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Bioerosion traces in bones of *Cuvieronius hyodon* from the Loltún Cave, Yucatán: First evidence of osteophagy by insects in Pleistocene caves of Mexico

Roberto Emmanuel Hernández Jasso and Alberto Blanco Piñón

ABSTRACT

This study describes and analyzes the first known case of osteophagy by insects in a continental cave setting from the Pleistocene of Mexico. The material consists of both bone and dental remains of *Cuvieronius hyodon* collected from layer X of the Lotun Cave, Yucatán, Mexico. The fossil remains expose a series of ovoid and ellipsoidal borings that strongly resembles the morphology and size reported for the ichnospecies *Cubiculum ornatus*, which has been attributed to pupal chambers of beetles of the family Dermestidae. The presence of these bioerosion traces in gomphother bones provides important information on its postmortem history, and the paleoenvironmental scenario established during the entire taphonomic process.

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INTRODUCTION

Bioerosion is the destruction of hard substrates resulting from biological activity (Neumann, 1966). Traditionally, bioerosion traces have been classically analyzed to determine and understand the nature of the producer. Furthermore, the bone-modification features provide critical insights into the postmortem histories of vertebrate fossil assemblages (Roberts et al., 2007). In recent years, studies of bioerosion traces in fossil bones have been used as an important tool not only for deciphering aspects related to the identification of producer organism, but also for getting valuable information on taphonomy, paleoclimate, and paleoecology (e.g., Cruickshank, 1986; Rogers, 1992; Currie and Jacobsen, 1995; Martin and West, 1995; Hasiotis et al., 1999; Bader et al., 2009; Saneyoshi et al., 2011; Gianechini and De Valais, 2015; Serrano-Brañas et al., 2018; Venegas-Gómez et al., 2024).

One of the most important groups involved in vertebrate decay in continental environments are the insects. Along with other carrion invertebrates, they play a critical role in the decomposition of soft tissues and, to a lesser degree, skeletal material (Campobasso et al., 2001; McHugh et al., 2020). Insects are the main macro-bioeroders that modify bones (e.g., osteophagous, and necrophagous taxa) and can leave distinctive traces on bone surfaces, which are relatively rare both in fossil and the present-day record (West and Martin, 2002; West and Hasiotis, 2007; Pirrone et al., 2014; Xing et al., 2015). Although taxonomic identification of osteophagous organisms to species level can be difficult through their traces, bioerosion features (often assigned to ichnospecies) represent a rich source of biological information concerning the general type and the diversity of the trace producers (Bertling et al., 2006), as well as the diversity of processes that involves the decomposer during the decay.

The oldest confirmed evidence of osteophagy produced by terrestrial invertebrates is represented by bioerosive structures in bone remains produced by the dermestid *Cubiculum inornatus*, from the Middle Triassic Santa María Supersequence in Brazil (Paes-Neto et al., 2016). Later, Cunha et al. (2023) noticed bioerosion traces in rhynchosaur bones from the Upper Triassic of Brazil, also from the Santa María Supersequence.

Fossil record of bioerosion by insects in bones increases significantly in Upper Jurassic (Hasiotis et al., 1999; Chin and Bishop, 2006; Britt et al., 2008; Bader et al., 2009; Augustin et al., 2021) and Cretaceous rocks (Rogers, 1992; Paik, 2000; Nolte et al., 2004; Roberts et al., 2007; Pirrone et al., 2014; Gianechini and De Valais, 2015; Serrano-Bañas et al., 2018; Venegas-Gómez et al., 2024). Finally, the most abundant records come from the Neogene (Dominato et al., 2009, 2010; Odes et al., 2017; Perea et al., 2020; Zonneveld et al., 2024), including bone remains of *Australopithecus* specimens (Odes et al., 2017). In Mexico, the only two known cases of bioeroded skeletal remains produced by insects is represented by bones of hadrosaur dinosaurs from the Upper Cretaceous Cerro del Pueblo Formation (deltaic foodplain scenario), affected by unidentified isopters (Serrano-Brañas et al., 2018) and dermestids (Serrano-Bañas et al., 2018; Venegas-Gómez et al., 2024).

Cenozoic evidence of bioerosion in bones in Mexico is scarce, and none of them were produced by insects until now. Bioeroded remains of *Cuvieronius* sp. produced by bacteria and fungi are known from the Pliocene of Tepeticpac, Tlaxcala, Central Mexico (Straulino et al., 2019). In the Holocene, traces of bioerosion in bones (e.g., dental inlays, cephalic deformations, cranial trepanation) have been reported in from the archaeological records (pre-Hispanic); nevertheless, it has been attributed to cultural (Romero-Molina, 1958; Tiesler, 1994) and/or unintentional factors (cuts, traumatic injury, traces, etc.) caused by fire or even produced by vertebrates activity (Coyoc-Ramirez et al., 2003), rather than insects. Concerning to other localities of Mexico, the presence of insect remains in funerary bundles has been documented in the states of Coahuila (Huchet et al., 2013) and Morelos (Muñiz-Vélez, 2001), however, no traces of bioerosion by insects has been documented in these caves or any other caves in Mexico.

The aim of this work is to report the first evidence of osteophagy by insects in Pleistocene mammal (*Cuvieronius hyodon*) skeletal remains found in cavernous environment (Loltún Cave) from southeastern Mexico, as well as to provide a discussion concerning the trace-producer and substrate (bone) interaction during the decay process, and the environmental conditions that prevailed in the Loltún Cave during the postmortem exposition.

LOCALITY AND GEOLOGICAL SETTING

The Loltún Cave is perhaps the most relevant archaeological-paleontological archive in the Yucatán Peninsula, with more than 4000 fossils and subfossils of Nearctic and Neotropical affinities (Schmidt, 1988; Arroyo-Cabrales-Álvarez, 2003; Morales-Mejía et al., 2009). This cave is located

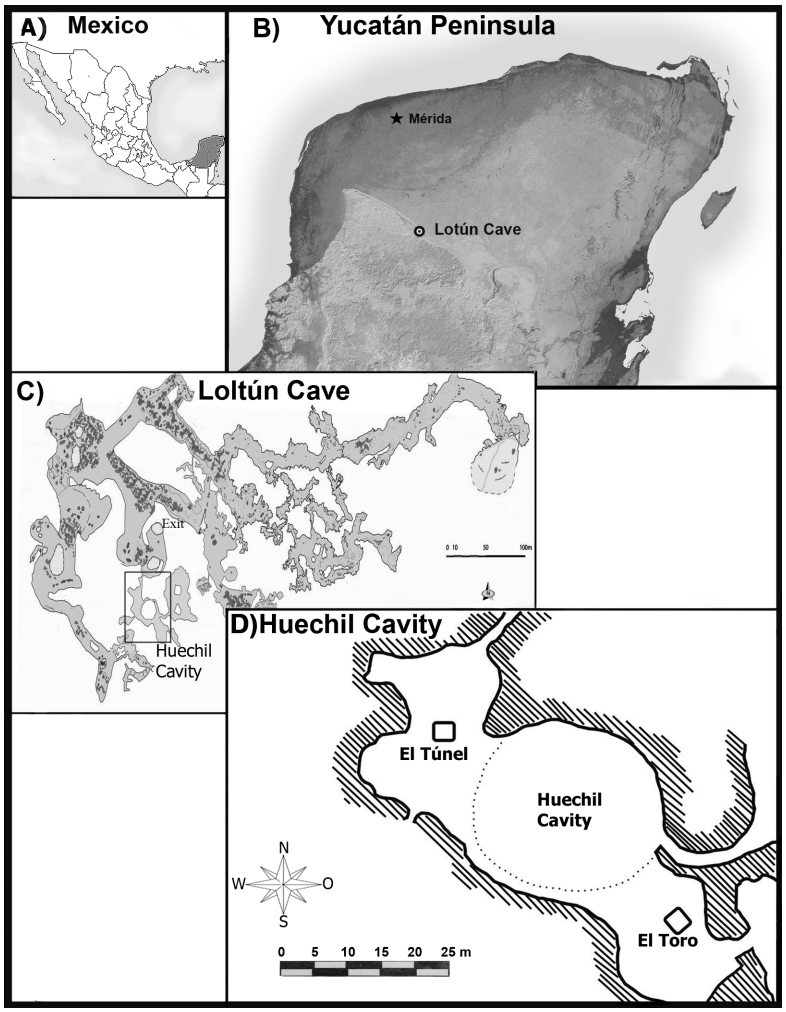

FIGURE 1. Geographic context. A) Location map of the Yucatán Peninsula in Mexico; B) Location of the Loltún cave in the state of Yucatán; C) General plan of Loltún (based on Arroyo-Cabrales and Álvarez (1990); D) Huechil Cavity and "El Toro" stratigraphic unit.

south-southwest of the municipality of Oxkutzcab, in the southwest of the state of Yucatán, México (Figure 1), within geographic coordinates 20°15'14.35" N and 89°27'20.82" W (Velázquez, 1978; 1980) The site is located on the foothills of the Sierra del Pu'uk (Álvarez and Polaco, 1982), also known as Sierra de Ticul, (Arroyo-Cabrales and Álvarez, 2003) where Miocene shallow water carbonates with a content of $CaCO_3$ higher than 89% were affected by acidic groundwaters (Estrada-Medina et al., 2019), that combined with a high precipitation rate in the area and a tropical climate (González-González et al., 2008) displaying different stages of the dissolution process that produced the tunnels and chambers of the complex subterraneous endokarstic systems of which the Loltún Cave is part (Arroyo-Cabrales and Álvarez, 2003).

