

The diversity of Glyptodontidae (Xenarthra, Cingulata) in the Tarija Valley (Bolivia): systematic, biostratigraphic and paleobiogeographic aspects of a particular assemblage

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With 3 figures and 1 table

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Abstract: A reevaluation on the main systematic, biostratigraphic and paleobiogeographic aspects of the Glyptodontidae fauna from the Pleistocene of Tarija Valley, Bolivia, are presented. The Glyptodontidae assemblage of this area is unique with respect to faunas known for other areas of South America. Some noteworthy features are the abundance of remains assignable to genus *Glyptodon* OWEN, and the scarcity or absence of others (*Panochthus* BURMEISTER and *Neosclerocalyptus* PAULA COUTO) that are very frequent in the fossil record of the Pampean and north-central regions of Argentina. The validity of *Hoplophorus echazui* HOFFSTETTER, as well as the presence of *H. euphractus* LUND and *P. tuberculatus* (OWEN) are questioned pending discovery of more complete materials. All specimens referred to *Neothoracophorus* AMEGHINO very probably correspond to subadult *Glyptodon* specimens. Biostratigraphically, all but one of the *Glyptodon* specimens resemble those from the Middle Pleistocene – Early Holocene (Bonaerian – Lujanian) of the Pampean region in Argentina. However, one of the specimens studied (MNPA-v 006118) from the locality Armados, corresponds to the species *G. munizi* AMEGHINO, restricted to the Ensenadan (Early Middle Pleistocene) in the Pampean region.

Key words: South America, Bolivia, Pleistocene, biostratigraphy, Glyptodontidae, *Glyptodon*, palaeobiogeography, systematics.

1. Introduction

The Tarija Valley (21° 31' S and 64° 43' W) is located approximately 1000 km southeast of La Paz (Bolivia; Fig. 1); Tarija city is situated within it. The valley extends for approx. 4500 km², at nearly 2000 m above sea level (MACFADDEN & SHOCKEY 1997; COLTORTI et al. 2007).

The paleontological importance of the Tarija Valley has been evident since the times of AMEGHINO (1902) and BOULE & THÉVENIN (1920), although the first

fossil findings in the area date back to 1602 (see BOULE & THÉVENIN 1920: 1; MARSHALL & SEMPERE 1991). In this context, one of the main problems that affects most of the collections of Pleistocene mammals from the area is the lack of precise stratigraphic and geographic data for exhumed materials (HOFFSTETTER 1963; MACFADDEN 2000; TONNI et al., in press). Nevertheless, despite the uncertain provenance and specific identification of the collected materials, these have been and are still being used to propose correlations and to establish biochron-

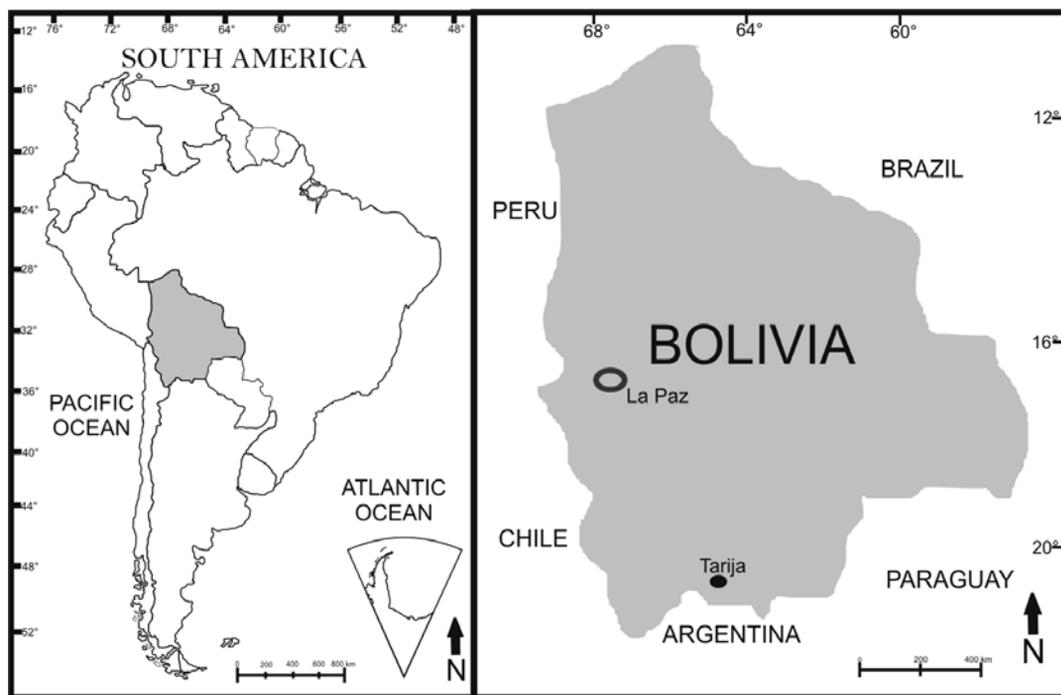


Fig. 1. Location map showing the Tarija Valley (Bolivia).

logical schemes, always in comparison to the scheme for the Pampean region of Argentina (e.g. CIONE & TONNI 1995, 1999; COLTORTI et al. 2007; CIONE et al. 2007).

