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A New Eocene Dasypodid with Caniniforms (Mammalia, Xenarthra, Cingulata) from Northwest Argentina

Claudia M. R. Herrera^{1,2} · Jaime E. Powell · Graciela I. Esteban¹ · Cecilia del Papa^{2,3}

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Abstract The aim of this work is to present a new genus and species of Dasypodidae from the Lumbreira Formation (“lower Lumbreira”), early-middle Eocene of Salta Province, northwest Argentina. The new taxon, documented by one specimen, consists of an incomplete skull and jaw with teeth housed in their alveoli, postcranial remains, and isolated osteoderms. *Lumbreratherium oblitum*, gen. et sp. nov., is characterized by heterodont dentition, with a caniniform as the first tooth, diastema between caniniform and first molariform, teeth with closed roots, and a peculiar morphology of the osteoderms. A phylogenetic analysis indicates that *Lumbreratherium oblitum*, gen. et sp. nov., and *Pucatherium parvum* belong to a monophyletic clade in a basal position within the Cingulata. The singularity of the morphological characteristics of these Paleogene armadillos of northwest Argentina reinforces the hypothesis of an intertropical origin

of mammal clades different from those of the Paleogene in more austral regions of Argentina.

Keywords New Dasypodidae · Early-middle Eocene · Lumbreira Formation · Northwest Argentina

Introduction

Xenarthra is a very peculiar group of the Neotropical fauna, with a long and successful evolutionary history during the Cenozoic in South America. The group is represented from the late Paleocene or early Eocene up to the present (Scillato-Yané 1976; Oliveira and Bergqvist 1998; Bergqvist et al. 2004; Gelfo et al. 2009). The early divergence of Xenarthra within placentals could have occurred during the Early Cretaceous (Delsuc et al. 2001, 2004; Kemp 2005; Rose and Archibald 2005; Meredith et al. 2011; dos Reis et al. 2012), although paleontological evidence does not support this hypothesis.

The armadillos represent the most diverse assemblage within the Xenarthra, with 13 genera and 31 species (Gaudin and Wible 2006; Delsuc and Douzery 2008). The group includes armored forms (Cingulata) and sloths and anteaters (Pilosa). Five families are recognized in Cingulata: Dasypodidae, Peltephilidae, Glyptodontidae, Pampatheriidae, and Palaeopeltidae (Carlini et al. 2008; Góis et al. 2013). Several morphological features support the monophyly of Cingulata (Gaudin and Wible 2006), but the relationships between these families are far from being resolved.

The oldest record of Cingulata is represented by dasypodid remains from the Itaboraian SALMA, late Paleocene (Cifelli 1983; Oliveira and Bergqvist 1998; Bergqvist et al. 2004) or early Eocene (Gelfo et al. 2009; Woodburne et al. 2014) of Brazil. One important feature of Dasypodidae is the presence of a dorsal armor integrated by independent but articulated

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osteoderms, which are frequently found and have a high diagnostic value (Scillato-Yané 1982; Krmpotic et al. 2009; Fernicola and Vizcaíno 2008).

Paleogene dasypodids from Patagonia, Bolivia, Peru, Brazil, and Chile have been the focus of several studies including osteology, systematics, and phylogenetics, and have also been employed in paleoenvironmental and stratigraphical studies (Cifelli 1985; Scillato-Yané 1986; Vizcaíno 1994; Oliveira and Bergqvist 1998; Bergqvist et al. 2004; Gaudin and Wible 2006; Croft et al. 2007; Ciancio and Carlini 2008; Carlini et al. 2009, 2010, 2013; Billet et al. 2011; Ciancio et al. 2012, 2013; Castro et al. 2013). However, dasypodid fossil records for the Paleogene of northwest Argentina are relatively scarce and mostly consist of isolated osteoderms (Pascual and Vucetich 1981; Alonso et al. 1988; López 1997). In the last decade, important evidence was obtained from findings in the Lumbrera (Salta Group), Casa Grande, Quebrada de los Colorados (Payogastilla Group), and Geste formations (Pastos Grandes Group) (Herrera and Powell 2007, 2009, 2013; Herrera et al. 2010, 2012; Herrera 2013). The dasypodids collected in these formations have increased our knowledge about northwest Argentina Paleogene faunistic associations (Powell et al. 2011; Ciancio et al. *in press*). Recently, a peculiar dasypodid *Pucatherium parvum* was described, based on associated osteoderms (Herrera et al. 2012).

The aim of this work is to present a new genus and species of Dasypodidae from the early-middle Eocene of northwest Argentina found in 1977. The fossil remains, which come from the Lumbrera Formation (“lower Lumbrera”) in Salta Province, are represented by an incomplete skull, jaw with teeth, postcranial remains, and isolated osteoderms. This finding is significant, because it has preserved the first known cranium for a dasypodid of this age. In addition, we perform a phylogenetic analysis to determine the relationships of this new taxon.

Materials and Methods

The specimen studied, PVL 4262, includes the left side of a partial skull, an almost complete jaw from which only the anterior region of the symphysis is missing, the upper and lower teeth in their alveoli, and postcranial remains. The last includes the atlas and axis, six lumbar and one caudal vertebrae, ribs, the sternum, the proximal region of the ulna, tibia, and fibula, one metacarpal, and three ungual phalanges. Isolated movable osteoderms have also been preserved.

The terminology used for skull descriptions follows the *Nomina Anatomica Veterinaria* (2005) and Wible and Gaudin (2004). The abbreviation for the molariform upper teeth is Mf. In order to describe the osteoderms, we followed Hill (2006), Krmpotic et al. (2009), and Herrera et al. (2012). For the descriptions of the step-like structure in the lateral side

of the movable osteoderms, we name the horizontal surface as “tread” and the vertical surface as “rise.”

A phylogenetic analysis of 23 taxa and 144 characters was performed for identifying phylogenetic relationships between the new fossil armadillo from the Lumbrera Formation and *Pucatherium parvum*, and their associations within the Dasypodidae. The ingroup is represented by 18 dasypodid genera (fossil and extant), one peltephilid, one pampatheriid, and one glyptodont, whereas the outgroup is integrated by the Folivora *Bradypus* and *Paramylodon*, following Gaudin and Wible (2006), Gaudin and Bramblett (2010), and Ciancio (2010) (Appendix 1). Twenty-one characters of the carapace and the osteoderm external morphology, and 123 craniodental characters were selected. Characters were selected from Carlini and Scillato-Yané (1996), Gaudin and Wible (2006), Abrantes and Bergqvist (2006), and Billet et al. (2011), although some of them were modified as indicated in the character list. In addition, we present 16 new characters (Appendix 2).

Characters that could not be directly observed were scored from descriptions and illustrations by Scott (1903–5), Stock (1925), Castellano (1958), Patterson et al. (1989), and Vizcaíno and Bargo (1998) (Appendix 1). The data matrix (Appendix 3) was analyzed with TNT 1.1 (Goloboff et al. 2008); heuristic searches were performed under the maximum parsimony criterium, followed by branch swapping through tree bisection reconnection. Fifteen characters were treated as additive. Support indices were calculated with the same program using Bremer supports.

Institutional Abbreviations – AMNH, American Museum of Natural History, New York, U.S.A.; CML, Colección de Mastozoología Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; FMNH, Field Museum of Natural History, Chicago, U.S.A.; LACM, Natural History Museum of Los Angeles County, Los Angeles, U.S.A.; MANC, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; MCL, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MPL, Museo de La Plata, Buenos Aires, Argentina; PVL, Paleontología Vertebrados Lillo, Tucumán, Argentina; YPM-PU, Princeton University collection housed at the Yale Peabody Museum, Yale University, New Haven, U.S.A.

