



The Cingulata Dasypodidae (Mammalia, Xenarthra) in the Tarija Valley (Bolivia): a particular assemblage in South America

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ABSTRACT - The Tolomosa Formation in southern Bolivia's Tarija Valley contains one of the most important Pleistocene assemblages of vertebrates in South America, in which Xenarthra are among the most recorded and diversified taxa. Within this clade, the Cingulata Dasypodidae has traditionally included four taxa: the Euphractinae Euphractini *Chaetophractus tarijensis* (a supposedly endemic species) and *Euphractus sexcintus*, and the Dasypodinae *Dasypodini* *Dasypus* and *Propraopus grandis*. However, a taxonomic revision together with new findings that include geographic and stratigraphic provenance reveals surprisingly low armadillo diversity; the only recorded taxa correspond to *Propraopus sulcatus* and *Chaetophractus villosus*. This is evident when compared with, for example, the Dasypodidae recorded in the Pampean region of Argentina that included more than six species in the Pleistocene. All of the new records come from the localities of Monte Sur (also called San Pedro), Monte Cercado and Río Rujero in the Tarija Valley, while the wide chronological distribution of these species does not allow us to infer the age of the Tolomosa Formation. This low Dasypodidae diversity is concordant with observations in other Cingulata clades, such as the Glyptodontidae.

RIASSUNTO - [I Cingulata Dasypodidae (Mammalia, Xenarthra) nella Valle di Tarija (Bolivia): una associazione peculiare dell'America meridionale] - La Formazione di Tolomosa, nella Valle di Tarija, contiene una delle associazioni a mammiferi del Pleistocene a maggior diversità tassonomica dell'America meridionale. Questa particolare associazione include sia taxa caratteristici di ambienti relativamente caldi e umidi (ad esempio *Tapirus* e *Neochoerus*), sia quelli adattati ad aree aride o semiaride e fredde. In questo scenario, gli Xenarthra sono uno dei più frequenti elementi faunistici e, tra loro, i Cingulata sono il clade con la più recente revisione sistematica. Nei Cingulata, Dasypodidae è l'unica famiglia priva di una moderna revisione tassonomica. A questo proposito, l'obiettivo di questo articolo è aggiornare la sistematica degli Xenarthra Dasypodidae della Valle di Tarija e discutere le loro implicazioni biogeografiche e paleobiogeografiche. Fino all'attuale lavoro, solo quattro specie erano tradizionalmente incluse nei Dasypodidae della Valle di Tarija: Euphractinae Euphractini *Chaetophractus tarijensis* (probabilmente una specie endemica) con *Euphractus sexcintus*, e i Dasypodinae *Dasypodini* *Dasypus* e *Propraopus grandis*. Ad ogni modo, le nuove analisi condotte su fossili precedentemente raccolti, insieme a nuovo materiale raccolto dagli autori, indicano che la diversità dei Cingulata Dasypodidae è minore di quanto tradizionalmente creduto. Questa nuova revisione tassonomica rivela una sorprendente bassa diversità degli armadilli, con gli unici taxa identificati corrispondenti a *Propraopus sulcatus* e *Chaetophractus villosus*. Inoltre, le uniche località dove Dasypodidae sono segnalati sono Monte Sur (noto anche come San Pedro), Monte Cercado e Río Rujero. Questa rarità diviene ancor più evidente se si confrontano questi dati con i ritrovamenti di Dasypodidae registrati in altre aree, come la Pampa argentina, da dove provengono almeno sei specie del Pleistocene. Anche attualmente la diversità dei Dasypodidae provenienti dalla Bolivia meridionale è maggiore (otto taxa) di quella del Pleistocene della Valle di Tarija. Comunque, una tale bassa diversità dei Dasypodidae è in accordo con quanto osservato in altri cladi di Cingulata, come Glyptodontidae e Pampatheriidae. In conclusione, l'ampia distribuzione cronologica delle specie di Dasypodidae considerate consente solo una generica attribuzione della Formazione di Tolomosa al Pleistocene.

INTRODUCTION

The fossil mammal fauna exhumed from the Pleistocene of the Tarija Valley (Bolivia) is among the most taxonomically diverse in South America, including ca. 55 species according to Hoffstetter (1963) or ca. 46 species, according to Tonni et al. (2009). This assemblage includes taxa characteristic of relatively warm and humid environments (e.g., *Tapirus* Brünich, 1772 and *Neochoerus* Hay, 1926) as well as those adapted to arid or semiarid and cold areas, where grazers are dominant (*Equus* Linnaeus, 1758, *Artiodactyla* Camelidae Gray,

1821, Xenarthra Glyptodontidae Burmeister, 1879) (MacFadden & Shockey, 1997).

In this context, the Xenarthra (Cingulata Illiger, 1811 and Pilosa Flower, 1883) are some of the most frequent faunal elements, and approximately 12 genera have been recognized (see Hoffstetter, 1963; Takai et al., 1982, 1984; Coltorti et al., 2007; Tonni et al., 2009). Within Xenarthra, Cingulata represents the clade with the most recent taxonomic revisions, especially in Glyptodontidae (Zurita et al., 2009) and Pampatheriidae (Rodríguez-Bualó et al., 2014b). On the other hand, Dasypodidae have only been mentioned in faunal listings (Tonni et al., 2009) and

lack modern taxonomic revision (but see Rodriguez-Bualó et al., 2014a). According to the most recent contributions (e.g., Coltorti et al., 2007; Tonni et al., 2009), four taxa correspond to Dasypodidae (Gray, 1821): *Chaetophractus* Fitzinger, 1871; *Euphractus* Wagler, 1830; *Dasypus* Linnaeus, 1758 and *Propraopus* Ameghino, 1881.

New materials have been exhumed (CT-2013-14, CT-2011-20, CT-2011-25, and CT-2013-4) in field studies carried out in the Pleistocene of the Tarija Valley (Bolivia). In this work, we update the taxonomy of Xenarthra Dasypodidae in the Tarija Valley (Bolivia); additionally, some biostratigraphic and paleobiogeographic implications are discussed.

GEOGRAPHIC AND STRATIGRAPHIC SETTINGS

The Tarija Valley is located in southern Republic of Bolivia, 1000 km from La Paz and 140 km north of the border with Argentina (Tarija city, 21° 31' S – 61° 44' W; Fig. 1).