Thus, from a historical perspective, the sedimentary sequences that crop out in Tarija Valley have been successively assigned to different ages and stages ranging from the Lower to the Upper Pleistocene (DE CARLES 1888; AMEGHINO 1902; ROVERETO 1914; BOULE & THÉVENIN 1920; KRAGLIEVICH 1934; OPPENHEIM 1943; PATTERSON & PASCUAL 1972; TAKAI et al. 1982, 1984; MACFADDEN et al. 1983; MACFADDEN & SHOCKEY 1997; MACFADDEN 2000; COLTORTI et al. 2007; MARSHALL et al. 1984: 33). More recently, and on the basis of a preliminary revision, SOIBELZON et al. (2007) and TONNI et al. (in press) have indicated that from a biostratigraphic viewpoint, Tarija includes taxa characteristic of the Ensenadan, Bonaerian and Lujanian interval (Early-Middle Pliocene – Early Holocene) included in the Pampean chronological standard (see CIONE & TONNI 2005).

From a geological and stratigraphical perspective, the Tarija Valley is part of a Quaternary sedimentation basin, filled with fluvio-lacustrine sediments that discordantly overlie a Paleozoic 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).

In this context, COLTORTI et al. (2007) included the entire Pleistocene sequence within the Tolomosa Formation, subdivided into two major Units: Ancón Grande Unit (AG) and San Jacinto Unit (SJ). The transition from AG Unit to SJ Unit is evident along most of the *badlands*. The upper part (SJ) is yellowish-gray and fine-grained. The lower part (AG) is reddish and coarser-grained (see more details in TONNI et al. in press).

The fossil mammal fauna exhumed from the Tarija Valley comprises a wide taxonomical diversity (ca. 55 species; HOFFSTETTER 1963; MACFADDEN 2000), including taxa characteristic for both forested or sub-forested, relatively warm and humid environments (e.g. *Tapirus* BRÜNICH, *Myocastor* KERR, *Neochoeerus* HAY) as well as others adapted to open, arid or semiarid and cold areas where grasslands are dominant (*Equus* LINNAEUS, Camelidae, Glyptodontidae) (MACFADDEN & SHOCKEY 1997). Some palynological studies (TAKAI et al. 1982) suggest that during most of the Pleistocene, the Valley was dominated by an open semiarid environment occupied by grasslands, with

scattered trees and shrubs that occurred along water courses.

The Xenarthra (Cingulata and Tardigrada) are some of the most frequent faunal elements; approximately 12 genera have been recognized (see HOFFSTETTER 1963; TAKAI et al. 1982, 1984; COLTORTI et al. 2007), 4 of which correspond to Glyptodontidae: *Neothracophorus* AMEGHINO, *Panochthus* BURMEISTER, *Hoplophorus* LUND, and *Glyptodon* OWEN.

Here, we discuss the taxonomical identifications of Xenarthra Glyptodontidae that allegedly occur in sediments from the Tarija Valley (Bolivia), their main paleobiogeographical features and their biostratigraphic implications.

Abbreviations: GCF, Grupo Conservacionista de Fósiles, Museo Paleontológico Fray Manuel de Torres (San Pedro, Buenos Aires, Argentina); MACN, Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina); MCA, Museo de Ciencias Naturales “Carlos Ameghino” (Mercedes, Buenos Aires, Argentina); MFCA, Museo Universitario “Florentino y Carlos Ameghino”, Universidad Nacional de Rosario (ex Instituto de Fisiografía y Geología “Alfredo Castellanos”) (Rosario, Argentina); MLP, Colección Paleontología de Vertebrados, Museo de La Plata (La Plata, Argentina); MMP, Museo Municipal de Ciencias Naturales del Mar del Plata “Lorenzo Scaglia” (Mar del Plata, Argentina); MNHNP, Muséum National d’Histoire Naturelle, Paris (France); MNK-PAL, Colección Paleontología del Museo de Historia Natural Noel Kempf Mercado (Santa Cruz de la Sierra, Bolivia); MNPA-V, Museo Nacional Paleontológico – Arqueológico, Vertebrados (Tarija, Bolivia).