Geology

The fossil material was collected in 1977 by Dr. José Bonaparte and his team in Pampa Grande locality (Salta Province). It was recovered in the lower deposits of the Lumbrera Formation, identified as “lower Lumbrera” (del Papa 2006), exposed in the Eastern Cordillera of northwest Argentina (Fig. 1).

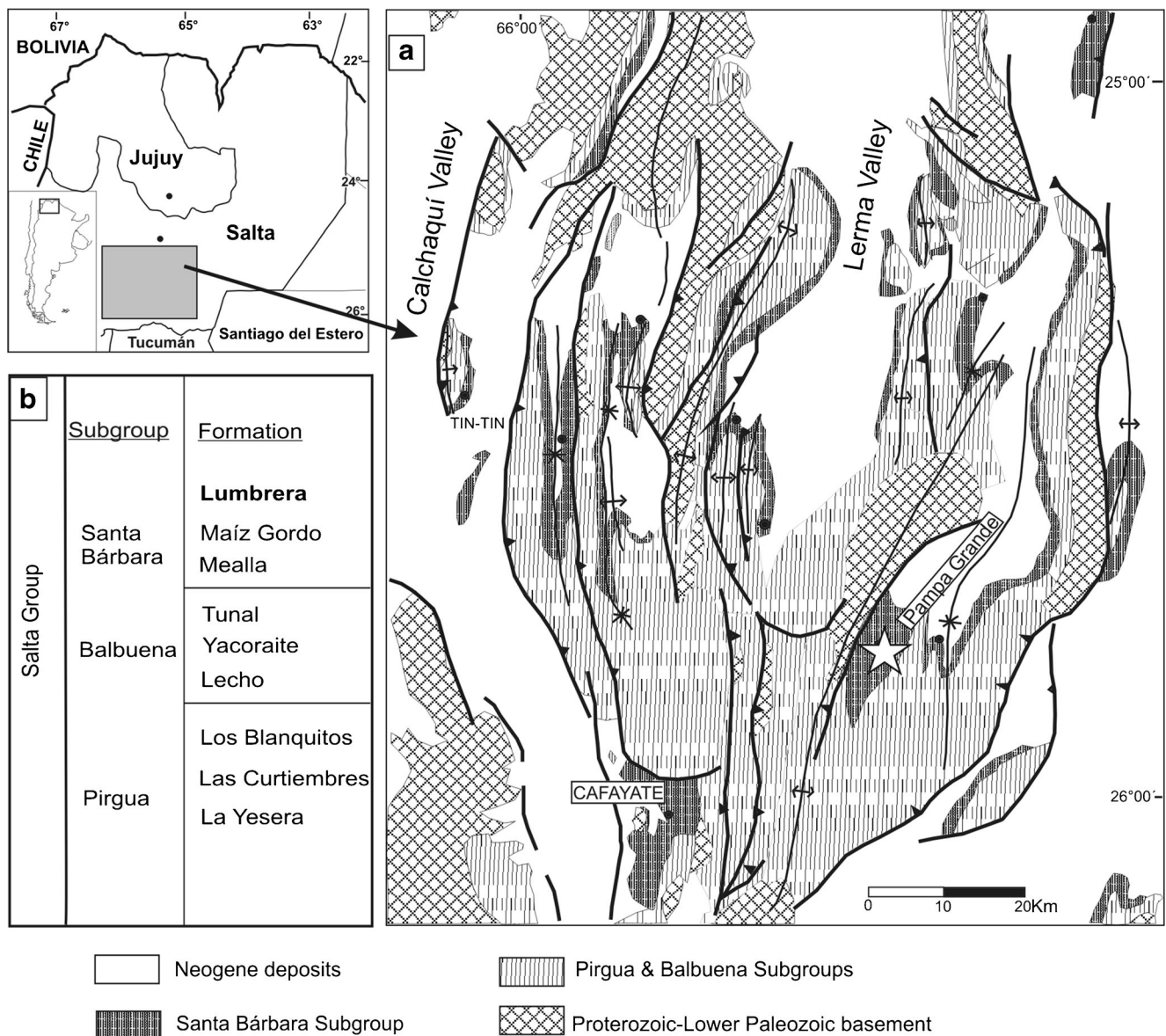


Fig. 1 Geological map. **a** geographic location of fossil sites in the central portion of the Valles Calchaquíes region and adjacent areas; **b** stratigraphic scheme showing ubication of the Lumbraera Formation in the Salta Group

In Pampa Grande region, the lower Lumbraera Formation has a mean thickness of 150 m and overlies the Maíz Gordo Formation towards the upper Lumbraera through a discontinuity - an omission surface (del Papa et al. 2010). The sedimentary facies are i) metric scale beds of lenticular conglomeratic sandstones to medium-grained sandstones with sharp bases and lateral accretion surfaces, internally trough cross-stratification, climbing ripple structures; ii) heterolithic facies composed of very fine-grained sandstones and red siltstones forming lobulated or tabular bodies; iii) tabular medium- to fine-grained bioturbated sandstones; and iv) sheet-like red mudstone massive, or with paleosols features. The overall sedimentary facies association suggests a fluvial

paleoenvironment of meandering type. Meandering systems imply the development of a main, migrating channel with the formation of levee, and fine-grained or cohesive lateral floodplains with vegetation (del Papa 2006). This fluvial system drained to a perennial freshwater lake-Faja Verde lake-characterized by clastic sedimentation and organic-rich facies (del Papa and Quattrocchio 2002). This scenario indicates extensive flat and low areas intensely vegetated, associated with stable water body with free water circulation developed under temperate climatic conditions. Based on the fossil records of mammals and palynomorphs, an early-middle Eocene Age (Casamayoran SALMA – Vacan Subage) is interpreted (Powell et al. 2011).

Systematic Paleontology

Superorder XENARTHRA Cope, 1889
 Order CINGULATA Illiger, 1811
 Superfamily DASYPODOIDEA Gray, 1821
 Family DASYPODIDAE Gray, 1821
 Dasypodidae incerte sedis

Lumbreratherium, gen. nov.

Type Species *Lumbreratherium oblitum*, sp. nov.

Diagnosis As for the single included species described below

Etymology Lumbrera from the Lumbrera Formation, where the specimen was recovered, + ‘*therium*’ from the greek *therion*, ‘beast’, a common generic suffix for mammalian taxa

Lumbreratherium oblitum, gen. et sp. nov.

Holotype PVL 4262. An incomplete skull that preserves part of the left side, including the maxilla, lacrimal, jugal, part of the squamosal, the basicranium, both almost complete hemimandibles, upper and lower caniniforms and molariforms. The postcranial elements include atlas and axis, six lumbar and a caudal vertebrae, some ribs, a fragment of sternum, proximal end of ulna, proximal end of tibia-fibula, a metacarpal, three ungual phalanges, and several movable osteoderms.

Etymology *oblitum* from the latin ‘*oblitum*’ forgotten.

Distribution Early to middle Eocene, Casamayoran SALMA, Vacan subage, Lumbrera Formation (“lower Lumbrera”), Pampa Grande, Guachipas department, Salta Province, Argentina.

