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Diversity and variation of dorsal carapace structures in the giant armadillo *Priodontes maximus* (Kerr, 1792) and their potential use for individual identification

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Abstract Dorsal carapace and osteoderm morphological features have traditionally been widely used in both extinct and extant armadillo systematics. However, the intraspecific variability at the carapace level represents a little studied aspect. In this contribution, we analyzed several dorsal carapaces of *Priodontes maximus* with the purpose of recording such variability. As a result, we describe a total of seven structures concerning the dorsal carapace osteoderm configuration, including distinct terminations of the osteoderm rows, and the most frequent aberrant shapes of the osteoderms. Though the same type of structure can be usually found in several specimens, its frequency and precise location within the carapace are unique to each individual. In this sense, besides improving anatomical descriptions, the identification of these structures can be potentially implemented as a complementary method to help recognize specific individuals being tracked. Moreover, it can represent a very effective recognition method even a long time after death. Given the general decreasing trend of *P. maximus* populations, it is important to develop as many monitoring tools as possible, in order to support conservation programs for this species.

Keywords: Cingulata, osteoderms, morphology, variability

Diversidad y variación de estructuras en la coraza dorsal del armadillo gigante *Priodontes maximus* (Kerr, 1792) y su potencial uso para la identificación de individuos

Resumen Las características morfológicas de la coraza dorsal y de los osteodermos han sido tradicionalmente muy utilizadas en la sistemática de armadillos, tanto extintos como actuales. Sin embargo, la variabilidad intraespecífica a nivel de coraza ha sido muy poco tratada en la literatura. En este trabajo se analiza una serie de corazas dorsales pertenecientes a *Priodontes maximus* con el objetivo de registrar dicha variabilidad. Como resultado, se describen un total de siete estructuras presentes en la configuración de osteodermos que conforman la coraza dorsal, incluyendo distintas terminaciones de las hileras de osteodermos, y las formas de osteodermos aberrantes más frecuentes. A pesar de que el mismo tipo de estructura puede estar presente en distintos ejemplares, su frecuencia y localización en la coraza son únicas de cada individuo. De esta manera, además de mejorar las descripciones anatómicas, la identificación de estas estructuras puede ser potencialmente implementada como un método complementario para reconocer individuos a los que se esté realizando un seguimiento. Además, también puede suponer un método de reconocimiento efectivo incluso pasado un largo tiempo tras la muerte del individuo. Dada la tendencia general a la disminución de las poblaciones de *P. maximus*, resulta importante desarrollar el mayor número posible de herramientas de monitoreo que puedan ayudar a los programas de conservación de esta especie.

***Palabras clave*:** Cingulata, morfología, osteodermos, variabilidad

Introduction

The giant armadillo *Priodontes maximus* (Kerr, 1792) of the subfamily Tolypeutinae (Xenarthra, Cingulata, Chlamyphoridae), has a wide distribution over most of South America, including habitats that range from tropical forests to open savannas (Abba & Superina, 2010). However, despite having such a wide geographical distribution, it is rare even in environments considered as "pristine" (Meritt, 2006), and is currently classified as Vulnerable by the IUCN Red List of Threatened Species (Anacleto *et al.*, 2014).

As reflected by its common name, it is the largest living representative of the order Cingulata ("armored xenarthrans"), reaching a total length of 150 cm and a body weight of up to 50 kg (Emmons & Feer, 1997; Nowak, 1999; Carter *et al.*, 2016; Desbiez *et al.*, 2019). It is a very efficient burrower with mainly nocturnal habits (Noss *et al.*, 2004; Silveira *et al.*, 2009), and its diet predominantly consists of

Table 1. List of specimens analyzed in this work.

