

PAMPATHERIIDAE (XENARTHRA, CINGULATA) FROM TARIJA VALLEY, BOLIVIA: A TAXONOMIC UPDATE

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Abstract. Pampatheriidae (Middle Miocene-late Pleistocene) constitutes an extinct clade of Cingulata widely dispersed in South America, entering in Central and North America during the Great American Biotic Interchange. In the Pleistocene of South America, two genera are recorded: *Pampatherium* (with three species) and *Holmesina* (with six species). In the Pleistocene palaeofauna of Tarija Valley (Bolivia) one of the most conspicuous recorded taxa are the Cingulata, including Pampatheriidae. Until this contribution, all the remains were classified as *P. typum* and *Pampatherium* sp. Here we present a modern taxonomic revision of the Pampatheriidae of the Tarija Valley, based on previous collected and published material together with new materials obtained from fieldwork carried out during 2011-2013. The evidence indicates that a single species of Pampatheriidae is present in the Tarija Valley (*Pampatherium humboldtii*), whereas the presence of *P. typum* is discarded. From a chrono-stratigraphic point of view, the biochron of this species is restricted to the late Pleistocene. This supports previous hypothesis on the age of the sediments of Tarija Valley (Tolomosa Formation).

Introduction

The Pampatheriidae Paula Couto, along with the Dasypodidae Gray, Glyptodontidae Burmeister, Peltephilidae Ameghino and Paleopeltidae Ameghino, comprise the clade Cingulata within the Xenarthra (McKenna & Bell 1997). The monophyly of the Pampatheriidae, which together with the Glyptodontidae comprise the

clade Glyptodontoidea, has been tested by several authors (Engelmann 1985; Carlini & Scillato-Yané 1993; Góis 2013).

The most distinctive anatomical feature of the Pampatheriidae (as well as of all the Cingulata) is the presence of a protective dorsal exoskeleton consisting of a cephalic shield, dorsal carapace, and caudal armor formed by osteoderms overlaid by horny epidermal scales (Edmund 1985; Góis et al. 2013; Góis 2013). The most evident synapomorphies of the family include: i) the scapular buckler, which is separated from the pelvic buckler by three rows of movable osteoderms (movable bands); 2) heterodont dentition, which differs from that of other armadillos by a short anterior series of oval or reniform, peglike teeth, and iii) a posterior set of bilobed teeth (Edmund 1985, 1996; Gaudin & Wible 2006).

From a chrono-stratigraphic point of view, the oldest record of an undoubted member of the Pampatheriidae is *Scirrotherium* (Edmund & Theodor 1997), from the middle Miocene of La Venta, Colombia. Later, two members of the family, *Holmesina* and *Pampatherium*, entered North America during the Great American Biotic Interchange (Scillato-Yané et al. 2005; Carlini & Zurita 2010).

During the Pleistocene and early Holocene (Ensenadan, Bonaerian and Lujanian Ages/Stages), two

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genera are recorded in South America, *Pampatherium* Gervais & Ameghino, and *Holmesina* Simpson, with different ecological requirements (see Vizcaíno et al. 1998; De Iuliis et al. 2000; Scillato-Yané et al. 2005; Góis et al. 2012b).

Góis (2013), who recognized eight Pleistocene species, carried out the most recent taxonomic and phylogenetic revision of the Pampatheriidae. In South America *Pampatherium humboldtii* (Lund), *P. typum* (Gervais & Ameghino), *Holmesina major* (Lund), *H. occidentalis* (Hoffstetter), *H. paulacoutoi* (Cartelle & Bohórquez) and *H. rondoniensis* (Góis, Scillato-Yané, Carlini & Ubilla) are present. *P. mexicanum* (Edmund) is from Central America while *Holmesina septentrionalis* (Leidy) came from Central and North America. Finally, *Holmesina floridana* (Robertson) is restricted to North America.