Diagnosis Osteoderms larger than those of *Pucatherium parvum*, but smaller than those of *Utaetus*, *Peltephilus*, and *Stegotherium*. External surface of the osteoderms less rough than in *P. parvum*. Anterior articular region with two or three poorly marked longitudinal elevations, separated by wide and shallow grooves, unlike *P. parvum*, which exhibits well-developed elevations and grooves and unlike the rest of the dasypodids, which present a flat articular region. Lateral surfaces with one step-like structure similar to *P. parvum*, but closer to the dorsal edge. Subrectangular main figure with rounded corners that do not reach the posterior edge of the osteoderm. Five peripheral figures, three anterior and two lateral. Well-defined grooves demarcating the main figure, with three pairs of foramina symmetrically arranged. In *P. parvum* the main figure reaches the posterior edge of the osteoderm, and is demarcated by weakly developed grooves with five to seven small perforations, and no peripheral anterior figures are

found. Posterior third of the inner surface of the osteoderms with two elevations close to the lateral margins, separated by a wide groove. In *P. parvum*, on the other hand, the inner surface of the osteoderms exhibits three to four short longitudinal elevations and grooves. Piliferous foramina only on the posterior edge, while in *P. parvum* they can be found on the posterior and lateral edges. Teeth in *L. oblitum* are protohypsodont (as in *Astegotherium*), first pair of teeth is caniniform; large diastema between caniniform and first molariform, unlike other dasypodids; one very large mental foramen; paroccipital process of the petrosal is freestanding, rounded, and rugose; straight and thin jugal.

Description

Osteoderms (Figs. 2, 3, 4)

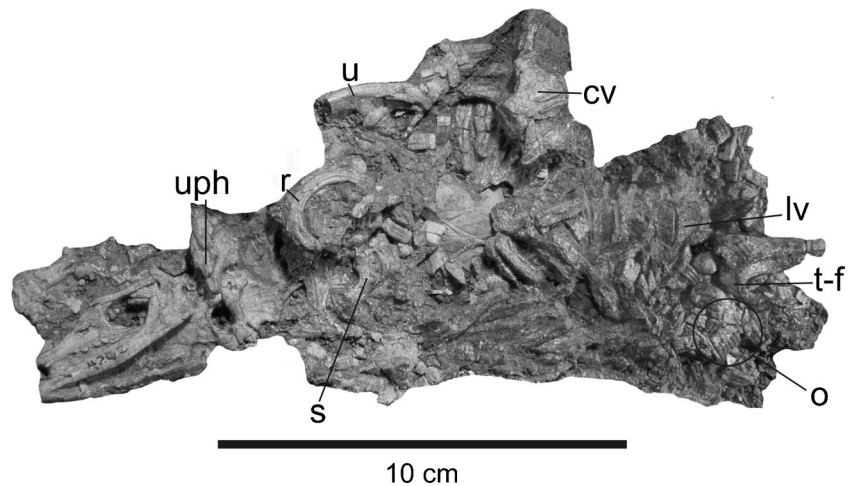
All the preserved osteoderms are movable. They are sub-quadrangular or sub-rectangular and small, but larger than those of *P. parvum*. In *L. oblitum* they vary from 6.14 to 8.20 mm length, 2.90 to 4.05 mm in width and 1.70 to 1.92 mm thick, while in *P. parvum* they vary from 3.43 to 5.17 mm in length, 2.75 to 3.75 mm in width and 1.09 to 1.89 mm thick. The anterior and posterior margins are almost straight. The exposed surface is less rugose than that of *P. parvum* and *Astegotherium*.

The outline of the lateral faces of the osteoderms is rhomboidal as found in *Stegotherium pascuali*. The lateral surfaces of the osteoderms of *L. oblitum* exhibit a step-like structure (“sls”) only along the exposed surface (it does not reach the anterior articular region: “aar”) (Figs. 3e, 4e); in contrast, in *P. parvum* this structure extends all along the lateral surface of the osteoderm (Figs. 3e, 4e). In *L. oblitum* the “tread” and “riser” are narrower and lower, respectively, than in *P. parvum* (Fig. 4c-f). The contact between adjacent osteoderms occurs on a flat surface below the step (Fig. 4c, e).

In *L. oblitum* and *P. parvum*, the external surface of the anterior articular region (“aar”) presents two or three longitudinal elevations separated by grooves. In *L. oblitum* these elevations and grooves are less marked than in *P. parvum* (Fig. 3a–e). In the rest of the dasypodids, the anterior articular region is flat (Fig. 4a). There is no transitional zone, as in *P. parvum*. On the external surface of the exposed region, the main figure is subrectangular with rounded corners and does not reach the posterior margin of the osteoderm. In *P. parvum*, this figure is similar but contacts the posterior edge. In *L. oblitum*, there are five peripheral figures, three anterior and two lateral. The former are small, sub-circular, convex, and delimited by well-defined grooves (Fig. 3a, b). The lateral figures are larger and elongated, accompanying the entire length of the main figure. In *P. parvum*, there are no anterior figures (Fig. 3e). In *L. oblitum*, there are three pairs of symmetrically arranged

Fig. 2 General view of *Lumbreratherium oblitum*, gen. et sp. nov. (PVL 4262).

Abbreviations: cv: caudal vertebra; lv: lumbar vertebrae; o: osteoderms; r: ribs; s: sternum; t-f: tibia-fibula; u: ulna; uph: ungual phalanges



foramina, located in the grooves delimiting the main figure, while in *P. parvum* they vary from three to five pairs. In *L. oblitum*, there are few piliferous foramina on the posterior edges, while in *P. parvum* these are located on the posterior and lateral edges of the osteoderms.

In *L. oblitum*, two elevations on the posterior third of the internal surface of the osteoderms can be found, situated close to the lateral margins. These are separated by a wide and shallow groove. In some osteoderms, a third shorter prominence

developed in this groove is found (Fig. 3c, d). Three to four short and well-marked elevations separated by deep grooves are present in *P. parvum* (Fig. 3f). The other dasypodids do not present such structures on the internal surface.

Skull (Fig. 5)

The premaxillary is not preserved. The facial surface of the maxilla is smooth. The maxillo-lacrimal and maxillo-jugal

Fig. 3 Movable osteoderms. **a–d**, *Lumbreratherium oblitum*, gen. et sp. nov. (PVL 4262); **e–f**, *Pucatherium parvum* (PVL 6398).

a osteoderm in external view with two elevations on articular surface; **b** osteoderm in external view with three elevations on articular surface; **c** osteoderm in internal view with two elevation in distal surface; **d** osteoderm in internal view with three elevation in the distal surface; **e** osteoderm in external view with three elevations on articular surface; **f** osteoderm in internal view with elevation in distal surface. Abbreviations: aar: anterior articular region; apf: anterior peripheral figure; ce: central elevation; cf: central figure; e: elevation; g: groove; le: lateral elevation; lpf: lateral peripheral figure; sls: step-like structure