The sedimentary sequences that crop out in the Tarija Valley document part of the Tolomosa Formation, and have been successively assigned to different ages and stages ranging from the lower to the upper Pleistocene (De Carles, 1888; Boule & Thévenin, 1920; Kraglievich, 1934; Oppenheim, 1943; Takai et al., 1982, 1984; MacFadden et al., 1983; Coltorti et al., 2007; Tonni et al., 2009; Zurita et al., 2009).

From a stratigraphic and chronological perspective, the Tarija Valley is part of a Quaternary sedimentary basin, filled with fluvio-lacustrine sediments that discordantly overlie a Paleozoic (Ordovician-Silurian) basement



Fig. 1 - Location Map showing the Tarija Valley (Bolivia).

(Suarez-Montero, 1996). The most outstanding feature of the area is the characteristic badlands landscape, with an irregular relief produced by differential sedimentary erosion (Oppenheim, 1943; Suarez-Montero, 1996). Recently Coltorti et al. (2010) included the entire Pleistocene sequence within the Tolomosa Formation, subdivided into three major Units: Ancón Grande (AG), Puente Phayo (PP) and the San Jacinto Unit (SJ).

Institutional Abbreviations

AAC: Colección Alfredo A. Carlini at Museo de La Plata (La Plata, Argentina); CTES-PZ: Colección Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (Corrientes, Argentina); CT: Campaña Tarija (collection year-material number); FMNH: Field Museum of Natural History, Chicago, Illinois, USA; MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP: Museo de la Plata, La Plata, Argentina; MNHN: Muséum National d’Histoire Naturelle, Paris, France; MNPA-V: Museo Nacional Paleontológico-Arqueológico, Vertebrados (Tarija, Bolivia); MUT: Museo de la Universidad de Tarija, Tarija, Bolivia; UCM: The University of Connecticut, United States; UF: University of Florida, Florida State Museum, United States; YPM: Yale Peabody Museum (PU, Princeton University Collection), New Haven, United States.

SYSTEMATIC PALEONTOLOGY

Superorder XENARTHRA Cope, 1889

Order CINGULATA Illiger, 1811

Family DASYPODIDAE Gray, 1821

Tribe EUPHRACTINI Winge, 1923

Genus *Chaetophractus* Fitzinger, 1871

Type species *Loricatus villosus* Desmarest, 1804

Chaetophractus villosus (Desmarest, 1804)

(Fig. 3)

Material - MACN 1611, distal portion of right hemimandible with seven preserved molariforms (m2-m8); MACN 1612, partial skull, incomplete right and left hemimandibles; MUT 128, partial carapace; MUT 295, anterior portion of skull, left and right hemimandibles (lost materials); FMNH 14184, portion of right hemimandible; FMNH 13785, five osteoderms, unguals and phalanges; FMNH 15131, partial dorsal carapace; YPM 16612, nearly complete skull, incomplete mandible, left humerus, right and left femur; CT-2013-14, two fixed osteoderms. Boule & Thévenin (1920: Pl. XXV) illustrated a portion of skull (attributed to *Euphractus sexcinctus* [Linnaeus, 1758]) and several osteoderms without a collection number.

Geographic and stratigraphic provenance - According to MacFadden et al. (1983) the material YPM 16612 comes from the San Pedro locality, which is of normal polarity and corresponds to the Subchron-Brunhes (0.78 Ma-present). This same locality was called Monte Sur by Coltorti et al. (2007), who mention *Dasypus* material

coming from the upper strata (F1 strata). Beneath the strata in which the *Dasypus* and other fossil remains were discovered (e.g., *Glyptodon* Owen, 1838; *Pampatherium* Gervais & Ameghino, 1880; *Lestodon* Gervais, 1855, and *Megatherium* Cuvier, 1796 among others), Coltorti et al. (2007) obtained two radiocarbon dates of 27,180 +/- 880 and 39,880 yr BP.

New material assigned to *C. villosus* (CT-2013-14) was collected during fieldwork from the Monte Cercado locality by the authors of this work. According to Coltorti et al. (2010) this locality belongs to the "San Jacinto sub-synthem" (late Pleistocene). The material housed in the FMNH (14184, 13785, 15131) comes from the Turomayo locality, which has not been previously mentioned in any publications related to the Tarija Valley. The materials MUT 128 and 295 belong to the "Echazú" Collection. This collection was listed and numbered by Takai et al. (1982, 1984) and lacks information on geographic and stratigraphic origin.

Description -

SKULL - The material MACN 1612 was already assigned to *C. villosus* by Rodríguez-Bualó et al. (2014a) on the basis of morphological and morphometric data (e.g., skull length from the back of the condyles to the foremost part of the pre-maxillary; length of the mandibular symphysis). The portion of the skull illustrated by Boule & Thévenin (1920) as *Euphractus sexcinctus* (Fig. 2) should be reassigned to *C. villosus*. This new assignment is based on: 1) the highly sculpted osteoderms of the cephalic shield, which include a central figure and several peripheral (5-8) figures, all convex, as observed in homologous *C. villosus* material (Scillato-Yané, 1982); 2) palatal size and morphology coinciding with *C. villosus*; Boule & Thévenin (1920) described a palatal width of 10 mm between fifth molars (M5), which is well within the range described for *C. villosus* (9.81-12.31 mm); 3) the cranial width at M3 is 23 mm, which is within the range described for *C. villosus* (21.35-24.66 mm) (Rodríguez-Bualó et al., 2014a).

MANDIBLE - In MACN 1611 (Fig. 3b), previously assigned to *Chaetophractus tarijensis* Ameghino, 1902, the mandibular symphysis is 18.9 mm long and the dorsoventral diameter of the horizontal ramus at the M8 alveolar level is 11.7 mm. Both measures are within the range described for *Chaetophractus villosus* (Rodríguez-Bualó et al., 2014a). FMNH 14184 (Fig. 3c) corresponds to the posterior portion of a horizontal ramus with angular apophysis and a small part of the ascending ramus. Seven molariforms are present (m4-m10). Molariform m10 is not visible from the labial perspective because it is located behind the mandibular ascending ramus, a feature characteristic of Dasypodidae Euphractinae. The dorsoventral diameter of the horizontal ramus at the m8 alveolar level is 10.9 mm, a measure that falls within the range typical of *C. villosus* (Rodríguez-Bualó et al., 2014a).