Museum/collection	Specimen	Anatomical element	Geographic provenance
American Museum of Natural History, New York, United States	AMNH-147493	Complete dorsal carapace	–
Colección Mamíferos, Facultad de Ciencias Naturales e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina	CML-06228	Complete skull and dorsal carapace	Chaco Province, Argentina
	CML-00137	Complete dorsal carapace	Chaco Province, Argentina
Museo Municipal de Ciencias Naturales Carlos Darwin, Punta Alta, Argentina	MD-	Complete dorsal carapace	–
Museo Ciencias Naturales Augusto Schulz, Resistencia, Argentina	–	Taxidermy specimen	Chaco province, Argentina
	–	Taxidermy specimen	Chaco province, Argentina
	–	Taxidermy specimen	Chaco province, Argentina
	–	Partial skeleton and complete dorsal carapace	Chaco Province, Argentina
	–	Complete dorsal carapace	Chaco Province, Argentina
	–	Complete dorsal carapace	Chaco Province, Argentina
	–	Complete dorsal carapace	Chaco Province, Argentina
	–	Complete dorsal carapace	Chaco Province, Argentina
	–	Complete dorsal carapace	–
	–	Complete dorsal carapace	–
	–	Complete dorsal carapace	–
	–	Complete dorsal carapace	–
	–	Complete dorsal carapace	–
	–	Complete dorsal carapace	–
	–	Complete dorsal carapace	–
Laboratorio de Paleontología de Vertebrados (CECOAL–UNNE–CONICET), Corrientes, Argentina	LPV-CO-56	Dessicated specimen, partially complete skeleton and complete dorsal carapace	Chaco Province, Argentina

ants and termites (Redford, 1985; Eisenberg & Redford, 1999). Each individual carapace presents a unique dark to light color pattern (Noss *et al.*, 2004), and is composed of a scapular and a pelvic shield separated by a variable number (11–13) of mobile bands (Nowak, 1999).

The dorsal carapace composed by hundreds of osteoderms is the main morphological feature that characterizes all cingulates (Gaudin & McDonald, 2008), and is believed to have strongly influenced the evolutionary history of the group (Superina & Loughry, 2012). As is the case with *P. maximus*, the carapace of all current armadillos can be divided into the same three well-differentiated portions (a scapular and a pelvic shield separated by a variable number of mobile bands), which provide greater limb and body flexibility. However, extinct cingulates developed a huge variety of carapace configurations. Among them, Eutatini armadillos (Euphractinae) are characterized by presenting a very rudimentary pseudo-scapular shield (Krmpotic *et al.*, 2009), and some extinct euphractine armadillos such as those belonging to the genus *Prozaedyus* Ameghino (1891) even developed a dorsal carapace that was composed just by mobile bands and a pelvic shield (Barasoain *et al.*, 2020). In turn, glyptodonts (Glyptodontidae) developed an undivided and rigid dorsal carapace composed by fixed osteoderms only (Zurita *et al.*, 2016).

The study of the dorsal carapace and osteoderm features has been traditionally considered as a valuable tool in both extinct and extant armadillo systematics. Moreover, the development in each species of a unique ornamentation pattern on the exposed surface of both the fixed and mobile osteoderms that compose the carapace has generated specific terminology that applies to each morphological character at the osteoderm level (Soibelzon *et al.*, 2010).

Intraspecific morphological variation at the carapace level has, however, not been studied. Our observations suggest that a high percentage of *P. maximus* individuals present a series of distinctive structures in the osteoderm configuration that compose their dorsal carapace. The purpose of this contribution is to compile, describe, and illustrate the main types of these structures present over a sample of carapaces belonging to the extant *P. maximus*. The proper characterization of these structures will serve to guide more comprehensive anatomical descriptions of both fossil and extant armadillo individuals. Moreover, given that carapaces can persist for a long time in natural environments, the previous documentation of these structures may provide a useful tool for the identification of specific individuals being monitored or under study even a long time after death.

Materials and Methods

This study is based on the analysis of several dorsal carapaces and taxidermy individuals belonging to the species *Priodontes maximus*, housed in several museums (**Table 1**). Each kind of structure identified is named, described in detail, and illustrated.

Since most of the samples consist of isolated carapaces with no available information on whether they belonged to a male or female individual or about their geographic provenance, these variables were not taken into consideration. In order to describe the structures, we consider as complete those rows of osteoderms that originate at one lateral border of the carapace and extend without interruption until they reach the opposite border. In turn, we consider as incomplete those rows of osteoderms that originate at one lateral border of the carapace and do not reach the opposite border, or that do not originate on either of the two lateral borders.

