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ARMADILLO OSTEODERMS ALTERED BY DIGESTION AND HOW TAPHONOMY CAN HELP TAXONOMY

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ABSTRACT: **Diverse modifications of the original morphological features occur throughout the taphonomic history of osteological remains, which may lead in erroneous interpretations about the formation of an accumulation as well as taxonomic misidentifications. Here, we present a neo-taphonomic study in order to analyze and interpret the modifications generated by digestion on osteoderms of the armadillo *Dasypus novemcinctus* obtained from scats produced by *Puma concolor*. Results reveal intense breakage and modifications of the articular and broken edges, dorsal surface, bone tissues, and ornamentation pattern of the osteoderms. This work describes for the first time the modifications caused by digestion in armadillo osteoderms, improving the knowledge of preservation of this type of skeletal element and providing a modern analog that can be used to distinguish archeological and paleontological accumulations formed by predators from those generated by other processes. The recognition that digestion modifies the original ornamentation pattern is particularly significant because ornamentation features are used in nearly all taxonomic and phylogenetic studies of fossil cingulates. We use this new information to re-evaluate osteoderms recovered from carnivore coprolites of the classic Middle Miocene La Venta site (Colombia), which formed the basis for recognizing and characterizing the dasypodid species *Nanoastegotherium prostatum*. We highlight the importance of knowing with certainty the origin and taphonomic history of remains since, in the particular case of cingulates, taxonomic identification also has important biostratigraphic, paleoecological, paleoenvironmental, and paleobiogeographical implications.**

INTRODUCTION

In recent decades, vertebrate taphonomy has had a remarkable development due to the data it provides about organisms, their relationship with the environment, and alterations that affect the remains from the moment of death and during its transition into the lithosphere (Fernández-Jalvo and Andrews 2016). All this information is very useful for interpreting the origin of fossiliferous sites and understanding the mechanisms of production and modification of the fossil record (e.g., Efremov 1940; Lyman 1994; Behrensmeyer et al. 2000).

Agents and processes involved in the taphonomic history of osteological remains produce modifications and sometimes loss of either macro- or microscopic original morphological features. On the one hand, the modifications may lead to erroneous interpretations about the origin of the accumulation (e.g., Fernández-Jalvo and Andrews 2016). On the other hand, the changes may also result in taxonomic misidentifications, sometimes even with phylogenetic implications. Knowing how a paleontological site was formed and how fossil remains were preserved can aid taxonomic identification; however, the relationship between taphonomy and taxonomy remains a poorly explored line of research within vertebrate paleontology (e.g., Arbour and Currie 2012; Hedrick and Dodson 2013; Tschopp et al. 2013; Kammerer et al. 2020).

Cingulata is a particular group of xenarthran mammals from the New World characterized by having protective armor formed by ossified dermal tissues known as osteoderms. This clade included diverse representatives of armadillos, glyptodonts, peltephilids, and pampatheriids during much of the Cenozoic; however, presently the diversity is reduced to armadillos of the families Dasypodidae and Chlamyphoridae (Gibb et al. 2016). Remains of cingulates are very abundant in archeological and paleontological sites from the Cenozoic of South America; this is mainly related to the great number of osteoderms present in a single dorsal carapace (i.e., ∼ 900 in armadillos, ∼ 1,800 in glyptodonts), which clearly increases the preservation potential of this element. Despite their abundance, taphonomic studies usually do not include osteoderms in analyses or describe alterations that affect them. Analyses that include taphonomic observations on osteoderms from other vertebrate groups (i.e., reptiles) are also scarce (e.g., Pereda-Suberbiola et al. 2000; Brand et al. 2003; Gillreath-Brown and Peres 2018).

Most of the taxonomic and phylogenetic arrangements proposed for fossil cingulates are mainly based on morphological features of the

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exposed surface of dorsal carapace osteoderms, such as shape, ornamentation pattern, and number, size, and location of foramina. However, the almost exclusive use of osteoderms as diagnostic elements to differentiate species (in several cases, isolated osteoderms without data on their provenance or certainty about their location in the dorsal carapace, among other factors) has led to several species being named that were later recognized to be invalid and an overestimation of the diversity of the clade (Zurita et al. 2016, 2017; Barasoain et al. 2022). Recently, taphonomic analyses have begun to be applied as a complementary tool to understand how osteoderms have been modified by taphonomic processes and, on this basis, to solve taxonomic issues involving Cenozoic representatives of this group. These studies have proposed that some taxa of glyptodonts (*Urotherium antiquum*, *U. simplex*, *Paraglyptodon chapadmalensis*, *Trachycalyptus chapadmalensis*, *Lomaphorus chapalmalensis*) were identified and characterized based on osteoderms affected by different processes (i.e., weathering, abrasion, soil corrosion) that modified the original ornamentation patterns and, therefore, resulted in taxonomic misidentifications (Zurita et al. 2016, 2017; Barasoain et al. 2022; Tomassini et al. 2023).

Considering that processes occurring in the past continue in the present, we carry out here a study based on modern taphonomy in order to improve knowledge of the preservation of fossil cingulate osteoderms. In this context, the goal of this work is to analyze and interpret the modifications generated by digestion on long-nosed armadillo (*Dasypus novemcinctus*) osteoderms obtained from scats produced by puma (*Puma concolor*) in northeastern Argentina (Mesopotamian region). Since armadillos were an important component of Cenozoic faunal communities of South America, this work should provide a useful framework for identifying archeological and paleontological accumulations formed by predators and differentiating them from those generated by other processes. We also provide new information about the characterization of the puma as a producer of small vertebrate accumulations. Finally, this is the first study that focuses specifically on analyzing the effects of digestion on cingulate osteoderms and their potential taxonomic repercussions. We use this information to re-evaluate fossil osteoderms recovered from carnivore coprolites of the classical middle Miocene La Venta site (Colombia) on which the armadillo *Nanoastegotherium prostatum* described in Carlini et al. (1997) was based.

SPECIES UNDER STUDY

The Prey: Dasypus novemcinctus

The genus of long-nosed armadillos or "mulitas", *Dasypus* (Dasypodidae, Dasypodinae), is the most species-rich among living xenarthrans (eight species *sensu* Feijó et al. 2018, 2019) as well as the most widely distributed (Wetzel et al. 2007; Hautier et al. 2017). Within the genus, the common long-nosed or nine-banded armadillo *Dasypus novemcinctus*, is currently distributed from southern South America (~ 35°S, Argentina), through Central America, to North America (~ 40°N, USA) (Wetzel et al. 2007; Loughry et al. 2014; Feijó et al. 2018) (Fig. 1). The fossil record of *D. novemcinctus* includes materials from the Late Pleistocene (and probably Holocene) of Argentina, Brazil, Uruguay, and Bolivia, mainly represented by isolated osteoderms (Castro 2014, 2015).

Dasypus novemcinctus armor is composed of three portions: the cephalic shield, the dorsal carapace (including well-defined scapular and pelvic bucklers, with 18 to 20 rows of fixed osteoderms, and 7 to 10 transverse movable bands of imbricated osteoderms), and the caudal sheath (McBee and Baker 1982; Hill 2006; Vickaryous and Hall 2006; Castro 2015) (Fig. 2). Osteoderms are dermal ossifications located within the integument, with epidermal (keratinous) scales covering the exposed dorsal surface (ornamented portion in the case of mobile and fixed osteoderms). From a histological viewpoint, osteoderms are composed of external and internal layers of compact bone surrounding a middle layer of cancellous bone (Hill 2006; Krmpotic et al. 2015). Internally, they are characterized by the presence of different types of cavities (based on their morphology and the soft tissues they encase), including marginal piliferous follicle cavities, glandular cavities, bone marrow cavities, and other small channels (Scarano et al. 2019; and references therein).

We provide here a description of the main morphological diagnostic characters of fixed, mobile, lateral (from the carapace margins), cephalic, and caudal osteoderms (Fig. 2), with more detail for the first two types due their relevance in taxonomic studies of fossil armadillos. This information is considered in the taphonomic analysis (see below).