CARAPACE - The carapace of Dasypodidae is formed by osteoderms and includes, from head to tail: cephalic shield, dorsal shield and caudal sheath. The dorsal shield comprises a scapular buckler, a region of movable bands

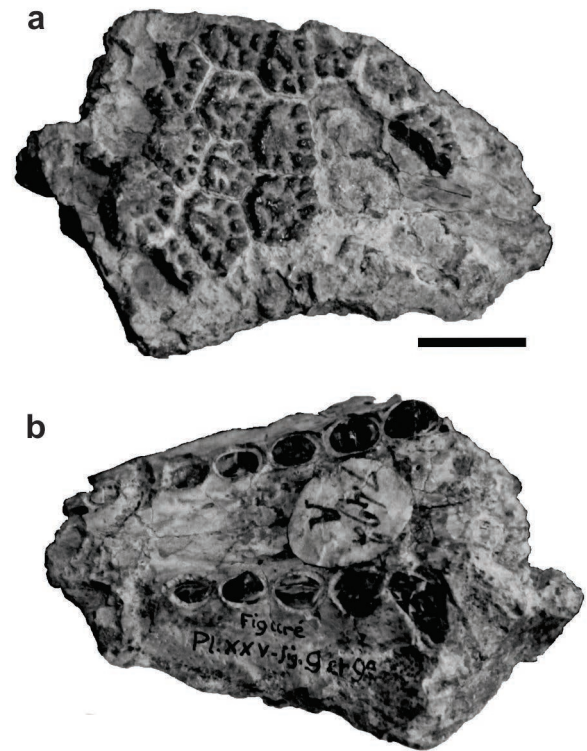


Fig. 2 - Portion of skull (identified as belonging to *Euphractus sexcinctus* [Linnaeus, 1758]) figured by Boule and Thévenin (1920: Pl. XXV) deposited in MNHN. a) Dorsal view. b) Ventral view. Scale bar is equal to 1 cm.

and a pelvic buckler. The fixed osteoderms of the scapular and pelvic bucklers (MUT 128, FMNH 13785, FMNH 15131 and CT-2013-14) (Fig. 3a, d) have an exposed, ornamented surface consisting of an elongated central figure, which occupies the posterior two-thirds of the osteoderm, and several smaller peripheral figures, located anteriorly and laterally to the central figure. Moreover, two rows of anterior peripheral figures are present on pelvic buckler osteoderms, which is characteristic and exclusive of *Chaetophractus villosus* (e.g., MLP 922, UCM 16591, AAC 166, AAC 167, CTES-PZ 7568). All figures are delimited by well-defined sulci with external surface foramina on it. The posterior margin of each osteoderm bears piliferous follicle foramina, as observed in *C. villosus* (Krmptotic et al., 2009). Movable osteoderms (MUT 128, FMNH 13785 and FMNH 15131) have three different regions: cranial portion (which is not exposed and lacks ornamentation), transverse depression (which has a striated appearance) and caudal portion (with the external surface ornamented similarly to that of the fixed osteoderms).

Remarks - The skull of *Chaetophractus villosus* is similar to the skulls of other Euphractini species (*C. vellerosus* Gray, 1865; *C. nationi* Thomas, 1894; *Zaedyx pichiy* Desmarest, 1804; and *Euphractus sexcinctus*); the most notable distinction being the relatively large size and robustness in *C. villosus* compared to *C. vellerosus* and *Z. pichiy*. Squarcia et al. (2007) conclude that the degree of hypertrophy of the auditory bullae is greater in *C. villosus* than in *Z. pichiy*. Both the skull and the mandible of *C.*