Results

After a detailed morphological analysis carried out on the scapular shield, mobile bands, and pelvic shield of the dorsal carapace of a total of 23 *P. maximus* adult individuals, we identified a total of seven distinct structures (**Fig. 1**).

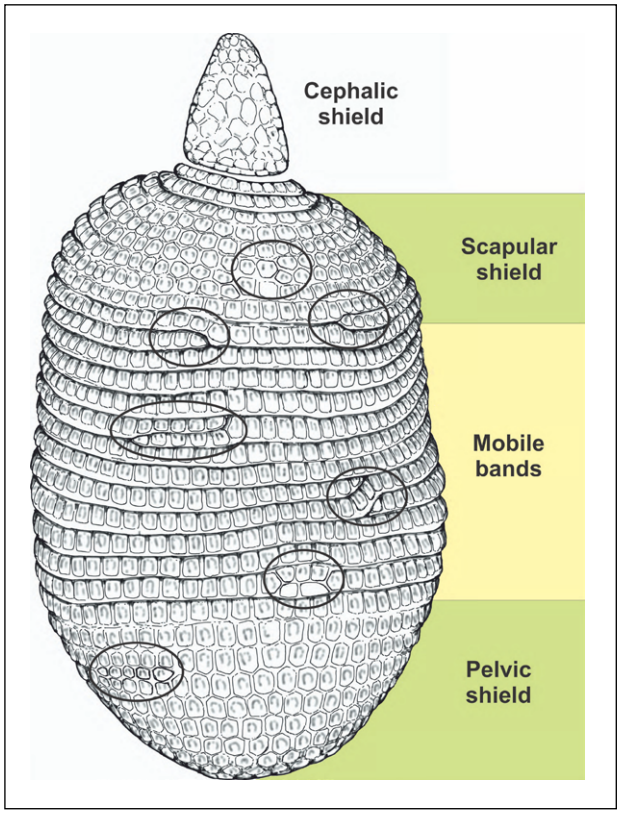

Figure 1. Division of the dorsal carapace of *Priodontes maximus*. Black ovals indicate examples of the structures identified.