Fixed osteoderms (Fig. 2) of the scapular and pelvic bucklers have irregular polygonal shapes that are variable (e.g., quadrangular, pentagonal, hexagonal) according to their position on the carapace. The ornamentation pattern of the dorsal surface includes a round, slightly raised, lageniform central figure partially surrounded by several (6 to 7) small and narrow peripheral figures. Central and peripheral figures are separated by a shallow central main sulcus, while peripheral figures are separated from each other by shallow radial sulci; all sulci are narrow but well-marked. A variable number (2 to 9, but generally 4) of circular to sub-circular foramina are present in the central main sulcus, usually in the intersections with the radial sulci. The central figure also includes numerous perforations, smaller than the foramina. The posterior margin has 1 to 4 (but generally 2 or 3) piliferous foramina.

Mobile osteoderms (Fig. 2) have a sub-rectangular shape and are anteroposteriorly longer than wide. They are divided into two portions. The anterior articular portion, overlapped and covered by the posterior portion (see below) of the next anterior movable band osteoderm, represents one-third of the osteoderm length and shows a smooth surface, except for small neurovascular foramina and some shallow and meandering grooves. The transition between the anterior and posterior portions is represented by a narrow zone (transverse depression) with a rough surface. The posterior portion displays an ornamented dorsal surface. The ornamentation pattern includes a lageniform central figure that is delimited by two shallow but well-marked main sulci that diverge toward the posterior margin and usually join each other anteriorly (V-shaped). A variable number of circular to sub-circular foramina are presents in these sulci (6 to 13, but generally 10). The central figure also includes numerous perforations, which are smaller than the foramina. The posterior margin has 1 to 4 (but generally 4) piliferous foramina.

Cephalic osteoderms (Fig. 2) are flat and, in general, have a polygonal shape. The dorsal surface is smooth, lacking a clear ornamentation pattern (i.e., central and peripheral figures) but with numerous small perforations. Piliferous foramina are present in the posterior and lateral margins.

Lateral osteoderms (Fig. 2), from the carapace margins, are fusiform and have rounded margins. The dorsal surface is mainly flattened and lacks a clear ornamentation pattern; two rows of small foramina may be present in the dorsal surface, while a row of larger foramina extends longitudinally across the ventral surface of the osteoderm.

The caudal sheath includes an anterior region divided in rings and a continuous posterior region. Each ring is composed of two rows of osteoderms with different morphologies. Osteoderms from the proximal row (Fig. 2) are divided into an articular and an ornamented portion; the ornamentation pattern includes two small anterior peripheral figures and small foramina in the lateral margins. Osteoderms from the distal row are pentagonal and have a flat and unornamented surface.

The Predator: Puma concolor

Puma concolor (Carnivora, Felidae) is a large felid with a wide distribution in the Americas (Fig. 1). It is a top predator, generalists and opportunistic hunters, with a diet including mainly meso- and large mammals, but also micromammals, birds, fishes, and mollusks (Mondini and Muñoz 2008; Stiner et al. 2012; Mondini 2017; Hockett 2018;

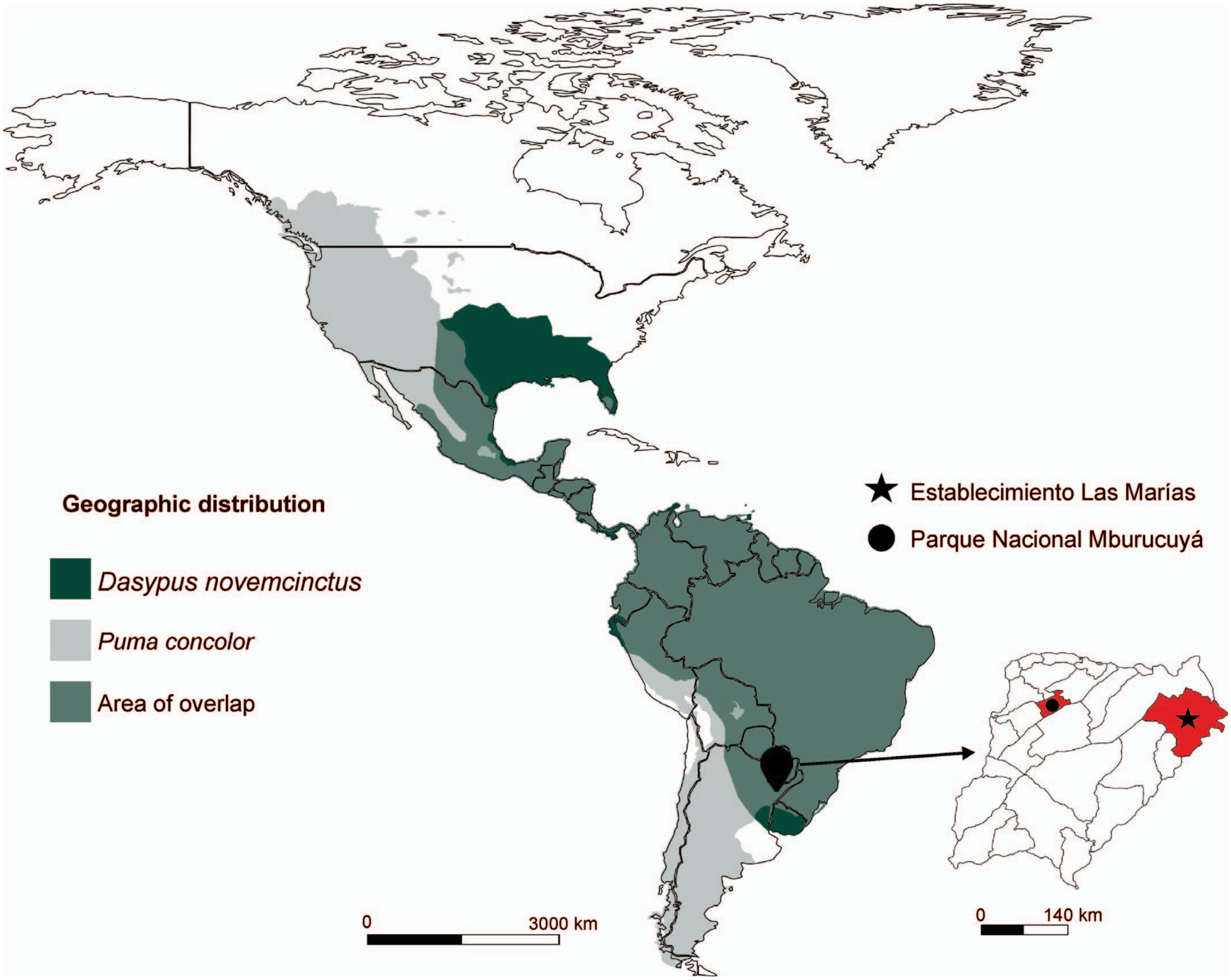

FIG. 1.—Map showing the geographic distribution of *Dasypus novemcinctus* and *Puma concolor* and the area of overlap. The detail map in lower right shows where the studied scats were collected (Establecimiento Las Marías -Departamento Santo Tomé-, and Parque Nacional Mburucuyá -Departamento Mburucuyá-, Corrientes Province, Argentina).

Montalvo and Fernández 2019; Álvarez et al. 2022). From a taphonomic viewpoint, this species was included in the maximum category of modification (extreme) based on the modifications it produces in osteological remains (of small mammals) that pass through the digestive tract, although it is variable according to the body mass of the prey (Montalvo et al. 2007; Montalvo and Fernández 2019). This relates to their very strong digestion chemistry (Stiner et al. 2012).

MATERIAL AND METHODS

A sample of 99 scats produced by *Puma concolor* was examined, and 23 of them contained osteoderms from different portions of the armor of *Dasypus novemcinctus*. Scats were collected between 2016 and 2021 at the Parque Nacional Mburucuyá (Departamento Mburucuyá; 28°02′S, 58°05′W) and Establecimiento Las Marías (Departamento Santo Tomé; 28°06′S, 56°03′W). Both sites are located in Corrientes Province, northeastern Argentina (Zaracho et al. 2017; Fig. 1). The specimens are housed at the Laboratorio de Ornitología y Mastozoología, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (Corrientes Province, Argentina). Other skeletal elements of *Dasypus novemcinctus* obtained in the samples but not considered in this taphonomic analysis include vertebrae and claws.