In this scenario, one of the most conspicuous elements of the paleofauna of the Pleistocene of Tarija Valley (Bolivia) among Xenarthra are the Pampatheriidae (see Tonni et al. 2009; Marshall & Sempere 1991; Hoffstetter 1963; Coltorti et al. 2007), mainly represented by osteoderms of the dorsal carapace. Since the first studies, most of these remains have been classified as belonging to *Pampatherium typum* (Tonni et al., 2009; Marshall & Sempere, 1991; Hoffstetter, 1963). This species has a biochron ranging from Ensenadan (early Pleistocene; Soibelzon et al. 2008) to Lujanian (late Pleistocene-early Holocene; Cione & Tonni 2005), mostly distributed in the Pampean Region and northeast of Argentina, Uruguay and Brazil (Oliveira et al. 2003; Kerber & Oliveira 2008; Oliveira & Pereira 2009; Scillato-Yané et al. 2005; Rodríguez-Bualó et al. 2009). However, and despite the abundance of remains of Pampatheriidae in Tarija Valley, no recent taxonomic revision of these pampatheres has been carried out until now.

As a result of the field work carried out during 2011, 2012 and 2013 (see Soibelzon et al. 2011; Rodríguez-Bualó et al. 2013) in many localities in the Tarija Valley, lots of remains assignable to Pampatheriidae were collected, documenting the presence of the family in new localities.

In this context, the main objectives of this study are: a) to carry out a taxonomic revision of the Pampatheriidae from Tarija Valley (Bolivia) with modern criteria; b) to discuss the chronostratigraphic implications.

Historical background of the Pampatheriidae in Tarija Valley

The first mention of a pampathere for Tarija Valley was by Hoffstetter (1963), who made the longest

and most useful fossil faunal list reported for this valley. During 1978 and 1980, paleontologists from the Research Institute of Evolutionary Biology (Tokyo, Japan) collected several fossils from Tarija Valley (see Takai et al. 1982, 1984). These researchers mentioned the presence of *Chlamytherium* (= *Pampatherium*) from the upper member of the “Tarija Formation” (= Tolomosa Formation).

Some years later, Marshall & Sempere (1991) revised the paleofaunistic contributions of Berta (1981, 1985, 1987, 1988), Liendo-Lazarte (1946), and Hoffstetter (1963, 1968, 1986), where *Pampatherium* was mentioned. In recent times, Coltorti et al. (2007) mentioned the presence of *Pampatherium typum* from the upper part of the Tolomosa Formation from the localities of Río Rugero and Monte Sur, but the material was not figured.

Finally, the last revision of the paleofauna from Tarija Valley was made by Tonni et al. (2009), who mentioned the presence of *Pampatherium* sp.

Material and methods

The chronological and biostratigraphic schemes used in this work correspond to those proposed by Cione & Tonni (2001, 2005) and Soibelzon et al. (2008), while the stratigraphy follows Coltorti et al. (2010). The systematics partially follows Edmund (1996), McKenna & Bell (1997), Scillato-Yané et al. (2005), and Góis et al. (2012b). The morphological terminology of the osteoderms follows Góis et al. (2013). All measurements were taken with a digital caliper with an error of 0.5 mm.

Institutional abbreviations:

CT: Materials collected during the field works (2011-2013), currently located in MNPA-V. CTES-PZ: Colección Paleozoología de la Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (Corrientes, Argentina). EPN: Museo de Historia Natural “Gustavo Orcés V.”, Quito, Ecuador. MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional Ameghino (A) and Colección Paleovertebrados (Pv), Ciudad Autónoma de Buenos Aires. MCL-PUC/MG: Museu de Ciências Biológicas da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte. MLP: Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Buenos Aires. MMP: Museo de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Mar del Plata, Buenos Aires, Argentina. MNPA-V: Museo Nacional Paleontológico – Arqueológico, Vertebrados, Tarija, Bolivia. PVE-F: Paleontología Villa Escolar, Formosa. UZM: Universitets Zoologisk Museum, Copenhagen, Denmark.