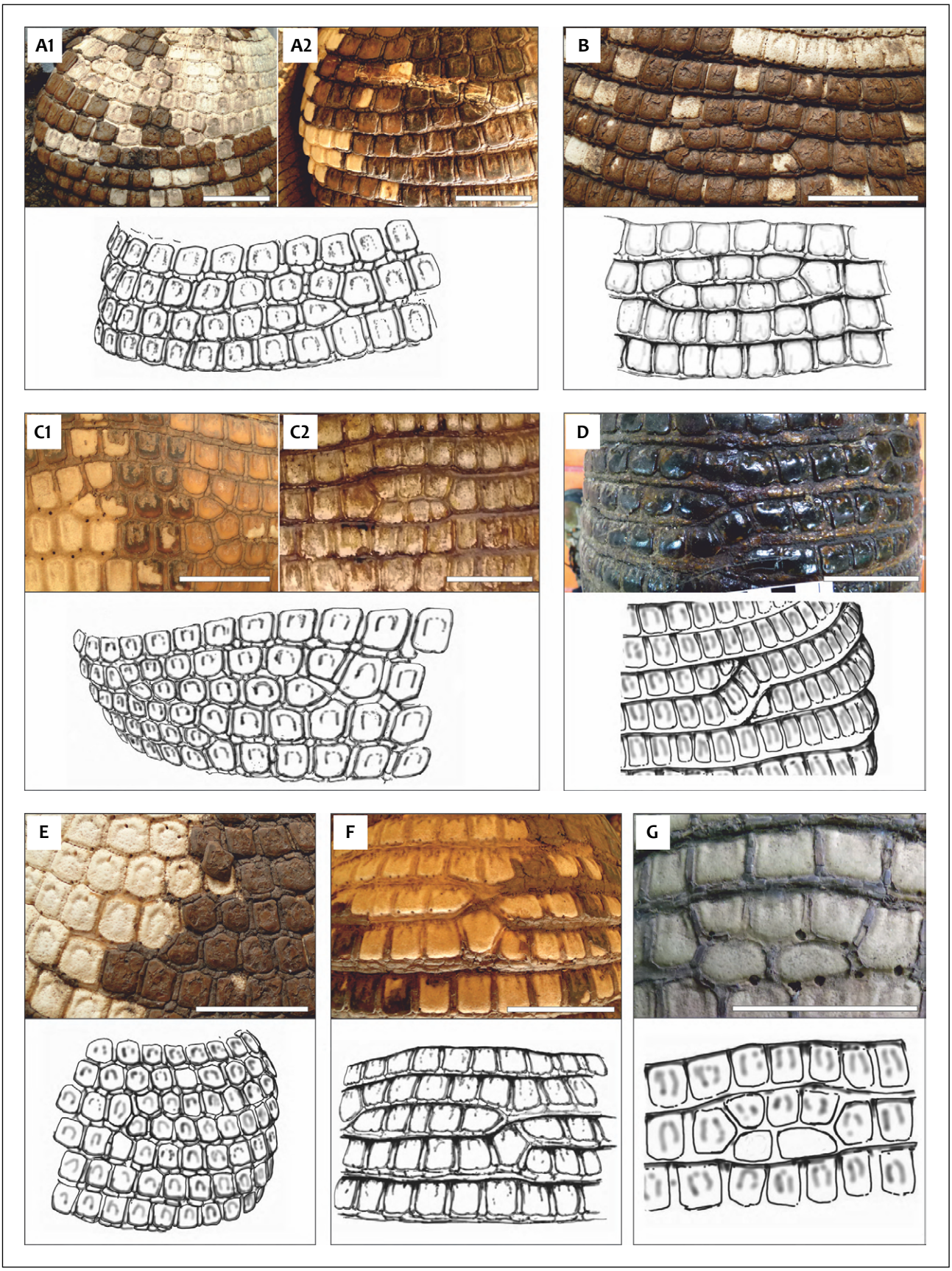

FIGURE 2. Structures identified together with schematic representations. **A.** Lateral wedging; **A1.** fixed osteoderms; **A2.** mobile osteoderms. **B.** Double lateral wedging. **C.** Isolated row; **C1.** fixed osteoderms; **C2.** mobile osteoderms. **D.** Crossed row. **E.** Confluent rows. **F.** Oversized osteoderm. **G.** Isolated osteoderms. Scale bars equivalent to 5 cm.

Structures identified

Lateral wedging. A row of osteoderms originates from one of the lateral borders of the carapace, and as it extends towards the dorsal area it is laterally wedged between the adjacent rows, becoming an incomplete row. The terminal osteoderm of the row can be identified as it develops a characteristic triangular or "wedged" shape. This wedging can occur at any point between the lateral border of the carapace where the row originates and the most dorsal area, but without reaching the opposite half of the carapace. This structure has been recorded for both the scapular and pelvic shield, and in the mobile bands (**Fig. 2A**).

Double lateral wedging. This structure is a special case of lateral wedging. Two consecutive rows of osteoderms originate from each lateral border of the carapace respectively, and as they extend towards the dorsal area they are wedged between each other and the adjacent rows, becoming incomplete rows. As it happens with the simple case of lateral wedging, the terminal osteoderms of the two wedged rows develop a triangular shape. However, unlike the simple case, this structure has only been recorded for the mobile bands, and not for the scapular and pelvic shields (**Fig. 2B**).

Isolated row. This structure consists of a row of osteoderms of variable extension that does not reach any of the lateral borders of the carapace. This happens as both endings of the row are laterally wedged between the adjacent rows. As in other wedged structures, terminal osteoderms from both sides of the row develop a triangular shape. The development of this incomplete row produces a deformation in the adjacent rows, with osteoderms reduced in size and displaced in order to adjust to the available space. This structure differs from the double lateral wedging in that it does not originate from any of the lateral margins of the carapace. It has been recorded for both the scapular and pelvic shields and for the mobile bands (**Fig. 2C**).