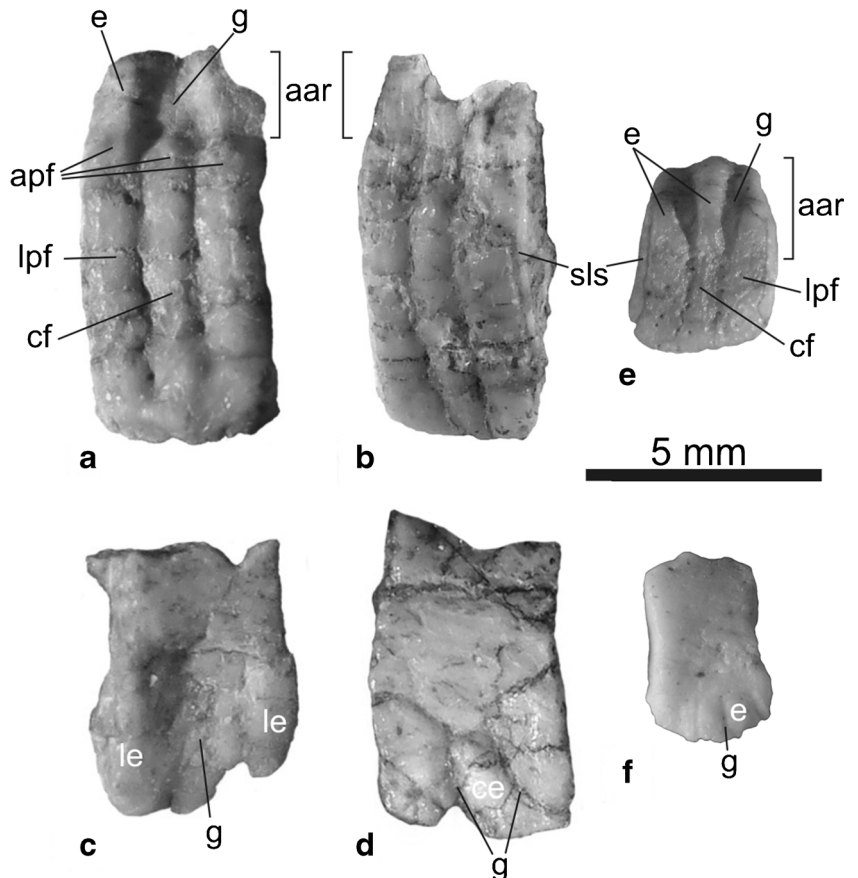
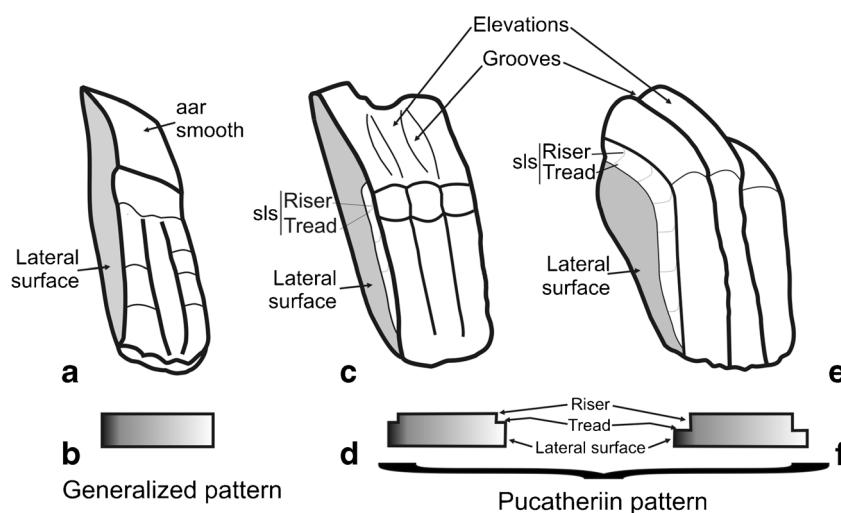


Fig. 4 Schematic representation of movable osteoderms. **a–b** *Prozaedyus* sp. (PVL 426); **c–d** *Lumbreratherium oblitum*, gen. et sp. nov. (PVL 4262); **e–f** *Pucatherium parvum* (PVL 6398). Hatched areas indicate articular lateral surface; **b** generalized pattern; **d–f** pucatheriin pattern



sutures are slightly concave, the latter directed obliquely towards the ventral edge of the jugal process, as in *Tolypeutes* (Fig. 5a).

The maxillary crest is less marked than in *Dasyopus*, *Euphractus*, and *Tolypeutes*. It begins at the level of the second molariform and projects towards the base of the zygomatic process of the maxilla, contacting the ventral margin of the lacrimal suture (Fig. 5a). In *Dasyopus*, *Euphractus*, *Chaetophractus*, and *Macroephractus*, the ridge continues in a well-defined lacrimal crest.

The infraorbital foramen opens at the level of the anterior margin of the fourth molariform as in *Cabassous*, and in contrast to *Dasyopus*, *Euphractus*, *Chaetophractus*, and *Macroephractus*, in which it opens at the level of the anterior margin of the sixth molariform. A shallow groove is observed anterior to the infraorbital foramen. The maxillary foramen opens in the orbital cavity as in *Euphractus*, *Chaetophractus*, and *Macroephractus*, contrasting with *D. yepesi*, *Cabassous*, and *Priodontes*, in which it opens below the ventral margin of the anterior root of the zygomatic arch (Billet et al. 2011). A small, slightly marked concavity for the origin of the masseter muscle is situated on the zygomatic process of the maxilla, ventral to the maxillo-jugal suture.

A small, wedge-shaped fragment of the nasal and of the ventral region of the lacrimal (with no evidence of the lacrimal foramen) has been preserved (Fig. 5a). The lacrimal portion situated below the maxillary crest is smaller than in *Dasyopus*, *Chaetophractus*, *Euphractus*, *Macroephractus*, and *Zaedyus*.

The body of the jugal is thin, cylindrical, and almost straight, unlike that of *Dasyopus*, *Zaedyus*, *Euphractus*, *Macroephractus*, and *Chaetophractus*, in which this bone expands ventrally and bows to form the ventral margin of the orbit (Fig. 5a). The medial portion of the maxillo-palatine suture is observed on the palatal surface of the maxilla. It is straight and runs from a point situated between Mf^3 and Mf^4 obliquely backward up to the axial plane of the palate. In *Chaetophractus*, *Euphractus*, *Macroephractus*, and

Zaedyus, the medial portion of the maxillo-palatine suture is straight and perpendicular to the axis of the palate, situated at the level of Mf^6 . In *D. novemcinctus* and *D. hybridus*, this suture is straight, but is located behind the posterior edge of the last molariform and perpendicular to the axis of the palate, while in *D. yepesi* the suture is placed behind the last molariform, but oriented forward up to the axial plane.

The basioccipital is nearly flat and very wide (twice the maximum width of the occipital condyle) (Fig. 5a), as in *Peltephilus*, while in *Dasyopus*, *Tolypeutes*, and *Chaetophractus* the basioccipital is narrow, less than one and a half times the maximum width of the condyle. There is a prominent crest along the axial plane, which originates at the level of the anterior margin of the petrosal and posteriorly becomes wider and more prominent, as in *Zaedyus* and *Chaetophractus*. In *Dasyopus*, this crest is prominent in the anterior region and less marked posteriorly. In *Tolypeutes*, *Cabassous*, *Euphractus*, and *Priodontes*, the crest is absent. In *L. oblitum*, two oval protuberances can be found on the basioccipital, near the axial plane, surrounded by a semicircular depression located in the medial margin. In *Dasyopus* and *Cabassous*, these are not as prominent and the semicircular depression is posterior and lateroposterior, respectively. *Chaetophractus* and *Zaedyus* exhibit two oval depressions that occupy the entire basioccipital. These structures serve as attachments of the m. longus capitis and m. rectus capitis ventralis (Wible and Gaudin 2004). The anterior margin of the foramen magnum exhibits a widely open U shape as in *Macroephractus*, whereas it is V-shaped in *Dasyopus*, *Tolypeutes*, *Zaedyus*, and *Euphractus*.

The odontoid notch of *L. oblitum*, located on the ventral margin of the foramen magnum, is similar to that of *Cabassous*, and more developed than in *Dasyopus*, *Chaetophractus*, and *Tolypeutes*. The anteroventral region of the articular surface of the occipital condyle is similar to that of *Euphractus* and *Cabassous*, and less convex than in *Dasyopus*, *Zaedyus*, *Chaetophractus*, and *Macroephractus*.

