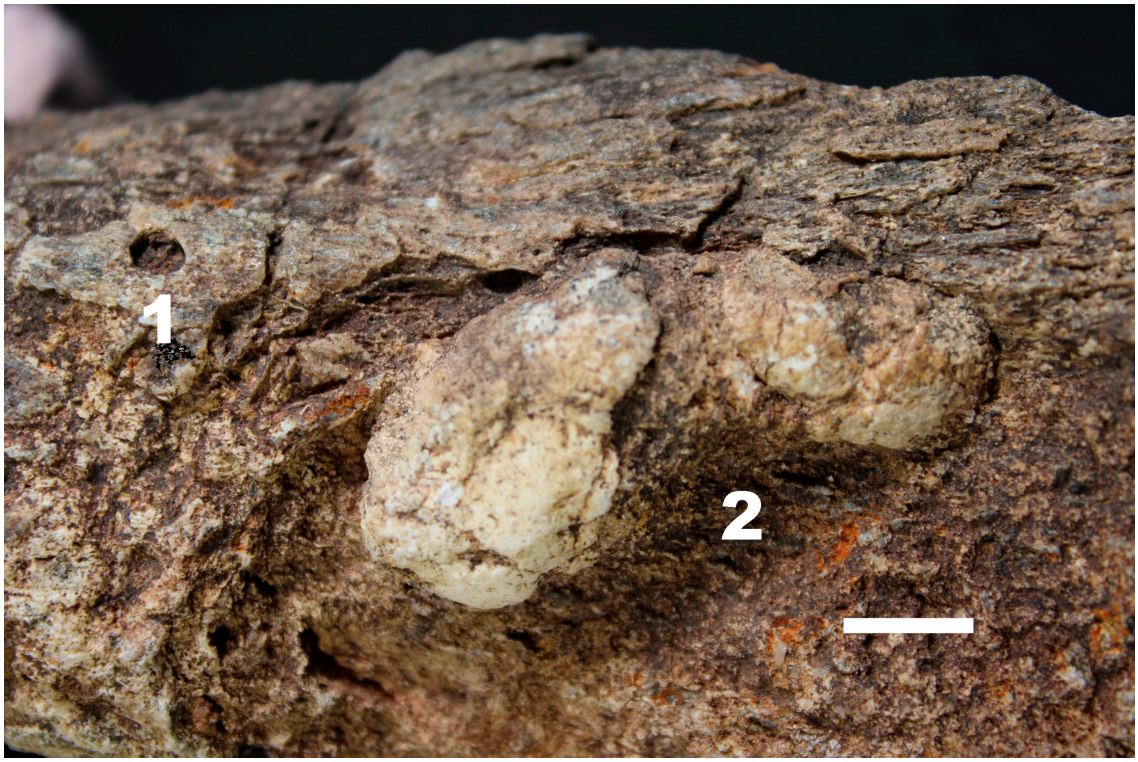

Figure 4. Metatacarpal fragment of *Udelartitan celeste* (FC.DPV-1900), showing bioerosion structures tentatively identified as cf. *Cubiculum* isp.: (1) an incipient bore-probe, (2) a chamber filled with minerals.

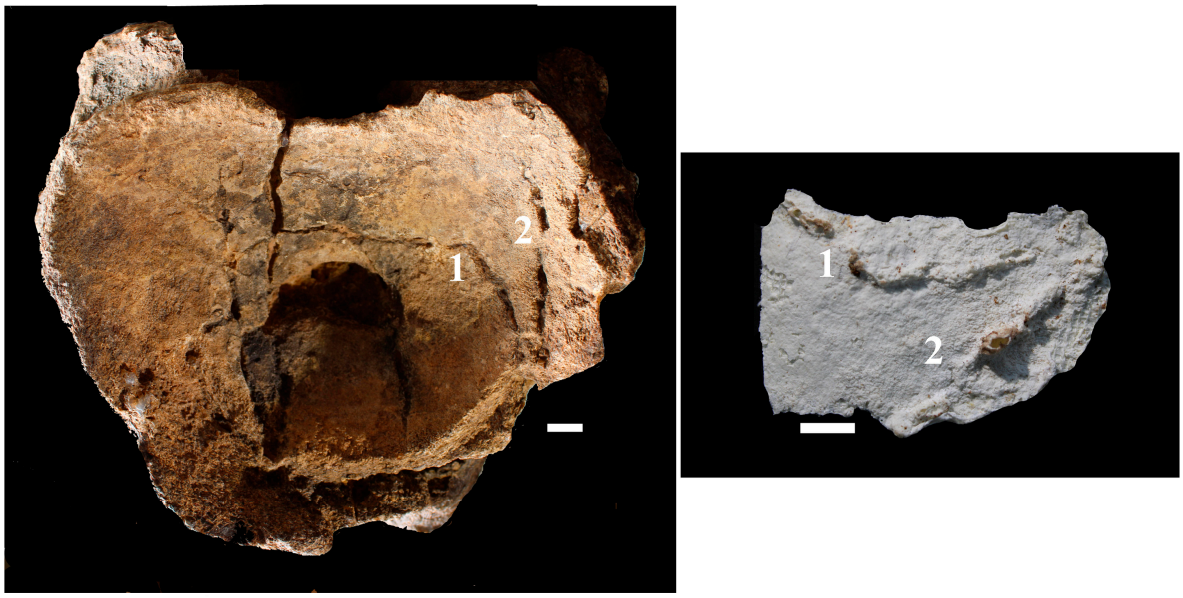

Figure 5. Cotyle of the third caudal vertebra centrum of the holotype of *Udelartitan celeste* (FC-DPV-3595) showing bioerosion structures tentatively identified as *Osteocallis* isp. (1 and 2). Latex casts on the right. Scale bar 1 cm.