Geological and chronostratigraphic context of Tarija Valley

Tarija Valley (21° 31' S and 64° 43' W) is located approximately 1000 km southeast of La Paz (Bolivia; Fig. 1) and extends for approximately 4500 km², at nearly 2000 m above sea level (MacFadden & Shockey 1997; Coltorti et al. 2007). The valley is part of a Quaternary sedimentation basin, filled with fluvio-lacustrine sediments that discordantly overlie a Paleozoic

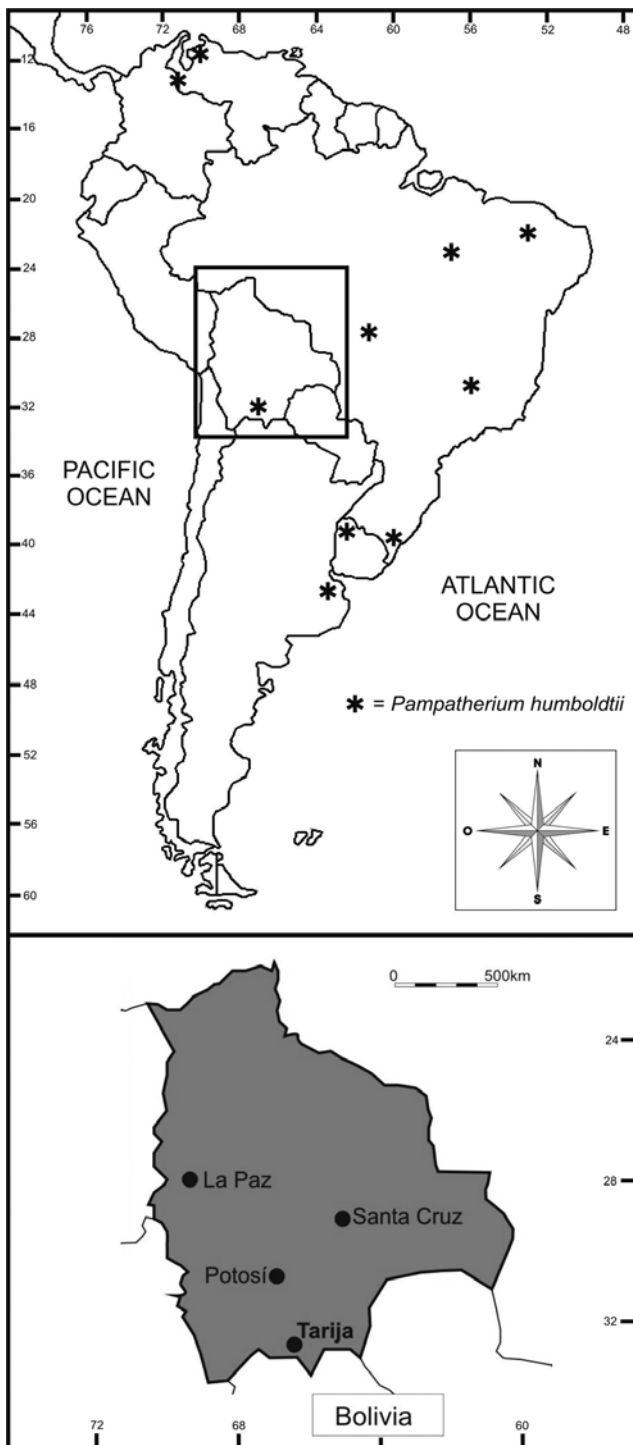


Fig. 1 - Location map showing Tarija Valley (Bolivia).

basement (Suárez-Montero 1996). The most outstanding feature of the area is the characteristic badlands landscape, with irregular relief produced by differential sediment erosion (Oppenheim 1943; Suárez-Montero 1996). Coltorti et al. (2007, 2010) included the entire Pleistocene sequence within the Tolomosa Formation, subdivided into three main subsynthem: Ancon Grande (AG), Puente Phayo (PP), and San Jacinto (SJ).

From a chrono-stratigraphic point of view, the age of the Tarija paleofauna remains problematic. Re-

cent studies, including magnetostratigraphy and numerical dating, suggest that the levels bearing fossil mammals are either Ensenadan (early Pleistocene; see MacFadden & Shockey 1997; MacFadden 2000, MacFadden et al. 2013), Lujanian (late Pleistocene; see Coltorti et al. 2007, 2010) or Ensenadan-Lujanian (Zurita et al. 2009; Tonni et al. 2009).