2. Taxonomic, biostratigraphic, and paleobiogeographic context of the Cingulata Glyptodontidae from the Tarija Valley, Bolivia

Cingulata Glyptodontidae are among the most frequent elements of the megafauna known for the Tarija Valley (HOFFSTETTER 1963; WERDELIN 1991; COLTORTI et al. 2007) and were first described by AMEGHINO (1902) and BOULE & THÉVENIN (1920), although the greatest contributions correspond to HOFFSTETTER (1963, 1964), TAKAI et al. (1982, 1984) and WERDELIN (1991).

From a taxonomical perspective, and taking into account the existing associations and the frequency of records, the ensemble of Cingulata Glyptodontidae exhumed from the Tarija Valley shows some significant differences with respect to the associations known for the Pleistocene of the Pampean region,

central-northern Argentina, Paraguay, western Uruguay and even with the locality Ñuapua (20° 52’ S and 63° 04’ W), in southeastern Bolivia. In these latter areas, the dominant taxa are the genera *Glyptodon*, *Neosclerocalyptus*, *Panochthus* and, to a lesser extent, *Doedicurus* BURMEISTER (AMEGHINO 1889; HOFFSTETTER 1968, 1978; MARSHALL et al. 1984; SCILLATO-YANÉ et al. 1995; CARLINI & SCILLATO-YANÉ 1999; CARLINI & TONNI 2000; BÁEZ-PRESSER et al. 2004; UBILLA 2004; ZURITA et al. 2004; Zurita 2007).

The composition of the glyptodont association is remarkably different in Tarija Valley, where more than 90% of the records correspond to the genus *Glyptodon*. In this sense, most of the materials have been traditionally assigned to the species *G. reticulatus* OWEN (AMEGHINO 1902; HOFFSTETTER 1963; TAKAI et al. 1982, 1984; WERDELIN 1991; MARSHALL & SEMPERE 1991; COLTORTI et al. 2007) and *G. clavipes* OWEN (BOULE & THÉVENIN 1920). However, and contrasting with the case of the North American Glyptodontinae that have been recently reviewed using modern systematic criteria (GILLETTE & RAY 1981), thus far, no similar updated study has been made for the South American taxa (SOIBELZON et al. 2006). In the South American case, several species included in the genus *Glyptodon* were recognized by numerous authors (e.g. OWEN 1839, 1845; BURMEISTER 1866; AMEGHINO 1881, 1883, 1889) mainly on the basis of dorsal carapace fragments. This clearly typological species concept (see MAYR 1996), characteristic of the 19th century (GIRAUDO 1997; TINAUT & RUANO 2000), has indubitably led to remarkable overestimation of the specific diversity of this genus (DUARTE 1997), a phenomenon that had already been noted by AMEGHINO (1889) himself. One of the direct consequences of this peculiar situation is the lack of morphological support for many species assignments. Despite this evident constraint, the numerous materials (mainly skulls, mandibles and dorsal carapaces) referable to *Glyptodon* deposited in the collections of MNPA-V (e.g. MNPA-V 006084, 006088, 006119, 006102, 006077) (Fig. 1A), in addition to the specimens illustrated by TAKAI et al. (1982: 26 f., 27, figs. 20-22), show morphological similarities to the specimens collected from the Middle Pleistocene – Early Holocene of the Pampean region (Bonaerian and Lujanian Stages; see BURMEISTER 1870-1874, pls. 25-28; AMEGHINO 1889, pl. 52, fig. 1; LYDEKKER 1894, pls. 4-5, MLP 18, MCA 2015, 1086) (Fig. 3; Table 1). Although most specimens lack precise stratigraphic and geographical provenance such data