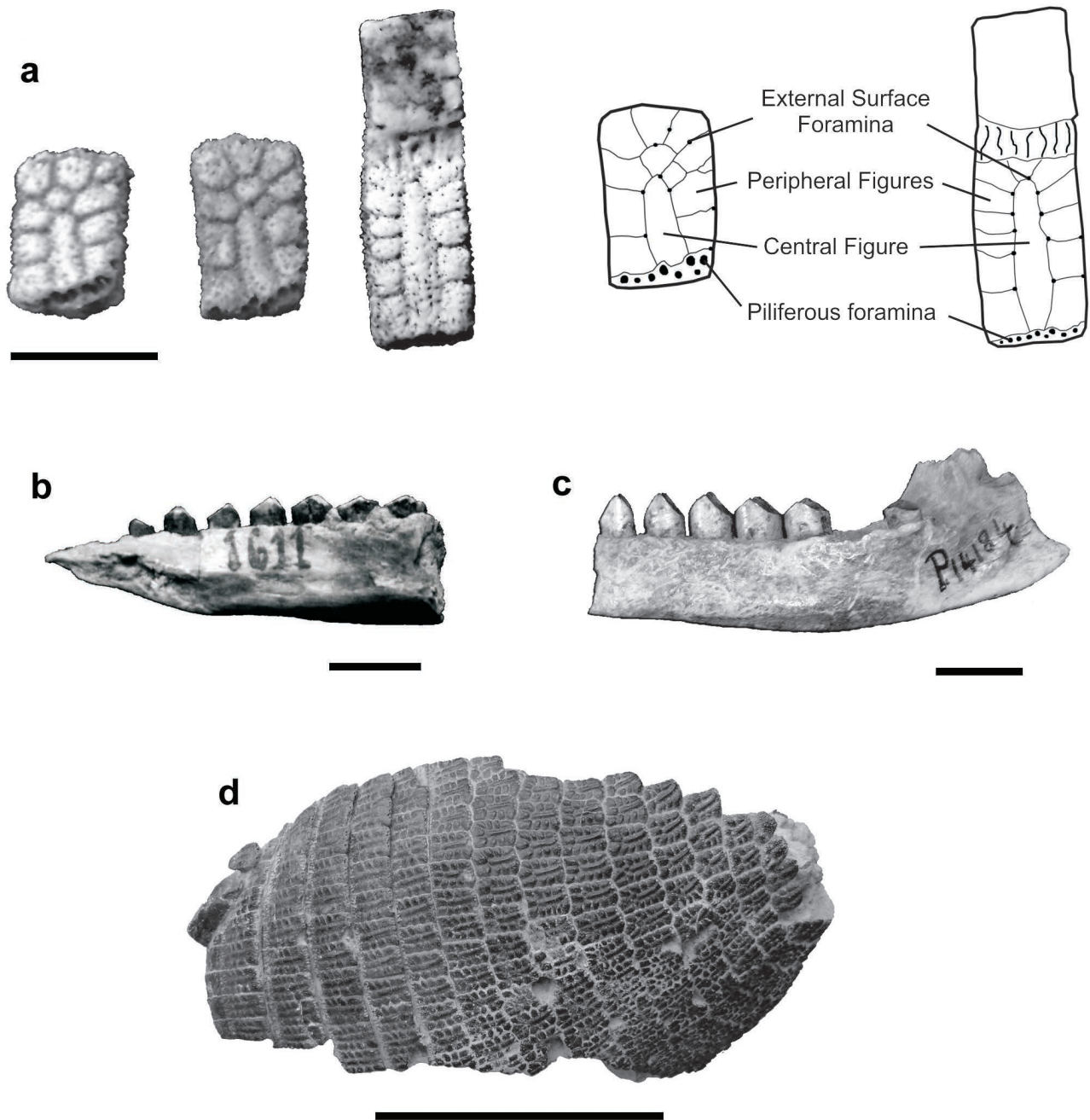


Fig. 3 - *Chaetophractus villosus* (Desmarest, 1804). a) Buckler and movable osteoderms. Line drawing of the major structures of buckler and movable osteoderms as mentioned in the text. Scale bar is equal to 1 cm. b) MACN 1611, distal portion of right hemimandible. Scale bar is equal to 1 cm. c) FMNH 14184, portion of right hemimandible. Scale bar is equal to 1 cm. d) MUT 128, partial carapace. Scale bar is equal to 10 cm.

villosus are 30% smaller than those of *E. sexcinctus*. The osteoderms of all three extant species of *Chaetophractus* are morphologically similar, but there are several characters that differentiate *C. villosus* from the others. The most noticeable feature is the size: the osteoderms (in homologous zones of the dorsal carapace) in *C. villosus* are about 20% larger than those of *Chaetophractus vellerosus* and *C. nationi* (Francia & Ciancio, 2013). Furthermore, the osteoderms from the pelvic buckler of *Chaetophractus villosus* present one or two additional anterior figures in front of the main figure (Scillato-Yané, 1982), a character absent in the other two living species of the genus.

Subfamily DASYPODINAE Gray, 1821

Genus *Propraopus* Ameghino, 1881

Type species *Propraopus grandis* Ameghino, 1881

Propraopus sulcatus (Lund, 1842)

(Fig. 4)

Material - MUT 187, a large portion of dorsal carapace preserving movable and fixed osteoderms; UF92404, a portion of dorsal carapace and isolated osteoderms; FMNH 13746, dorsal carapace, isolated osteoderms and

complete caudal sheath; CT-2011-20, several isolated osteoderms; CT-2011-25, several isolated osteoderms and other indeterminate remains; CT-2013-4, several isolated osteoderms. Takai et al. (1982) illustrated the material MUT 10 (a portion of dorsal carapace with movable osteoderms) but this material was not found in the collections of the MNPA-V.

Geographic and stratigraphic provenance - *P. sulcatus* is registered in the following localities of Tarija Valley: 1) San Pedro (=Monte Sur of Coltorti et al., 2007) (UF92404), which is of normal polarity and corresponds to the Subchron Brunhes (MacFadden et al., 2013). Coltorti et al. (2007) obtained a C_{14} date of 27,180 +/- 880 yr BP in this locality; 2) Rio Rujero, most of the materials recovered by the authors of this work are from this locality (CT-2011-20, CT-2011-25, and CT-2013-4). Coltorti et al. (2007) mentioned that Rio Rujero corresponds to the San Jacinto sub-synthem and they obtained a C_{14} date of 20,840 +/- 100 yr BP for the fossil-bearing sequences; 3) Turomayo locality (FMNH 13746), which has not been previously mentioned in any publications related to the Tarija Valley.

Description -

CARAPACE - The fixed osteoderms have a hexagonal or pentagonal shape. The ornamented exposed surface is smooth, with a posteriorly displaced subcircular central figure that is near to margin of the osteoderm, and surrounded by the principal sulcus. This sulcus separates the central figure from the anterior peripheral figures (3 to 5). There are two to five glandular foramina in the sulci (three to six in *Dasypus novemcinctus* Linnaeus, 1758), which are restricted to the anterior part of the osteoderm, and are never located at the intersection of the principal and the radial sulci (see Fig. 4b-c). Movable osteoderms have two anteriorly separated principal sulci on the ornamented surface that diverge posteriorly, delimiting a subtriangular figure, generally with four foramina in the sulci (six to 14 in *D. novemcinctus*) (see Fig. 4b-c).

CAUDAL SHEATH - In the specimen FMNH 13746 (Fig. 4a), eight of 12 caudal rings are preserved (e.g., MLP 69-IX-9-9), which decrease in size distally. Each of these rings is comprised of two rows of osteoderms. The distal row of osteoderms in each ring runs above and joins the proximal row of osteoderms of the contiguous distal ring. The external morphology of the osteoderms is different in the two rows that form the ring. The osteoderms in the proximal row have a pair of sulci that originate at the proximal end of the osteoderm and extend distally, curving markedly until they reach the lateral margins of the osteoderm. One or two foramina are located above each sulcus. The second row of osteoderms (distal) are rhomboid in the proximal rings and quadrangular in the more distal rings (see Fig. 4d).

Remarks - *Propraopus grandis* Ameghino, 1881, the type species of the genus, was founded based on several osteoderms from the Pleistocene of the Buenos Aires Province, Argentina. Hoffstetter (1952, 1958) assigned *Dasypus magnus* Wolf, 1875 (Pleistocene of Ecuador), *Dasypus bellus* Simpson, 1929 (Pleistocene of U.S.A.), *D. punctatus* Lund, 1842, and *D. sulcatus* Lund, 1842 (both

from the Pleistocene of Brazil), to *Propraopus*. Several authors (Scillato-Yané, 1982; Rincon et al., 2008; Oliveira & Pereira, 2009) have questioned the validity of these *Propraopus* species.

