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An exceptional Pleistocene specimen of *Panochthus* Burmeister (*Xenarthra*, *Glyptodontoidea*) from Bolivia: Its contribution to the understanding of the Early-Middle Pleistocene *Panochthini*

Un spécimen exceptionnel de Panochthus Burmeister (Xenarthra, Glyptodontoidea) du Pléistocène de la Bolivie : sa contribution à la compréhension des Panochthini du Pléistocène inférieur-moyen

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ABSTRACT

Knowledge of the Early-Middle Pleistocene (Ensenadan Age/Stage; ca. 1.8–0.4 Ma) South American Glyptodontidae (Cingulata) is still poor compared with the Late Pleistocene–Early Holocene taxa (Lujanian Age/Stage). This is especially true for the Glyptodontidae *Panochthini*, in which it is possible to recognize two Ensenadan species from the Pampean region of Argentina, *Panochthus intermedius* and *P. subintermedius*, known only by their type material. Prior to this contribution, the knowledge of *P. intermedius*, a taxon with bios-tratigraphic importance for being considered as a guide taxon of the Ensenadan Age/Stage of South America, was limited to a dorsal carapace. The finding of an exceptional almost complete specimen from the Early-Middle Pleistocene of Bolivia has allowed us to greatly improve the morphological characterization of this species, and discuss some taxonomic aspects related to the other Ensenadan *Panochthini*. This specimen represents the most completely known *Panochthini* and one of the most complete Glyptodontidae from the Early-Middle Pleistocene of South America.

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R É S U M É

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La connaissance de Glyptodontidae (Cingulata) de l'étage/âge Ensenadéen (1,8–0,4 Ma) d'Amérique du Sud est encore pauvre, en comparaison des taxons de la période fini – Pléistocène – début de l'Holocène (étage/âge Lujanéen). Cela est particulièrement vrai pour les Glyptodontidae *Panochthini*, chez lesquels il est possible de reconnaître deux espèces de l'Ensenadéen provenant de la Pampa argentine, *Panochthus intermedius* et *P. subintermedius* connues, seulement par leur matériel type. Avant le travail ici présenté,

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la connaissance de *P. intermedius*, taxon d'importance biostratigraphique suffisante pour être considéré comme un taxon guide de l'étage/âge Ensenadéen d'Amérique du Sud, était limité à une carapace dorsale. La découverte d'un spécimen exceptionnel, presque complet du Pléistocène inférieur-moyen de Bolivie nous a permis d'améliorer grandement la caractérisation morphologique de cette espèce et de discuter de certains aspects taxonomiques en relation avec d'autres Panochthini ensenadéens. Ce spécimen représente le Panochthini le plus complet connu et l'un des Glyptodontidae le plus complet du Pléistocène inférieur-moyen d'Amérique du Sud.

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1. Introduction

Among the Cingulata Glyptodontidae (Xenarthra) from South America, one interesting taxon is the tribe Panochthini. The first record of this clade corresponds to the genus *Nopachthus*, *N. coagmentatus* (Ameghino, 1888a, 1888b) and *N. trouessarti* (Moreno, 1888), from the "Brocherense" (*sensu* Castellanos, 1942a; Late Miocene-Pliocene?), and from the Monte Hermoso Formation (Montehermosan Age/Stage, Late Miocene-Pliocene) of the current territory of Argentina, respectively (Castellanos, 1942a, 1942b). Recently, Zamorano et al. (2011) have suggested that *N. trouessarti* does not belong to this genus, but to *Phlyctaenopyga*. If this is the case, this species could be interpreted as belonging to the tribe Plophorini ("Hoplophorinae"). The other Tertiary genus is *Propanochthus*, *P. bullifer* (Burmeister, 1870–1874), coming from the "Brocherense" of Córdoba province (Castellanos, 1942b; Lydekker, 1894).

Later, in the Pleistocene (ca. 2.588–0.0117 Ma), the only recorded genus in the tribe Panochthini is *Panochthus* Burmeister. From a paleobiogeographic point of view, this Pleistocene taxon seems to be restricted to the southern and northeastern regions of South America (Chaco-pampean and Mesopotamic regions of Argentina, Tarija (Bolivia), Paraguay, western sector of Uruguay and southern and northeastern Brazil (Carlini and Tonni, 2000; Porpino and Bergqvist, 2002; Porpino et al., 2004; Ubilla et al., 2004; Zurita et al., 2009). The main synapomorphy characterizing the genus includes a particular reticular pattern of the exposed surface of the osteoderms of the dorsal carapace, especially evident in its dorsal area. In addition, the caudal tube shows a similar ornamentation pattern in its dorsal and ventral surfaces, and the lateral margins present some very characteristic depressions (five to seven) with rough surface, which probably represent the area of insertion of conical spines (Castellanos, 1927, 1942b).