Taxonomic identification of the osteoderms was carried out following McBee and Baker (1982), Vickaryous and Hall (2006), and Castro (2014, 2015), and used comparative specimens housed at the Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (Corrientes Province, Argentina). *Dasypus novemcinctus* was the only taxon of armadillo identified in the sample. We determined and interpreted the macroscopic modifications resulting from puma digestion in all of the osteoderms (see below). The specimens were examined under a Motic SMZ168 binocular light microscope (20× and 40×) belonging to the Departamento de Geología, Universidad Nacional del Sur (Bahía Blanca, Argentina).

Some previous works that analyzed modern (Montalvo et al. 2007) and fossil (Ballejo et al. 2022) vertebrate assemblages accumulated by predators briefly mentioned and described modifications identified in osteoderms as result of digestion. We propose here a categorization of different taphonomic features, discriminating according to the type of

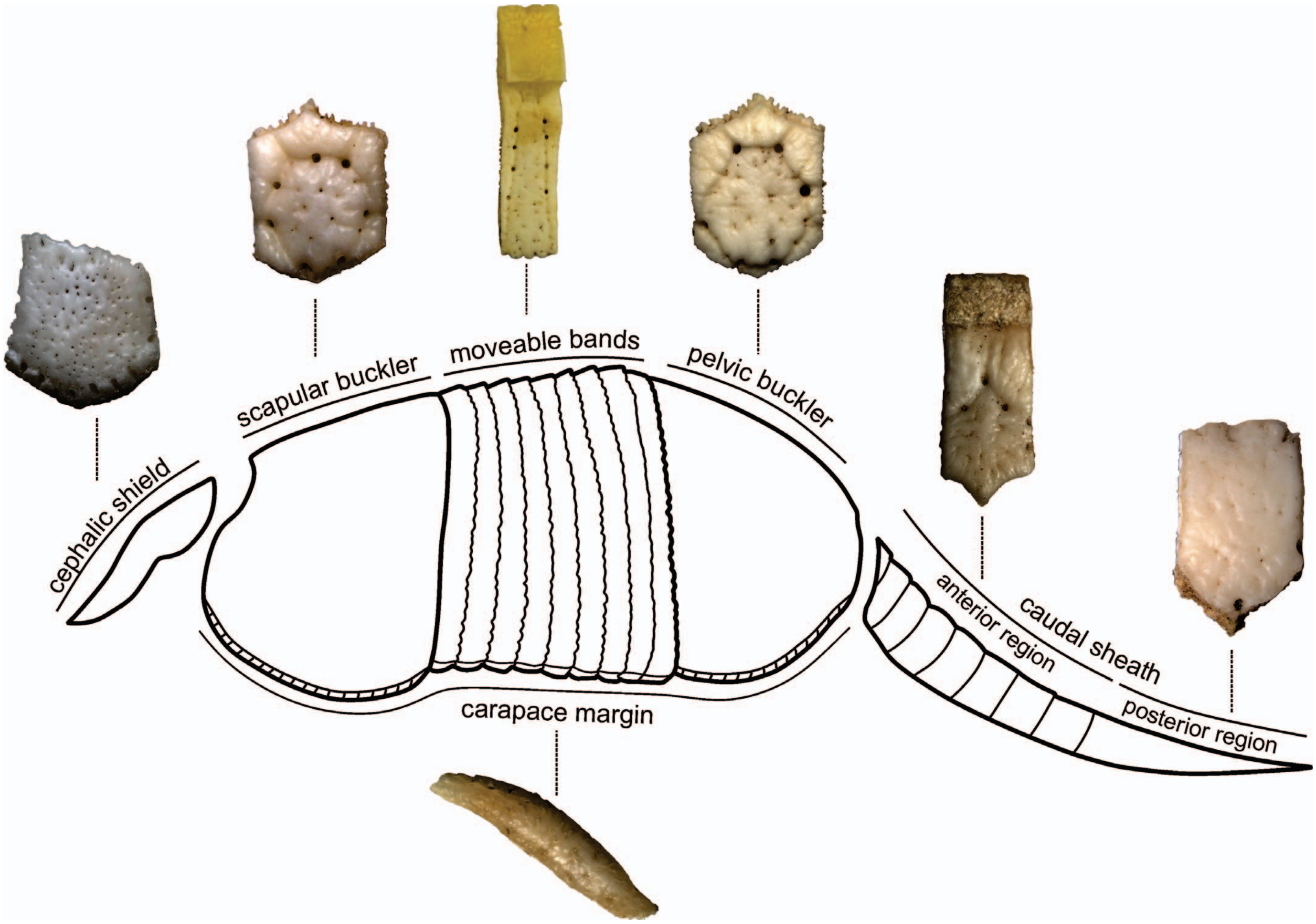

FIG. 2.—Schematic (not to scale) of the armor of *Dasypus novemcinctus* and osteoderms from the different regions.

osteoderm, in order to make a more detailed evaluation of the effects of the digestion process on this particular skeletal element and the possible taxonomic consequences.

1. Breakage and type of fracture. Osteoderms were classified according to whether they were complete ($\geq$95% of the element preserved) or incomplete (<95% of the element preserved). Type of fracture was defined based on the angle formed by the fracture plane and the antero-posterior axis of the osteoderm: longitudinal, oblique, and transverse. These types of fractures may also be combined in a single specimen. In the case of mobile osteoderms, we recorded the preserved portion (anterior articular, posterior ornamented, or part of both portions).
2. Modification of articular and broken edges includes three categories: (1) intact edges; (2) rounded edges; and (3) thinned edges.
3. Modification of the surface includes three categories: (1) intact surface; (2) smoothed surface; and (3) polished surface.
4. Modification of bone tissues includes four categories: (1) intact tissues; (2) slightly degraded (irregular surface) compact bone, without exposed cancellous bone; (3) highly degraded compact bone, with exposed cancellous bone; and (4) extremely degraded compact and cancellous bones; only a thin layer of compact bone is preserved.
5. Modification of original ornamentation pattern includes three categories: (1) intact ornamentation; (2) slightly modified ornamentation; and (3) intensely modified ornamentation. In each case, we determined changes in central and peripheral figures, main and radial sulci, and dorsal foramina (Fig. 3A, 3B). Assignment to a specific category depended on the intensity of the changes in each of these morphological features. We evaluated this attribute only in fixed and mobile osteoderms, considering its relevance in taxonomic and phylogenetic analyses of fossil armadillos (see above).

In the particular case of the dorsal foramina, we performed a statistical analysis to determine possible changes in size as a result of digestion. The area of each complete foramen from the sulci of fixed osteoderms (osteoderms from scapular and pelvic bucklers were evaluated together; n osteoderms measured = 20; n foramina measured = 83) and mobile osteoderms (n osteoderms measured = 61; n foramina measured = 392) was measured using the software ImageJ. Data obtained were analysed through a Levene test for equal variances applied in R software (R Core Team 2022), where H_0 assumes equal variances in the size of the foramina of fixed and mobile osteoderms (p-value $>$ 0.05) and H_1 assumes that variances are not equivalent (p-value $<$ 0.05). Piliferous foramina of the posterior margin were not considered, since they are open and, therefore, the area cannot be calculated.

