



NEW CINGULATA (MAMMALIA, XENARTHRA) FROM THE UPPER LUMBRERA FORMATION (BARTONIAN, MIDDLE EOCENE), SALTA PROVINCE, ARGENTINA

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ABSTRACT – We describe isolated remains of a Paleogene cingulate from El Simbolar locality, Upper Lumbrera Formation (Bartonian), southern Salta Province, northwestern Argentina. The material consists of numerous fixed, movable, and caudal sheath osteoderms. The specimen has large-sized osteoderms, with a lageniform main figure, as in *Utaetus buccatus*, *U. laxus*, *U. argos*, ?*U. deustus*, *Punatherium catamarcensis*, and the basal euphractin *Archaeutatus*. The combination of morphological characters, in addition to its large size, allows us to recognize a new species of “Utaetini” for the Paleogene of northwestern Argentina. This new species of ?*Utaetus* represents the oldest record of Euphractinae in this region, and strengthens the endemic condition of its Paleogene faunas.

Keywords: Cingulata, osteoderms, El Simbolar, Paleogene, Salta, Argentina.

RESUMO – Nós descrevemos restos isolados de cingulado do Paleógeno da localidade de El Simbolar, Formação Lumbrera Superior (Bartoniano), sul da Província de Salta, noroeste da Argentina. O material consiste em numerosos osteodermos das bandas fixas, móveis e caudais. Os osteodermos têm tamanho grande, com uma figura principal de aspecto lageniforme, como em *Utaetus buccatus*, *U. laxus*, *U. argos*, ?*U. deustus*, *Punatherium catamarcensis*, e o euphractino basal *Archaeutatus*. A combinação de caracteres morfológicos, em adição ao seu grande tamanho, nos permite reconhecer uma nova espécie de “Utaetini” para o Paleógeno do noroeste da Argentina. Esta nova espécie de ?*Utaetus* representa o registro mais antigo para Euphractinae nesta região e fortalece a condição endêmica das faunas paleógenas no noroeste da Argentina.

Palavras-chave: Cingulata, osteodermos, El Simbolar, Paleógeno, Salta, Argentina.

INTRODUCTION

Cingulata are a diverse and relatively abundant group of eutherian mammals characteristic of the South American Cenozoic. The evolutionary history of cingulates in particular, and xenarthrans in general, is deeply linked to the protracted isolation of South America (SA) and the concomitant evolution of endemic faunas in the continent. During the late Pliocene (~ 3.5 Ma), at the beginning of the Great American Biotic Interchange (GABI), cingulates spread into Central and North America (Patterson & Pascual, 1968; Cione *et al.*, 2015), currently occupying different biomes between approximately 40° N and 40° S in the Americas (Castro, 2015; Soibelzon *et al.*, 2015).

The external morphology of osteoderms has played an important role in traditional systematic assessments of the group (Carlini *et al.*, 2009; Ciancio, 2016 and references therein), given that the isolated osteoderms are the most frequently preserved elements of the Cingulata skeleton in the fossil record (Carlini *et al.*, 2010). The earliest record of cingulates is represented by isolated osteoderms of *Riostegotherium* (Astegotheriini), from the early Eocene locality of São José de Itaboraí in Southeast Brazil (Oliveira & Bergqvist, 1998; Bergqvist *et al.*, 2004; Gelfo *et al.*, 2009; Woodburne *et al.*, 2014). The rich Cenozoic fossil record of cingulates from Argentina comprises the bulk of the current

knowledge on the systematics of the group. In Patagonia, the oldest cingulate comes from the early Eocene (Simpson, 1948). In the Paso del Sapo Fauna, all the cingulate remains have been assigned to different Astegotheriini species, representing the most diverse record of the group (Tejedor *et al.*, 2009; Carlini *et al.*, 2010; Ciancio *et al.*, 2013). By the middle Eocene, cingulates become more diverse and the first undoubtedly Euphractinae, *Utaetus* Ameghino, 1902 is recorded (Simpson, 1948; Carlini *et al.*, 2010). Significantly, there is a subsequent reversal in the relative abundance of the major groups, with Euphractinae becoming dominant over Dasypodinae by the late Eocene (Ciancio, 2016).

In northwestern Argentina (NWA), several Paleogene geological units have produced a rich record of continental mammals (Río Loro, Mealla, Maíz Gordo, Lower Lumbreira, Upper Lumbreira, Casa Grande, Quebrada de los Colorados, and Geste formations), spanning from the Paleocene to the late Eocene (del Papa *et al.*, 2017). Despite the abundant record of mammals (mainly South American native ungulates) in these units, the record of armadillos is sparse and limited to levels from the early to the late Eocene (Lower Lumbreira, Upper Lumbreira, Casa Grande, Quebrada de los Colorados, and Geste formations; Table 1) (Babot *et al.*, 2012, 2017; Ciancio *et al.*, 2016; Herrera & Powell, 2009; Herrera *et al.*, 2010, 2012, 2016, 2019; Fericola *et al.*, 2021).

Table 1. Comparative chart of cingulate present in the different Eocene localities of Northwestern Argentina (Herrera & Powell, 2009; Herrera *et al.*, 2010, 2012, 2016, 2019; Babot *et al.*, 2012, 2017; Ciancio *et al.*, 2016; Fericola *et al.*, 2021). **Abbreviations:** (localities grouped by provinces): **CTT**, Cerro Tin Tin; **ES**, El Simbolar; **JR**, Juramento river; **LC**, Los Cardones; **LP**, Laguna de Los Pozuelos; **LV**, Luracatao valley; **PG**, Pampa Grande (Salta Province); **AS**, Antofagasta de la Sierra (Catamarca Province); **MA**: Mina Aguilar (Jujuy Province).