Unlike *Dasypus*, the buckler osteoderms of *Propraopus* have a deep principal sulcus and two or three foramina, which are not placed at the intersection between the main and radial sulci; the pelvic osteoderms are larger and have more elongated main figures. The main differences between *Propraopus* and *Dasypus* are: the most lateral section of the pelvic buckler is composed by sharp projecting osteoderms that form a denticulate border (these are not denticulate in *Dasypus*); and the pelvic buckler is much longer than the scapular buckler in *Propraopus* (these bucklers are almost the same length in *Dasypus*) (Ameghino, 1895).

According to Castro et al. (2013), the differences in the lengths of the mobile and fixed osteoderms between *P. grandis* and *P. sulcatus* are not sufficient to define two distinct species. Likewise, the qualitative differences are minor and are related to intraspecific variation in the taxon. This work concludes that the only valid species is *Propraopus sulcatus* (Castro et al., 2013).

DISCUSSION AND RESULTS

This new analysis of previously collected materials alongside with the new materials collected by the authors indicates that the diversity of Cingulata Dasypodidae is less than traditionally has been believed. Various authors have recognized the presence of *Chaetophractus tarijensis*, *Euphractus sexcinctus*, *Dasypus* spp., and *Propraopus grandis* (see Hoffstetter, 1963; Marshall & Sempere, 1991 and Tonni et al., 2009). However, this new analysis establishes the presence of only two species: *P. sulcatus* and *C. villosus* in the Pleistocene of the Tarija Valley. The presence of *Dasypus* could not be confirmed because the materials mentioned by Coltorti et al. (2007) could not be located in the collections of the MNPA-V in Tarija. It is worth noting that Coltorti et al. (2007) are the only authors to have described the presence of this taxon in the Tarija Valley.

The localities with records of Dasypodidae in the Tarija Valley correspond to Monte Sur (also known as San Pedro in MacFadden, 1983), Monte Cercado and Río Rujero.

From a chronological and geographical perspective, *P. sulcatus* is recorded in the Ensenadan-Lujanian SALMAs of the Pampean and Mesopotamian regions of Argentina (Cione & Tonni, 2005; Francia, 2014). In Uruguay it is recorded as *Propraopus* sp. in the Sopas and Dolores Formations, both assigned to the Lujanian SALMAs (upper Pleistocene) (Ubilla & Perea, 1999; Ubilla et al., 2004). In Brazil, *P. sulcatus* is recorded in various locations, and is often assigned to the late Pleistocene (e.g., Touro Paso, Arroio Chuí, Linha de Praia and the Aurora do Tocantins Formations) (Cartelle, 1999; Ribeiro & Scherer, 2009). In Venezuela, Rincón et al. (2008) identified *P. sulcatus* in the Mene de Inciarte tar pits (late Pleistocene), which is the northern most locality known so far for the genus.

C. villosus is a species with a wide chronological distribution; it has been recorded from the Chapadmalalan (Pliocene; Scillato-Yané, 1982; Carlini & Scillato-Yané,

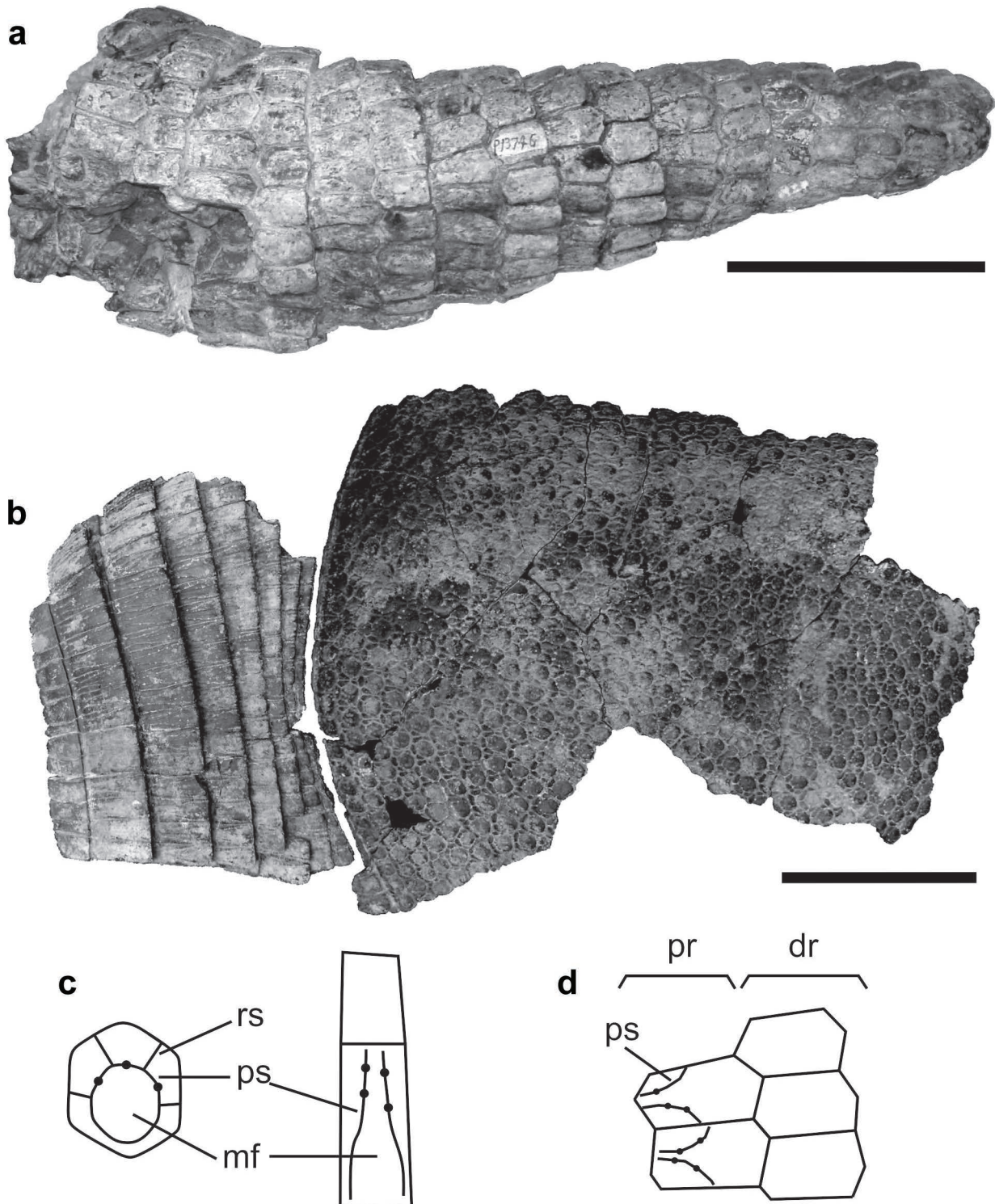


Fig. 4 - *Propraopus sulcatus* (Lund, 1842). a) FMNH 13746, complete caudal sheath; scale bar is equal to 10 cm. b) MUT 187, a large portion of dorsal carapace preserving movable and fixed osteoderms; scale bar is equal to 10 cm. c) Line drawing of the major structures of buckler and movable osteoderms of the dorsal carapace as mentioned in the text. d) Line drawing of the major structures of osteoderms of the caudal sheath as mentioned in the text.