The last taxonomic revision of the genus was carried out by Castellanos (1942), who recognized six species: *P. intermedius* (Lydekker, 1894), *P. subintermedius* (Castellanos, 1942b), *P. frenzelianus* (Ameghino, 1889), *P. morenoi* (Ameghino, 1881), *P. vogthi* (Ameghino, 1889), and *P. tuberculatus* (Owen, 1845), and described three new species: *P. rusconii*, *P. oliveira-roxoi* and *P. greslebini*. Later, Moreira (1965) recognized a new intertropical species, *P. jaguaribensis*. Porpino and Bergqvist (2002) synonymized *P. oliveira-roxoi* with *P. greslebini*.

From a morphological perspective, the species of the Ensenadan Age/Stage (Early-Middle Pleistocene),

P. intermedius and *P. subintermedius*, preserve a rosette pattern (a central figure surrounded by one or more rows of peripheral figures) in the osteoderms located in the anterior and/or posterior and lateral areas of the dorsal carapace (Cruz et al., 2010; Lydekker, 1894); in contrast, the most derived forms (*P. tuberculatus*, *P. frenzelianus*, *P. morenoi*, *P. vogthi*, but see Zamorano, 2009) from the Lujanian Age/Stage (Late Pleistocene-early Holocene) show an almost entire reticular pattern in its dorsal carapace (Castellanos, 1942b).

As already mentioned, the only two valid species from the Ensenadan Age/Stage are *P. intermedius* and *P. subintermedius*, the former of which has biostratigraphic relevance because it has been interpreted by many authors as an exclusive taxon of the Ensenadan Age/Stage (Early-Middle Pleistocene; ca. 1.8–0.4 Ma) (Cione and Tonni, 1995, 1999, 2005; Soibelzon et al., 2010). Until now, *P. intermedius* was known only by the type material (MLP 16-36), consisting of a nearly complete dorsal carapace. Recently, a partial skull (MLP 84-IX-2-44) from the Ensenadan of La Plata (ca. 0.78 Ma), Buenos Aires province, Argentina, was first tentatively associated with this species (Scillato-Yané and Carlini, 1998; Tonni et al., 1999; Zamorano and Scillato-Yané, 2006), but later classified as *Panochthus* sp. (Zamorano, 2009).

The finding of a new exceptional specimen coming from the Early-Middle Pleistocene (Sacaba Formation) of western Bolivia (Cochabamba) (Fig. 1) has allowed us to greatly improve the knowledge of *P. intermedius*. In fact, this notable record constitutes the most complete Glyptodontidae Panochthini from the Early-Middle Pleistocene of South America. Finally, taking this new record into account, we discuss some taxonomic aspects related to the other Ensenadan Panochthini recorded.

2. Materials and methods

The chronological and biostratigraphic schemes used in this work correspond to those proposed by Cione and Tonni (2001, 2005) and Soibelzon (2008). The systematics partially follows Fernicola (2008), Hoffstetter (1958), McKenna and Bell (1997), and Paula Couto (1979).

All the values included in tables are expressed in millimeters (mm), with an error range of 0.5 mm (Table 1). Measurements smaller than 150 mm were taken with "vernier" calipers; measurements greater than this value were taken using an anthropometric spreading caliper. The description and terminology for