The Loltún Cave has been studied under different proxies and objectives for several decades. From the late nineteenth century to the mid-twentieth century, several foreign expeditions were made to the cavern (e.g., Mercer, 1896; Hatt et al., 1953). However, paleontological and archeological excavations were carried out at the end of the 1970s by archeologists Norberto González Crespo, Ricardo Velázquez-Valadés, and other members of the Instituto Nacional de Antropología e Historia (INAH) (Velázquez, 1978, 1980; Álvarez and Polaco, 1982).

The excavations were carried out with a metric grid, with quadrants with units of 1 m^2, and areas of 2 m wide × 2 m (or more depending on the need) and controlled stratigraphy during four seasons. The first excavations were carried out in 1977 at the Nahakab entrance, but no remains of

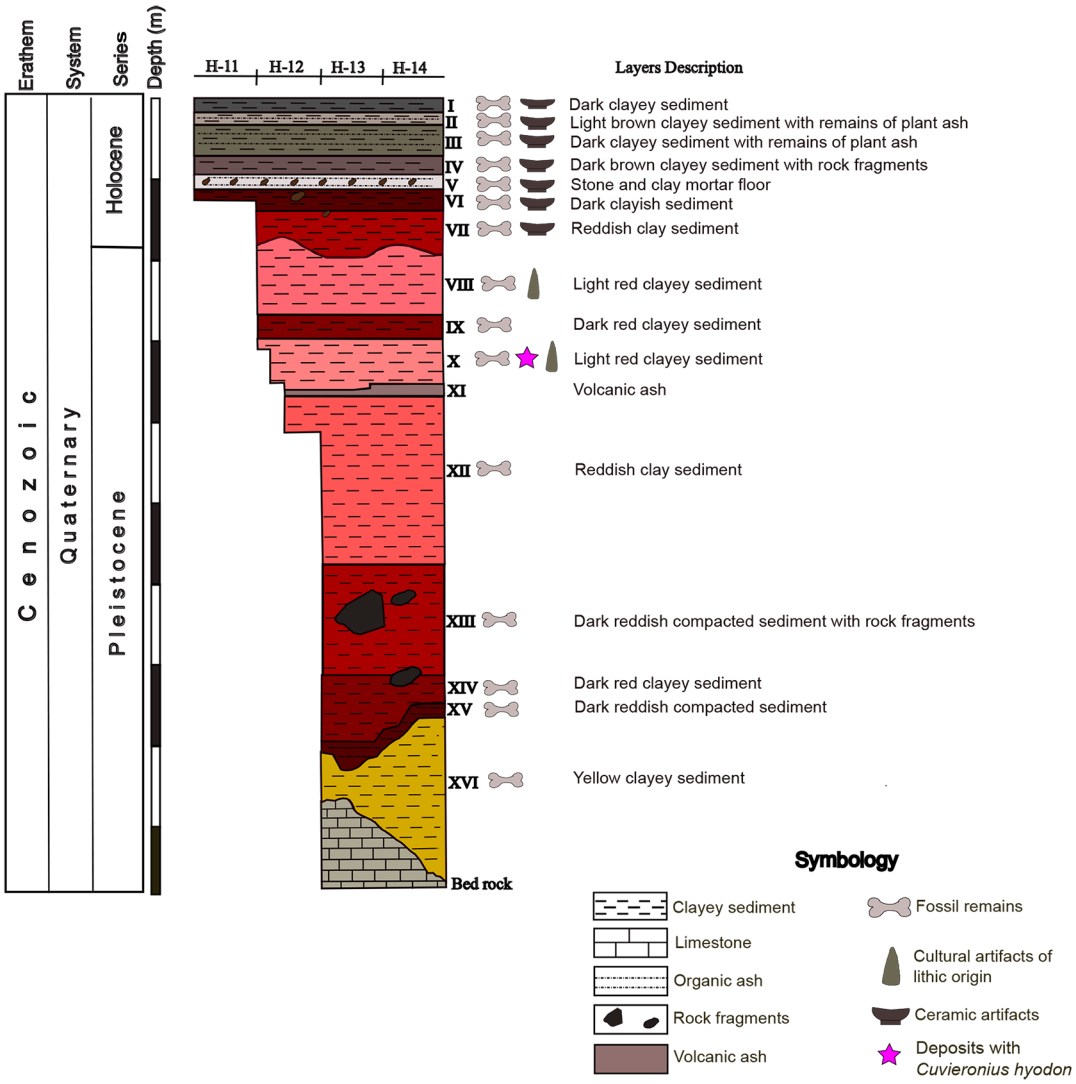

FIGURE 2. Stratigraphic column (redrawn from Álvarez and Polaco, 1982) of El Toro Unit, Loltún cave, Yucatán peninsula. H 11-14, excavation boxes. The stratigraphic layer with *Cuvieronius hyodon* remains is represented by the magenta star.

pre-ceramic materials were found (Velázquez, 1978). Subsequently, several excavation seasons were carried out (1977–1980) in the Huechil chamber, obtaining the stratigraphic sequence in two units, which correspond to the "El Tunel" Unit and the "El Toro" Unit. In the first unit, seven strata or layers are recognized at a depth of 4.8 m. The second unit exhibits sixteen layers with a depth of 9.5 m (Figure 2). Velázquez (1978) recognized 16 horizons, which were enlisted from the oldest (Layer XVI) to the youngest (Layer I). The levels or layers of the sequence can be divided into three main groups (Schmidt, 1988; Arroyo-Cabrales and Álvarez, 2003) numbered top down but described here in profile-up order:

Group 3. Layers IX to XVI are Pleistocene in age, without any cultural material. These layers are formed from reddish clayey sediments except layer XI, composed of volcanic ash correlated to the Rosseau tephra was dated to 28,400 yr by radiocarbon method (uncalibrated, Rampino et al., 1979).

Group 2. Layer VIII is from the Pre-Ceramic Stage; it includes some lithic elements and extinct fauna.

Group 1. Layers I to VII are from the Ceramic Stage (Holocene), but extinct animal remains are found at the bottom of level VII. This group includes layers with clayey sediments of light to dark brown tones.

The remains of *Cuvieronius hyodon* were found in the last metric level of layer X, at a depth between 3.39 and 3.50 m. This layer is composed of clasts of clayey sediments of light reddish tones, small fragments of carbonate and rocks. Other mammals such as *Equus conversidens, Pecari tajacu, Mazama,* and *Odocoileus virginianus*, birds, and reptiles have been found at this same level. The relative age of this layer is calculated ca. 28,400 years, based on the date calculated for the volcanic ash of layer XI (Rampino et al., 1979) as well as 32,782 ±296 yr (Cruz et al., 2016) and confirm the assignation of that level to the Late Pleistocene.