RESULTS

The sample obtained from 99 scats comprises a total of 185 osteoderms belonging to *Dasypus novemcinctus* (Fig. 4A–4C). Osteoderms from different region of the armor are represented, including cephalic shield (n = 28), dorsal carapace (movable bands n = 113; scapular buckler n = 15;

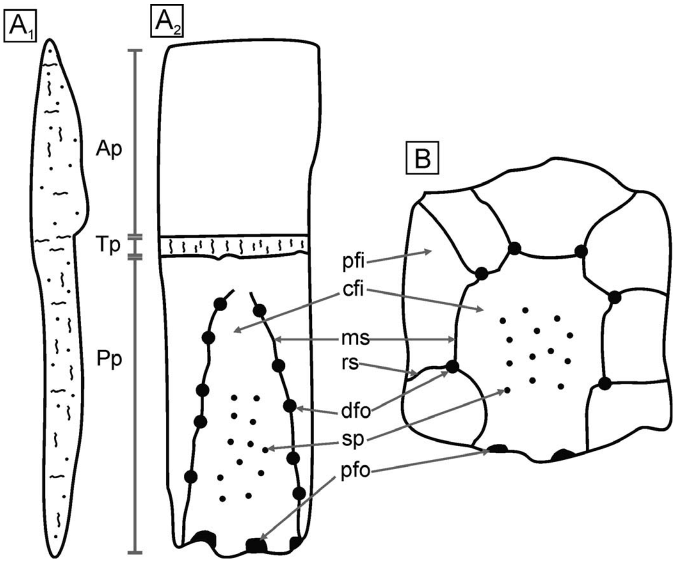

FIG. 3.—Diagrams (not to scale) of *Dasypus novemcinctus* osteoderms showing morphological characteristics and ornamentation patterns. **A**) Mobile osteoderm in lateral (A$_1$) and dorsal (A$_2$) views. **B**) Fixed osteoderm in dorsal view. Abbreviations: Ap = anterior articular portion; cfi = central figure; dfo = dorsal foramen; ms = main sulcus; pfi = peripheral figures; pfo = posterior piliferous foramen; Pp = posterior ornamented portion; rs = radial sulcus; sp = small perforations; Tp = transitional portion.

pelvic buckler n = 19; and undetermined laterals n = 3) and caudal sheath (n = 7). The number of osteoderms by sample varies from 1 to 45. From the 23 scats analyzed, only 10 have osteoderms from different regions of the armor, while the remaining 13 include osteoderms from a single region. One of the samples has three small portions of pelvic buckler with 3–4 articulated osteoderms.

Complete specimens (30.8% of the total sample) predominate among the different types of osteoderms, except in the mobile osteoderms (Fig. 5). Different types of fractures are recognized among the incomplete osteoderms (Fig. 6A–6E), with a marked predominance of transverse and combined (Table 1). We highlight that most of the incomplete mobile osteoderms (65%) are broken at the level of the transitional portion and represented by the ornamented portion; the remaining mobile osteoderms include parts of both articular and ornamented portions.

Modifications of the articular and broken edges are present (93.5% of the total sample) in the different types of osteoderms (Fig. 5), represented by rounding (Category 2; Fig. 7A, 7B) and thinning (Category 3; Fig. 7C, 7D). The scarce intact specimens (Category 1) only correspond to complete mobile and fixed osteoderms; all broken osteoderms, including different types of fractures, show rounded edges. Thinning affects the margins (which represent less thick zones; see Fig. 3A$_1$) of mobile and caudal osteoderms; in the anterior margin of the articulated portion, cancellous bone is exposed, whereas in the posterior margin of the ornamented portion, jagged ends are present, which generate a significant distortion or loss of the piliferous foramina.

The surface is altered in most osteoderms (99% of the total sample; Fig. 5). Intact specimens (Category 1) only include mobile and fixed osteoderms. Cephalic, fixed, mobile, and caudal osteoderms show both smoothed (Category 2; Fig. 7E) and polished (Category 3; Fig. 7F) surfaces, while lateral osteoderms only have smoothed surfaces (Category 2).

Most of the osteoderms (55.6% of the total sample) show loss of bone tissues (Fig. 5). Intact specimens (Category 1) include all types of osteoderms. All affected cephalic, caudal, and lateral osteoderms, as well as some fixed and mobile osteoderms, only show a slight degradation of the compact bone (Category 2; Fig. 7G), evidenced by a surface with irregular aspect. Several fixed and mobile osteoderms have a high degradation of the compact bone (Category 3; Fig. 7H, 7I), which implies areas with exposed cancellous bone. In mobile osteoderms, the exposure of cancellous bone generally affects both the articular and ornamented portions. Only some mobile osteoderms reach an extreme modification degree, represented by an intense degradation of the bone tissues (Category 4; Fig. 7J) and the preservation of only a thin layer of compact bone, in all cases corresponding to the dorsal surface of the ornamented portion.

Some mobile osteoderms have subcircular/suboval perforation located in the transitional portion (which represent a less thick zone; see Fig. 3A$_1$) that may partially (n = 9) or totally (n = 6) cross the bone tissue (Fig. 7K, 7L). This modification is mainly present in those osteoderms that show highly modified bone tissues (categories 3 and 4).

The ornamentation pattern of the exposed surface shows changes in most of the osteoderms (Fig. 5), being more evident in mobile osteoderms (92.9%) than in fixed (52.9%). Modifications of the ornamentation pattern include smoothing of central and peripheral figures, deepening and widening of sulci, and increase in size of the dorsal foramina (and the small perforations present in the central figure) (Fig. 7M–7Q). These modifications can appear independently (mainly in osteoderms with slight modifications) or combined (mainly in osteoderms with intense modifications). Most affected fixed osteoderms only show slight modifications (Category 2); only one osteoderm has intense modifications (Category 3). Among mobile osteoderms, those with slight modification predominate (Category 2), although there are several specimens with intense modifications (Category 3); in some mobile osteoderms included in Category 3, the great modification practically obliterates all the original features of the ornamentation (Fig. 7Q).

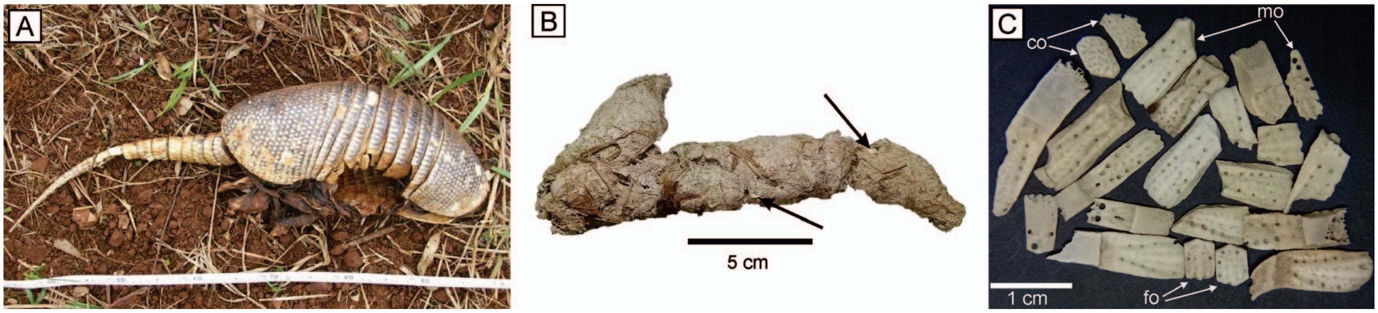

FIG. 4.—Evidence of *Puma concolor* and *Dasypus novemcinctus* interactions. **A**) Carcass modified by predator activity. Note the damage produced in the inferior portion of the movable bands region. **B**) Scat with presence of several osteological remains; arrows indicate osteoderms. **C**) Osteoderms obtained from one of the studied specimens, showing different degrees of modification by digestion. Abbreviations: co =cephalic osteoderm; fo = fixed osteoderm; mo = mobile osteoderm.