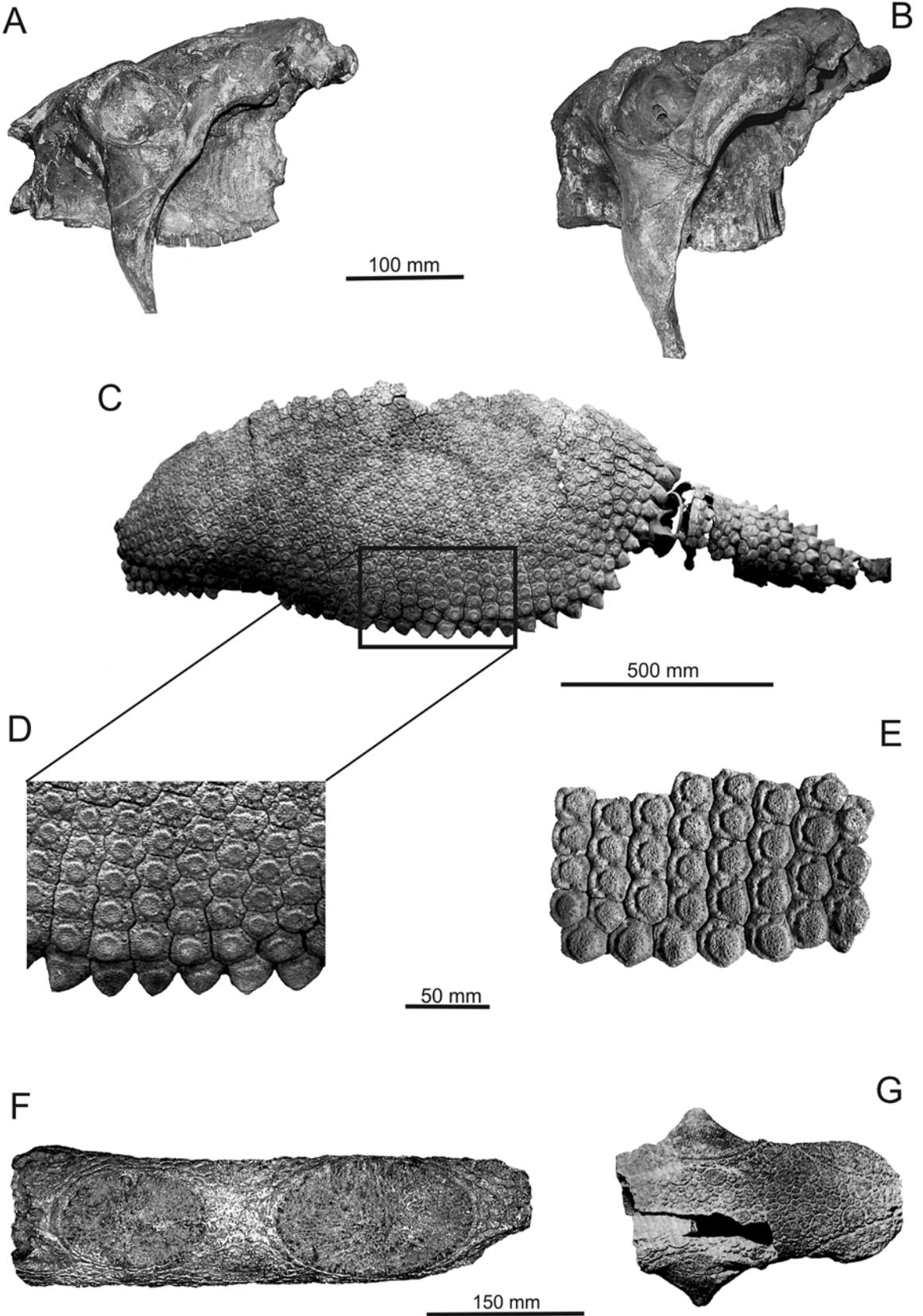


Fig. 2 (Legend see p. 229)

Table 1. Comparative measurements (in mm) of the Glyptodontinae species present in the Tarija Valley.

Taxa	<i>Glyptodon munizi</i> (MNPA V - 006118)	<i>Glyptodon</i> sp.		
		MNPA V - 006084	MNPA V - 006088	MNPA -V 006103
Measurements				
Skull				
Length	280	295	281	----
Maximum transverse diameter between zygomatic arches	265	251	280	----
Transverse diameter between lacrimals	170	142	150	----
Transverse diameter of postorbital region	112	111	112	----
Height of skull (M8 sagittal crest)	199	180	210	----
Height of narial aperture	85	71	79	----
Transverse diameter of narial aperture	95	90	85	----
Length of palate	235	230	234	----
Length of toothrows	185	200	200	----
Mandible				
Length	----	----	345	270
Length of toothrows	----	----	216	205
Anteroposterior diameter of ascending ramus at alveolar level	----	132	148	106

are available for at least some of them [MNPA-V 006088 from the locality San Pedro, Tarija Valley; and the materials illustrated by TAKAI et al. (1982: 27, fig. 21), from the upper member of “Tarija” Formation (= Tolomosa Formation; see SUÁREZ SORUCO & DÍAZ MARTÍNEZ 1996) (*sic* TAKAI et al. 1982: 11).

Recently, SOIBELZON et al. (2006) have provided an enhanced morphological and stratigraphical characterization of *G. munizi* AMEGHINO, which is at present the only species of *Glyptodon* that occurs with certainty in the Ensenadan Stage (Early-Middle Pleistocene), outcropping at the “Toscas” del Río de La Plata (MACN 8706), San Pedro (GCF 10) and Mar del Plata (MMP 3985), in the Pampean region of Argentina). Furthermore, a specimen assignable to *G.*

munizi (MNPA-V 006118), exhumed from the locality Armados, 40 km South from Tarija, has been found in the collections of MNPA (see TAKAI et al. 1984: 55) (Fig. 2B). This species is characterized by a robust skull with great dorso-ventral diameter; in addition, the skull is more elongated than that of Middle Pleistocene – Late Pleistocene forms, with markedly narrow region between the postorbital apophyses and the supraoccipital crest; clearly developed antero-inferior margin of the orbital notch and lower third of descending processes of maxillaries, and first molariform with more primitive morphology (see SOIBELZON et al. 2006) (Table 1). The presence of this glyptodontine in the Tarija Valley represents an important biostratigraphical observation, because it im-