Age	early Eocene		middle Eocene				late Eocene		
	Formation		Upper Lumbreira		Quebrada de los Colorados		Casa Grande	Geste	
	NWA locality	Lower Lumbreira	JR	ES	CTT	LV	MA	AS	LP
CINGULATA									
								X	
ASTEGOTHERIINI									
								X	
					X	X			
								X	
							X		
								X	
EUPHRACTINAE									
								X	X
				X					
CINGULATA incertae sedis									
		X	X		X	X	X	X	X
		X							
								X	
		X							

Here we describe numerous fixed, movable, and caudal sheath osteoderms, all from the same individual, of a new large-sized Cingulata recovered at El Simbolar locality, Upper Lumbrera Formation, in southern Salta Province, NWA. We discuss the significance of these new findings within the evolutionary history of the group in the context of early Cenozoic faunal evolution in SA intermediate-latitudes.

MATERIAL AND METHODS

The specimen of *?Utaetus magnum* sp. nov. (IBIGEO-P 109) here described includes several isolated fixed, movable, and caudal sheath osteoderms, all from the same individual, which are deposited in the Colección de Paleontología, Instituto de Bio y Geociencias del Noroeste Argentino, Rosario de Lerma (Salta, Argentina).

Specimens used for comparison include *Utaetus buccatus* (MACNA-11622A, MPEF PV 5426), *Utaetus latus* (MACN 10424, 11295), *Utaetus argos* (MACN 10445), *?Utaetus deustus* (MACN 10431), *Pucatherium parvum* (PVL 6384, MHAS 068-072), *Lumbreratherium oblitum* (PVL 4262), *Riostegotherium yanei* (MCN-PV 1774), *Astegotherium dichotomus* (MACN A-10421), *Stegosimpsonia chubutana* (MACNA-10438), *Pseudostegotherium glangeaudi* (MACN A-12679), *Parastegosimpsonia peruana* (LACM 150608), *Punatherium catamarcensis* (MLP 93-VI-1-18, MLP 86-V-6-24), *Parutaetus punaensis* (MLP 83-XI-3-2, MHAS 017–020, 029, PVL 6416, 6575, 6403, 6413–6415, 6407, 6417, 6568), *Orthutaetus* (MPEF PV 7633B), *Anteutatus* (MACNA-11621), *Yuruatherium tropicalis* (LACM 150606), and *Archaeutatus malaspiniensis* (MACN A-10440).

Institutional Abbreviations: **IBIGEO-P**, Colección de Paleontología Instituto de Bio y Geociencias del Noroeste Argentino, Rosario de Lerma, Salta, Argentina; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina;

MCN-PV, Museo de Ciencias Naturales, Secretaria do Meio Ambiente e Infraestrutura do Rio Grande do Sul, Porto Alegre, Brazil; **MHAS**, Museo del Hombre de Antofagasta de la Sierra, Antofagasta de la Sierra, Catamarca, Argentina; **MLP**, Museo de La Plata, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata, Buenos Aires, Argentina; **MPEF PV**, Museo Paleontológico Egidio Feruglio, Paleontología Vertebrados, Trelew, Chubut, Argentina; **PVL**, Colección Paleontología Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, UNT, Tucumán, Argentina.

GEOLOGICAL SETTINGS

The outcrops of the Upper Lumbrera Formation at El Simbolar, Guachipas Department, Salta Province (Figure 1) are composed of a thick succession of reddish siltstones and sandy siltstones, with sporadic and localized intercalations of fine-grained sandstones and nodules of gypsum/anhydrite. The most outstanding features of this geological unit are its homogeneous lithology and the presence of conspicuous paleosol layers (del Papa *et al.*, 2017). The paleoenvironmental reconstruction suggests that the Upper Lumbrera Formation represents sedimentation in a fine-grained plain, with localized fluvial and ephemeral lacustrine deposits (del Papa, 2006). Indeed, based on granulometric and petrographic analysis of the Upper Lumbrera sediments at El Simbolar, Lapiana *et al.* (2016) suggested a paleoenvironment of open plains constructed by the aggradation of reworked loess. The fossil-bearing sedimentary layer is formed by red sandy siltstones with root traces, carbonate nodules, ped structures and clay cutans typical of paleosols with wet/dry cycles. The age of the Upper Lumbrera Formation has been estimated in 39.9 +/- 0.4 Ma (U/Pb zircon recovered from a tuff layer close to the upper contact, see del Papa *et al.*, 2010). The age of the fossil is therefore considered as middle Eocene (Bartonian).

Table 2. Compared dimensions (in mm) of movable and fixed osteoderms of *?Utaetus magnum* sp. nov. (IBIGEO-P 109), with *?U. deustus*, *U. buccatus*, *U. argos*, and *U. latus* (Ameghino, 1902).