INSTITUTIONAL ABBREVIATIONS

LSAF, Laboratorio de la Sección de Antropología Física, **CINAHY,** Centro INAH-Yucatán (Instituto Nacional de Antropología e Historia), **MRAMPC,** Museo Regional de Anttopología de Yucatán, Palacio Cantón

MATERIALS AND METHODS

The bone remains of *Cuvieronius hyodon* with bioerosion structures from the Loltún Cave analyzed in this study, are deposited in two collections in Mérida, Yucatán: the CINAHY (previously known as the Centro Regional del Sureste), and The Museo Regional de Antropología de Yucatán, Palacio Cantón (MRAMPC). The CINAHY houses limb remains such as right and left humerus; calcaneum; carpal bones [pyramidal and trapezoid]; and unidentified bones (Figure 3A); cranial elements such as fragments, dental pieces, and the left hemimandible (Figure 3B), all of them registered under the catalog number CINAHY:LOLTUN(P): 1978.2.1. The Museo Regional de Antropología de Yucatán, Palacio Cantón (MRAMPC), curates the largest remains of *C. hyodon* (Figure 3C) under the following catalogs: upper right incisor (tusk): MM1988.33:1 (10-347041INV); and first right rib: MM1998-33:3(10-347042INV)The bone remains with bioerosion signatures reported in this document were described in the Laboratorio de la Sección de Antropología Física of the Centro INAH-Yucatán, by using optical instruments such as stereoscopic microscope (Trinocular Stereoscopic Microscope AMSZOOM 3.5X – 90X). Morphological aspects, measurements, and classification were reviewed based on the work of Roberts et al. (2007); Pirrone et al. (2014); and Xing et al. (2015). The depth and diameter of the perforations (bioerosions) were measured by using a Lion Tool Q-1500 mm digital caliper (vernier). The recognition of the morphology of the perforations was possible by making silicone molds. Fossil material were photographed by using a digital camera (Canon EOs Revel T7) and included in a database for further analysis in order to recognize the producer organisms and to understand the taphonomic processes involved in the bioerosion structures.

The bioerosive structures reported in this study were described as tunnels, notches, and holes, and assigned at the ichnospecies level, following the terminology used by various authors for morphologically similar structures (see Roberts et al., 2007; Britt et al., 2008; Pirrone et al., 2014; Xing et al., 2015; Paes Neto et al., 2016; Parkinson, 2016; Serrano Brañas et al., 2018; Benyoucef and Bouchemla, 2023; Trifiglio et al., 2023; Venegas-Gómez et al., 2024; Alves-Silva et al., 2024).

SYSTEMATIC ICHNOLOGY

Ichnogenus *CUBICULUM*
Roberts, Raymond and Foreman (2007)

Type ichnospecies. *Cubiculum ornatus* Roberts, Raymond and Foreman, 2007

Emended Diagnosis (Venegas-Gómez, 2024). “Discrete hollow ellipsoidal to drop-shaped borings considered chambers bored into the surface of inner spongy, outer cortical bone or as subcortical borings with a spongy bone base and a compact bone ceiling. The bases are flat to rounded with smooth to engraved walls perpendicular to the bone surface. The bases can be flat or tapered towards one side. Structures may be isolated but commonly form dense, locally overlapping concentrations. They appear as single-chamber borings or as a composite trace connected with entrance tubes. The chamber is two to six times longer than its diameter”.

See Roberts et al. (2007) for original diagnosis.

Ichnospecies *Cubiculum ornatus*
Roberts, Raymond, and Foreman (2007)
(Figure 3, Table 1)

Diagnosis. “Discrete ovoid borings in bone. Hollow, elliptical chambers with concave flanks bored into inner spongy and outer cortical bone surfaces. Chamber length three to four times greater than diameter or width. May be isolated, but observed more commonly in dense, sometimes overlapping concentrations. Walls roughened commonly, composed of shallow, arcuate (apparently paired) grooves” (after Roberts et al., 2007).

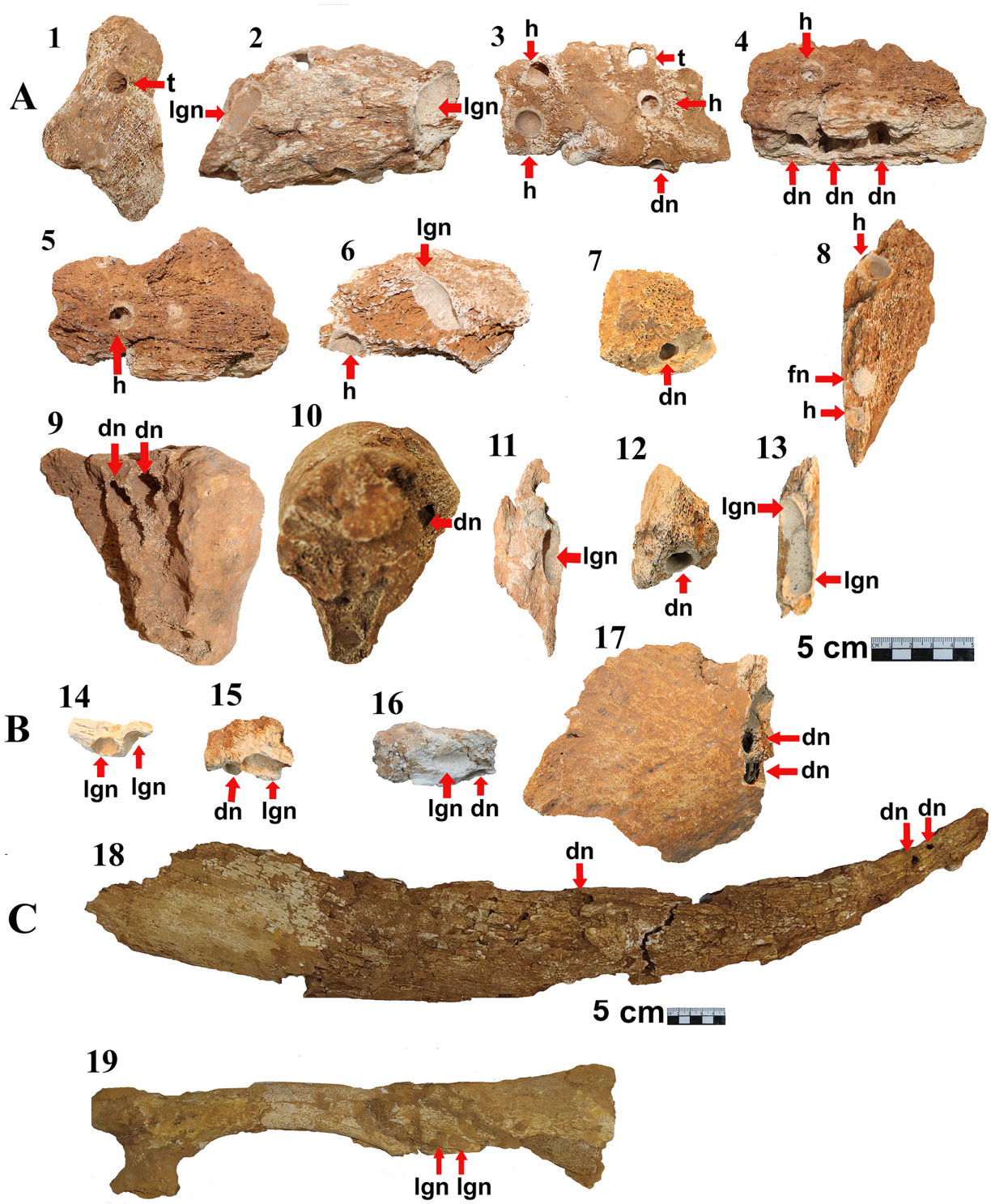

FIGURE 3. Bone and dental remains of *Cuvieronius hyodon* from the Loltún cave, with biotraces assigned to *Cubiculum ornatus*: A) limb remains (CINAHY:LOLTUN(P):1978.2.1) [1) pyramidal (carpal bone); 2-4) unidentified limb bones; 5) left calcareous; 6-8) unidentified limb bones; 9) humerus right; 10) humerus left; 11-13) unidentified limb bones]; B) cranial elements (CINAHY:LOLTUN(P):1978.2.1): [14-16) dental fragment (dentin); 17) mandibular fragment]; C) remains of *C. hyodon* from the Canton Palace collection: MM1988.33:1 (10-347041$_{INV}$) [18) left tusk]; and MM1998-33:3(10-347042$_{INV}$) [19) right first rib]. Tunnels (t), lateral growth notches (ln), holes (h), deep notches (dn), filled notches (fn). Scale bar equals 5 cm.

TABLE 1. Morphological characters (in millimeters) of the bioerosion structures of *Cubiculum ornatus* in fossil bones of *Cuvieronius hyodon* from the Loltún Cave (Abreviations: BS= Total of bioerosive structures, D= Depth, DIA= Diameter, L= length, W= Width).