Crossed row. This very particular structure consists in a complete row of osteoderms that at some point is diagonally displaced until it occupies the position that would correspond to the immediately superior or inferior row. The osteoderms located at the transition point develop a normal morphology but in a diagonal position, generating the lateral wedging of the adjacent rows at the point where the displacement occurs. This structure has only been recorded for the mobile bands (**Fig. 2D**).

Confluent rows. This structure involves a total of three incomplete rows of osteoderms. Two consecutive rows extend from one lateral border of the carapace, while a third one extends from the opposite border until encountering the first two. At this point, the osteoderms of the consecutive rows are approximately half the size of those of the opposite row, and both terminal osteoderms of these bands are laterally limited with the terminal osteoderm of the opposite band. Unlike in lateral wedging, terminal osteoderms of the confluent rows maintain their original shape, but are modified in size. This structure has been recorded for both the scapular and pelvic shields (**Fig. 2E**).

Oversized osteoderm. A random osteoderm of a complete row is greatly oversized, extending either towards the anterior or posterior part of the carapace, and therefore occupying the space that would correspond to two adjacent rows. In turn, this generates the lateral wedging of the affected rows at both sides of the oversized osteoderm, giving place to two incomplete rows. This structure has been recorded for the scapular shield and the mobile bands (**Fig. 2F**).

Isolated osteoderms. This structure is composed of a variable number of isolated osteoderms that are surrounded by complete rows. This produces a deformation in the adjacent rows, with osteoderms reduced in size and displaced in order to adjust to the available space. Contrary to the isolated row structure, these osteoderms do not compose a defined row, as they develop aberrant morphologies and those on the extremes are not laterally wedged. This structure has only been recorded between the last mobile band and the first row of fixed osteoderms of the pelvic shield (**Fig. 2G**).

Discussion

Both extant and extinct armadillos exhibit wide variability in the morphology of their dorsal carapace. Far beyond the evident differences between different species, intraspecific variability is also considerable. Each individual *P. maximus* that we examined presented a unique carapace pattern. Individual variation has been noted for other extant species such as *Zaedyus pichiy* (Desmarest, 1804) (see Superina & Abba, 2014), but has not been analyzed in detail.

Among the structures we identified, some appear to be very common, while others may not be. The simple case of lateral wedging was the most common structure we observed; it was present in all our specimens. Other structures such as confluent rows or oversized osteoderms were common, present in more than half of the sample. In turn, we found isolated rows and isolated osteoderms in less than half of the sample. The rarest structures in our sample are the double lateral wedging, in two individuals, and the crossed row, in just one individual.