	<i>?Utaetus magnum</i>	<i>?U. deustus</i>	<i>U. buccatus</i>	<i>U. argos</i>	<i>U. latus</i>
Fixed osteoderms					
Length	17.6–23.1	13	14	11	16
Width	13.1–17.7	15	9–13	8	11
Thickness	6.2–7	6	4–6	2.5	5
Movable osteoderms					
Length	41.3–45.5	30 - 40	20–22	----	18.6
Width	11.2–17.5	15	7–9	----	8.64
Thickness	4.3–4.7	----	3	----	----
Subtriangular osteoderms					
Length	18.8–24.6	----	----	----	----
Width	12.8–15.4	----	----	----	----
Thickness	4.3–5.5	----	----	----	----

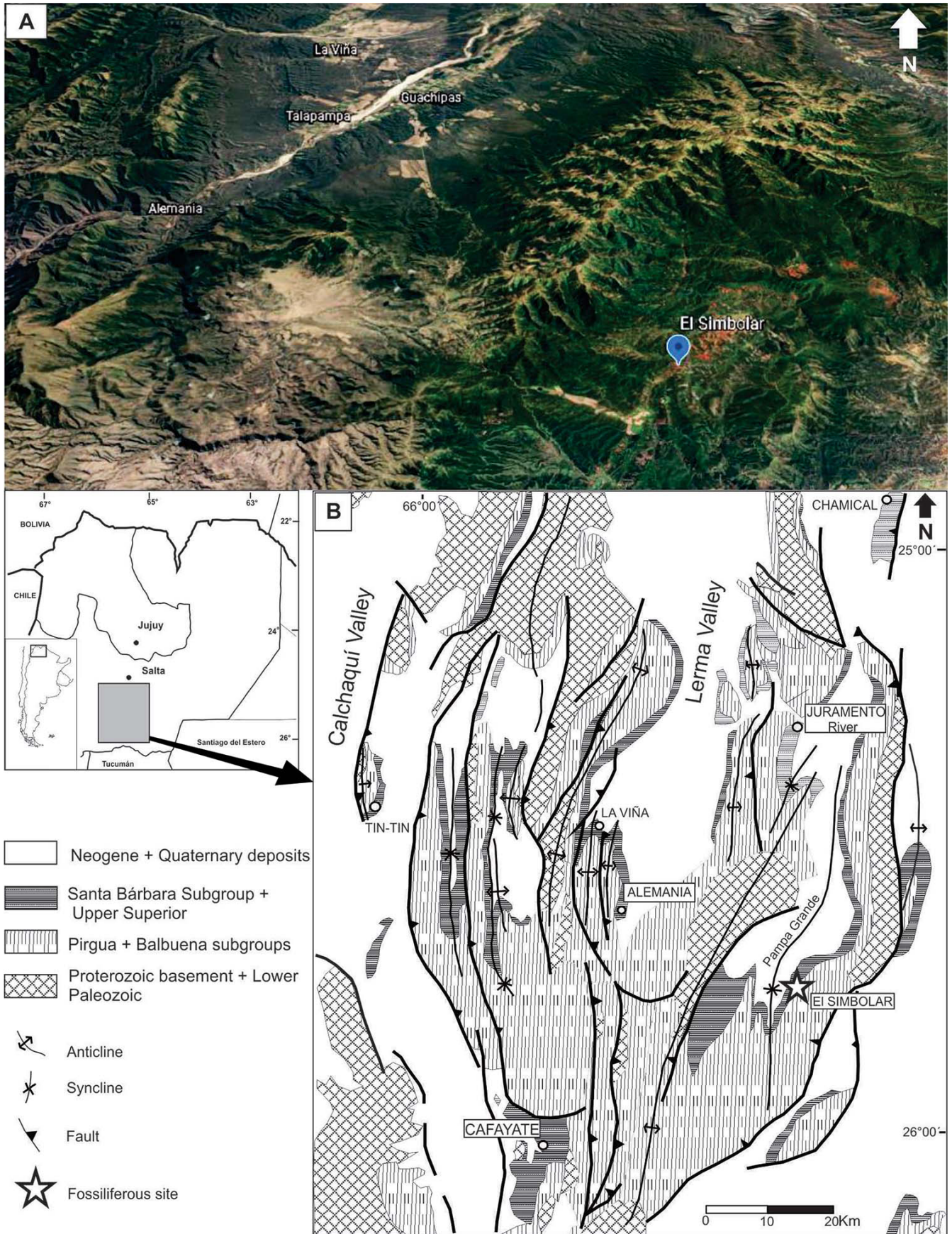


Figure 1. Location of the studied area. **A**, geographic location of El Simbolar locality, Guachipas Department, Salta Province, Argentina; **B**, geological map and synthesized stratigraphy showing the location of the fossiliferous site (Upper Lumbreira Formation).

SYSTEMATIC PALEONTOLOGY

XENARTHRA Cope, 1889

CINGULATA Illiger, 1811

CHLAMYPHORIDAE Pocock, 1924

EUPHRACTINAE Winge, 1923

“UTAETINI” Simpson, 1945

Utaetus Ameghino, 1902**Type Species.** *Utaetus buccatus* Ameghino, 1902.*?Utaetus magnum* sp. nov.

urn:lsid:zoobank.org:act:AB845C91-605B-4609-BDB8-1E90E7A23BBF

(Figure 2)

Etymology. *magnum* from the Latin *magna*, large or superior, in reference to the large size of the new taxon in comparison to other closely related forms.

Holotype. IBIGEO-P 109, 11 fixed, two movables, and eight caudal complete osteoderms, in addition to numerous fragmentary osteoderms, all from the same individual.

Geographic and Stratigraphic Provenance. El Simbolar (25°43'34.5''S – 65°24'35.4''W), Guachipas Department, Salta Province, Argentina (Figure 1). Upper Lumbreira Formation, middle Eocene (Bartonian). The fossiliferous layer is 23 m above the base of the unit.