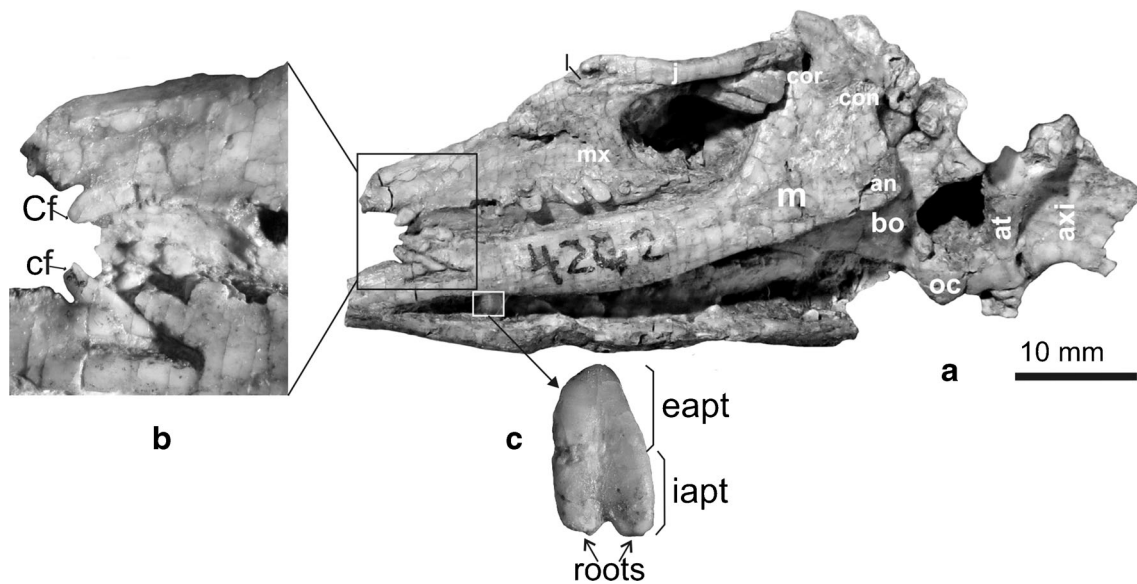


Fig. 5 Skull in lateroventral view of *Lumbretherium oblitum*, gen. et sp. nov. (PVL 4262). **a** photograph of skull; **b** labial view of upper and lower caniniforms; **c** protohypsodont molariform with two well-defined closed roots. Abbreviations: an: angular process; at: atlas; axi: axis; bo:

basioccipital; Cf: upper caniniform; cf: lower caniniform; cor: coronoid process; con: condylar process; eapt: extra-alveolar portions; iapt: intra-alveolar portions; j: jugal; l: lacrimal; m: mandible; mx: maxilla; oc: occipital condyle

No suture of the exoccipital with the basioccipital has been recognized in *L. oblitum*. The hypoglossal foramen is located anterodorsal to the occipital condyle, with the jugular foramen opening above that of the hypoglossal (Fig. 6a, b). The hypoglossal foramen is similar in size and position to those of *D. hybridus*, *D. novemcinctus*, and *D. yepesi*. The jugular foramen is larger in *Tolypeutes*, *Cabassous*, *Zaedyus*, *Macroeuphractus*, and *Priodontes*.

The paroccipital process of the petrosal (=mastoid process) is completely preserved, freestanding, rounded, well developed in the mediolateral plane, and characterized by a rough surface. It is located anterolateral to the occipital condyle and slightly posterior to the jugular foramen (Fig. 6a, b). This process is present in *Dasypus*, *Priodontes*, *Tolypeutes*, *Cabassous*, *Euphractus*, and *Chaetophractus*. In those taxa with bullae it is wider in the mediolateral plane, but appressed to the posterior surface of the ectotympanic/external auditory meatus. In those taxa without bullae it is wider in the anteroposterior plane, and freestanding. The postglenoid process is poorly developed.

No tympanic bulla is found, as in dasypodines and tolypeutines. The tympanic surface of the promontory is slightly globular. The cochlear fenestra is rounded and large. The stylomastoid foramen is rather oval and opens lateral to the petrosal (Fig. 6a, b).

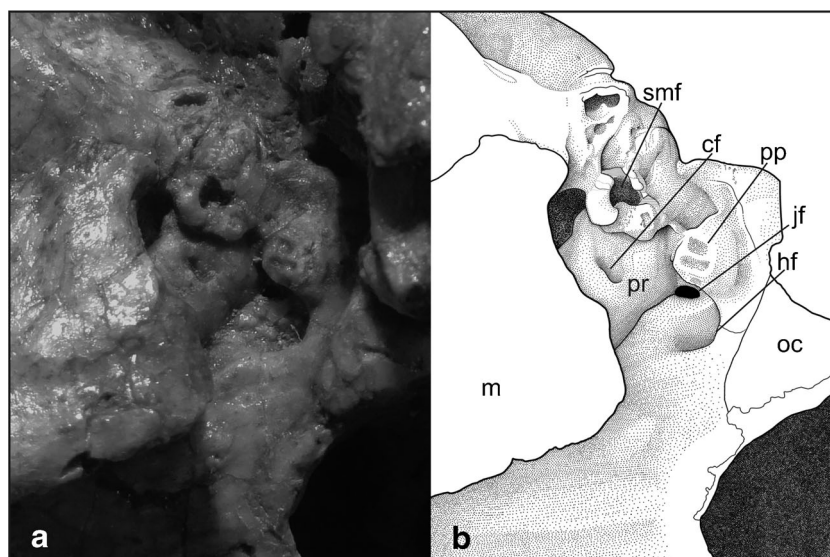
Jaw (Figs. 5, 7)

The jaw is more robust than in *Dasypus* and less robust than in *Utaetus*, *Zaedyus*, *Chaetophractus*, *Cabassous*, *Euphractus*, and *Tolypeutes* (Table 1). In *L. oblitum*, the ventral edge is

convex in the molariform region but straight in the anterior and posterior portions, while in *Utaetus*, *Tolypeutes*, and *Cabassous* it is more convex in the molariform region. In *Dasypus*, *Chaetophractus*, *Euphractus*, and *Priodontes* the ventral edge is convex in all its length. The edentulous region of the jaw ends behind the posterior edge of the symphysis as in *Dasypus* and *Priodontes*. In *Cabassous* and *Tolypeutes*, the symphysis ends in front of the first molariform (Fig. 5a). In *Utaetus*, *Euphractus*, *Zaedyus*, and *Chaetophractus*, on the other hand, the symphysis ends at the level of the second or third molariform. The jaw in *L. oblitum* exhibits a large mental foramen that occupies the space between the posterior edge of the symphysis and the first molariform (Figs. 5a, 7a, b). This condition is unique among dasypodids.

The anterior edge of the coronoid process elevates in a 56° angle until it reaches the level of the articular process, and approximately in a 71° angle from the latter process. The base of the coronoid process in *L. oblitum* is wide and the anterior and posterior edges are sub-parallel as in *Utaetus*, *Euphractus*, *Chaetophractus*, *Zaedyus*, and *Tolypeutes*. In *Dasypus*, *Priodontes*, and *Cabassous*, in contrast, the anterior and posterior edges converge on the dorsal end. The condylar process exhibits a short neck, as in *Utaetus*. *Dasypus*, *Priodontes*, *Zaedyus*, *Tolypeutes*, *Euphractus*, and *Chaetophractus*, while in *Cabassous*, it exhibits a long neck. In *L. oblitum*, the angular process is larger and more rounded, but less individualized than in *D. novemcinctus*, *D. hybridus*, and *D. yepesi*. This process is located below the alveolar level, whereas in *Utaetus*, *Tolypeutes*, *Euphractus*, *Chaetophractus*,

Fig. 6 Basicranial region in lateroventral view of *Lumberatherium oblitum*, gen. et sp. nov. (PVL 4262). **a** photograph; **b** schematic representation. Abbreviations: cf.: cochlear fenestra; hf: hypoglossal foramen; jf: jugular foramen; oc: occipital condyle; pp: paroccipital process of the petrosal; pr: promontorium of the petrosal; smf: stylomastoid foramen



Cabassous, and *Dasypus* is located above the alveolar line. The coronoid, condylar, and angular processes are essentially equidistant (Fig. 5a).