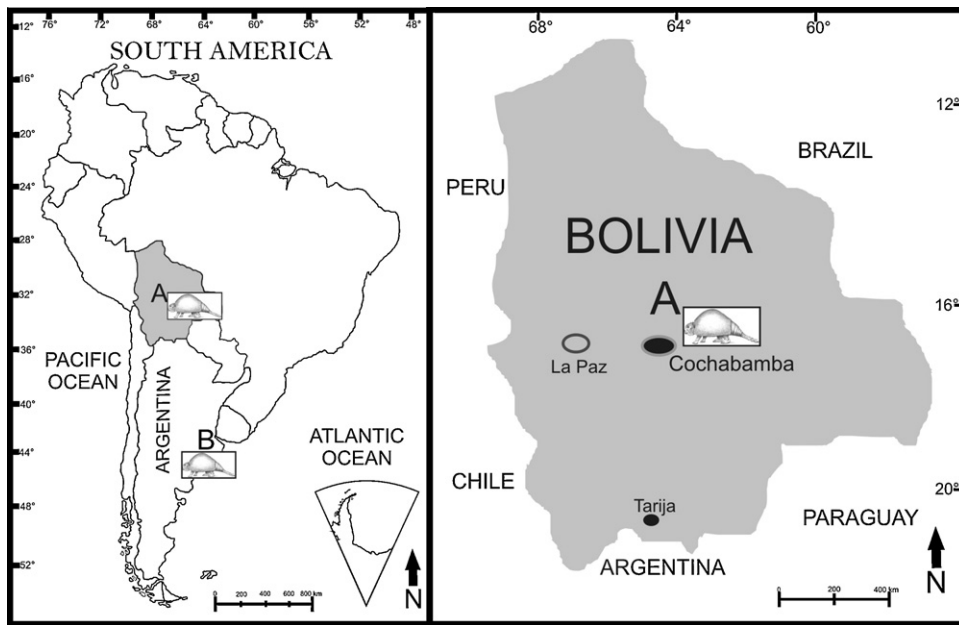


Fig. 1. Geographic location of *Panochthus intermedius* Lydekker. A. MLP 16-36. B. MHNC-13491.

Fig. 1. Carte montrant l'emplacement de *Panochthus intermedius* Lydekker. A. MLP 16-36. B. MHNC-13491.

osteoderms follow mainly Zurita (2007) and Krmpotic et al. (2009).

Institutional abbreviations. AMNH: American Museum of Natural History, New York, USA; MACN: Sección Paleontología Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MD: Museo Municipal de Ciencias Naturales de Punta Alta Charles Darwin; DGM: Departamento de Geología e Mineralogía, Rio de Janeiro, Brazil; IESC: Instituto de Ensino Superior do Cariri, Crato, Ceará, Brazil; MLP: División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; MMNP: Municipal de Nueva Palmira "Francisco Lucas Roselli", Nueva Palmira, Colonia, Uruguay; MNRJ: Museu Nacional, Rio de Janeiro, Brazil; MHNG: Musée d'Histoire Naturelle, Genève, Switzerland; MHNC: Museo de Historia Natural de Cochabamba "Alcide d'Orbigny", Bolivia.

Other abbreviations: M, m: upper and lower molari-forms respectively.

2.1. Systematic palaeontology

Magnorder *Xenarthra* Cope, 1889
 Order: CINGULATA Illiger, 1811
 Suborder: GLYPTODONTIA Ameghino, 1889
 Superfamily: GLYPTODONTOIDEA Gray, 1869
 Family: GLYPTODONTIDAE Gray, 1869
 Subfamily: "HOPLOPHORINAE" Huxley, 1864
 Tribe PANOCHTHINI Castellanos, 1927
 Genus *Panochthus* Burmeister, 1866

Type species: *Panochthus tuberculatus* Owen, 1845

Panochthus intermedius Lydekker, 1894
 (Figs. 2, 3)

Holotype: MLP 16-36, a nearly complete dorsal carapace.

Geographic and stratigraphic provenance: Port of Buenos Aires (currently "Ciudad Autónoma de Buenos Aires"), Buenos Aires province, Argentina. Early-Middle Pleistocene (Ensenadan Age/Stage).

Referred material: MHNC-13491, a nearly complete specimen: skull and mandible, cephalic armor; complete appendicular skeleton; proximal half of the caudal tube and some partial caudal rings; numerous fragments of associated osteoderms that compose most of the dorsal carapace, except the most posterior-dorsal area, which is missing (Figs. 2 and 3).

Geographic and stratigraphic provenance: approximately 20 km west of Cochabamba, Bolivia. Sacaba Formation (Late Pliocene-Middle Pleistocene; Soruco and Díaz Martínez, 1996) (Fig. 1).