Locality and stratigraphic level. Town of Araújo, near Quebracho, Paysandú department, Guichón Formation (Figure 1).

Description. Shallow trails of grooves in the cortical bone. They form curved lines that are approximately parallel to the external contour of the cotyle or condyle of each vertebra.

Comments: The bones from this locality are less well preserved than the first described specimens FC-DPI-9924 and 9925. They have a rougher and more worn surface, which makes it more difficult to distinguish traces on their surface.

5. Discussion

5.1. Tracemakers and Biology

Machichnus bohemicus could represent a small terrestrial reptile or mammal, probably a multituberculate given the morphology of the traces attributed to the effect of gnawing [38] and the context of its geological age.

Cubiculum isp. (Figure 2A) is considered to represent pupal chambers of scavenger or osteophagous insects, probably dermestid beetles [5,22,25]. However, there is not enough experimental evidence to assign the bowl-shaped trace FC-DPI-9925 to dermestid pupation chambers [23]. This trace has a hole general morphology [6], and according to the definitions used by Britt et al. [2], it could be an incipient bore-probe.

Osteocallis probably corresponds to the feeding tracts of insects [8,25,39]. The furrows can be interpreted as an "external mining/harvesting" structure [2], in which the width of the trace reflects the growth of the larva. "The general use of this ichnogenus to accommodate all shallow trails of grooves in cortical bone" was suggested by Paes-Neto et al. [8].

5.2. Taxonomy of Bones

As described, the three first vertebrae of the holotype of *Udelartitan celeste* FC-DPV-3595 have probable traces attributed to sarcosaprophagous insects. The bone material from Arroyo Malo (FC-DPI-9924 and 9925), showing the presence of most of the ichnotaxa described here, including those referred to small gnawing vertebrates, could also be assigned tentatively to *Udelartitan celeste*, particularly the vertebral remain FC-DPV- 9925, given that it shows an hexagonal cotyle border, an autapomorphic trait of the species [34].

5.3. Taphonomy, Ecology of the Tracemakers, and Environment

Different degrees of preservation are observed in the ichnofossils analyzed, depending on the geographic location from which they originate. This is closely linked to the degree of preservation of the bones that contain them. The dinosaur bones FC-DPI-9924 and 9925, from Arroyo Malo Town, have a less abraded surface than those from Araújo Town (FC-DPV-1900 and 3595). In both locations, the deposits of the Guichón Formation are made up of sandstones and conglomerates of probable fluvial origin. In this context, the bones of *Udelartitan celeste* (FCDPV-1900 and 3595) from Araújo probably underwent greater transport processes than those from Arroyo Malo (FCDPI-9924 and 9925).

The gnawing activity inferred for *Machichnus bohemicus* was perhaps related to obtaining dry organic matter or minerals from bones [38]. According to laboratory experiences, as well as taphonomical and forensic observations, all suggested insect tracemakers should have a better development in a terrestrial warm and dry environment [1,12,13,15,17,40,41]. This is also supported by the interpreted paleoenvironment for the Guichón Formation, i.e., fluvial deposition in arid to semi-arid climate, interspersed with long intervals of no deposition [31].

It is also possible to infer subaerial exposure of the bones prior to their burial, since the traces represent the activity of a sarcosaprophagous and scavenger fauna commonly associated with the last stages of terrestrial vertebrate decomposition, although a transient burial can favor the development of certain insects [39].

In particular, the dermestid beetles, whose body fossils are undoubtedly registered since the Late Cretaceous [5], are scavengers that develop better in dry organic matter at intermediate temperatures (e.g., [15,41–43]).

6. Conclusions

The first traces of bioerosion in dinosaur bones are reported from Uruguay. They were identified in sauropod remains coming from the Upper Cretaceous Guichón Formation, which crops out in the Paysandú department, northwestern Uruguay.

The bone specimens FC-DPI-9924 and 9925, from Arroyo Malo, the better-preserved ones, bear the more conspicuous traces described herein: *Machichnus bohemicus and Cubiculum* isp. Traces tentatively assigned to *Cubiculum* isp. and *Osteocallis* isp. are described for the vertebrae of the holotype specimen of *Udelartitan celeste* FC-DPV-3595, along with some other material attributed to this species from the same locality (FC-DPV-1900). These last two numbers correspond to bones that are less well preserved, perhaps due to greater rolling.

Some of the bioerosion traces described (*Cubiculum* and *Osteocallis*) are attributed to sarcosaprophagous beetles, probably dermestids, while others, attributed to *Machichnus bohemicus*, could be interpreted as the gnawing activity of a small scavenger vertebrate, probably a multituberculate mammal.

The insects probably responsible for the bioerosion fossil traces studied herein point to depositional conditions characterized by dry and non-depositional episodes in a warm climate for the referred stratigraphical unit.

The action of this scavenging fauna indicates a period of subaerial exposure of the bones before their final burial.

Author Contributions: Conceptualization (D.P., M.V., M.S., V.M. and F.M.); methodology (D.P., M.V., V.M., M.S. and F.M.); software (D.P., M.V. and V.M.); data curation (D.P., M.V. and V.M.); writing—reviewing and editing (D.P.). All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflicts of interest.

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