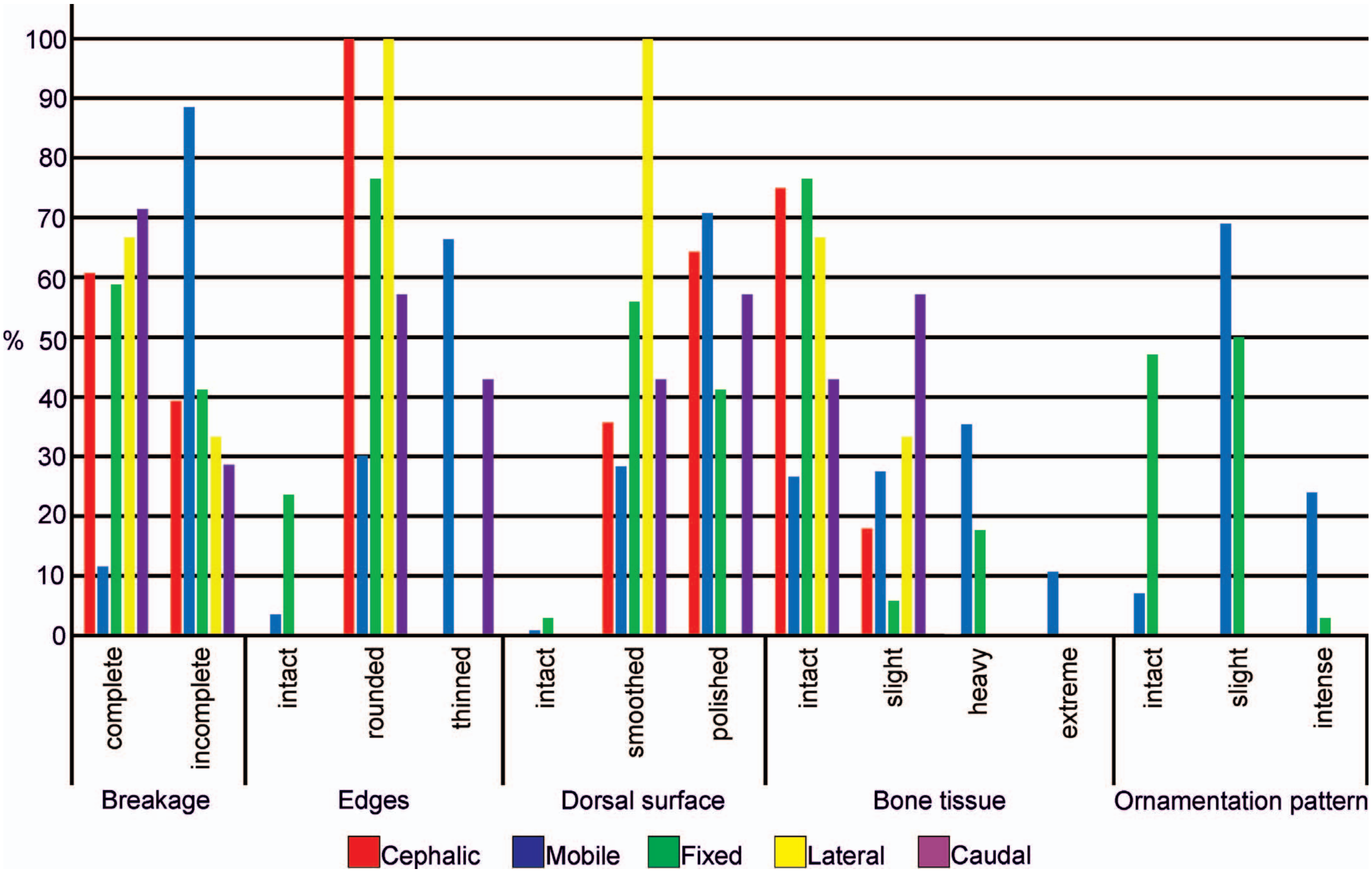

FIG. 5.—Bar graph showing the proportions of taphonomic modifications identified in different types of osteoderms.

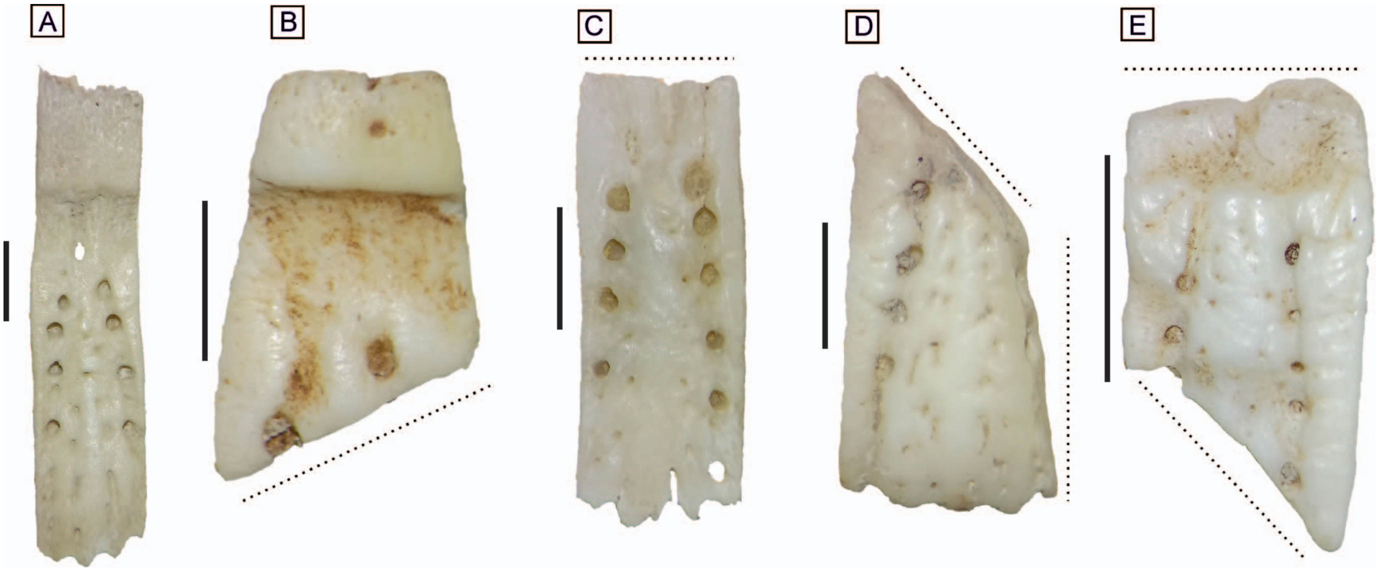

FIG. 6.—Examples of mobile osteoderms with different degrees of breakage and types of fractures (note dotted lines). **A**) Complete osteoderm. **B**) Oblique fracture (preservation of both articular and ornamented portions). **C**) Transverse fracture at level of the transitional portion (preservation of ornamented portion). **D**) Combined fracture (longitudinal + oblique; preservation of ornamented portion). **E**) Combined fracture (oblique + transverse; preservation of both transitional and ornamented portions). Scale bars = 0.25 cm.

TABLE 1.—*Diversity of fractures in different types of osteoderms.*

	Fracture type							
	Transverse		Oblique		Longitudinal		Combined	
Osteoderm type	n	%	n	%	n	%	n	%
Mobile	34	34	16	16	0	0	50	50
Fixed	5	35.71	2	14.29	3	21.43	4	28.57
Lateral	1	100	0	0	0	0	0	0
Cephalic	7	63.63	0	0	1	9.1	3	27.27
Caudal	0	0	1	50	0	0	1	50

The general increase in the size of the dorsal foramina is evident in several mobile osteoderms (Fig. 7P, 7Q); likewise, in those cases where there is a significant loss of compact and cancellous bone (categories 3 and 4, see above), foramina tend to cross the entire thickness of the osteoderm (Fig. 7Q). On the contrary, only some dorsal foramina of a few fixed osteoderms show a clear size change (Fig. 7O). A brief description of the coefficients summarizing the studied data set is shown in Table 2; differences in mean, standard deviation, minimum, median, and maximum values are observed between these two types of osteoderms. Statistical analyses (Fig. 8) support these observations and indicate that more variation of dorsal foramina size occurs in mobile osteoderms than in fixed osteoderms (Levene test, p-value = 0.000).

DISCUSSION

Taphonomic Interpretation of the Sample

Records of predation on *Dasypus novemcinctus* have been reported in several regions of the Americas. Predators include various carnivorous mammals, such as puma, jaguar, ocelot, lesser grisson, coyote, American black bear, northern raccoon, and fox. Apart from terrestrial mammals, other predators of the armadillo include avian raptors such as harpy eagle and owls, as well as the reptiles black-and-white tegu and American alligator (McBee and Baker 1982; Loughry and McDonough 2013).

Osteoderms of different armadillo species are commonly identified in pellets and scats of diverse predators (Montalvo et al. 2007, 2016; Ballejo et al. 2012; López et al. 2021; Álvarez et al. 2022), although their ingestion is considered to be accidental (see below). They also appear in accumulations of leftover prey remains (Kaufmann 2016; Montalvo et al. 2016). On the other hand, although armadillos are abundant in the fossil record, the presence of osteoderms in archeological and paleontological accumulations produced by non-human predators is scarce (e.g., Carlini et al. 1997, see below; Ballejo et al. 2022), and they are not usually evaluated from a taphonomic perspective.