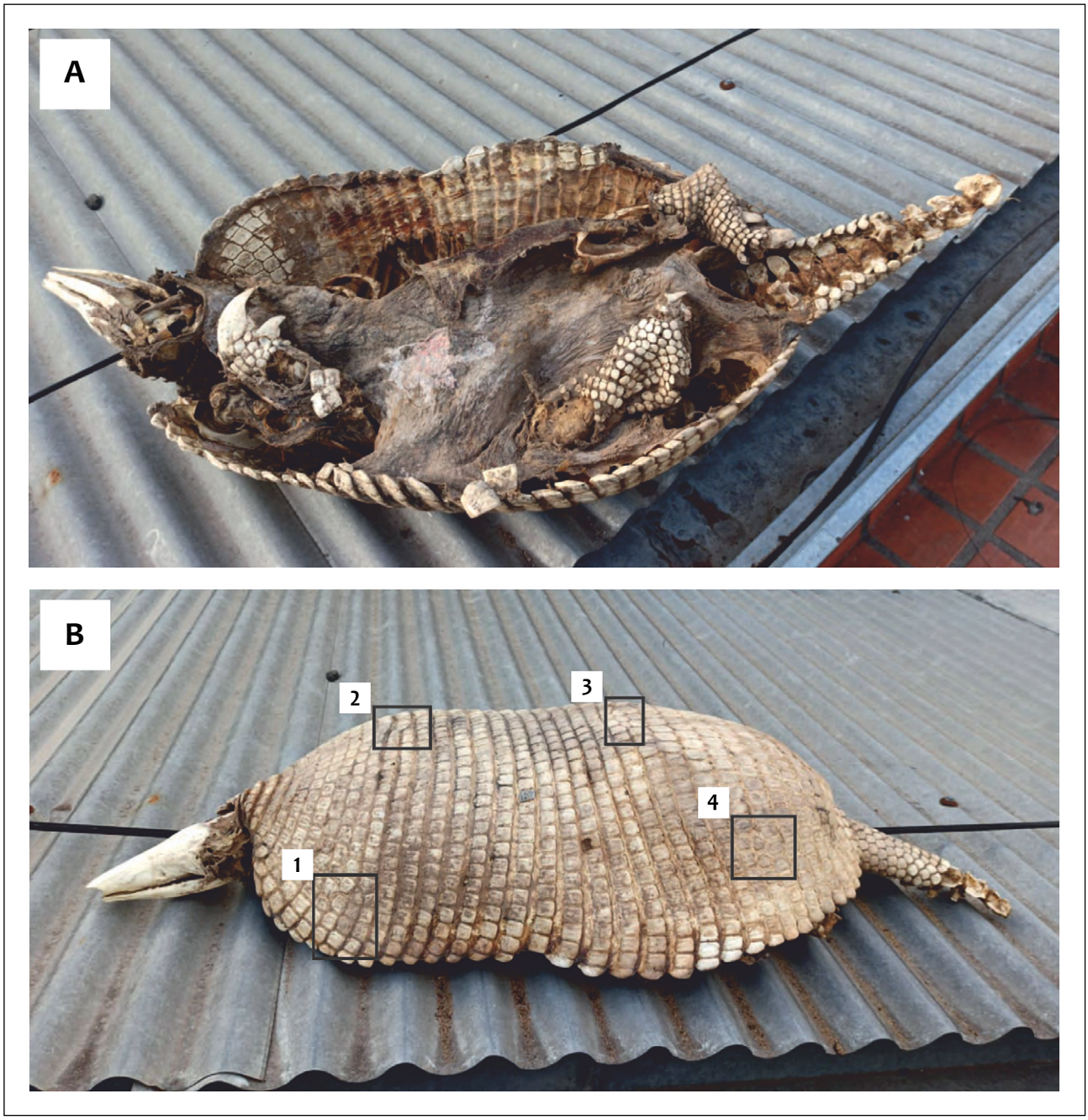

FIGURE 3. Structure identification in a desiccated specimen (LPV-CO-56). **A.** Ventral view. **B.** Dorsal view. **1.** Lateral wedging in the scapular shield. **2.** Confluent rows. **3.** Isolated row. **4.** Lateral wedging in the pelvic shield.

The precise location and number of times that these structures appear on each carapace is unique to each individual.

According to the principal osteoderm development studies carried out for extant armadillos, osteoderm ossification occurs during the embryonic stage, so the configuration pattern of the osteoderms that compose the dorsal carapace is already defined prior to parturition (Cooper, 1930; Vickaryous & Hall, 2006). We assume therefore that the structures we identified are already present at birth and are preserved through the individual's entire lifespan.

The structure we describe can help to recognize specific individuals in field studies, particularly when the animals are captured. Recently, Massocato & Desbiez (2019) published a series of guidelines to help in the identification of *P. maximus* individuals recorded by camera traps, including scale patterns, coloration patterns, and natural marks. Though the recognition of the proposed structures and their variations can be more challenging in camera trap photos because they provide only partial and sometimes distorted views of the animals, our structures can be a complementary method for camera trap studies. The main benefit of documenting these

structures may reside in the potential recognition of particular individuals even a long time after death (**Fig. 3**), because the carapace can be preserved for a long time in natural environments even after the decomposition of the soft tissues and the disarticulation of the axial skeleton (Muñoz, 2015).

Priodontes maximus is globally classified as Vulnerable by the IUCN Red List, and the population overall is decreasing. In Argentina, its situation is even worse, and it is classified as Endangered (Di Blanco & Superina, 2019). In this context, we strongly believe in the importance of implementing as many tools and monitoring strategies as possible, in order to maximize the effectiveness of conservation efforts.

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