Systematic palaeontology

Superorder *Xenarthra* Cope, 1889

Order *Cingulata* Illiger, 1811

Family Pampatheriidae Paula Couto, 1954

Pampatherium Gervais & Ameghino, 1880

Pampatherium humboldtii (Lund, 1839).

Fig. 2

1839 *Chlamydothorium humboldtii* Lund p. 69.

1839 *Chlamytherium humboldtii* Örsted, lapsus pro Lund, 1839: 69.

1987 *Holmesina humboldtii* - Edmund, p. 4.

Syntype: UZM 150, right hemimandible fragment and one osteoderm; UZM 618, part of the left hemimandible.

Geographic and stratigraphic provenance: Caves of Lagoa Santa, Minas Gerais, Brazil. Lujanian Age/Stage, late Pleistocene – Holocene (Winge 1915; Edmund 1996).

Referred material: Many osteoderms of the dorsal carapace found in spatial and stratigraphic association, suggesting that they belong to a single specimen. This material was originally listed by Takai et al. (1984) as RIEB-CM407, and later changed to MNPA-V-005688. As mentioned, additional materials resulting from the expeditions carried out by the authors during 2011–2013, include five different individuals: CT2011-5: 25 osteoderms of the dorsal carapace; CT2011-12: 40 osteoderms of the dorsal carapace; CT2011-19: nine osteoderms of the dorsal carapace; CT 2013-1: two fixed osteoderms; CT2013-2: several osteoderms of the dorsal carapace.

Geographic and stratigraphic provenance: MNPA-V-005688, CT2011-5, CT2011-12, and CT2011-19 come from Río Rugero (21° 42' 18,8"S – 64° 45' 32,9"W). CT2013-1 comes from Monte Cercado (21°27'41.1"S-64°42'10.8"W) and CT2013-2 from Monte Sur (21°21'42.1"S-64°41'48.4"W). Until now, all the material is recovered from the San Jacinto sub-synthem, late Pleistocene in age sensu Coltorti et al. (2010).

Description

The exposed surface of the osteoderms of the pampathers from the Tarija Valley (MNPA-V-005688, CT2011-5, CT2011-12, CT2011-19, CT2013-1 and CT2013-2) shows an external ornamentation similar to those of *Pampatherium humboldtii* (MCL 900). The osteoderms of *P. humboldtii* shows a more ornate and rugose morphology than that of *P. typum*, but less than that of *P. mexicanum* and *Holmesina* spp. (see Góis, 2013). Two groups of osteoderms are described (the material used for comparison is listed in the appendix).