Diagnosis. Large cingulate of inferred size similar to the extant *Euphractus sexcintus*. Osteoderms larger than *?Utaetus deustus*, and one and a half times larger than *Utaetus buccatus*, *U. laxus*, and *U. argos*. Lateral contact area straight, with denticular projections in their entire surface, as in Euphractinae. Fixed and movable osteoderms with a lageniform main figure, as in “Utaetini”, in *Punatherium catamarcensis*, and the basal euphractins *Archaeutatus*. Convex main figure, with a sharp and elevated central keel. In those osteoderms with large foramina on their surface, the main figure and keel rise above the level of the peripheral figures. Peripheral figures very convex to globose unlike *U. buccatus*, *U. laxus*, *U. argos*, and *?U. deustus*.

Description. Fixed and movable osteoderms of *?Utaetus magnum* sp. nov. have a slightly rough external surface (Figure 2A–G, I–M; Table 2), as in certain Euphractinae, and Astegotheriini, except for *Astegotherium dichotomus*, in which it is completely smooth (Vizcaíno, 1994). The lateral contact areas between osteoderms are straight, with denticular projections in their entire surface (Figure 2H), similar to the condition observed in the paleogene Euphractinae *Archaeutatus*, and in the Cingulata *incertae sedis* *Punatherium catamarcensis*. In *Utaetus* the lateral faces are straight but, according to Ameghino (1902), the denticular projections are scarce or absent. By contrast, in Astegotheriini these surfaces are concave and smooth, and in *Parutaetus punaensis* they are concave with small and dispersed denticular projections (Ciancio *et al.*, 2016). In *?U. magnum* sp. nov. the piliferous system is underdeveloped. One or two conspicuous foramina can be

observed in the posterior third of one or both lateral margins, as well as one or two small foramina can be observed in the posterior margin. Similar condition is present in “Utaetini”, Astegotheriini, *Archaeutatus*, and *Parutaetus* (Simpson, 1948; Carlini *et al.*, 2009, 2010; Ciancio *et al.*, 2016). By contrast, the foramina are large and located in the posterior and lateral margins in *P. catamarcensis*. In most Euphractinae (Eutatini in particular) the piliferous system is well developed.

Ciancio *et al.* (2016) mentioned that rectangular and pentagonal fixed osteoderms are recognized in *Parutaetus punaensis*, and that the former would correspond to the lateral portion of the carapace, while the pentagonal ones would correspond to the middle region. In *?U. magnum* sp. nov. the same variation in the shape of the osteoderms is observed.

The main figure of the rectangular osteoderms (Figure 2A–D) is lageniform, very convex, and it has a sharpened central keel that extends nearly to the posterior margin of the osteoderm but not reaching it. These figures have a long, wide neck, reaching approximately one third of the osteoderms total length. *Utaetus buccatus*, *U. argos*, and *?U. deustus* have a lageniform and convex main figure without keel. *U. laxus* has a flat main figure without keel. On the other hand, *?U. deustus* has a convex main figure, with a low and not sharpened keel. The lageniform figure is also present in Astegotheriini and some euphractins like *Orthutaetus*, and *Anteutatus*. In “Utaetini”, Astegotheriini, and some Eocene Euphractinae, the neck is comparatively shorter (Ameghino, 1902; Carlini *et al.*, 2010; Ciancio *et al.*, 2013).

The new species has four peripheral polygonal figures, two anterior and two lateral, all convex or globose and similarly sized. In *Utaetus buccatus*, *U. laxus*, and Astegotheriini there are three to four flat or slightly convex and similarly sized anterolateral figures. *Archaeutatus malaspiniensis* has two peripheral polygonal anterior figures that are well developed, and two smaller triangular lateral figures. In osteoderms of *Punatherium catamarcensis* there are three peripheral anterior figures and two slightly convex lateral figures.

In *?U. magnum* sp. nov. the main figure is delimited by a wide, concave, and deep groove. Some of these osteoderms have a well-developed circular foramen at the intersection of the central groove with the radial groove, which delimits the anterior figures. In *Utaetus buccatus* and *U. laxus* the groove that delimits the main figure is narrow and has two to five circular foramina in the anterior region. In Astegotheriini, in general, the groove is narrow, shallow, and has two to 20 foramina of various sizes. A particular case is *Pseudostegotherium* in which the foramina of the anterior region are very well developed. In *A. malaspiniensis* the groove that delimits the main figure is wide, concave and has two to four circular foramina. In *Punatherium catamarcensis* there are three circular foramina delimiting the anterior region of the main figure.

The fixed pentagonal osteoderms (Figures 2E–G) have very convex to globose figures. The main figure has a high, sharp keel that elevates above the level of the peripheral figures. In *Utaetus buccatus* and *U. laxus* the figures are not as convex, and the main figure does not rise above the level of the peripheral figures. There are two to three peripheral



Figure 2. Osteoderms of *?Utaetus magnum* sp. nov., IBIGEO-P 109. Quadrangular fixed osteoderms (A–D), pentagonal fixed osteoderms (E–G), lateral contact area in fixed osteoderm (H), movable osteoderms (I–K), caudal sheath osteoderms (L, M), osteoderms A–M are at the same scale. Cross section of osteoderms showing the foramen connected with glandular subspherical cavities, marked by the dotted line (N). **Abbreviations:** ch, channel; gc, glandular cavity. Scale bars = 10 mm.

anterior figures and two lateral figures. The grooves that delimit the figures are deep and narrow. In the anterior region, the main figure has three large subcircular foramina. These large foramina are also found in *U. buccatus* (four or five), *?U. deustus* (three or four), and *U. laxis* (two) (Ameghino, 1902; Ciancio & Carlini, 2008; Carlini *et al.*, 2010). In *?U. magnum* sp. nov., the large foramina are connected with glandular

subspherical cavities, that are well developed, through a short and very wide channel, as is observed in an osteoderm transversely cut (Figure 2N). A similar morphology has been described in the *Stegosimpsonia* and in the *U. buccatus*, which show hypertrophied glands (Ciancio *et al.*, 2019).