N	Ichnospecies	Material	Tunnels (mm)	Lateral growth chambers (mm)	Deep chambers (mm)	Filled chambers (mm)	Holes (mm)
1	*Cubiculum ornatus*	Pyramidal CINAHY:LOLTUN(P):1978.2.1	BS: 1 D: 15 DIA: 30	BS: 1 L: 12 W: 7	BS: 1 D: 16 DIA: 12-16	BS: 0 D: DIA:	BS: 0
2	*Cubiculum ornatus*	unidentified limb bone 1 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 1 L: 2.0 W: 0.9	BS: 4 D: 17-26 DIA: 11-15	BS: 1 D: ? DIA:9-11	BS: 0
3	*Cubiculum ornatus*	unidentified limb bone 2 CINAHY:LOLTUN(P):1978.2.1	BS: 1 D: 10 DIA: 9	BS: 3 L: 20-24 W: 9-10	BS: 1 D: 30 DIA: 10	BS: 1 D: 23 DIA:11	BS: 8 D: 8-11 DIA: 8-10
4	*Cubiculum ornatus*	unidentified limb bone 12 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 1 L: 25 W: 10	BS: 0	BS: 2 D: 16-18 DIA: 9-10	BS: 0
5	*Cubiculum ornatus*	Left calcaneus CINAHY:LOLTUN(P):1978.2.1	BS:1 D:30 DIA: 11	BS: 1 L: 12 W: 7	BS: 0	BS: 0	BS: 0
6	*Cubiculum ornatus*	unidentified limb bone 7 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 0	BS: 0	BS: 0	BS:10 Dp: 7 Dm: 7
7	*Cubiculum ornatus*	unidentified limb bone 11 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 1 L: 20 W: 10	BS: 1 D: 17 DIA: 11	BS: 2 D: 30 DIA: 9-10	BS: 1 D: 6 DIA: 8
8	*Cubiculum ornatus*	unidentified limb bone 18 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 2 L: 16-30 W: 11-12	BS: 0	BS: 0	BS: 1 D: 11 DIA: 11
9	*Cubiculum ornatus*	Humerus right CINAHY:LOLTUN(P):1978.2.1	BS: 1 D: 20-35 DIA: 10	BS: 0	BS: 4 D: 12-35 DIA: 9-11	BS: 0	BS: 1 D: 5 DIA: 10
10	*Cubiculum ornatus*	Humerus left CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 1 L: 21 W: 10	BS: 2 D: 24-25 DIA: 09-11	BS: 0	BS: 0
11	*Cubiculum ornatus*	Unidentified limb bone 5 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 1 L: 17 W: 9	BS: 1 D: 18 DIA: 10	BS: 0	BS: 0
12	*Cubiculum ornatus*	Unidentified limb bone 4 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 1 L: 16 W: 11	BS: 0	BS: 0	BS: 0
13	*Cubiculum ornatus*	Unidentified limb bone 9 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 0	BS: 0	BS: 0	BS: 1 Dp: 5 Dm: 10
14	*Cubiculum ornatus*	Dental fragment (dentin) II CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 2 L: 14-22 W: 10-11	BS: 0	BS: 0	BS: 0
15	*Cubiculum ornatus*	Dental fragment (dentin) III CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 2 L: 17-18 W: 9-11	BS: 0	BS: 0	BS: 0
16	*Cubiculum ornatus*	Dental fragment (dentin) IV CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 0	BS: 1 D: 21 DIA: 10	BS: 0	BS: 0

TABLE 1 (continued).

N	Ichnospecies	Material	Tunnels (mm)	Lateral growth chambers (mm)	Deep chambers (mm)	Filled chambers (mm)	Holes (mm)
17	*Cubiculum* indet. *C. ornatus*	Mandible fragment I CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 2 Lg: 14-17 Wd: 8-10	BS: 0	BS: 0	BS: 1 Dp: 5 Dm: 10
18	*Cubiculum ornatus*	Left tusk MM1988.33:1 (10-347041INV)	BS: 0	BS: 0	BS: 4 D: 17 -20 DIA: 11	BS: 0	BS: 1 D: 6 DIA: 10
19	*Cubiculum ornatus*	Right first rib MM1988.33:3 (10-347042INV).	BS: 0	BS: 5 L: 12-22 W: 09-11	BS: 1 D: 18 DIA: 10	BS: 0	BS: 0
20	*Cubiculum ornatus*	Trapezium CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 0	BS: 1 D: 20 DIA: 09	BS: 0	BS: 0
21	*Cubiculum ornatus*	unidentified limb bone 13 CINAHY:LOLTUN(P):1978.2.1	BS: 1 Dp: 7 Dm: 7	BS: 2 L: 11 -12 W: 8-9	BS: 1 D: 15 DIA: 10	BS: 0	BS: 0
22	*Cubiculum ornatus*	unidentified limb bone 14 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 0	BS: 1 D: 20 DIA: 10	BS: 0	BS: 0
23	*Cubiculum ornatus*	unidentified limb bone 15 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 1 L: 27 W: 11	BS: 0	BS: 1 D: 19 DIA:12	BS: 0
24	*Cubiculum ornatus*	unidentified limb bone 16 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 5 L: 13-24 W: 9-11	BS: 0	BS: 0	BS: 0
25	*Cubiculum ornatus*	unidentified limb bone 17 CINAHY:LOLTUN(P):1978.2.1	BS: 1 Dp: 13 Dm: 10	BS: 0	BS: 1 D: 25 DIA: 10	BS: 0	BS: 0
26	*Cubiculum ornatus*	unidentified limb bone 8 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 0	BS: 1 D: 22 DIA: 10	BS: 2 D: 3-4 DIA: 9-10	BS: 0
27	*Cubiculum ornatus*	unidentified limb bone 19 CINAHY:LOLTUN(P):1978.2.1	Bs:0	BS: 1 L: 24-13 W: 11	BS: 5 Dp: 09-11 Dm: 10: 0	BS: 0	BS: 0
28	*Cubiculum ornatus*	unidentified limb bone 20 CINAHY:LOLTUN(P):1978.2.1	BS: 1 Dp: 11 Dm: 10	BS: 0	BS: 0	BS: 0	BS: 0
29	*Cubiculum* indet. *C. ornatus*	Mandible fragment III CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 3 L: 10-22 Wd: 09-10	A: 6 D:14-22 DIA: 9-11	A:1 D:? DIA: 1.0	A: 0
30	*Cubiculum ornatus*	unidentified limb bone 6 CINAHY:LOLTUN(P):1978.2.1	BS: 0	BS: 0	A: 1 D: 8 DIA: 11	BS: 0	A: 2 D: 13-17 DIA: 9-10
Total			BS = 7	BS = 36	BS = 37	BS = 10	BS = 26

Description of Bioerosion Structures from the Loltún Cave

A total of 116 bioerosion traces (borings) were recognized in the bones of *Cuvieronius hyodon* within layer X of the Loltún Cave (Table 1). Ninety-three borings were observed in postcranial bones (six in a complete rib and 87 in 23 small bones or fragments). In the cranial region, 23 traces were found, of which 13 borings in mandible fragments and 10 in teeth (five in a tusk and five in molar fragments). Borings were abundant in fragments and