Fig. 2. Skull in lateral view. **A** – *Glyptodon* sp. (MNPA-V 006084). **B** – *Glyptodon munizi* (MNPA-V 006118). **C** – *Glyptodon* cf. *elongatus*, dorsal carapace of a juvenile specimen (MCA 2017). **D** – Detail of lateral osteoderms (MCA 2017). **E** – *Glyptodon* sp. (originally classified as *Neothoracophorus*), lateral osteoderms of a juvenile specimen (MNPA-V 005423). **F** – *Panochthus* sp., proximal fragments of a caudal tube (MNPA-V 006598). **G** – *Hoplophorus echezui*, distal portion of a caudal tube (MNPA-V 142).

plies the presence of some levels of Ensenadan age, at least at the locality Armados (Fig. 3). Another remarkable aspect is that the fossilization type of this specimen is quite different from that of most materials referred to Tarija Valley, as it is heavily mineralized (in contrast to the very poor mineralization of other materials).

The other taxon that occurs exclusively in the Ensenadan of the Pampean region and has been found in Tarija Valley is the Ursidae *Arctotherium angustidens* GÉRAVIS & AMEGHINO; regrettably, the material lacks well-defined geographical or stratigraphical provenance (SOIBELZON 2004; SOIBELZON et al. 2005). It is noteworthy that its fossilization type is the same as that of the *G. munizi* specimen.

From a palaeobiogeographical perspective, the species of *Glyptodon* were the most frequent Pleistocene Glyptodontidae from approximately 22° S to 4° N (BOMBIN 1981; MARSHALL et al. 1984; MARSHALL & SALINAS 1991; PUJOS & SALAS 2004; CARLINI et al. 2008a, b) probably following “para-Andean” corridors (CARLINI & ZURITA 2007; CARLINI et al. 2008a). In the region of the Cusco Valley, Peru, remains of *Glyptodon* cf. *G. clavipes* have been cited at an altitude of 3350 m above sea level (HOFFSTETTER 1970; PUJOS & SALAS 2004), while MARSHALL & SALINAS (1991) have reported the presence of this genus in Ulloma Formation, Bolivia, at over 3880 m above sea level. In this context, BENJAMIN et al. (1987) estimate that the uplift of Eastern Cordillera in Bolivia and Peru accelerate at the beginning of the Quaternary, reaching a uplift rate of 0.7 mm/yr (see also REGUERO et al., 2007). In Venezuela, the Glyptodontidae from the Late Pleistocene that had traditionally been assigned to *Glyptodon* (see BOCQUENTIN VILLANUEVA 1982; AGUILERA 2006; RINCÓN et al. 2008) actually correspond to the genus *Glyptotherium* Osborn (see CIONE et al. 2007; CARLINI et al. 2008a).

Glyptodon is also one of the most frequent taxa recorded on the “Atlantic” eastern slope in southern Brazil, but in this area it is associated with other Glyptodontidae, particularly *Panochthus*, as far as 5° S (PAULA COUTO 1979; PORPINO & BERGQVIST 2002; PORPINO et al. 2004; DANTAS & ZUCON 2005; DA SILVA et al. 2006). The presence of the Equidae *Equus* (A.) *neogeus* LUND associated with *Glyptodon* at these latitudes allows the existence of open savanna-type environments to be inferred during the Late Pleistocene of that region (see ALBERDI et al. 2003). The genus has also been recorded in Bahia (Brazil) synchronically associated with typical “pampean”

forms (e.g. *Toxodon platensis* OWEN, *Morenelaphus* sp.) as well as intertropical taxa (e.g. *Trigonodops lopesi*, *Xenorhinotherium bahiense*) (CARTELLE & DE IULIIS 1995). An association of *Panochthus* – *Glyptodon* has also been observed in the south-western Amazon region, in sediments corresponding to the Last Glacial Maximum (RANCY 1992; LATRUBESSE & FRANZINELLI 1995; RANZI 2000). The remarkable absence of Cingulata Glyptodontidae in the area of the Amazon Basin could be related to the existence of a cold-arid to warm-humid climatic and environmental gradient with a north-western orientation (MARSHALL et al. 1984; CARTELLE & LESSA 1988; OLIVEIRA 1996). Nevertheless, the evidence suggests that during the latest Pleistocene, the dominant habitats in Brazil were characterized by open or semi-forested environments (MARSHALL et al. 1984; PASCUAL & ORTIZ-JAUREGUIZAR 1990; PENNINGTON et al. 2000), although fluvial systems were present that could have acted as biogeographical barriers. Southwards (Rio Grande do Sul State, western Uruguay and Argentine Mesopotamia) this association also includes the genus *Neuryurus* AMEGHINO and, in much lower proportion, *Doedicurus* (CARLINI et al. 2004, 2008; NORIEGA et al. 2004; UBILLA 2004; UBILLA et al. 2004; RIBEIRO et al. 2007).