1999) to the present (Soibelzon et al., 2006) in the current territories of Argentina, Chile, Paraguay and Bolivia.

A comparative analysis with other South American Pleistocene associations reveals a very uneven Dasypodidae diversity. The ones that record the presence of a single taxon are: Southern Brazil (Touro Passo Fm.) (*P. sulcatus*)

and Entre Rios province, Argentina (Arroyo Feliciano Fm.) (*P. sulcatus*). In the Tarija Valley (Tolomosa Fm.) and Formosa province, Argentina (Rio Bermejo Fm.), the same two taxa are recorded: *P. sulcatus* and *C. villosus*. In western Uruguay (Sopas Fm.) two dasypodids are registered (*D. aff. novemcinctus* and *Propraopus* sp.). In

the eastern Corrientes province, Argentina (Toropí/Yupoí Fm.) three taxa were registered (*P. sulcatus*; *E. sexcinctus* and *C. villosus*), and in the Buenos Aires province, Argentina (Lujan Fm.) six Pleistocene Dasypodidae have been recorded (*P. sulcatus*; *Eutatus seguini*; *Dasyopus hybridus*; *C. villosus*; *Zaedyus pichi*; *Tolypeutes matacus*).

It is worth noting that the Dasypodidae species currently recorded in southern Bolivia correspond to *Dasyopus novemcinctus*, *D. yepesi*, *D. hybridus*, *Chaetophractus villosus*, *C. vellerosus*, *Euphractus sexcinctus*, and *Tolypeutes matacus* (Emmons, 1999; Abba et al., 2012). This is a far greater diversity than that of the Pleistocene of the Tarija Valley.

The Xenarthra Cingulata association exhumed from the Tarija Valley (Bolivia) is substantially different from the known assemblages in other regions of South America (e.g., western Uruguay; Southern Brazil; Pampean, Mesopotamian, and Chacoan regions). Of the glyptodonts, the dominant taxon is *Glyptodon*, and to a lesser extent, *Panochthus* and *Hoplophorus*. In contrast, some genera that are very frequent in the Chaco-Pampean plains, such as *Neosclerocalypus*, are absent in Tarija's fossil record (Zurita et al., 2009). Among the Pampatheriidae, *Pampatherium humboldtii* (Lund, 1839) is the only taxon registered in the valley.

CONCLUSIONS

1. The Cingulata Dasypodidae documented in the Pleistocene sediments of the Tarija Valley (Tolomosa Formation) are restricted to *Chaetophractus villosus* and *Propraopus sulcatus*.

2. The presence of *Euphractus sexcinctus* and the endemic taxa *Chaetophractus tarijensis* can be discarded, and the materials previously assigned to these taxa are now interpreted as *Chaetophractus villosus*.

3. The localities within the Tarija Valley with records of Dasypodidae are Monte Sur (also known as San Pedro in MacFadden et al., 1983), Monte Cercado and Río Rujero.

4. From a biostratigraphic point of view, the presence of *C. villosus* and *P. sulcatus* in the valley does not allow us to infer the age of the Tolomosa Formation sediments, because both taxa have a wide temporal distribution (throughout the Pleistocene).

5. It is remarkable that the Dasypodidae assemblage from the Pleistocene of the Tarija Valley differs from known assemblages in the Pampean Region (PR), southern Brazil (Br) and southern Uruguay (Ur). Notably, *Propraopus* records are frequent in the Tarija Valley (also present in PR, Br and Ur) but *Eutatus*, *Zaedyus* and *Euphractus* (a taxa widely distributed in the PR) are absent, and *Chaetophractus* (absent in Br) is the only Euphractini present.