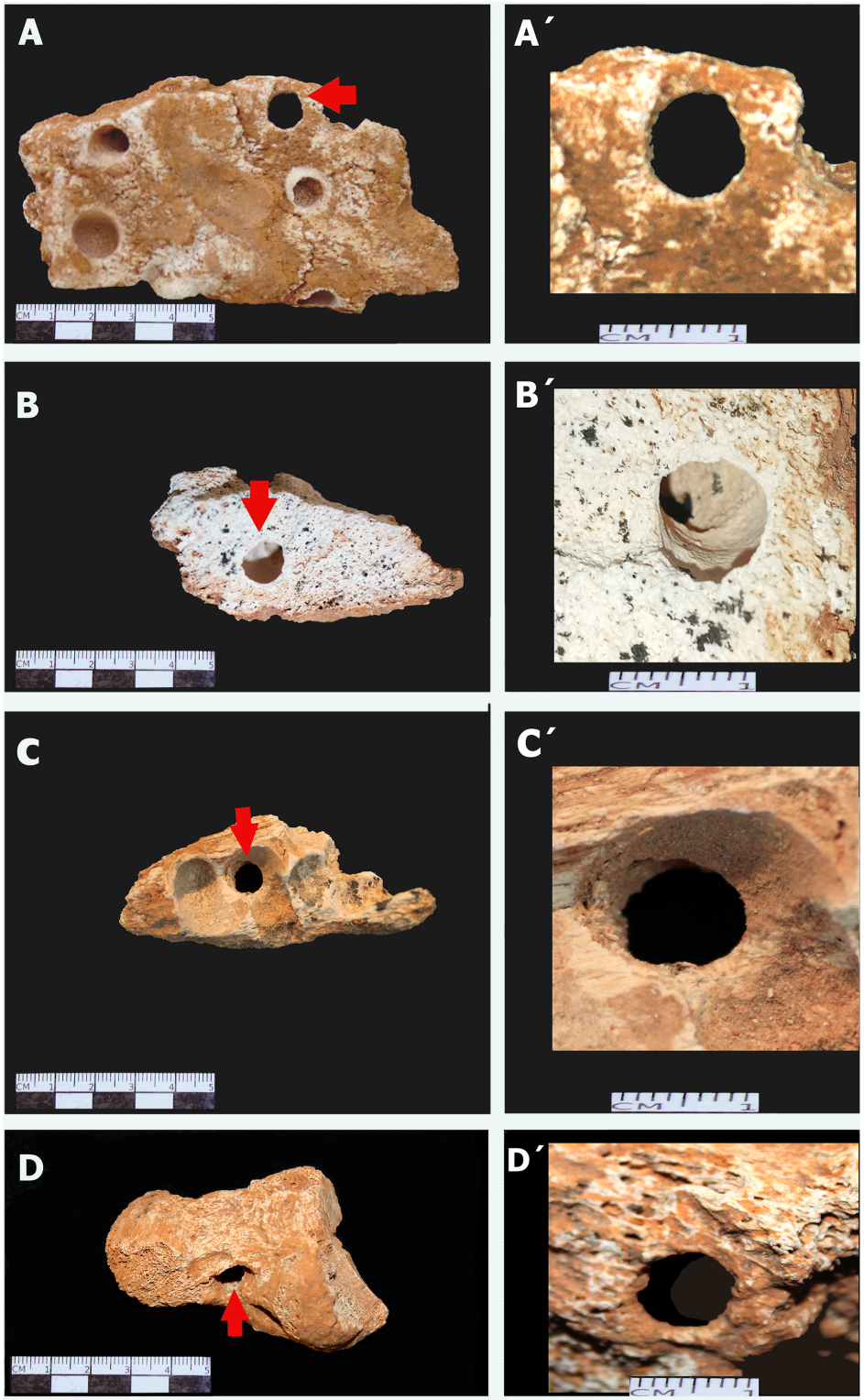

FIGURE 4. Bioerosive structures of *Cubiculum ornatus* in fossil bones of *Cuvieronius hyodon* (CINAHY:LOLTUN(P):1978.2.1) from the Loltún Cave interpreted as tunnels (red arrows): A) bone remain No. 3 (unidentified limb bone 2), A') magnified view of tunnel of A (red arrow); B) bone remain No. 28 (unidentified limb bone 20); C) bone remain No. 21 (unidentified limb bone 13); D) bone remain No. 5 (left calcaneus). A', B', C', and D', represent magnified view of traces (red arrow) illustrated in figures A, B, C, and D respectively. Scale bar in the images A, B, C, and D equals 5 cm; scale bar in the images A', B', C', and D' equals 1 cm.

small bones, whereas in large bones and teeth, the number of traces were scarce. They occur in isolated structures or forming overlapping concentrations.

Tunnels. They consist of straight traces with oval entrance that penetrate the bone vertically/parallel to the bone surface They expose a length that varies from 10 mm to 30 mm with ends having diameters from 8 mm to 11 mm (Figure 4). This type of trace fossils represents the less common bioerosion structure found in *Cuvieronius hyodon* bone remains from Loltún Cave (N= 7). They were observed in one right humerous, a left calcaneus, and in the limb of three unidentified bones. They are not filled by sediment.

Notches. They represents the most abundant type of trace recorded and is present in all bone and dental remains. They are represented by elongated openings with an ovoid or ellipsoidal outline. According to their depth angle, two types of notches are recognized:

a) Lateral growth notches (Figure 5): They represent the second most abundant of all bioerosion traces (N= 36) and are characterized by having an slightly ellipsoidal and shallow chamber at one end, giving the appearance of lateral growth. However, towards the interior of the structure, the chamber becomes slightly more perpendicular until it reaches the other end, which becomes concave with respect to the wall. This type of chamber has an approximate length-width ratio of 3:1, with a range between 12 mm to 30 mm long, and 9 mm to 11 mm wide. The trace was found in spongy, compact bone or between both, as well as in the dentin of the molar and tusk. It may or may not have filling and the walls have bioglyphs.

b) Deep notches (Figure 6): They are the most abundant kind of borings (N= 37). They are also showing a quite-similar shallow end to the previous one. However, the trace is distinguished from the previous one in that it is inserted perpendicularly or obliquely to the line of bone growth. Its end is also convex. The chamber has a length-width ratio similar to the lateral growth notch, although its depth (length) may be slightly greater. Likewise, they can be found in spongy, compact bone or dentin. It may or may not have filling and the walls have bioglyphs.

Holes. They are the third most abundant borings in bones (N= 26), but are rare in teeth. They can be found individually, together, or associated with other types of borings. The chamber entrance is a circular or ovoid pit (Figure 7). Its interior is shallow and slightly oblique, and its end is convex. In general, the holes have a diameter-depth ratio of between 1:1 and 1:2. With a diameter range that ranges from 8 mm to 11 mm and a depth that varies from 5 mm to 10 mm. The holes were only observed in spongy bone or dentin. It may or may not have filling and the walls have bioglyphs.

REMARKS

The characteristics of the bioerosive structures described in skeletal remains of Loltún closely resemble those reported in the emended diagnosis of Venegas-Gómez et al. (2014) for the ichnogenus *Cubiculum*, and mentioned by Roberts et al. (2007), Dominato et al. (2009); Xing et al. (2015); Paes-Neto (2016); Parkinson (2016); Serrano-Brañas et al. (2018), and Venegas-Gómez et al. (2024) for *Cubiculum ornatus*. This ichnospecies is characterized by ovoid cavities entrances, ellipsoidal chambers present in bones and teeth, with concave wall flanks bored into inner cortical bone surfaces, in spongy bone, and the dentin; the chamber length in most of them is approximately three times longer than the width in the notches. They occur in isolated structures or in concentrations overlapping or in close contact each other, and the presence of well-developed bioglyphs, considered as ichnotaxobases for the ichnogenus. In contrast, *Cubiculum inornatus* maintains a gross ellipsoidal morphology, has a more pronounced apical constriction, does not exhibit concave walls, and lacks bioglyphs (Xing et al., 2015; Paes-Neto et al., 2016; El Hedeny el al., 2023); *C. levis*, exhibits a sharply constricted upper margin that detail its particular bowl-shaped morphology and, as well as *C. inornatus*, bioglyphs are absent (Pirrone et al., 2014, Xing et al., 2015); *C. cooperi* does not expose concave flats, the trace length is three to four times its diameter, and it also lacks of bioglyphs (Parkinson, 2016); *C. atsintli* also lacks bioglyphs and exhibits a characteristic drop-like chambers (Serrano-Brañas et al., 2028) and *C. subcorticalis* has a subcortical natures and exhibits a bone ceiling, features absent in the rest ichnospecies of *Cubiculum* (Venegas-Gómez, 2024).

DISCUSSION

On the Nature of the Bioerosion Traces on the Skeletal Remains of *Cuvieronius hyodon*

Traces in *Cuvieronius hyodon* are not comparable in size and morphology to those pits, holes, perforations, or traces produced by the bite action