The movable osteoderms (Figures 2I–K) have a lageniform convex main figure, with a blunt central keel that does not

reach the posterior margin and is less prominent than in fixed osteoderms. *?Utaetus deustus* also has a low central keel, while *U. buccatus* and *U. laxus* do not have this structure. The osteoderms have a long, wide neck that does not reach the anterior margin of its exposed region. Only a pair of peripheral figures limit the neck, each extending in the anterior and lateral region, which are slightly convex and extend up to half the length of the exposed region. A similar condition is observed in *U. laxus*, while in *U. buccatus* the main figure is open in the anterior margin of the exposed region and presents only one pair of lateral peripheral figures (Ciancio & Carlini, 2008). Movable osteoderms are unknown for *U. argos*. *Parastegosimpsonia peruana* also has a long neck, but it is surrounded by two pairs of peripheral figures, with an anterior pair and a lateral pair (Ciancio *et al.*, 2013). In the other Astegotheriini, the main figure can be lageniform or triangular, flat or slightly convex, and in certain cases it has a short, blunt central keel. The neck extends up to the anterior margin of the exposed region; it is open and is limited by two lateral figures. In *?U. magnum* sp. nov. the groove that delimits the main figure is deep and, around the neck, one to three circular foramina of smaller size than those of the fixed osteoderms occur. The transition zone is concave, short, and smooth. In *U. buccatus*, and *U. laxus* the transition zone is well developed and somewhat rough. In Astegotheriini, in general, the groove is narrow, shallow, and has circular foramina that vary in size and number (from one to eight). The transition zone is more developed; it is concave and can be smooth or rough.

The subtriangular osteoderms (Figures 2L, M) have a wide and rounded anterior edge, with a short articular region, as in *Utaetus buccatus* (MPEF PV 5426) from the middle Eocene of Patagonia, Argentina (Carlini *et al.*, 2010). The transition zone is concave and deep. The exposed surface is rough, and the main figure is elongated, with an elevated keel, which does not reach the posterior margin of the osteoderm. There are no well-defined peripheral figures. The ventral surface is very concave in the transversal axis. These osteoderms are here regarded as part of the caudal sheath.

Size comparisons. The Euphractinae *Utaetus buccatus*, *U. laxus*, *Parutaetus*, *Orthutaetus*, *Anteutatus*, and the Cingulata *incertae sedis Yuruatherium tropicalis*, are medium-sized, similar to *Chaetophractus villosus* (movable osteoderms between 14–26 mm length, 5–11 mm width, 2.5–4.5 mm thick) (Ciancio & Carlini, 2008; Carlini *et al.*, 2010). The Astegotheriini (*e.g. Riostegotherium*, *Prostegotherium*, *Parastegosimpsonia*, *Stegosimpsonia*) are small to medium-sized, similar to the extant *Dasypus hybridus* or *D. novemcinctus* (movable osteoderms between 10–16 mm length, 5–8 mm width, 2–4 mm thick) (Oliveira & Bergqvist, 1998; Tejedor *et al.*, 2009). The only Stegotheriini from the Eocene is smaller than the above-mentioned taxa (Ciancio *et al.*, 2013). Among the Eocene cingulate recorded in NWA, Astegotheriini, Euphractinae, and *Punatherium catamarcensis*, have similar sizes to those recorded for other latitudes. A particular case is *?U. deustus*, which is larger than the other *Utaetus* species from Patagonia (movable osteoderms between 30–40 mm length, 15 mm width; Ameghino, 1902). On the other hand,

Lumbreratherium oblitum and *Pucatherium parvum* (known by more complete specimens) are medium-sized forms, similar to *D. novemcinctus* but with proportionally very small osteoderms (movable osteoderm between 4.82–9.60 mm length, and 4.07–5.58 mm width) (Herrera *et al.*, 2012, 2016, 2019; Ciancio *et al.*, 2016).

DISCUSSION

The new species presents similar morphological characters to *Utaetus* Ameghino (1902), such as the lageniform main figure, the presence in some osteoderms of large foramina on the external surface, and areas of lateral contact with denticular projections. The genus *Utaetus* comprises four species of which *U. buccatus*, *U. laxus*, and *U. argos* are of medium size, and only *?U. deustus* is a large form (around two times larger than the others). The osteoderms of *?U. magnum* sp. nov. are larger compared to *?U. deustus* and other Eocene cingulates. Unlike all *Utaetus* species mentioned above, *?U. magnum* sp. nov. has the main figure convex, the peripheral figures convex or globose, and the central keel sharp and raised.