Teeth (Figs. 5, 7)

Six upper and lower teeth are recognized. In this work, the first upper and lower pair of teeth are named caniniforms (Figs. 5a, b; 7a, b). These are straight and conical with a blunt apex, an oval cross section, procumbent, and with a single closed root. The upper caniniform exhibits a slight labial orientation with a narrowing close to the level of the alveolus. The lower caniniform is located at the anterior edge of the mental foramen, in the same transverse plane as the upper caniniform, and the latter occludes in front of the lower. Behind the caniniforms, there is a long diastema equivalent to one-third of the molariform series length (Table 1). None of these features are present in any of the described dasypodids.

Molariforms are protohypsodont; their total height is greater than their width and length (Ciancio et al. 2014). They exhibit two well-defined closed roots. No neck develops between the extra- and intra-alveolar portions. Roots are short

(approximately one-sixth of the total height of the teeth) and separated by a wide notch (Fig. 5c).

In the upper left molariform series, only the alveolus of Mf^1 has been preserved. Mf^2 , Mf^3 , and Mf^4 are completely preserved while Mf^5 conserves only the intra-alveolar part. Teeth are separated from each other by a variable distance: the distance between Mf^1 and Mf^2 is equal to the anteroposterior length of Mf^2 , whereas the distance between Mf^2 and Mf^3 is equal to the anteroposterior length of Mf^3 . In the other teeth, this separation is small (Table 1; Figs. 5a, 7a, b).

Mf^2 , Mf^3 , and Mf^4 have approximately the same size, and exhibit an oval cross section and rounded edges. The labial surface is slightly convex and exhibits a medial basal groove that reaches half the extra-alveolar height of the tooth. Mf^5 is smaller and its cross section is sub-circular at the alveolar level. Mf^3 and Mf^4 are slightly posteriorly oriented (Figs. 5a, 7a, b). The lingual surface of the lower molariforms is convex and exhibits a slightly marked middle groove that reaches the lower half of the extra-alveolar surface (Fig. 5c).

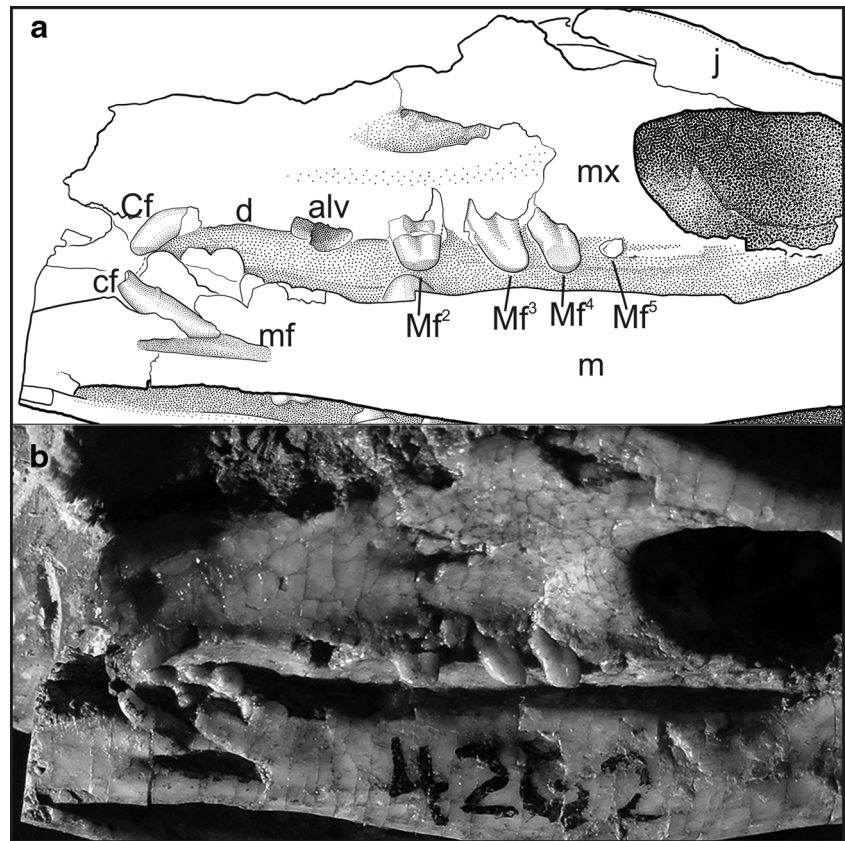
Table 1 Length of mandible, upper tooth row, and diastemata (in mm) of *Lumberatherium oblitum*, gen. et sp. nov. (PVL 4262)

Dimensions (mm)	<i>L. oblitum</i>
Mandible length from the back of the symphysis	41,65
Horizontal branch length from the back of the symphysis	28,66
Length of upper tooth row (including caniniform)	18,84
Length of upper tooth row (excluding caniniform)	12,32
Diastema length Cf – Mf^1	4,69
Diastema length Mf^1 – Mf^2	1,65
Diastema length Mf^2 – Mf^3	1,65

Postcranium (Figs. 2, 5, 8)

The atlas, articulated to the cranium and axis, is exposed only in ventral view. It is slightly narrower than in *Chaetophractus* and *Tolypeutes*. The ventral surface is short and smooth, and it lacks the posteroventral medial tuber. In *Chaetophractus* and *Tolypeutes*, this structure is present. The left transverse process shows a rounded transverse foramen situated in front of the posterior tuberosity, similar to *Chaetophractus*. In *Tolypeutes*, the transverse foramen is situated dorsal to the posterior tuberosity in the lateral face. Only the

Fig. 7 Teeth in lateroventral view of *Lumbreratherium oblitum*, gen. et sp. nov. (PVL 4262). **a** schematic representation; **b** photograph. Abbreviations: alv: alveolus; Cf: upper caniniform; cf: lower caniniform; d: diastema; j: jugal; m: mandible; mf: mental foramen; Mf^{2-5} : upper molariforms; mx: maxilla



ventral face of the axis is observed. Over the right side, part of the articular facet for the atlas is slightly convex (Fig. 5a). The ventral face shows longitudinal striations similar to those in *Chaetophractus*. These striations are not present in *Tolypeutes*.

There are five articulated lumbar vertebrae exposed in ventral view (Fig. 8c). The vertebral bodies are more robust and wider than in *Chaetophractus*. A ventral anapophysis has been almost completely preserved in one vertebra. One isolated caudal vertebra exhibits a subcylindrical centrum, with the length being less than double the width. Ventrally, a pair of sharp, elevated medial crests are found, which extend over the posterior two-thirds of the centrum, forming a deep and concave groove. The transverse processes are well developed and exhibit a sharp edge on their lateral margin (Fig. 8a).

One nearly complete rib and many fragments have been preserved. In the proximal end, there are two articular surfaces: the tuberculum and capitulum. The distal end is not observed. The shaft of the rib is wide with a groove in the middle of the length of the shaft, which possibly corresponds to the attachment for the intercostal muscles. The curvature of this element suggests it might be an anterior rib (Fig. 8b).

The manubrium has been preserved. It is approximately rhomboidal, with the anterior region broader than the posterior

region and a marked stretching in the medial region. The anterior and posterior edges are convex. On the ventral area, there is a marked keel, which is more prominent towards the anterior end.