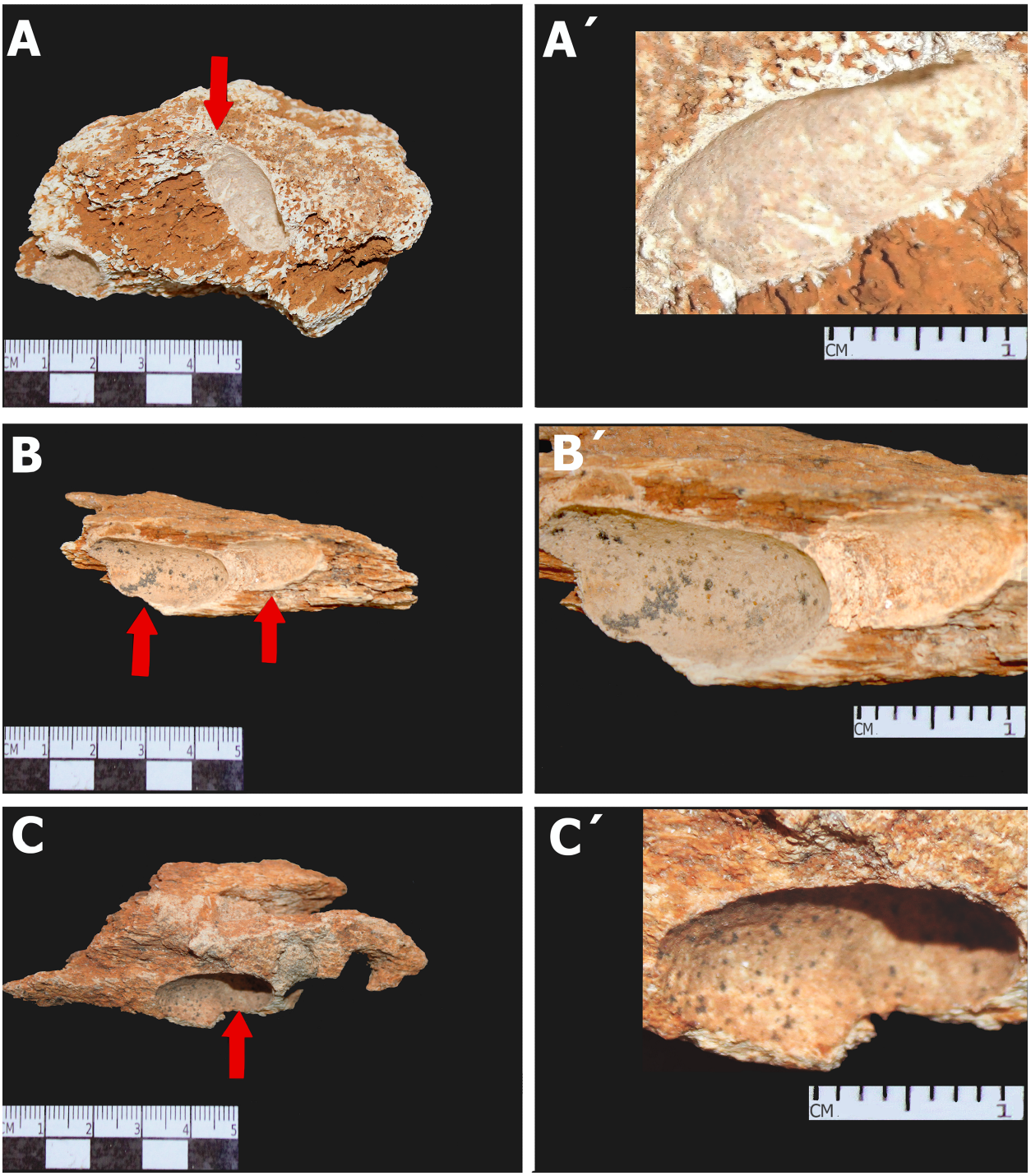

FIGURE 5. Bioerosive structures of *Cubiculum ornatus* in fossil bones of *Cuvieronius hyodon* (CINAHY:LOLTUN(P):1978.2.1) from the Loltún Cave. Lateral growth notches (Lgn): A) bone remain No. 13 (unidentified limb bone 9); B) bone remain No. 28 (unidentified limb bone 20); C) bone remain No. 4 (unidentified limb bone 12). A', B', and C', represent magnified view of traces (red arrow) illustrated in figures A, B, and C respectively. Scale bar in the images A, B, C, and D equals 5 cm; scale bar in the images A', B', C', and D' equals 1 cm.

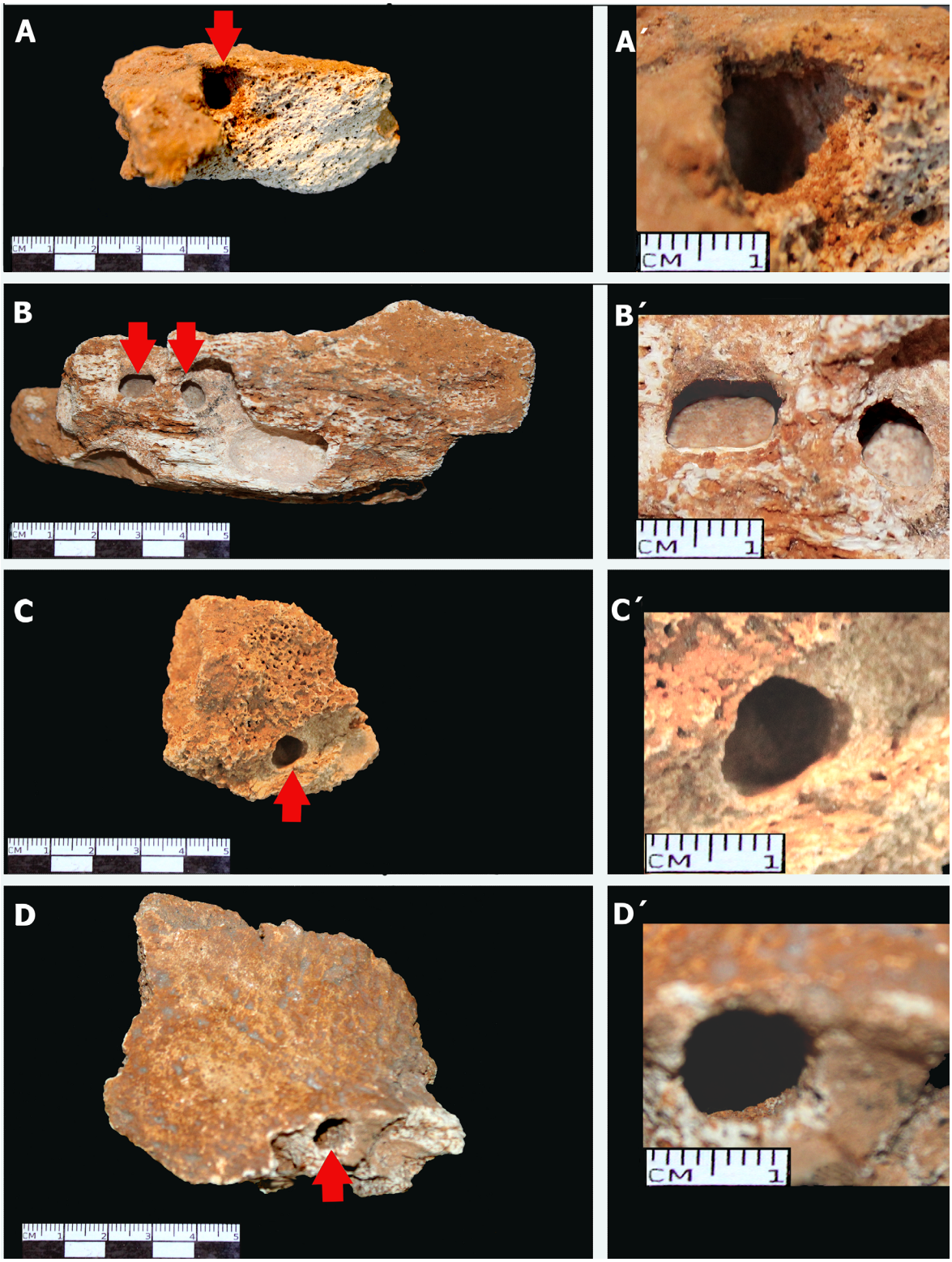

FIGURE 6. Bioerosive structures of *Cubiculum ornatus* in fossil bones of *Cuvieronius hyodon* (CINAHY:LOLTUN(P):1978.2.1) from the Loltún Cave. Deep notches (Dn): A) bone remain No. 22(unidentified limb bone 14); B) bone remain No. 2 (unidentified limb bone I); C) bone remain No. 11 (Unidentified limb bone 5); D) bone remain No. 29 (mandible fragment III). A', B', C', and D', represent magnified view of traces (red arrow) illustrated in figures A, B, C, and D, respectively. Scale bar in the images A, B, C, and D equals 5 cm; scale bar in the images A', B', C' and D' equals 1 cm.