Another interesting feature of the Tarija Valley is the absence of genera such as *Neosclerocalyptus* (see ZURITA 2007) and the evident scarcity of others such as *Panochthus*. Remarkably, *Neosclerocalyptus*, which is one of the most common forms in the Pampean region and north-central Argentina (ZURITA et al. 2005; ZURITA 2007), is recorded again further northwards, at the locality of Santa Cruz de la Sierra (17° 47' S and 63° 11' W), and at much lesser altitude (ca. 439 m); this material, deposited in MNK-PAL, also represents the northernmost record of this genus.

Panochthus is very rare in the Tarija Valley; this genus is represented only by one isolated osteoderm from the mid-central region of the dorsal carapace and fragments of a caudal armor (MNPA-V 006598) (Fig. 2F). A new analysis of these specimens indicates that the original assignation made by HOFFSTETTER (1964: 131-132) as *Panochthus* cf. *P. tuberculatus* has no morphological support, and that it can only be sustained at the genus level (Fig. 3). Particularly, the reticular ornamentation pattern of the dorsal carapace osteoderm and fragments of caudal armor is a character useful for generic identification only (see CASTELLANOS 1941; PORPINO & BERGQVIST 2002,

Ma	EPOCHS	AGE	S. AMERICAN STAGES	BIOCHRON OF THE TAXA IN THE PAMPEAN REGION (ARGENTINA)					
				1	2	3	4	5	
	HOLOCENE		PLATAN						
		LATE	LUJANIAN	■		■	■		
		MIDDLE	BONAERIAN	■					
0.5	PLEISTOCENE	EARLY	ENSENADAN		■	■			
1					■	■		■	
2									

Fig. 3. Chronological distribution in the Pampean region of the Cingulata Glyptodontidae (except *Hoplophorus*) present in the Tarija Valley. 1 – *Glyptodon* sp. 2 – *Glyptodon munizi*. 3 – *Panochthus*. 4 – *Hoplophorus*. 5 – *?Neothoracophorus*.

among others). Future findings of more complete materials may allow a more precise determination.

Hoplophorus echazui HOFFSTETTER is a species that thus far has only been recorded in this area (HOFFSTETTER 1964); it is known only from the holotype (MNPA-V 142; distal portion of a caudal armour), several dorsal carapace fragments, and one caudal ring osteoderm (MNPA-V 141) (Fig. 2G). Among others, the diagnostic characters provided by its author that distinguish this taxon from the other recognized species (*H. euphractus*), an intertropical form from the late Pleistocene of Minas Gerais, Brazil (LUND 1839; PAULA COUTO 1957; CARTELLE & DE IULIIS 1995; RANZI 2000), include the following: a) lateral margins of distal end of caudal armor more parallel to each other than in *H. euphractus*, b) sheath tip more rounded, with fewer peripheral figures on its dorsal surface, and c) central figures that tend to be more clearly circular than in *H. euphractus*. It is worth noting that these morphological characters show high intraspecific variability in the Hoplophorinae Hoplophorini (ZURITA 2007). In addition, the ornamentation of the dorsal carapace osteoderms does not show any diagnostic features, and these plates are virtually identical to those of *H. euphractus*, as recognized by the author himself (HOFFSTETTER 1963: 128). Each osteoderm is characterized by a central figure encircled by a row of peripheral figures, creating the rosette-type pattern typical of the Hoplophorinae

Hoplophorini, with parabolic transversal section of both main and radial sulci (ZURITA 2007). To sum up, the extremely fragmentary nature of this material, together with the lack of clear diagnostic characters, suggest that the validity of this species should be provisional, pending the discovery of more complete materials. HOFFSTETTER himself (1964: 131) acknowledged this limitation when he stated: “*Il conviendra cependant de réviser cette interprétation provisoire lorsqu’ on connaîtra plusieurs tubes caudaux de chacune de ces formes, et qu’ on sera en mesure de préciser leurs variations respectives*”. Consequently, although this material undoubtedly corresponds to the genus *Hoplophorus* (Fig. 3), the validity of the species *H. echazui* is uncertain.