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REFERENCES

- Abba A.M., Tognelli M.F., Seitz V.P., Bender J.B. & Vizcaíno S.F. (2012). Distribution of extant xenarthrans (Mammalia: Xenarthra) in Argentina using species distribution models. *Mammalia*, 76: 123-136.
- Ameghino F. (1881). La antigüedad del hombre en el Plata. Tomo segundo. XIV. 640 pp. Masson editor, Paris.
- Ameghino F. (1895). Sur les édentés fossiles de l'Argentine (Examen critique, révisión et correction de l'ouvrage de M.R. Lydekker "The extinct Edentates of Argentina"). *Revista del Jardín Zoológico de Buenos Aires*, III: 97e192.
- Ameghino F. (1902). Notas sobre algunos mamíferos fósiles nuevos o pocos conocidos del Valle de Tarija. *Anales del Museo Nacional de Buenos Aires*, 8: 225-261.
- Boule M. & Thévenin A. (1920). Mammifères fossiles de Tarija. Paris, Imprimerie National, 4: 1-256.
- Brünnich M.T. (1772). Zoologiae fundamenta praelectionibus acad. Acomodata. *Transaction of the Linnean Society of London*, 7: 241.
- Burmeister H. (1879). Description physique de la République Argentine d'après des observations personnelles et étrangères. 3: animaux vertébrés, 1: Mammifères vivants et éteints: 1-555. Paul-Emile Coni Editor. Buenos Aires.
- Carlini A.A. & Scillato-Yané G.J. (1999). Evolution of Quaternary Xenarthrans (Mammalia) of Argentina. In Rabassa J. & Salemme M. (eds), *Quaternary of South America and Antarctic Peninsula*, 12: 149-175.
- Cartelle C. (1999). Pleistocene mammals of the cerrado and caatinga of Brazil. In Eisenberg J.B. & Redford K.H. (eds), *Mammals of the Neotropics*. University of Chicago Press, Chicago: 27-46.
- Castro M.C., Avilla L.S., Freitas M.L. & Carlini A.A. (2013). The armadillo *Propraopus sulcatus* (Mammalia: Xenarthra) from the late Quaternary of northern Brazil and a revised synonymy with *Propraopus grandis*. *Quaternary International*, 317: 80-87.
- Cione A.L. & Tonni E.P. (2005). Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina. In De Barrio R.E., Etcheverry R.O., Caballé M.F. & Llambias E. (eds), *Geología y Recursos Minerales de la Provincia de Buenos Aires*, XVI Congreso Geológico Argentino, La Plata, 9: 183-200.
- Coltorti M., Abbazzi L., Ferretti M., Lacumin P., Paredes Ríos F., Pellegrini M., Pieruccini P., Rustioni M., Tito G. & Rook L. (2007). Last Glacial mammals in South America: a new scenario from the Tarija Basin (Bolivia). *Naturwissenschaften*, 94: 288-299.
- Coltorti M., Pieruccini P. & Paredes Ríos F. (2010). Late Pleistocene stratigraphy, sedimentology and paleoenvironmental evolution of the Tarija-Padcaya basin (Bolivian Andes). *Proceedings of the Geologists' Association*, 121: 162-179.
- Cope E.D. (1889). The Edentata of North America. *American Naturalist*, 23: 657-664.
- Cuvier G. (1796). Notice sur le squelette d'une très grande espèce de quadrupède inconnue jusqu'à présent, trouvé au Paraguay, et déposé au cabinet d'histoire naturelle de Madrid. *Magasin encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 1: 303-310.
- De Carles E. (1888). Noticias sobre un viaje a Tarija (Bolivia). *Boletín del Instituto Geográfico Argentino*, 9: 35-40.
- Desmarest A. (1804). Tableau methodique des mammiferes. Nouveau dictionnaire d'histoire naturelle. Deterville, Libraire, Paris, 24: 5-58.
- Emmons L.H. (1999). Mamíferos de los bosques húmedos de América Tropical: Una guía de campo. Primera edición en español. 298 pp. Editorial F.A.N., Bolivia.
- Fitzinger L.J. (1871). Die natürliche Familie der Gurtelthiere (Dasypodes). *Sitzungsberichte Mathematisch-Naturwissenschaftliche Klasse der Akademie der Wissenschaften, Wien*, 64: 209-276.