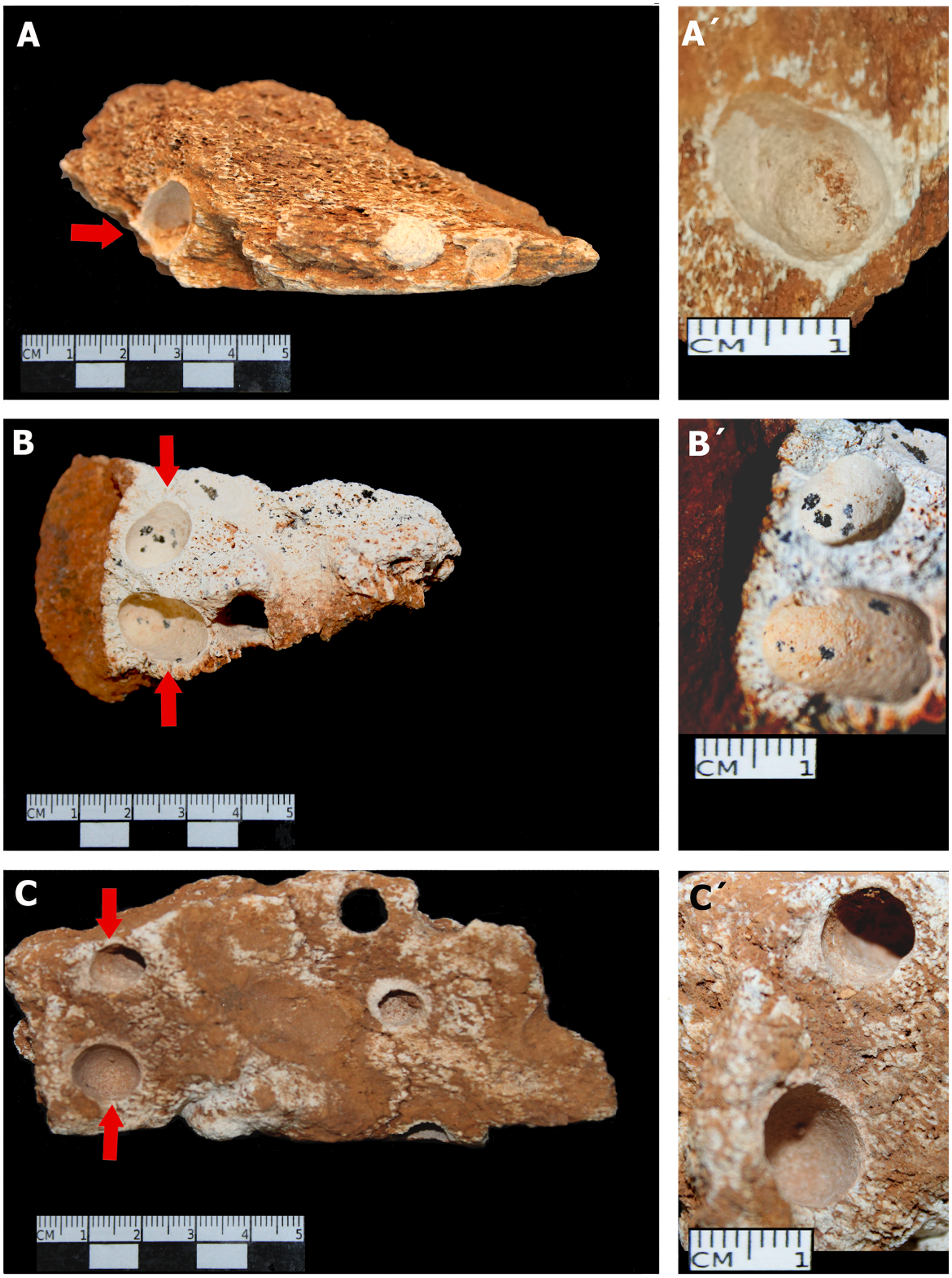

FIGURE 7. Bioerosive structures of *Cubiculum ornatus* in fossil bones of *Cuvieronius hyodon* (CINAHY:LOLTUN(P):1978.2.1) from the Loltún Cave. Hole (H): A) bone remain No. 26 (unidentified limb bone 8); B) bone remain No. 30 (unidentified limb bone 6); C) bone remain No. 3 (unidentified limb bone 2). A', B', and C', represent magnified view of traces (red arrow) illustrated in figures A, B, and C, respectively. Scale bar in the images A, B and C equals 5 cm; scale bar in the images A', B', and C' equals 1 cm.

of some known continental predators and/or scavengers from the Pleistocene (e.g., rodents, birds, reptiles) present in the Loltún Cave and the surrounding area (Goff, 1993; Morales-Mejía et al., 2009). Although it is assumed that they also were involved during the decay processes of *C. hyodon* and the remaining stages of decomposition, consuming soft tissues and/or some bones.

Loltún traces preserved in bone and teeth remains of *Cuvieronius hyodon* consist of shallow, ellipsoidal borings with oval entrances, disposed in isolated structures or forming isolated or concentrations. They occur in the cortical bone surface as well as the cancellous bone, and within the dentine in teeth. Traces with walls displaying concave flanks; with a length approximately three times bigger than the diameter; and they are characterized by the presence of bioglyphs. Those characters agree with those in Roberts et al. (2007), Dominato et al. (2009), Xing et al. (2015), Paes-Neto (2016), Parkinson (2016), Serrano-Brañas et al. (2018), and Venegas-Gómez et al. (2024) for *Cubiculum ornatus*, and make the Loltún traces clearly distinguishable of the other five ichnospecies of the ichnogenus *Cubiculum* (see the section of remarks).

The anatomy and sizes of the bioerosion traces of the Loltún structures suggest that they were created by osteophagous activity in a postmortem stage. For instance, the presence of well-developed bioglyphs on the internal walls of the traces here studied, could be an evidence of the progressive bone perforation made by the mandibula of dermestid larva, as suggested by Laudet and Antoine (2004), Britt et al.(2008), and Parkinson (2022), and documented by Fernández-Jalvo and Marín-Monfort (2008) under laboratory conditions.

In addition, several authors have also suggested that some ichnospecies of the ichnogenus *Cubiculum* are pupal chambers as a consequence of osteophagus activity of dermestid beetles (Robets et al., 2007; Britt et al., 2008; Parkinson, 2016; Trifilio et al., 2023; Alves-Silva et al., 2024; Venegas-Gómez et al., 2024; Perea et al., 2025). Schwanke and Kellner (1999) described cylindrical borings as supposed dermestid pupation chambers in Triassic vertebrate bones from Brazil, which according to Roberts et al. (2007) could be referable the ichnogenus *Cubiculum*. These traces could represent the ancient record of this ichnogenus.

Concerning *C. ornatus*, traces referable to this ichnospecies (see Roberts et al., 2007) and interpreted as dermestid chambers were described from the Neogene of Germany (Tobien, 1965) Plio-Pleistocene of South Africa (Kitching, 1980) and Pleistocene of USA (Martin and West, 1995). Dominato et al. (2009) also associated borings of *C. ornatus* observed in mastodont cervical vertebrae from the Pleistocene of Brazil to dermestid activity.

The dominance of dermestid beetle marks and the absence of ichnospecies other than *C. ornatus* in the bones and teeth of Loltún remains unknown, and represents a curious phenomenon that allows discussion about behavioral biology, taphonomy, and preservation vias. Caves often have limited scavenger access, stable microclimates, and slower decay rates conditions ideal for dermestid colonization (Gatta et al., 2021), but less favorable for other osteophagous groups that require open air condition (termites) or specific humidity (darkling beetles). In this context, *C. ornatus* traces on Pleistocene bone and teeth remains of the gomphotheriid *Cuvieronius hyodon* likely reflect both the behavioral adaptations of dermestid and the taphonomic filtering on the cave of Loltún, which selectively preserved their osteophagus activity.

According to Cruz et al. (2016), during the Late Pleistocene nearby the Loltún Cave was dominated by an evergreen seasonal forest, tropical deciduous forest, and scrub forest, based on fossil herpetofauna assemblages, contrasting to the current tropical semi-deciduous forest. At that time, the mean annual temperature was of about 25 °C whereas the mean annual precipitation was of around 1,183 mm (Cruz et al., 2016). Those conditions were optimal for the development of large communities of different groups of insects such as Coleoptera (including Dermestidae), Diptera, Blattodea, Lepidoptera, Ephemeroptera, and Himenoptera (Noonan, 1988; Britt et al., 2008), that contain scavenging species. Of these, Diptera and Coleoptera dominated the decomposition process (fresh, swelling, and decay stages according to Goff (1993) within the Loltún Cave by the reasons due the selectivity of the cave. It seems, beetles were responsible for the most disintegration stages in dry soft tissues and bone damages, representing the only bioerosion traces producers.