During the Eocene, the succession of changes in the composition of cingulate faunas was different between high-latitude (Patagonia) and intermediate-latitude (NWA) deposits. The oldest records in Patagonia correspond to the early Eocene. In this period, the armadillos with the greatest diversity and abundance are Astegotheriini (Tejedor *et al.*, 2009; Ciancio, 2016). In the middle Eocene, this group diversity decreased, simultaneously with the appearance of the first record of Euphractinae (*Utaetus*). Towards the late Eocene, the diversity of Euphractinae surpassed that of Astegotheriini and Stegotheriini.

In NWA, the sediments bearing Cingulata correspond to the span between the early to late Eocene (Powell *et al.*, 2011; Ciancio *et al.*, 2016; Herrera *et al.*, 2012, 2016, 2019; Babot *et al.*, 2017; Fernicola *et al.*, 2021). In the early Eocene only two armadillos of uncertain affinities, unique to the NWA (*Pucatherium parvum* and *Noatherium emilioi*), are recorded. During the middle Eocene, the new species described here (*?U. magnum* sp. nov.) represents the oldest record of Euphractinae for this region. *P. parvum* and *Lumbreratherium oblitum*, exclusive forms of the NWA, are also recorded. In the late Eocene the most diverse group is Astegotheriini, while Euphractinae are represented by *Parutaetus punaensis*. Other taxa of uncertain affinities, such as *Pucatherium parvum*, and *Punatherium catamarcensis*, are recorded. To the present, some cingulate taxa that are frequently found in Patagonia, such as Stegotheriini, and Eutatini (Euphractinae), have not been yet recorded in NWA (Ciancio, 2016).

According to Fernicola *et al.* (2021), in the early Eocene deposits of the NWA there are three possible morphotypes of cingulate carapace. The first of them corresponds to a carapace formed entirely by transverse movable bands (*Pucatherium parvum* and *Lumbreratherium oblitum*); the second to a carapace with a scapular and pelvic shield separated by transverse movable bands (possibly *Noatherium emilioi*), and the third model with the entire anterior region formed by

movable bands and a short pelvic shield (possibly *N. emilioi*). In the middle Eocene (Upper Lumbreira Formation), the *P. parvum* record show the presence of a carapace formed by movable bands; on the other hand ?*U. magnum* sp. nov. could present a carapace formed by movable bands, scapular shield, and pelvic shield or a carapace with movable bands and pelvic shield. Until now, no sufficiently complete specimen has been recovered to confirm the coexistence of these latter models throughout the Eocene. In relation to the articulation between contiguous osteoderms, ?*U. magnum* sp. nov. presents lateral contact areas straight with denticular projections in their entire surface, which allows us to infer a firm union between these osteoderms and little lateral mobility. On the other hand, *P. parvum* would present an exoskeleton with a high degree of lateral mobility between osteoderms (Herrera *et al.*, 2019).

The identification of this new species assigned to ?*Utaetus* (?*U. magnum* sp. nov.) represents the oldest record of Euphractinae in NWA. In Patagonia and southern Brazil, the oldest records of *Utaetus* also come from the middle Eocene (Barrancan SALMA). Sedor *et al.* (2017) recognize, in addition to *Utaetus*, the cingulates *Proeocoleophorus*, *Machlyotherium*, *Astegotheriini* indet., *Euphractinae* indet., *Meteutatus*, and *Parutaetus* and points out that the fauna from Guabirota Formation (Southern Brazil), shares taxa with those of Patagonia (high-latitudes) and NWA (intermediate-latitudes). However, with the latter it only shares the genus *Parutaetus*, since *Punatherium*, *Pucatherium*, *Lumbretherium*, and *Noatherium* represent an exclusive set of endemic cingulates for NWA. The recognition of this new species, an exclusive cingulate from the Upper Lumbreira Formation, strengthens the endemic character of the Paleogene faunas of NWA. This region was interpreted as an important Eocene diversification center for a variety of endemic South American lineages (Reguero *et al.*, 2008). In the case of Cingulata, *Pucatherium parvum* and *Lumbretherium oblitum*, a basal monophyletic clade, constitute a clearly different lineage from all other armadillos, and are peculiarly characterized by size, general morphology, and articulation of osteoderms (Herrera *et al.*, 2016). Besides xenarthrans, NWA served as an area of origin of intertropical clades of notoungulates, which have striking taxonomical differences compared to those originating in the Paleogene of southern SA, and Patagonia in particular (Reguero *et al.*, 2008; García-López & Powell, 2011; Powell *et al.*, 2011). Therefore, this pattern of archaic endemism evidenced in cingulates is supported by notoungulates and also observed among crocodiles, with the presence of unique forms of sebecids that contribute to the singular fauna found in this region (Bravo, 2019).