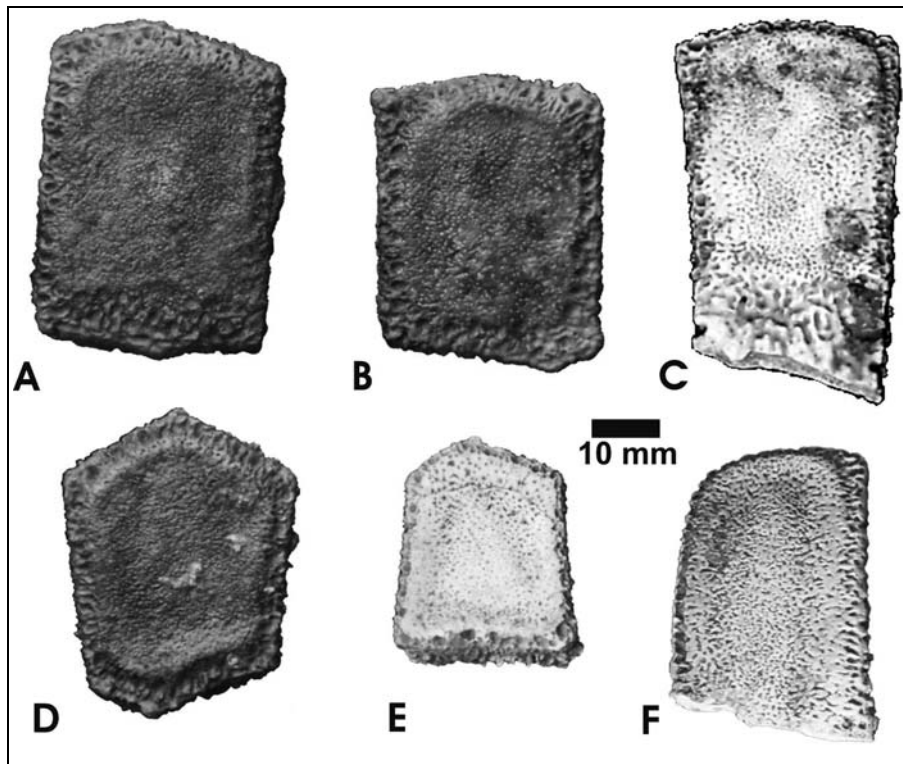


Fig. 2 - *Pampatherium humboldtii*. A, B, D, E) fixed osteoderms. C, F) Fragments of mobile osteoderms. A, B: MNPA-V-005688; C: CT2011-5; D: CT2013-1; E: CT2011-12; F: CT2013-2.

Fixed osteoderms: the osteoderms of the scapular and pelvic bucklers are 8.4 – 11.2 mm thick, as in *P. humboldtii*, this is thicker than those of *P. typum* and *H. occidentalis* but thinner than those of *H. paulacoutoi*. The wide of the lateral margins of the Tarija specimens (2.3 – 3.2 mm) falls within those of MCL 900, this wide is similar to that of *P. mexicanum* and wider than in *P. typum*. The marginal elevation is wider and higher than that of *P. typum*, but slightly less pronounced than that of *P. mexicanum* and very similar to *P. humboldtii*. The longitudinal depressions in the studied materials are as in *P. humboldtii*, and deeper than those of *P. typum* but less than those of *P. mexicanum*. The longitudinal central elevation is similar to that of *P. humboldtii* and *P. mexicanum*, but higher than that of *P. typum* and shallower than in *Holmesina*.

Mobile and semi-mobile osteoderms: most of the osteoderms from the Tarija Valley are partially preserved. They show a larger and more rugose intermediate portion than those of *P. typum* and *Holmesina* spp., similar to *P. humboldtii*. The lateral margins are 2.5 – 3.3 mm wide (as in MCL 900); this is clearly narrower than those of *Holmesina*.

Discussion

Pampatherium humboldtii has a wide paleontological record in South America. In Venezuela, it has been recorded in Zulia state (McDonald et al. 1999; Rincón et al. 2008; Rincón & White 2007; Góis et al. 2012b) from the late Pleistocene (Lujanian). In Brazil, it has been

recorded in Mato Grosso, Minas Gerais (Lagoa Santa), Tocantins (Aurora do Tocantins), Ceará and Rio Grande do Sul state (Lund 1839; Winge 1915; Edmund 1996; Scillato-Yané et al. 2005; Oliveira & Pereira 2009; Góis et al. 2012b; Avilla et al. 2012). Stratigraphic studies have been carried out only in Rio Grande do Sul, in Santa Victoria and Touro Passo Formations, both corresponding to the late Pleistocene (Oliveira & Pereira 2009). In Uruguay *P. humboldtii* has been recorded in Artigas Department (Sopas Formation, late Pleistocene) (Martinez & Ubilla 2004; Ubilla et al. 2004a, b). In Argentina, it has been recorded in Berazategui, Buenos Aires province, late Pleistocene (Góis et al. 2012a), and in Tezano-Pintos Formation (Lujanian; ca 36-9 ka; Kröhling 1999), Santa Fe province (Góis 2013).

The presence of *P. humboldtii* in the Pleistocene of Tarija Valley has biogeographic and chronological implications. From a biogeographic point of view, this is the first undoubted record of the species in Bolivia.