Emended diagnosis (modified from Lydekker (1894: 34–35)): large Glyptodontidae. Dorsal carapace retaining rosette pattern ornamentation in the lateral, postero-dorsal and antero-dorsal regions, and a reticular pattern in the other regions. Skull with a lower degree of pneumatization of its fronto-nasal region compared with *P. tuberculatus*, *P. vogthi* and *P. frenzelianus*; frontals and nasals not so ventrally inclined (ca. 50°) as seen in the Lujanian species (ca. 60°), with a greater transverse diameter distally; narines with a middle lateral notch not as marked as in *P. tuberculatus*, *P. frenzelianus* and *P. vogthi*, and a much more developed upper notch. Orbits posteriorly opened, as in *P. frenzelianus* and MLP 84-IX-2-44; zygomatic arches and the upper half of the

Table 1
Comparative measurements (in millimeters) of *Panochthus* spp.

Tableau 1
Mesures comparatives (en millimètre) de *Panochthus* spp.

Measurements	Taxa			
	<i>P. intermedius</i> (MHNC-13491)	<i>P. subintermedius</i> (MACN 5130)	<i>Panochthus</i> sp. (MLP 84-IX-2-44)	<i>P. tuberculatus</i> (MLP 16-38)
<i>Skull</i>				
Length	420	400
Maximum transverse diameter between zygomatic arches	310	...	344	320
Transverse diameter between lacrimals	214	223
Transverse diameter of occipital	174	...	197	171
Transverse diameter between infraorbital foramina	156	150
Height of narial aperture	79
Transverse diameter of narial aperture	118	160
Length of toothrows	201	...	250	230
<i>Mandible</i>				
Length	325	380
Length of toothrows	197.63	240
Anteroposterior diameter of ascending ramus at alveolar level	133.50	155
Dorsoventral diameter of ascending ramus	269.33	305
<i>Cephalic armor</i>				
Maximum transverse diameter	340
Anteroposterior diameter	328
<i>Carapace</i> (MLP 16-36)				
Length	1900	1720
Anteroposterior length along dorsal curvature	2030	1770
Maximum transverse half-circumference	1017	910
<i>Caudal tube</i>				
Length	...	960	...	750
Dorsoventral diameter in its proximal portion	100	201.20	...	152
Transverse diameter in its proximal portion	173	198.14	...	164
<i>Scapula</i>				
Transverse diameter	406	495
<i>Humerus</i>				
Length	352	370
<i>Radius</i>				
Length	180	160
<i>Ulna</i>				
Length	265	270
<i>Femur</i>				
Length	479	550	...	470

descending process of the maxillae much more robust than those of *P. tuberculatus*, *P. vogthi* and *P. frenzelianus*, resembling MLP 84-IX-2-44 in its morphology. Cephalic armor constituted by large osteoderms; each central figure surrounded by only one or two rows of peripheral figures. Caudal tube clearly different from that of the other species of *Panochthini*, bearing central figures surrounded by one row of peripheral figures in its dorsal and ventral surfaces. Humerus and femur showing a gracile morphology.

2.2. Comparative description

2.2.1. Skull

The skull is almost complete, except part of the frontal and parietal areas. It is similar in size to that

of *P. tuberculatus* (e.g., MLP 16-38, MD 08-02), but much smaller compared to MLP 84-IX-2-44 (Table 1). In lateral view (Fig. 2B), the zygomatic arch and the upper half of the descending process of the maxillae are clearly much more robust than those of *P. tuberculatus*, *P. vogthi* (MHNG P-S.E 1.1) and *P. frenzelianus* (AMNH 11243–11245), resembling in this sense the Ensenadan specimen MLP 84-IX-2-44. Its lower margin is noticeably straight, whereas in *P. tuberculatus*, *P. frenzelianus* and *P. vogthi* this margin is concave. The orbital notch is dorsoventrally elongated, and morphologically similar to that seen in *P. frenzelianus* and MLP 84-IX-2-44, but different from that of *P. tuberculatus* and *P. vogthi*, in which this structure is more nearly circular. As in *P. frenzelianus* and MLP 84-IX-2-44, the orbit is posteriorly opened, whereas in *P. tuberculatus* and *P. vogthi* it is closed by a postorbital