Beyond the advances in recent decades in the study of modern and fossil vertebrate accumulations generated by diverse predators of South America (Fernández et al. 2017; Mondini 2017; Montalvo and Fernández 2019; and references therein), it is worth mentioning that, at the moment, little is known about how the ingestion and digestion processes affect osteoderms. The analysis performed herein on a sample of *D. novemcinctus* osteoderms obtained from *Puma concolor* scats provides novel data on different modifications that can occur. Although some of these modifications (i.e., rounding, polishing, loss of bone tissue) have been mentioned in previous works related to other skeletal elements (e.g., bones, teeth; Andrews 1990) of different mammal taxa, others (i.e., distortion of the ornamentation pattern) are specific to osteoderms and are described in detail here for the first time.

The number of ingested osteoderms that were not destroyed by the digestion process, considering both the whole sample and each scat individually, is very low with respect to the number of osteoderms included in the armor of a single individual of *D. novemcinctus*. There is a marked predominance of osteoderms from the movable bands, with osteoderms from the other regions identified to a lesser extent; this situation is likely related to the hunting strategy of the puma and how it obtains nutrients. Once a puma kills a *D. novemcinctus*, access to the internal organs occurs through the carapace edges; in many cases, this occurs in the movable bands area (Fig. 4A) (M.L. Chatellenaz personal observation 2017), which causes the accidental ingestion of osteoderms.

The high percentage of broken osteoderms (~ 70%) is likely related to killing and ingestion of prey. According to different authors (Montalvo et al. 2007; Mondini 2017), skeletal elements of micromammals consumed by *P. concolor* are practically swallowed whole without chewing due to their small size. However, a differential response is expected in the case of *D. novemcinctus*, considering its body mass (~ 3–8 kg for adult individuals; McBee and Baker 1982), which makes it a mesomammal, and the structural differences that exist between osteoderms and other skeletal elements. The sample here analyzed indicates that different types of fractures (i.e., longitudinal, oblique, transversal, and combined) are produced during ingestion but that transverse ones predominate. With respect to this, Stiner et al. (2012) studied a sample of puma scats from North America and recorded a high percentage of transverse fractures among long bones. Among mobile osteoderms, the predominance of specimens represented only by the ornamented portion is probably related to the fact that breakage affects the transitional portion most easily, a thin and weak zone of the element. Variations in the breakage pattern may be the result of different anatomical characteristics (e.g., size, shape, and structural density) that exist among the different types of osteoderms.

The absence of tooth marks is consistent with the proposal of accidental ingestion, since the consumption of this type of skeletal element does not provide nutrients. Other taphonomic works that have analyzed scats of *P. concolor* have highlighted the scarcity of bone remains with chewing evidence, particularly those of small prey (Montalvo et al. 2007; Stiner et al. 2012; Mondini 2017; Álvarez et al. 2022).

Localized rounding of bone remains is a characteristic modification of digestion produced by mammalian carnivores (Andrews 1990), and *P.*

TABLE 2.—*Descriptive statistics of dorsal foramina measured for mobile and fixed osteoderms.*

	n	Mean	Standard deviation	Minimum	Q1	Median	Q3	Maximum
Mobile osteoderms	392	0.189	0.121	0.038	0.115	0.156	0.234	1.021
Fixed osteoderms	83	0.087	0.031	0.038	0.063	0.081	0.110	0.184

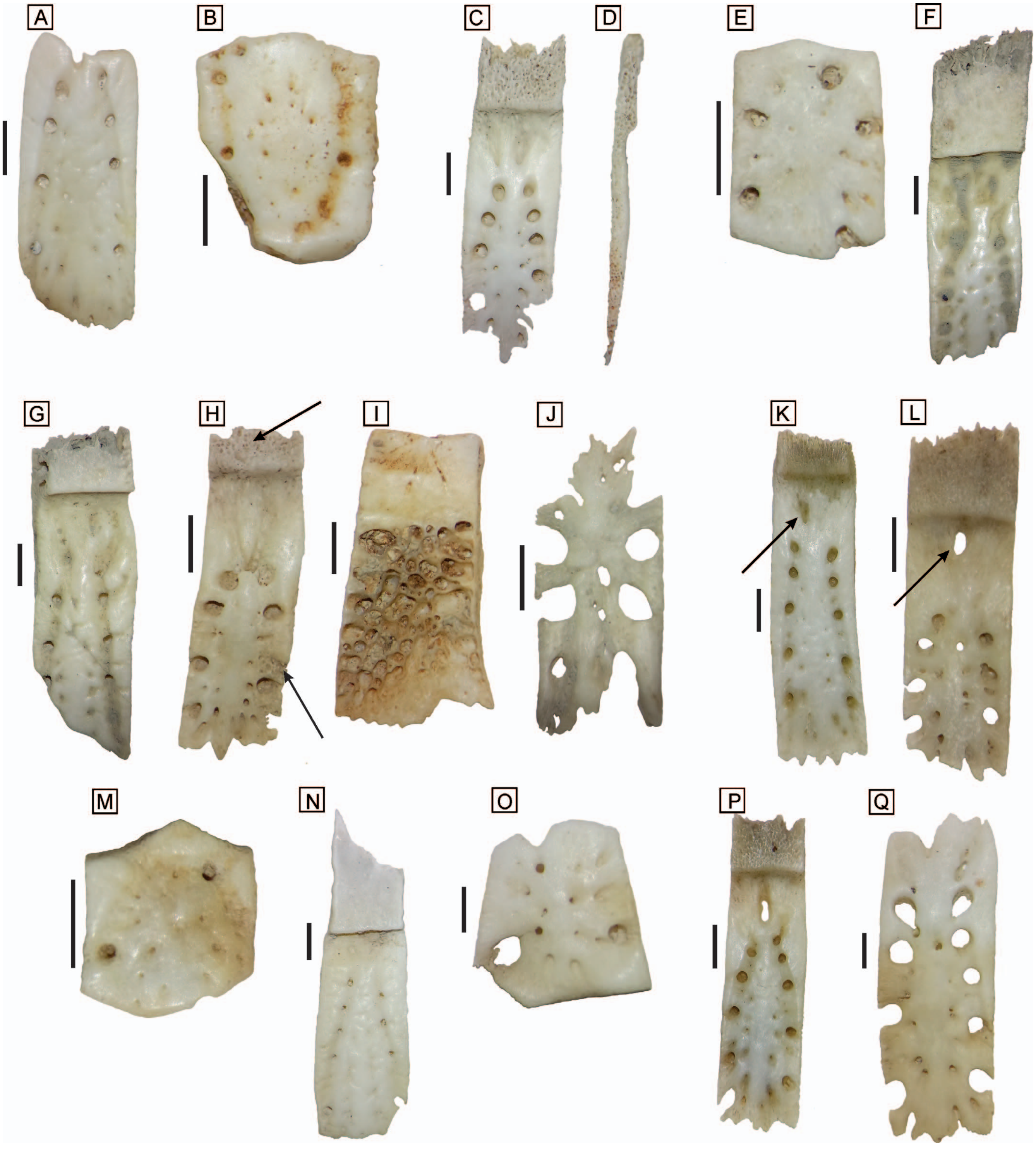

FIG. 7.—Taphonomic modifications caused by digestion. **A**, **B**) Rounded edges in mobile (A) and fixed (B) osteoderms. **C**, **D**) Thinned edges in mobile osteoderms in dorsal (C) and lateral (D) views. **E**) Smoothed surface in fixed osteoderm. **F**) Polished surface in mobile osteoderm. **G**) Slightly degraded compact bone (irregular surface in the ornamented portion) in mobile osteoderm. **H**) Highly degraded compact bone (cancellous bone exposed in the articular and ornamented portions; see arrows) in mobile osteoderm. **I**) Highly degraded compact bone (cancellous bone exposed throughout the entire ornamented portion) in mobile osteoderm. **J**) Extremely degraded compact bone (only a thin layer of compact bone preserved) in mobile osteoderm. **K**) Partial perforation (see arrow) in the transitional portion of a mobile osteoderm. **L**) Complete perforation (see arrow) in the transitional portion of a mobile osteoderm. **M**) Slightly modified ornamentation in fixed osteoderm. **N**) Slightly modified ornamentation in mobile osteoderm. **O**) Intensely modified ornamentation in fixed osteoderm (note the enlargement of some dorsal foramina). **P**) Intensely modified ornamentation in mobile osteoderm (note the enlargement of several dorsal foramina and the deepening of the main sulcus). **Q**) Intensely modified ornamentation in mobile osteoderm (note the obliteration of the original ornamentation pattern). Scale bars = 0.2 cm.