Lastly, TAKAI et al. (1984, pl. 20, figs. 50-52), as part of a paleofaunal survey, have reported and illustrated *H. euphractus* in the Pleistocene of Tarija, represented by approximately six isolated dorsal carapace osteoderms. As in the case of *H. echazui*, these osteoderms show only the typical rosette-type ornamentation. The absence of diagnostic features, combined with the scarcity and poor preservation of the material, preclude any specific assignment. As in the previous case, referral to the genus *Hoplophorus* is supported by the rugosity of the exposed osteoderm surface, greater than that of *Neosclerocalyptus* (PAULA COUTO 1957; ZURITA 2007).

Another Glyptodontidae recognized for the Tarija Valley is *Neothoracophorus* AMEGHINO. The occurrence of this taxon has been mentioned by several authors, including HOFFSTETTER (1963, 1964), MARSHALL et al. (1984) and COLTORTI et al. (2007), although none of these workers have justified this assignation or illustrated the materials in question. The dorsal carapace of this genus is formed by small but extremely thick osteoderms, with practically no visible lateral sutures. Each osteoderm comprises a relatively large and elevated central figure surrounded by a series of large foramina (AMEGHINO 1889; CASTELLANOS 1951). Currently, this Pleistocene genus includes one species, *N. elevatus* (NODOT) (Fig. 3), which is only known from isolated dorsal carapace osteoderms. The holotype of this species (MNHN BRD 20; see MONES 1994) consists of a fragmentary dorsal carapace in relatively poor preservation state; the latter circumstance, according to AMEGHINO (1889: 791), precluded detailed study of the specimen. However, the characters provided originally by NODOT (1857) and later by AMEGHINO (1889) imply that this could actually be a juvenile specimen (e.g. small-sized osteoderms, large foramina and lax sutures). In addition, its stratigraphic provenance is not precise, although it has been tentatively assigned to the Pleistocene (MONES 1986). As a consequence of these factors, this is certainly the least known and worst characterized of the Pleistocene Glyptodontidae (PAULA COUTO 1979). For the Tarija Valley, only COLTORTI et al. (2007: 7, fig. 3a) have illustrated the material, consisting of 9 osteoderms from the lateral region of a dorsal carapace. However, this specimen cannot be referred to *Neothoracophorus* because the exposed surface of the osteoderms is flat and smooth, and they are larger, with no evident foramina. This combination of characters refutes the assignation made by these authors. In this context, the remarkable morphological similarity between the dorsal carapace osteoderms of juvenile *Glyptodon* specimens (see LYDEKKER 1894; RINDERKNECHT 2000) and those that have been referred by different authors (e.g. CASTELLANOS 1951) to *Neothoracophorus*, together with the evident scarcity of records, suggest that this latter genus is probably a synonym of *Glyptodon*, something that had already been noted by certain authors (see CASTELLANOS 1951: 74-75). Furthermore, the type species was originally assigned to genus *Glyptodon* (*G. elevatus* NODOT) and later transferred to *Thoracophorus* by GERVAIS & AMEGHINO (1880). Finally, AMEGHINO (1889) replaced the genus name (since it was pre-

occupied), and erected *Neothoracophorus* (see CASTELLANOS 1951).

The examination of the materials deposited in the Museo Nacional Paleontológico – Arqueológico de Tarija (Bolivia) that have been referred to *Neothoracophorus* does not reveal significant differences when compared to dorsal carapace osteoderms from juvenile *Glyptodon* specimens (e.g. MCFA 760, MCA 2017, LYDEKKER 1894, pl. 2) (Fig. 2C-D). In particular, the dorsal carapace osteoderms of these juveniles are characterized by: a) relatively small but very thick osteoderms, mostly pentagonal or hexagonal, b) presence of a protruding central figure, surrounded by a row of poorly defined peripheral figures, c) evident foramina at the intersection of the main and radial sulci, d) poorly co-ossified sutures between osteoderms (Fig. 2D). In a word, this morphology is not much different from the diagnostic features of *Neothoracophorus*. Furthermore, in the locality Rugero (situated about 40 km south of Tarija), one of the richest fossiliferous sites of the Tarija Valley (see TAKAI et al. 1982; COLTORTI et al. 2007), large fragments of *Glyptodon* carapace have been observed in close spatial and stratigraphic association with smaller fragments with similar morphology to that of the materials assigned to *Neothoracophorus* (Fig. 2E)

To sum up, most of the evidence strongly suggests that, at least in Tarija Valley, the records assigned to *Neothoracophorus* actually correspond to juvenile *Glyptodon* specimens. Along these lines, it cannot be ruled out that *Neothoracophorus* is a synonym of *Glyptodon*, although testing this hypothesis would require a more complete revision.