The proximal half of the right tibia-fibula is preserved. The medial condyle is not observed, whereas the lateral condyle is oval and convex. The intercondylar eminence is strongly projected proximally, as occurs in *Dasypus*. On the other hand, in *Priodontes* and *Chaetophractus* the intercondylar eminence is less developed. Over the shaft of the tibia, the tibial crest is shorter and less developed than in *Dasypus*, *Priodontes*, and *Chaetophractus* (Fig. 8d).

The proximal end of the ulna is observed in postero-internal view and it is somewhat deformed by compression. The olecranon is well developed, and its end exhibits a sharp curvature.

One metacarpal has been preserved, with a cylindrical, flattened shaft in dorsopalmar orientation. In the distal end, the trochlea exhibits a deep groove. The medial crest, described in other dasypodids, is not observed.

Three ungual phalanges were found, but only one remains complete. The ungual process is conical and slightly curved. There is a groove on the lateral face along its length. The articular surface is concave. The discoidal area, at the base of the proximal end, is higher and more compressed than in *Dasypus* and *Chaetophractus* (Fig. 8e).

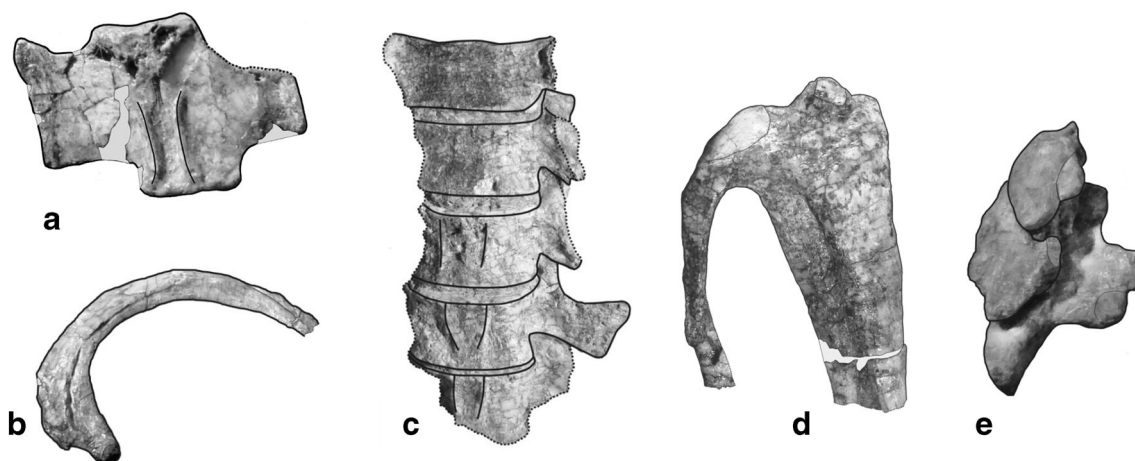


Fig. 8 Postcranial elements of *Lumbretherium oblitum*, gen. et sp. nov. (PVL 4262). **a** caudal vertebra; **b** rib; **c** lumbar vertebrae, **d** proximal half of the right tibia-fibula; **e** ungual phalanges

Phylogenetic Analysis

The phylogenetic analysis resulted in two most parsimonious trees of 515 steps. The strict consensus is shown in Fig. 9. The indices of the present cladogram are: consistency index =0.38 and retention index =0.48.

The Cingulata (clade A) are a monophyletic group. *Peltephilus* is the sister taxon to all the remaining cingulates, consistent with previous studies (Abrantes and Bergqvist 2006; Gaudin and Wible 2006). Clade B includes *P. parvum* + *L. oblitum* as the sister group of a diverse clade that includes dasypodines, tolypeutines, euphractines, and glyptodontoids. Clade C (*L. oblitum* + *P. parvum*) is clearly distinguished by the following unambiguous synapomorphies: dorsal carapace formed only by movable bands [2(0)], articular anterior surface of the osteoderms with elevations and grooves [12(0)], posterior edge of the internal surface of the movable osteoderms with elevations and grooves [13(0)], lateral contact area between osteoderms flat and smooth [14(2)], and step-like structure in the lateral surface of the osteoderms [15(1)]. *Lumbretherium oblitum* exhibits three anterior and two lateral peripheral figures on the osteoderms [8(0)], whereas *P. parvum* does not exhibit peripheral anterior figures. In contrast, *P. parvum* differs from *L. oblitum* because the main figure reaches the posterior edge of the osteoderm [10(1)] and the articular surface is developed (representing more than 35 % the total length of the osteoderm) [17(0)].

Clade D includes *Utaetus* and the remaining dasypodines, pampatheres, and glyptodonts. This clade is supported by four unambiguous synapomorphies: extension of the main figure of the osteoderm contacting the posterior edge [10(0)], small piliferous foramina, located in the posterior margin of the osteoderm [16(0)], nine lower teeth [23(4)], and three or more mental foramina [35(2)]. Simpson (1945, 1948) proposed the inclusion of the genus *Utaetus* in the Utaetini tribe, based on a set of characters that are considered primitive. Some authors

considered Utaetini as a tribe within Euphractinae (Scillato-Yané 1980; McKenna and Bell 1997). Recently, Carlini et al. (2010) questioned the validity of Utaetini as a distinct tribe and considered that *Utaetus* is closely related to Euphractinae. The euphractines analyzed in this study are not recovered as a monophyletic group, which agrees with results obtained in previous phylogenetic studies (Engelmann 1985; Gaudin and Wible 2006; Abrantes and Bergqvist 2006; Billet et al. 2011). *Macroeuphractus* + *Proeuphractus* (Clade F) are basal to the euphractines, eutatines, pampatheres, glyptodonts, and Dasypoda.

In the present analysis, Clade G is an unresolved trichotomy. This grouping includes *Eutatus* as a sister taxon to Clade H and Clade K. Clade H is a monophyletic group formed by (*Zaedyus pichiy* + *Calyptophractus retusus*) (*Chaetophractus vellerosus* + *Euphractus sexcinctus*). Gaudin and Wible (2006) considered this clade as Euphracta. Wetzel (1985) and Delsuc et al. (2012) considered the Chlamyphoriinae as a subfamily that differs from Euphractinae.

Clade L has (*Proeutatus* (*Propalaeohoplophorus* + *Vassallia*)). The eutatini *Proeutatus* is the sister taxon of Glyptodontoidea, in agreement with studies by Gaudin and Wible (2006), Gaudin and Bramblett (2010), and Billet et al. (2011). Clade M is composed of Pampatheriidae + Glyptodontidae. The relationship between pampatheres and glyptodonts has been suggested by different authors (Patterson and Pascual 1972; Carlini and Scillato-Yané 1993; McKenna and Bell 1997; Gaudin and Wible 2006; González 2010).