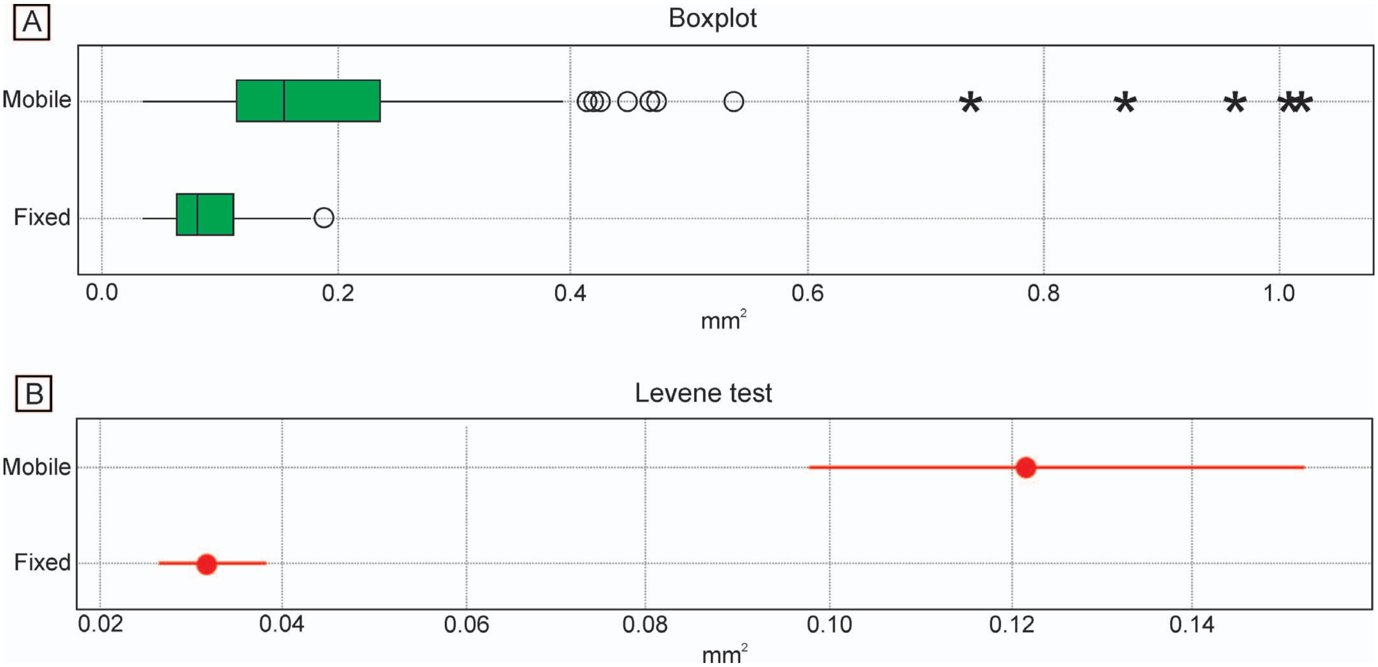

FIG. 8.—Statistical analyses of dorsal foramen size in mobile and fixed osteoderms. **A**) Box and whisker plot obtained through descriptive statistics showing the great variation in foramen area in both types of osteoderms. Circles and asterisks = outliers. **B**) Levene test graph showing the different variance values of both types of osteoderms, considering the 95% of confidence interval.

concolor in particular produces extreme rounding in bone remains (Fernández-Jalvo and Andrews 2016). In the sample studied here, this rounding affects both articular and broken edges of most specimens of the different types of osteoderms. Based on the obtained results, it seems that the edges of the broken osteoderms are more susceptible to being modified.

Thinning is evident in both anterior and posterior margins of some elongated (mobile and caudal) osteoderms, which represent less thick zones. This attribute was used in other skeletal elements to differentiate digestion (the edges of cancellous bone are thinner) and abrasion (the edges of cancellous bone are thick and homogeneously rounded) (Fernández-Jalvo et al. 2014; García-Morato et al. 2019).

Smoothing and polishing of the surface of osteological remains are other characteristic modifications produced by digestion (Fernández-Jalvo et al. 2014; Fernández-Jalvo and Andrews 2016). In osteoderms, thinning, smoothing, and polishing are represented in almost all the specimens of the sample and affect different types of osteoderms similarly.

Digestive acids cause loss of bone tissue in osteoderms as has also been observed in bone skeletal elements (Andrews 1990; Fernández-Jalvo and Andrews 2016). It is likely that the numerous external foramina, perforations, and internal cavities that osteoderm have (plus breakage produced during the ingestion) represent pathways that favor the access and distribution of acids throughout the element. Some authors think that the keratinous scale, when present, protects the exposed dorsal surface of an osteoderm from the effects of the acids (Montalvo et al. 2007; Mondini 2017).

Most damaged osteoderms only show a slight degradation of the compact bone, while several fixed and mobile osteoderms show a greater intensity of damage that exposes cancellous bone. In mobile osteoderms in which exposure of cancellous tissue is restricted to the articular portion, we interpret that the keratinous scale remained for some time and protected the dorsal surface of the ornamented portion. Degradation of tissues also generates perforations in the transitional portion of mobile osteoderms, probably taking advantage of the lesser thickness of this sector and the presence of internal cavities located there.

In some mobile osteoderms, extreme modification only left a thin layer of compact bone corresponding to the dorsal surface of the ornamented portion. In these cases, we believe that the keratinous scale protected the dorsal surface of the ornamented portion and the degradation of the tissues advanced from the ventral surface of the osteoderm, causing the loss of the internal layer of compact bone and the middle layer of cancellous bone.

Variations in the degree of bone tissue modification could be related to the proportions in which the diverse internal structures (e.g., compact bone, glandular cavities, marginal follicle cavities, medullary cavities, neurovascular ingressions; *sensu* Scarano et al. 2019, see above) are represented in the different types of osteoderms. In this framework, based on the values obtained by Scarano et al. (2019, fig. 4) for *D. novemcinctus*, the greater degradation (both in number of affected specimens and in the intensity of the process) observed in mobile osteoderms compared to fixed osteoderms would be linked to lower proportions of compact bone and higher proportions of internal cavities. Histotaphonomic studies currently in progress may provide more detailed information about the changes that occur at a microstructural level.

The ornamentation pattern of the dorsal surface of osteoderms is of great diagnostic value in Cingulata, particularly for fossil representatives. In this study, changes produced by digestive acids in the central and peripheral figures, sulci, and foramina have been identified, all of them usually used in species identification of fossil representatives. Although changes are identified in both mobile and fixed osteoderms, the intensity is generally higher in the former; in some specimens that displayed extreme modification of the bone tissue, the original ornamentation pattern is almost completely lost, making a reliable taxonomic assignment difficult. Therefore, the modification of original features may lead to taxonomic misinterpretations. This is the first description of the different modifications generated in the ornamentation of cingulate osteoderms as result of the digestive process.

Cingulate osteoderms are generally found isolated in the archeological and paleontological records, which increases difficulties in the interpretation of their possible origins. Thus, without a taphonomic study that supports the anatomical analysis, it is possible to fall into the mistake of thinking that the observed features are the original ones when, in fact, they represent modified patterns caused by post-mortem modifications.