As mentioned above, the age of the Tolomosa Formation is a debated topic among the researchers that worked there (see Tonni et al. 2009; MacFadden et al. 2013), with ages that range between the Ensenadan Stage/Age (early Pleistocene, see MacFadden et al. 1983, 2013) and the Lujanian Stage/Age (late Pleistocene, see Coltorti et al. 2007, 2010), or Ensenadan-Lujanian (Zurita et al. 2009; Tonni et al. 2009). Until now, *P. humboldtii* has a biochron restricted to the late Pleistocene (Lujanian) (Góis 2013). Thus, the presence of this taxon in the Tolomosa Formation has two possible

explanations: a) accepting the age mentioned by MacFadden (1983, 2013), this could be the earliest record in sediments attributable to the Ensenadan Stage, which would expand the range of the taxon until the beginning of the Pleistocene; b) accepting the interpretation by Tonni et al. (2009) and Zurita et al. (2009) and according to its paleofaunistic content, the Tolomosa Formation would present a section with sediments only attributable to the upper Pleistocene (Lujanian), from which the materials here described were obtained. Moreover, the presence of this taxon in the localities of Río Rugero, Monte Cercado and Monte Sur is consistent with the recent chronostratigraphic interpretation carried out by Coltorti et al. (2007, 2010), who, through numerous C¹⁴ dates, have indicated an age limited to the late Pleistocene (between 44 ka and 21 ka).

From a paleoecological point of view, *P. humboldtii* is mostly associated with faunas that are not as eremic as those of the Late Pleistocene of the Pampean region of Argentina. In at least one case (Sopas Formation, Uruguay; see Ubilla & Perea 1999), *P. humboldtii* has been associated with fauna that may be correlated with the last Interglacial period (isotopic stage 5e). De Iuliis et al. (2000) and Scillato-Yané et al. (2005) have suggested that this species was adapted for grazing on less abrasive plants than those thought for *P. typum*.

Finally, the presence of *P. humboldtii* in Tarija Valley, together with that of other taxa such as *Neochoerus tarijensis* (Hydrochoeriidae) and *Tapirus tarijensis* (Tapiridae), indicates humid and warm conditions, in at least some periods in the Pleistocene of Tarija Valley.

Conclusions

a) The Cingulata Pampatheriidae present in the Pleistocene of Tarija Valley are restricted to *Pampather-*

ium humboldtii on the basis of the following morphological characteristics: 1) thicker osteoderms of the scapular and pelvic bucklers than those of *P. typum* and *H. occidentalis*; 2) wider lateral margins than those of *P. typum*; 3) wider and higher marginal elevation than that of *P. typum*; 4) deeper longitudinal depressions than those of *P. typum*; 5) higher longitudinal central elevation than that of *P. typum*; 6) larger and more rugose intermediate portion in mobile osteoderms than that of *P. typum* and *Holmesina* spp. Therefore, the presence of *Pampatherium typum* in the Tarija fauna is now discarded.

b) *P. humboldtii* is now recorded in Río Rugero, Monte Cercado, and Monte Sur.

c) The chrono-stratigraphic records of *P. humboldtii* in South America are limited to the Lujanian Age /Stage (late Pleistocene-early Holocene).

d) The presence of *P. humboldtii* suggests the development of humid and warm conditions during some time intervals in the Tarija Valley.

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Appendix.

List of materials used for comparison:

Pampatherium typum: PVE-F- 5; 13; 27; 35; 36; 51; 52; MLP 52-IX-28-20; 76-VIII-2-6; CTES-PZ 7332; 7518; 7516; MMP S216.

Pampatherium humboldtii: MLP 76-VIII-2-7; 81-X-30-1; MACN Pv 8490; 11681; 11905; 13731; 14264; 14737; MCL 900; 2308.

H. occidentalis: EPN, V. 1176; 1068; 1166; 1169.

H. paulacoutoi: MCL 501; MLP 69-XII-26-3; MACN Pv 11905; PVE-F 28; 55; 61; CTES-PZ 3581.

P. mexicanum: INAH 6201

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