The modifications of bones vary depending on the producing insect and its life stage; termites and beetles (e.g., families Silphidae, Hysteridae, Tenebrionidae, and Dermestidae) are the only insects bearing the mandibular structure capable of damaging bones; and the dermestids specifically generate destruction of small bones, boring through spongy bones, grooves on the articular surfaces, and depressions in the form of holes (notches, pits,

and chambers, as observed in the specimen of *C. hyodon* in Loltún) for shelter and pupa formation (Roberts et al., 2007; Britt et al., 2008; Pirrone et al., 2014; Xing et al, 2015; Zanetti et al., 2019).

Biostratinomic Processes

The presence of bioerosion traces in the bones of *C. hyodon* provides important information about its postmortem history, especially concerning taphonomic processes (biostratinomic), as well as paleoecological (biological interactions) and paleoclimatic approaches (Hasiotis, 2004; Holden et al., 2013).

Immediately after the death of the specimen of *C. hyodon* in Loltún Cave, both internal chemicals and enzymes (autolysis) and microorganisms (putrefaction) stas breaking down its tissues initiating the decomposition process, creating an optimal microenvironment that allowed the colonization of necrophagous invertebrate such as blow flies (Calliphoridae), common flies (Muscidae), and flesh flies (Sarcophagidae), within a few hours to begin laying their eggs on the corpse. Later, other insects such as beetles (e.g., Silphidae, Histeridae) arrive and lay their eggs in natural orifices. Internal gases, a product of both autolysis and putrefaction processes, produced swelling and eventual skin breakdown leading to the active and later to the advanced decay. At that time, infestation by larvae and adult forms of flies, beetles, and their predators (parasitoid wasps, canibism in beetles) occur in the decaying microenvironment, as well as the occurrence of other groups of insects (lepidopters, hymenopters), which are attracted by visceral liquids. Finally, when soft parts start to dry and get harder, dermestid coleoptera arrive to consume dry soft tissues, keratinized parts and bones.

Infestation by beetles, particularly the Dermestidae family, can occur in stages before decomposition (swelling). However, such infestation commonly occurs sometime later, during the dry decomposition stages and the post-decay (Beal, 1991; Richards et al., 1997); as a strategy to avoid competition with other necrophagous insects (Smith, 1986; Britt, 2008; Byrd and Castner, 2009). Male and female dermestids mate and feed on moist or dry muscle tissue, as well as remnants of ligamentous tissue left behind by other carrion insects (Braack, 1987). They also have a jaw strong enough to chew hard parts such as bones (Schroeder et al., 2002). Dermestid infestation not only depends on the state of decomposition of the corpse, but climatic conditions are also undoubtedly an important factor, for example, the temperature of the environment must be above 20 °C (Wilches et al., 2016); The optimum being between 25 - 35 °C, with a preferably dry environment (Richardson and Goff, 2001; von Hoermann et al., 2011; Parkinson, 2016), which is consistent to paleoclimatic data provided by Cruz et al. (2016).

During oviposition and hatching of the dermestids, the larvae feed on the remains of soft tissues, especially on dry skin left by the adults, who have already left the site at this point (Parkinson, 2016). The consumption of the soft parts and carcasses by the deremestids could take weeks or even months, as occurs in the remains of large mammals (Sullivan and Romney, 1999). According to the body dimensions of the specimen of *C. hyodon* of Loltún, the complete decay process could take over one year or even more. After nutrient depletion, the larvae reach their final period of development, which under normal conditions pupation would occur within the larval mold or away from the decomposing body, as a strategy to avoid predation or cannibalism (Kreyenberg, 1928).

So far, the reason why only dermestid borings are exposed in the *Cuveronius* bones remains unknown, since extant species commonly feed on soft or dry tissues. Backwell et al. (2012) propose that these bone modifications occur as an indicator of environmental stress, since when the colony of dermestids has little food and nesting substrates they cause greater damage to the bones. On the other hand, Parkinson (2022), considers the smaller the amount of food, the less damage the insects produce, which means that under stress conditions, the insects do not have enough energy to mark the bone remains. In the case of Loltún Cave, during the stages of decomposition of the body of *C. hyodon*, the dermestid colony could only have thrived under warm climatic conditions, with a prolonged period of drought, indicated by the tolerance ranges of the dermestids themselves (Richardson and Goff, 2001). The large body dimensions of the *C. hyodon* allowed it to nourish the colony for a long time (one or more years), as extrapolated in the gomphoter from Aráxa, Brazil (Dominato et al., 2009). After this time, the colony would enter its stress phase, since the bone remains would remain the only source of food and substrate available for pupation.

After the decomposition process, the bones of *C. hyodon* were exposed to the elements inside the Huechil chamber. The whitening of the bone remains indicates that they were exposed for a long period to the sun's UV rays that enter directly through the hole. This suggests that the *C. hyodon*

of Loltun died in the cavity area of the Huechil chamber, and not within the "El Toro" rock shelter where the material was found. Furthermore, access from other galleries of the cavern to the Huechil chamber is very narrow, which makes it impossible for large animals to pass from the interior, with the cavity being the only access route (Chan-Mau, 2018). The Huechil chamber is a sinkhole that presents different light, temperature, and humidity conditions than other chambers in the cave, allowing the establishment of plant communities and access for some animals, which in some cases functioned as a natural trap (Xelhuantzi, 1986). It is likely that, in the rainy seasons, water currents formed capable of dragging the skeletal remains of *C. hyodon* into the "El Toro" rock shelter. The movement caused by the water would cause abrasion in the bones, which over time would be expressed as a superficial rounding in most bone remains. The manganese stains on some bones would indicate that they were underwater for a long time before being buried.

The Temporal Distribution of *Cubiculum* and Their Known Ichnospecies.

The geologic record of the six ichnospecies of the ichnogenus *Cubiculum* is well known. So far, *C. ornatus* was first described in the late Cretaceous of Madagscar by Roberts et al. (2007). Subsecquent discoveries are known from the Upper Cretaceous of Morocco (Ibrahim et al., 2014) and the Pleistocene of Brazil (Dominato et al., 2009). Nevertheless, according to Roberts et al. (2007) traces that display morphological similarities to those observed in *C. ornatus* are known from Jurassic to Pleistocene deposits of North America, Asia, Europe, and Africa, and represents the ichnospecies with the larger stratigraphic rank and the widest world distribution, showing a remarkable ichnotaxonomic stability as well as a biogeographic continuity through time.

C. inornatus has been described from the Middle Triassic (Paes-Neto et al., 2016) and Pleistocene (Alves-Silva et al., 2024) and the Middle Jurassic of China (Xing et al., 2015). The bowl-shaped *C. levis*, is known only from the Cretaceous of Argentina (Pirrone et al., 2014), *C. cooperi* is known from the Upper Cretaceous of Mexico (Serrano-Brañas et al., 2018) and the Pleistocene of South Africa (Parkinson, 2016), whereas the Mexican ichnospecies *C. atsintli* and *C. subcorticalis* have been reported only from the Upper Cretaceous of Northeastern Mexico.

The finding of *C. ornatus* in the Pleistocene of Yucatán extends the known range of the ichnogenus into tropical karstic regions of North America, particularly in the northern lowland tropics of the Neotropical realm. During the Pleistocene, climatic variations played an important role in the distribution of dermestids. In the Nearctic realm, they were restricted to areas around 40 °N latitude during interglacial episodes, but during glacial episodes, their distribution was more limited to seasonality (Martin and West, 1995; Holden et al., 2013). Neotropical species, on the other hand, may have been larger and more active in tropical environments between latitudes 20 °N and 20 °S, based on records from Yucatán, Mexico (this work), and Minas Gerais, Brazil (Dominato et al., 2009; 2011).

CONCLUSION

The boring in *C. hyodon* bones, and teeth of Loltún Cave, are one of the few records of osteophagy by insects in fossil bones documented for continental environments in Mexico. However, it is the first to be documented in a continental cavernous environment during the Pleistocene in Mexico. There are probably other continental Pleistocene records with insect perforations in Mexico, rather than human or other factors as suggested by Romero-Molina, (1958) and Tiesler (1995), among others.

The importance of the bioerosion traces in bones of the study material is not only in the identification of the ichnospecies *Cubiculum ornatus* and its producer as an osteophagous beetle of the Dermestidae family. Its discovery allows us to recapitulate the post-mortem history of *C. hyodon*, providing valuable taphonomic (biostratonomic), paleoecological (interspecific interactions), and paleoclimatic (temperature and humidity) information. The finding of *C. ornatus* in the Pleistocene of Yucatán represent the first record of the ichnogenus and the ichnospecies in to tropical North America.

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