Taphonomic studies including cingulate osteoderms recovered from modern and fossil accumulations produced by predators are scarce (Montalvo et al. 2007, 2016; Ballejo et al. 2012, 2022; López et al. 2021; Álvarez et al. 2022). Nevertheless, the brief descriptions of the different attributes identified in these works coincide with the results obtained herein. Some of the highlighted issues include rounding of edges, polishing, presence of large holes, intense loss of bone tissue, and absence of tooth marks. In particular, Montalvo et al. (2007) and Álvarez et al. (2022) mentioned different degrees of digestion in osteoderms of the euphractin armadillos *Chaetophractus* sp. and *Zaedyus pichiy* respectively obtained from *P. concolor* scats, with effects ranging from negligible (i.e., fully intact) to highly polished and limited to areas of cancellous bone. On the other hand, since these works were mainly focused on identifying the category of predator, there are no specific references to the changes in the ornamentation pattern.

The sample analyzed herein also reflects a clear variability in the modification suffered by *D. novemcinctus* osteoderms that pass through the digestive tract of *P. concolor*. Variations recorded among the different types of osteoderm are related to their particular anatomical characteristics (see above); these differences were not described in previous taphonomic studies that included cingulate osteoderms (Montalvo et al. 2007; Álvarez et al. 2022; Ballejo et al. 2022). Even the same type of osteoderm displays differences in a single scat, which indicates a differential response to digestion. These observations, especially in mobile and fixed osteoderms, are relevant for analyses of fossil cingulates, since both types of osteoderms commonly form the basis for taxonomic studies.

It is expected that the interpretations proposed here of the changes produced by digestion cannot be totally extrapolated to accumulations where other cingulate taxa are recorded, even if the producer was *P. concolor*, since there are differences in the size, shape, ornamentation pattern, and structural characteristics between osteoderms of different lineages. This situation has been proposed for other skeletal elements that also respond differentially to digestive action according to the taxonomy (i.e., rodent molariforms; Andrews 1990; Fernández-Jalvo and Andrews 2016; Fernández et al. 2017; Montalvo and Fernández 2019). Finally, it should also be considered that the processes of both ingestion and digestion vary among the diverse predators that feed on *Dasypus novemcinctus* (see above), so it is expected to record different taphonomic responses in the osteoderms.

Implications of Digestive Modifications for Taxonomic Analyses: Coprolites from the Middle Miocene of La Venta (Colombia)

Carlini et al. (1997) recognized a new fossil species of Astegotheriini (Dasypodidae), *Nanoastegotherium prostatum*, from the middle Miocene (La Victoria and Villevieja formations, Honda Group) of the La Venta locality (Colombia), based on isolated osteoderms obtained from three coprolites (possibly from crocodiles, according to the authors, but without further details). The material includes several fixed osteoderms (possibly from pelvic buckler) and a single caudal sheath osteoderm (Carlini et al. 1997).

In an evolutionary context, *Nanoastegotherium prostatum* represents the last record of the tribe Astegotheriini, an ancient lineage within dasypodid armadillos, with most of its evolutionary history restricted to southern South America. Carlini et al. (2014) highlighted the presence of one of the oldest representatives of the Dasypodini tribe in the same locality, *Anadasypus hondanus*, with which *N. prostatum* shares several features (see Vizcaíno 1994; Carlini et al. 1997; Castro 2014, 2015; Castro et al. 2014). Carlini et al. (1997) considered that "the presence of anterior and lateral peripheral figures [identified by the authors in *N. prostatum*] heralds the condition characteristic of the Dasypodini".

Considering that osteoderms of *N. prostatum* come from carnivore coprolites, we expect that modifications caused by digestion will be present. Such modification would be even more pronounced if the coprolites were produced by crocodiles, which generate an extreme degree of degradation in ingested bone remains (Fisher 1981; Fernández-Jalvo and Andrews 2016). In this context, it is worth noting that the description of this species includes features (see below) that, according to the results obtained herein on *D. novemcinctus* osteoderms, may have been generated by the action of digestive acids.

Osteoderms of *N. prostatum* show a morphological gradation from specimens with a well-developed lageniform central figure to specimens with very large foramina located in the central sulcus (absent in *A. hondanus*) that, in some cases, occupy almost the entire exposed dorsal surface (Carlini et al. 1997, fig. 13.1.A; Carlini et al. 2014); these latter specimens were interpreted as part of a particular portion of the carapace (middle axis or middle pelvic region *sensu* Carlini et al. 1997). As mentioned above, digested osteoderms of *D. novemcinctus* show an increase in foramen size compared to non-digested osteoderms; although this modification is more evident in mobile osteoderms, it is also observed in fixed osteoderms. In the case of fixed osteoderms, there are specimens with no apparent change in foramen size (see Fig. 7B) and others with remarkable enlargement (see Fig. 7O).

Another characteristic of *N. prostatum* osteoderms is the presence of main and radial sulci that are wider and deeper than in other representatives of Astegotheriini (Carlini et al. 1997, fig. 13.1.A). Several of the digested fixed and mobile osteoderms of *D. novemcinctus* show deepening and widening of sulci with respect to non-digested osteoderms.

Finally, the absence of a longitudinal keel in the central figure (present in *A. hondanus* but absent in *A. aequatorianus* from the late Miocene of Ecuador) was indicated as a feature of *N. prostatum* osteoderms (Carlini et al. 2014). With respect to this point, it is important to note that: (1) digestion generates smoothing of central and peripheral figures in osteoderms of *D. novemcinctus* that modifies the original morphology; and (2) states of this character (absence, presence, or development degree of the keel) are quite variable among osteoderms of the same region of the carapace in both extant and extinct Dasypodidae (D. Barasoain personal observation 2021). *Nanoastegotherium prostatum* is represented by too few materials to adequately evaluate these differences.

Other taphonomic features could not be evaluated in the fossil osteoderms of *N. prostatum* since we were not able to study the original material firsthand and the available images (Carlini et al. 1997, fig. 13.1.A) do not provide further details. Carlini et al. (1997) highlighted the absence of mobile osteoderms of *N. prostatum* in the recovered coprolites; however, the *D. novemcinctus* sample studied herein reveals that the representation of different types of osteoderms in scats is very variable.

The information available in previous works and the results obtained herein indicate that: (1) remains of *N. prostatum* have only been recovered from coprolites; (2) *N. prostatum* (the last representative of Astegotheriini) is present in the same locality as *A. hondanus* (the oldest representative of Dasypodini), overlaps this species stratigraphically, and shares anatomical characters at level of the carapace osteoderms; and (3) some of the anatomical differences proposed to distinguish *N. prostatum* from *A. hondanus* may be linked to modifications generated by the digestion process in ingested osteoderms. Based on these points, we think that the material attributed to *N. prostatum* could correspond to *A. hondanus* and that a detailed taxonomic review of *N. prostatum* should be carried out to test this hypothesis. Despite the fact that taphonomic analyses are not usually considered in taxonomic studies, it is possible that these aspects have not been considered in the previous works (e.g., Carlini et al. 1997,

2014) since, as observed in the *D. novemcinctus* sample, fixed osteoderms do not show an intense degree of modification.

CONCLUSIONS

This neo-taphonomic study provides new information about accumulations of osteological remains formed by the *Puma concolor*, an important top predator of the Americas. In this case, we improve characterization of this felid as producer of small vertebrate accumulations based on the analysis of several scat samples with *Dasypus novemcinctus* osteoderms.

This is a pioneering work in which the modifications in cingulate osteoderms caused by digestion are described in detail for the first time. Although osteoderms are found mostly isolated in late Cenozoic sites of South America, paleontological and archeological record evidence that cingulates were preyed upon (and their remains accumulated) by carnivorous mammals (including humans) and diurnal birds of prey. The development of this type of modern analog helps identify modifications that different producers generate in this particular type of skeletal element and, therefore, to identify fossil accumulations formed by predators and differentiate them from those generated by other processes.

The importance of taphonomic studies to differentiate original features of skeletal elements from post-mortem modifications is highlighted, since it may prevent potential taxonomic and phylogenetic misidentifications. This is particularly relevant for the study of fossil cingulates, because features of the osteoderm ornamentation (e.g., figures, sulci, dorsal foramina) that are frequently used to define and characterize taxa are significantly altered by the digestion process. This observation highlights the need to know with certainty the origin and taphonomic history of the remains since, in the particular case of cingulates, taxonomic identification also has biostratigraphic, paleoecological, paleoenvironmental, and paleobiogeographical implications. This study also lays the groundwork for analyzing the fossil record of these peculiar "armored" xenarthrans from other perspectives.

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