3. Discussion of results

As previously discussed, the association of Cingulata Glyptodontidae exhumed from the Tarija Valley (Bolivia) is substantially different from the assemblages known for other regions of South America (e.g. Chacoan-Pampean region, continued in the eastern “Atlantic” sector of south Brazil, and subandean areas) and permits the paleofaunal and paleobiogeographical characterization of this particular region, situated between the Andean Altiplano, the Amazon region and the Chacoan-Pampean area (MOURGUIART et al. 1997). As stated by COLTORTI et al. (2007), the mammalian faunal assemblage exhumed from Tarija Valley includes taxa characteristic of both flatlands and higher altitude environments (*Hippocamelus* LEUCKART, *Cuvieronius hyodon* FISCHER).

In this context, the almost exclusively dominant glyptodonts in Tarija Valley belong to genus *Glyptodon*; eastwards and northwards, and in parallel to subandean areas, this taxon is practically the only glyptodont occurring up to 4° N (BOMBIN 1981; MARSHALL & SALINAS 1991; PUJOS & SALAS 2004; CARLINI et al. 2008a).

In contrast, some genera that are very frequent in the Chaco-Pampean plains, such as *Neosclerocalyptus*, are absent from Tarija's fossil record. Others, such as *Panochthus*, which have a good record in the lateral eastern portion of South America between 5° S and 22° S, are quite poorly represented in the Tarija Valley. In addition, the validity of *H. echazui* and the presence of an intertropical taxon such as *H. euphractus* (see RANZI 2000; CARTELLE & DE IULIIS 1995) in Tarija Valley are unconfirmed until new and more complete specimens are found. The current available evidence only allows confirmation of the presence of the genus *Hoplophorus*.

Apart from this, the presence and validity of the poorly known genus *Neothoracophorus* is highly uncertain. This is due, on one hand, to the fact that the published records were never illustrated or their assignments justified, and on the other hand, the analysis of those materials deposited in the collections of MNPA-V strongly suggests that these correspond to juvenile *Glyptodon* specimens.

From a biostratigraphical perspective, the Glyptodontidae (*Glyptodon*) are important for the resolution of the problematic chrono-stratigraphy of this area. On several occasions, MACFADDEN and collaborators have supported an age of 1.1 to 0.7 Ma for the entire sequence (see MACFADDEN & SHOCKEY 1997; MACFADDEN et al 1983; MACFADDEN 2000). However, a possible Lujanian age had already been suggested by some authors (e.g. CASAMIQUELA 1969; MARSHALL et al. 1984; HOFFSTETTER 1986), for at least some areas of the Tarija Valley. More recently, COLTORTI et al. (2007), adopting a completely different perspective, have proposed a much younger age of between 44 and 21 ka. Likewise, TONNI et al. (in press) remark that the paleofaunal association of Tarija Valley comprises taxa whose biochrons in the Pampean region fall within the Ensenadan-Lujanian interval (Early-Middle Pliocene – Early Holocene) (see CIONE & TONNI 1995, 1999, 2005), and that at present it is not possible to assume that the entire sequence necessarily corresponds to only one of those intervals.

It is also important to remark that, although the species of *Glyptodon* are in need of urgent revision, the morphology of all the exhumed specimens but one is similar to that of the specimens known from the Middle Pleistocene (Bonaerian) and Late Pleistocene – Early Holocene (Lujanian) of the Pampean region. However, the exceptional specimen deposited in the collection MNPA-V, from the locality Armados, corresponds to the species *G. munizi*, whose stratigraphic distribution in the Pampean region is limited to the Ensenadan (AMEGHINO 1881; SOIBELZON et al. 2006). This specimen, in addition to being the first record of the taxon outside the Pampean region, would be the only Ensenadan taxon with precise geographical provenance.

4. Conclusions

From a taxonomic perspective, the Glyptodontidae present in the Tarija Valley (Bolivia) are represented with certainty by the genera *Glyptodon*, *Panochthus* and *Hoplophorus*.

The presence of the species *H. echazui*, *H. euphractus* and *P. tuberculatus* is conditional pending discovery of more complete materials.,

The records of *Neothoracophorus* correspond with high probability to juvenile *Glyptodon* specimens.

From a taxonomical-stratigraphic viewpoint, the great majority of *Glyptodon* specimens are morphologically similar to those exhumed from the Middle Pleistocene – Early Holocene of the Pampean region in Argentina (Bonaerian-Lujanian stages).

Nevertheless, one of the specimens (from the locality Armados) is assignable to the species *G. munizi*, whose stratigraphic distribution is restricted to the Ensenadan Stage (Early – Middle Pleistocene) in the Pampean region of Argentina, and this is the first record of this taxon outside this region.

The assemblage of Cingulata Glyptodontidae from the Tarija Valley differs from those known for the Chacoan-Pampean region, southern Brazil and western Uruguay. In this context, the remarkable frequency of *Glyptodon* records and the scarcity of *Panochthus*, as well as the absence of *Neosclerocalyptus*, one of the commonest taxa in the chacoan-pampean plains, are noteworthy.

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