Clade N includes *Prozaedyus* as sister taxon of Clade O. This clade has (*Tolypeutes matacus* (*Dasypus novemcinctus* + *Stegotherium*) (*Priodontes maximus* + *Cabassous*)). Gaudin and Wible (2006) defined this clade as Dasypoda. *Dasypus* and *Stegotherium* remain as a basal monophyletic group in the analyses by Abrantes and Bergqvist (2006); Gaudin and Wible (2006), and Billet et al. (2011). In this analysis, the

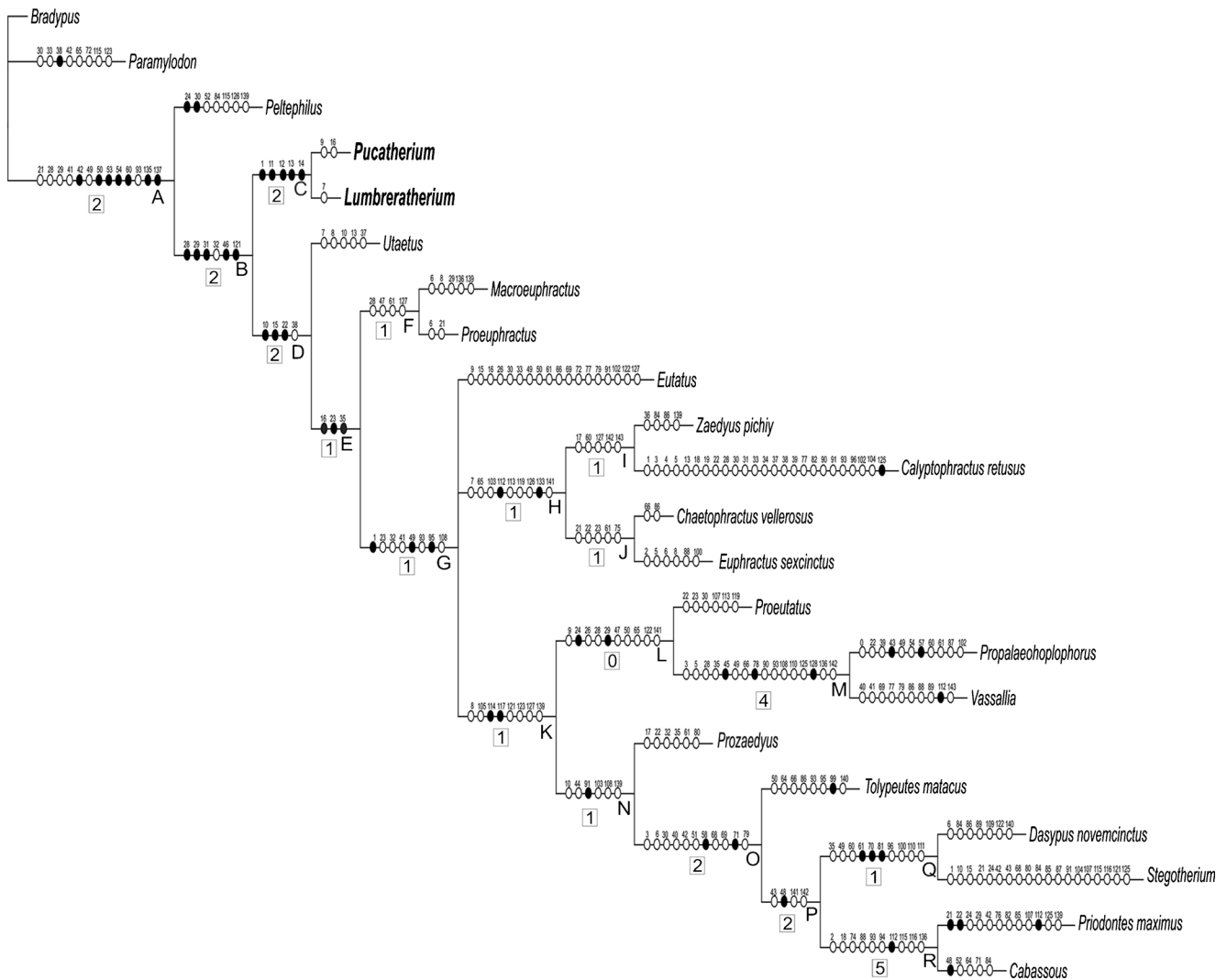


Fig. 9 Phylogeny of cingulates based on the cladistic analysis of 23 taxa and 144 characters. Capital letters represent the clades, discussed in the text *black circles* correspond to unambiguous synapomorphies, *white*

circles correspond to ambiguous synapomorphies, and framed numbers are values of Bootstrap support at nodes

subfamily Tolypeutinae sensu McKenna and Bell (1997) is not recovered as a monophyletic group.

Discussion

Paleogene armadillos of the early-middle Eocene of northwest Argentina are known from cranial remains, associated post-cranial elements, and articulated or isolated osteoderms (Herrera 2013). This contrasts with the majority of the Eocene dasypodids, which are only known by isolated osteoderms and associated postcranial remains.

Pucatherium parvum and *L. oblitum* are recovered as a new basal clade of dasypodids. This clade is characterized by the articulation between osteoderms of successive bands and the articulation between adjacent osteoderms of the same band. The former occurs between the anterior articular region with

the internal face of the distal region of the anterior osteoderm (Fig. 3). Both regions are sculptured with grooves and elevations that lock together. The latter occurs between the lateral face, located immediately below the step (Fig. 4c–f).

This set of characteristics, which we define as “pucatheriine pattern” (Fig. 4c, e) clearly differs from the morphology in the rest of dasypodids (Fig. 4a).

The first tooth is caniniform and behind it there is a large diastema, the length of which is approximately equal to one-third of the preserved molariform series. This tooth is described as caniniform due to its morphology and position. Caniniforms are conical and their major axis is anterolabially oriented; the upper tooth exhibits a distal wearing surface, which suggests that the lower tooth occludes behind it. This heterodont condition is more similar to mylodontoids and megalonychids than to that specified for armadillos. Vizcaíno (2009) pointed out that in *Macroephractus* the

second upper tooth is modified as a “powerful caniniform” (Vizcaíno 2009:349). However, this tooth looks like a well-developed molariform, and is larger than the remaining teeth.

In *L. oblitum*, the first lower right molariform is displaced from its alveolus, which allows the observation of its complete morphology (Fig. 5c). This tooth is protohypsodont, presents no neck, and has short closed roots separated by a wide notch. The extra-alveolar region corresponds to the upper half of the tooth, while the roots represent approximately only one-sixth of the total height of the tooth. Recently, Ciancio et al. (2014) described two protohypsodont closed-rooted molariforms in a mandibular fragment referred to *Astegotherium*. These teeth are different from those in *L. oblitum* because the extra-alveolar region is shorter (restricted to the upper third) and the roots are longer (one third of the total height of the tooth). These authors determined that this *Astegotherium* specimen corresponds to an adult specimen due to the presence of closed rooted teeth and the absence of the tooth germ underneath (Ciancio et al. 2014). *Lumbreratherium oblitum* is considered as an adult individual, due also to the obliteration of the sutures of the basicranial region (basisphenoid-basioccipital and basisphenoid-presphenoid).

The reduced number of teeth, the presence of intermolariform diastemata, and the gracefulness of the jaw have been mentioned as features of dasypodids, which feed mainly on social insects (Vizcaíno 2009; Ciancio et al. 2014). As the new taxon described in this study does present these characteristics, it is inferred that *L. oblitum* was probably an insectivorous species.

Conclusions

Lumbreratherium oblitum is a new dasypodid from northwest Argentina, due to its very distinctive dental characters and the morphology of the osteoderms. This new taxon comes from the early-middle Eocene Lumbra Formation (“lower Lumbra”), Casamayoran SALMA, Vacan subage in Salta province, Argentina. As a result of the phylogenetic analysis of Cingulata, *Pucatherium parvum*, and *L. oblitum* form a monophyletic group with a basal position within Dasypodidae. Several authors proposed that the notable presence of basal forms indicates that northwest Argentina was an important region of the early diversification for many notoungulate lineages (Pascual et al. 1996; Goin et al. 1998; Reguero et al. 2008; García López and Powell 2011; Powell et al. 2011). The basal position of these Paleogene armadillos of northwest Argentina reinforces the hypothesis of an intertropical origin of mammal clades, different from those in the Paleogene of more austral regions of Argentina.

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