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REFERENCES

- Ameghino, F. 1902. Notices préliminaires sur des mammifères nouveaux des terrains crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias en Córdoba*, 17:5–70.
- Babot, M.J.; García-López, D.A.; Deraco, V.; Herrera, C.M. & del Papa, C. 2017. Mamíferos paleógenos del subtropical de Argentina: síntesis de estudios estratigráficos, cronológicos y taxonómicos. In: C.M. Muruaga & P. Gross (eds.) *Ciencias de la Tierra y Recursos Naturales del NOA*, Relatorio del XX Congreso Geológico Argentino, p. 730–753.
- Babot, M.J.; García-López, D.A. & Gaudin, T.J. 2012. The most ancient xenarthran petrosal: morphology and evolutionary significance. *Journal of Vertebrate Paleontology*, 32:1186–1197. doi:10.1080/02724634.2012.686466
- Bergqvist, L.P.; Abrantes, É.A.L. & Ávila, L.S. 2004. The Xenarthra (Mammalia) of São José de Itaboraí Basin (upper Paleocene, Itaboraian), Rio de Janeiro, Brazil. *Geodiversitas*, 26:323–337.
- Bravo, G.G. 2019. *Estudio morfológico y sistemático de un registro de Sebecidae (Mesoeucrocodylia, Sebecosuchia) para la Formación Mealla (Paleógeno), provincia de Jujuy, Argentina*. Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, B. S. Thesis, 84 p.
- Carlini, A.A.; Ciancio, M.R.; Flynn, J.J.; Scillato-Yané, G.J. & Wyss, A.R. 2009. The phylogenetic and biostratigraphic significance of new armadillos (Mammalia, Xenarthra, Dasypodidae, Euphractinae) from the Tinguirirican (Early Oligocene) of Chile. *Journal Systematic Palaeontology*, 7:489–503. doi:10.1017/S1477201908002708.
- Carlini, A.A.; Ciancio, M.R. & Scillato-Yané, G.J. 2010. Middle Eocene–Early Miocene Dasypodidae (Xenarthra) of southern South America: faunal succession at Gran Barranca—biostratigraphy and paleoecology. In: R.H. Madden; A.A. Carlini; M.G. Vucetich & R.F. Kay (eds.) *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*, Cambridge University Press, p. 106–129.
- Castro, M.C. 2015. Sistemática y evolución de los armadillos Dasypodini (Xenarthra, Cingulata, Dasypodidae). *Revista del Museo de La Plata*, 15:1–50.
- Ciancio, M.R. 2016. Los armadillos (Dasypodidae, Xenarthra) del Cenozoico temprano-medio de Argentina: aspectos evolutivos, bioestratigráficos y biogeográficos. *Contribución del Museo Argentino de Ciencias Naturales*, 6:231–247.
- Ciancio, M.R. & Carlini, A.A. 2008. Identificación de ejemplares tipo de Dasypodidae (Mammalia, Xenarthra) del Paleógeno de Argentina. *Revista del Museo Argentino de Ciencias Naturales*, 10:221–237.
- Ciancio, M.R.; Carlini, A.A.; Campbell, K.E. & Scillato-Yané, G.J. 2013. New Palaeogene cingulates (Mammalia, Xenarthra)