- Flower W.H. (1883). On the arrangement of the Orders and Families of existing Mammalia. *Proceedings of the Zoological Society of London*, 51: 178-186.
- Francia A. (2014). Vertebrados cuaternarios de Corrientes, paleoambientes, paleoclima y diversidad. Un análisis comparativo con faunas continentales equivalentes del Cono Sur de América del Sur. Tesis Doctoral. 323 pp. Universidad Nacional del Nordeste. Facultad de Ciencias Exactas, Naturales y Agrimensura.
- Francia A. & Ciancio M.R. (2013). First record of *Chaetophractus villosus* (Mammalia, Dasypodidae) in the late Pleistocene of Corrientes Province (Argentina). *Revista del Museo de La Plata, Sección Paleontología*, 13: 1-9.
- Gervais H. (1855). Recherches sur les mammifères fossiles propres à l'Amérique méridionale. *Mémoires de la Société Géologique de France*, 40: 1112-1114.
- Gervais H. & Ameghino F. (1880). Los mamíferos fósiles de la América del Sur. 235 pp. Sabih e Igon, Paris y Buenos Aires.
- Gray J.E. (1821). On the natural arrangement of vertebrate animals. *London Medical Repository*, 5: 296-310.
- Gray J.E. (1865). Revisión on the genera and species of entomophagous, Edentata, founded on examination of the specimens in British Museum. *Proceedings of the Zoological Society of London*, 33: 359-386.
- Hay O.P. (1926). A collection of Pleistocene vertebrates from southwestern Texas. *Proceedings of the United States National Museum*, 68(2625): 1-18.
- Hoffstetter R. (1952). Les Mammifères pléistocènes de la République de l'Équateur. *Mémoires de la Société Géologique de France, Nouvelle Serie*, 31: 1-391.
- Hoffstetter R. (1958). Xenarthra. In Piveteau J. (ed.), *Traité de Paléontologie*, 6, 2: 535-636.
- Hoffstetter R. (1963). La faune pléistocène de Tarija (Bolivie). *Bulletin du Muséum National d'Histoire Naturelle*, 35: 194-203.
- Illiger C. (1811). *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, XVIII, Salfeld, Berolini*: 1-301.
- Kraglievich L. (1934). La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron, Imprenta El Siglo Ilustrado: 1-133.
- Krmpotic C.M., Ciancio M.R., Barbeito C., Mario R.C. & Carlini A.A. (2009). Osteoderm morphology in recent and fossil euphractinae xenarthrans. *Acta Zoologica*, 90: 339-351.
- Linnaeus C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.
- Lund P.W. (1839). Blik paa Brasiliens Dyreverden för Sidste Jordomvaeltning Anden Afhandling: Pattedyrene. *Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematisk Afhandlinger*, 8: 61-144.
- Lund P.W. (1842). Forstatte bemaerkninger over Brasiliens uddøde dyrskabning. *Det kongelige Danske Videnskabernes. Selskabs naturvidenskabelige og mathematisk Afhandlinger*, 9: 121-136.
- MacFadden B.J. & Shockey B.J. (1997). Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: Morphological and isotopic evidence. *Paleobiology*, 23: 77-100.
- MacFadden B.J., Siles O., Zeitler P., Johnson N.M. & Campbell Jr K.E. (1983). Magnetic polarity stratigraphy of the middle Pleistocene (Ensenadan) Tarija Formation of southern Bolivia. *Quaternary Research*, 19: 172-187.
- MacFadden B.J., Zeitler P.K., Anaya F. & Cottle J.M. (2013). Middle Pleistocene age of the fossiliferous sedimentary sequence from Tarija, Bolivia. *Quaternary Research*, 79: 268-273.
- Marshall L.G. & Sempere T. (1991). The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: A review. *Revista Técnica de YPFB, Fósiles y Facies de Bolivia*, 1: 631-652.
- Oliveira É.V. & Pereira J.C. (2009). Intertropical cingulates (Mammalia, Xenarthra) from the Quaternary of Southern Brazil: systematic and paleobiogeographical aspects. *Revista Brasileira de Paleontologia*, 12: 167-178.
- Oppenheim V. (1943). La cuenca fosilífera de Tarija, Bolivia. *Notas del Museo de La Plata, Geología*, 8: 179-190 (English version: The fossiliferous basin of Tarija, Bolivia. *Journal of Geology*, 51: 548-555).
- Owen R. (1838). Fossil Mammalia, Part 1, In Darwin C. (ed.), *The Zoology of the voyage of H.S.M. Beagle*. 40 pp. Smith Elder and Co., London.
- Ribeiro A.M. & Scherer C.S. (2009). Mamíferos do Pleistoceno do Rio Grande do Sul. In Ribeiro A.M., Bauermann S.G. & Scherer C.S. (eds), *Quaternário do Rio Grande do Sul. Integrando conhecimentos*, Porto Alegre, Sociedade Brasileira de Paleontologia: 171-191.
- Rincón A.D., White R.S. & McDonald H.G. (2008). Late Pleistocene cingulates (Mammalia: Xenarthra) from Mene de Inciartaripis, Sierra de Perijá, western Venezuela. *Journal of Vertebrate Paleontology*, 28: 197-207.
- Rodríguez-Bualó S., Soibelzon E., Scarano A.C. & Zurita A.E. (2014a). *Chaetophractus tarijensis* (Xenarthra, Dasypodidae) ¿Un endemismo del Valle de Tarija (Bolivia)? Implicancias paleobiogeográficas. *Revista Brasileira de Paleontologia*, 17: 59-68.
- Rodríguez-Bualó S., Zurita A.E., Góis F., Miño-Boilini A.R., Soibelzon E. & Paredes-Ríos F. (2014b). Pampatheriidae (Xenarthra, Cingulata) from Tarija Valley, Bolivia, a taxonomic update. *Rivista Italiana di Paleontologia e Stratigrafia*, 120: 253-159.
- Scillato-Yané G.J. (1982). Los Dasypodidae (Mammalia, Edentata) del Plioceno y Pleistoceno de Argentina. Tesis Doctoral (Inédita) Facultad de Ciencias Naturales y Museo. 159 pp. Universidad Nacional de La Plata, La Plata.
- Simpson G.G. (1929). Pleistocene mammalian fauna of the Seminole field, Pinellas County, Florida. *Bulletin of the American Museum of Natural History*, 56: 561-599.
- Soibelzon E., Carlini A.A., Tonni E.P. & Soibelzon L. (2006). *Chaetophractus vellerosus* (Mammalia: Dasypodidae) in the Ensenadan (Early-Middle Pleistocene) of the southeastern Pampean region (Argentina). Paleozoogeographical and paleo-climatic aspects. *Neues Jahrbuch für Geologie und Paläontologie*, 12: 734-748.
- Squarcia S.M., Sidorkewicz N.S. & Casanave E.B. (2007). The Hypertrophy of the Tympanic Bulla in Three Species of Dasypodids (Mammalia, Xenarthra) from Argentina. *International Journal of Morphology*, 25: 597-602.
- Suarez Montero M. (1996). Geología del Cuaternario de la cuenca pleistocena de Tarija. XII Congreso Geológico de Bolivia, Memorias: 455-463.
- Takai F., Arozqueta B., Mizuno T., Yoshida A. & Kondo H. (1984). On fossil mammals from the Tarija department, Southern Bolivia. *The Research Institute of Evolutionary Biology*, 4: 1-63.
- Takai F., Mizuno T., Iwasaki Y., Tanaka K. & Yoshida A. (1982). Tarija mammal-bearing formation in Bolivia. *The Research Institute of Evolutionary Biology*, 3: 1-72.
- Thomas O. (1894). On a new specie of armadillo from Bolivia. *Annals and Magazine of Natural History*, 13: 70-72.
- Tonni E.P., Soibelzon E., Cione A.L., Carlini A.A., Scillato-Yané G.J., Zurita A.E. & Paredes Ríos F. (2009). Mammals from the Pleistocene of the Tarija Valley (Bolivia). Correlation with the Pampean chronological standard. *Quaternary International*, 210: 57-65.
- Ubilla M. & Perea D. (1999). Quaternary vertebrates of Uruguay: a biostratigraphic, biogeographic and climatic overview. *Quaternary of South America and Antarctic Peninsula*, 12: 75-90.
- Ubilla M., Perea D., Goso C. & Lorenzo N. (2004). Late Pleistocene vertebrates from northern Uruguay: tools for biostratigraphic, climatic and environmental reconstructions. *Quaternary International*, 114: 129-142.

- Wagler J.G. (1830). Natürliches System der Amphibien: mit vorangehender Classification der Säugethiere und Vögel. 354 pp. J.G. Cotta'schen Buchhandlung, München.
- Winge H. (1923). Pattedyr Slaegter. I- Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata. 360 pp. Hagarup, Copenhagen.
- Wolf T. (1875). Geognostische Mittheilungen aus Ecuador, Kritische Zusammenstellung der in Ecuador stattgefundenen Vulkan-Ausbrüche und Erdbeben seit der Zeit der Conquista. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*: 152-170, 449-472, 561-584.
- Zurita A.E., Miño-Boilini A.R., Soibelzon E., Carlini A.A., Gasparini G.M. & Paredes Ríos F. (2009). The diversity of Glyptodontidae (Xenarthra, Cingulata) in the Tarija Valley (Bolivia): systematic, biostratigraphic and paleobiogeographic aspect of a particular assemblage. *Neues Jahrbuch für Geologie und Palaontologie, Abhandlungen*, 251/2: 225-237.
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APPENDIX

Specimens examined for the comparative study

- Chaetophractus villosus* (Desmarest, 1804): AAC 98, 100, 105, 106, 122, MLP 30.XII.02.41, MLP 7.V.10.3, UCM 19930, MACN 47221.
- Propraopus grandis* Ameghino, 1881: MACN 17989, 7027, MACN-A 10989, 11108, MLP 69-IX-9-9, 69-VIII-22-3, 58-IX-3-26.
- Euphractus sexcinctus* (Linnaeus, 1758): AAC 183, 184, UCM 20492, 15963.