- from Santa Rosa, Perú and their importance in the context of South American faunas. *Journal Systematic Palaeontology*, **11**:727–741. doi:10.1080/14772019.2012.704949.
- Ciancio, M.R.; Herrera, C.M.; Aramayo, A.; Payrola, P. & Babot, M.J. 2016. Diversity of cingulates (Mammalia, Xenarthra) in the middle-late Eocene of Northwestern Argentina. *Acta Paleontologica Polonica*, **61**:575–590. doi:10.4202/app.00208.2015
- Ciancio M.R.; Krmpotic, C.M.; Scarano, A.C. & Epele, M.B. 2019. Internal morphology of osteoderms of extinct armadillos and its relationship with environmental conditions. *Journal Mammalian Evolution*, **26**:71–83. doi:10.1007/s10914-017-9404-y
- Cione A.L.; Gasparini, G.M.; Soibelzon, E.; Soibelzon, L.H. & Tonni, E.P. 2015. *The Great American Biotic Interchange. A South American Perspective*. New York, London, Springer, 106 p.
- del Papa, C.E. 2006. Estratigrafía y paleoambientes de la Formación Lumbreira, Grupo Salta, Noroeste Argentino. *Revista de la Asociación Geológica Argentina*, **61**:313–327.
- del Papa, C.; Aramayo, A.; Payrola Bosio, P.; Hongn, F.; Montero López, C.; Do Campo, M.; Deraco, V.; Herrera, C.; Petrinovic, I. & Lapiana, A. 2017. La cuenca de antepaís Eocena-Oligocena en el NOA: primeros indicios de deformación intra-cuenca. In: C.M. Muruaga & P. Grosse (eds.) *Ciencias de la tierra y recursos naturales del NOA*, Relatorio del XX Congreso Geológico Argentino, Asociación Geológica Argentina, p. 237–253.
- del Papa, C.E.; Kirschbaum, A.; Powell, J.E.; Brod, A.; Hongn, F. & Pimentel, M. 2010. Sedimentological, geochemical and paleontological insights applied to continental omission surfaces: a new approach for reconstructing an Eocene foreland basin in NW Argentina. *Journal of South American Earth Sciences*, **29**:327–345. doi:10.1016/j.jsames.2009.06.004
- Fernicola, J.C.; Zimicz, A.N.; Chornogubsky, L.; Cruz, L.E.; Bond, M.; Arnal, M.; Cárdenas, M. & Fernández, M. 2021. New assemblage of cingulates from the Quebrada de Los Colorados Formation (middle Eocene) at Los Cardones National Park (Salta Province, Argentina) and the Casamayoran SALMA problem at Northwestern Argentina. *Journal of South American Earth Sciences*, **111**:103476. doi:10.1016/j.jsames.2021.103476
- García-López, D.A. & Powell, J.E. 2011. *Griphotherion peiranoi*, gen. et sp. nov., a new Eocene Notoungulata (Mammalia, Meridiungulata) from northwestern Argentina. *Journal of Vertebrate Paleontology*, **31**:1117–1130. doi:10.1080/02724634.2011.599464
- Gelfo J.N.; Goin, F.J.; Woodburne, M.O. & Muizon, C. 2009. Biochronological relationships of the earliest South American Paleogene mammalian faunas. *Palaeontology*, **52**:251–269. doi:10.1111/j.1475-4983.2008.00835.x
- Herrera C.M.; del Papa C.E. & Hongn, F. 2010. Nuevos registros de dasipódidos eocenos para la Formación Quebrada de Los Colorados en el tramo central del Valle Calchaquí (Salta, Argentina). In: CONGRESO ARGENTINO DE PALEONTOLOGÍA Y BIOESTRATIGRAFÍA, X, CONGRESO LATINOAMERICANO DE PALEONTOLOGÍA, 7, 2010. *Libro de resúmenes*, Buenos Aires, p. 63.
- Herrera, C.M.R.; Esteban, G.I.; Ciancio, M.C. & del Papa, C. 2019. New specimen of *Pucatherium parvum* (Xenarthra, Dasypodidae), a singular dasypodid of the Paleogene (Eocene) of Northwest Argentina. Importance in the early evolution of armadillos. *Journal of Vertebrate Paleontology*, **39**:4. doi:10.1080/02724634.2019.1670669.
- Herrera, C.M. & Powell, J.E. 2009. Primer registro de astegoterinos (Dasypodidae, Cingulata) de la Formación Quebrada de los Colorados (Grupo Payogastilla) en la Provincia de Salta. *Ameghiniana*, **46**:18.
- Herrera, C.M.; Powell, J.E. & del Papa, C. 2012. Un nuevo Dasypodidae (Mammalia, Xenarthra) de la Formación Casa Grande (eoceno) de la provincia de Jujuy, Argentina. *Ameghiniana*, **49**:267–271. doi:10.5710/AMGH.v49i2(502)
- Herrera, C.M.R.; Powell, J.E.; Esteban, G.I. & del Papa, C. 2016. A new Eocene dasypodid with caniniforms (Mammalia, Xenarthra, Cingulata) from Northwest Argentina. *Journal Mammalian Evolution*, **24**:275–288. doi:10.1007/s10914-016-9345-x
- Lapiana, A.T.; del Papa, C. & Gaiero, D. 2016. Los depósitos limolíticos eocenos de la Formación Lumbreira superior (Salta, Argentina): discusión sobre el posible origen eólico. *Latin American Journal of Sedimentology and Basin Analysis*, **3**:743–758.
- Oliveira, E.V. & Bergqvist, L. 1998. A new Paleocene armadillo (Mammalia, Dasypodoidea) from the Itaboraí basin, Brazil. *Asociación Paleontológica Argentina*, **5**:35–40.
- Patterson, B. & Pascual, R. 1968. Evolution of mammals on southern continents. *Quarterly Review of Biology*, **43**:409–451.
- Powell, J.E.; Babot, M.J.; García-López, D.A.; Deraco, M.V. & Herrera, C. 2011. Eocene vertebrates of northwestern Argentina: annotated list. In: J.A. Salfity & R.A. Marquillas (eds.) *Cenozoic Geology of the Central Andes of Argentina*, SCS Publisher, p. 349–370.
- Reguero, M.A.; Croft, D.A.; Lopez, G.M. & Alonso, R.N. 2008. Eocene archaeohyracids (Mammalia: Notoungulata: Hegetotheria) from the Puna, Northwest Argentina. *Journal of South American Earth Sciences*, **26**:225–233. doi:10.1016/j.jsames.2008.05.004
- Sedor, F.; Oliveira, E.V.; Silva, D.D.; Fernandes, L.A.; Cunha, R.F.; Ribeiro, A.M. & Dias, E.V. 2017. A new South American Paleogene Land Mammal Fauna, Guabirotuba Formation (Southern Brazil). *Journal of Mammalian Evolution*, **24**:39–55. doi:10.1007/s10914-016-9364-7
- Simpson, G.G. 1948. The beginning of the age of mammals in South America. Part I Introduction. Edentata, Condylarthra, Liptoterna, and Notioprogonia. *Bulletin of the American Museum of Natural History*, **91**:1–232.
- Soibelzon, E.; Avilla, L.S. & Castro, M. 2015. The cingulates (Mammalia: Xenarthra) from the late Quaternary of northern Brazil: fossil records, paleoclimates and displacements in America. *Quaternary International*, **377**:118–125. doi:10.1016/j.quaint.2015.02.052
- Tejedor, M.F.; Goin, F.J.; Gelfo, J.N.; López, G.M.; Bond, M.; Carlini, A.A.; Scillato-Yané, G.J.; Woodburne, M.O.; Chornogubsky, L.; Aragón, E.; Reguero, M.A.; Czaplewski, N.J.; Vincon, S.; Martin, G.M. & Ciancio, M. 2009. New early Eocene mammalian fauna from Western Patagonia, Argentina. *American Museum Novitates*, **3638**:1–43.
- Vizcaíno, S.F. 1994. Sistemática y Anatomía de los Astegotheriini Ameghino, 1906 (Nuevo Rango) (Xenarthra, Dasypodidae, Dasypodinae). *Ameghiniana*, **31**:3–13.
- Woodburne, M.O.; Goin, F.J.; Raigemborn, M.S.; Heizler, M.; Gelfo, J.N. & Oliveira, E.V. 2014. Revised timing of the South American early Paleogene land mammal ages. *Journal of South American Earth Sciences*, **54**:109–119. doi:10.1016/j.jsames.2014.05.003Get