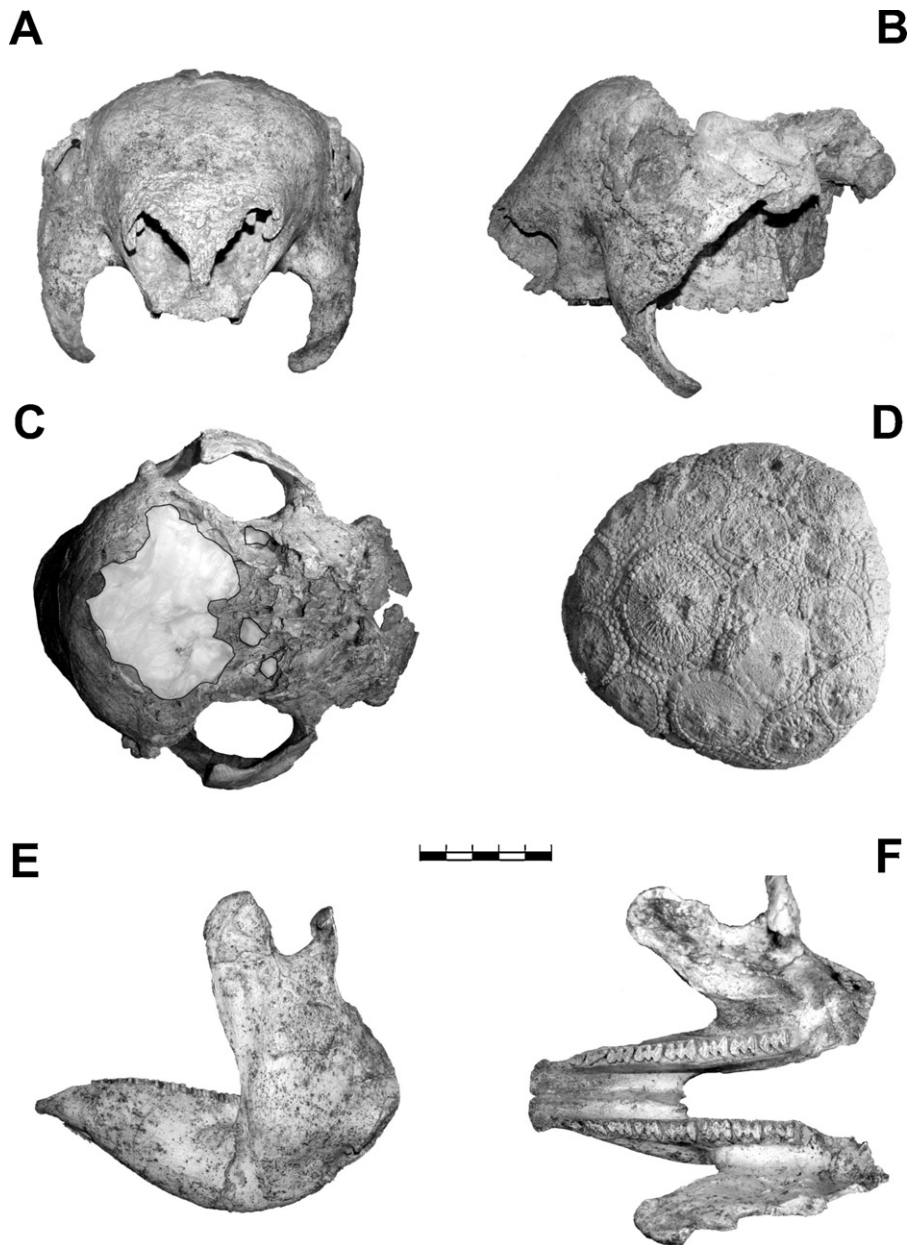


Fig. 2. *P. intermedius* (MHNC-13491). A–C, skull in: A: frontal; B: lateral; C: dorsal views. D. Cephalic armor in dorsal view. E–F, mandible in: E: lateral; F: occlusal views. Scale bar: 100 mm.

Fig. 2. *P. intermedius* (MHNC-13491). A–C, crâne en vues : A : frontale ; B : latérale ; C : dorsale. D. Bouclier céphalique en vue dorsale. E–F, mandibule en vues : E : latérale ; F : ventrale. Échelle : 100 mm.

bar. The anterior edge of this orbital notch bears some irregular facial osteoderms, with morphology comparable to that observed in the Glyptodontinae *Glyptodon munizi* (Soibelzon et al., 2006). The rostral area located ahead of the orbitals is pneumatized, showing an intermediate state of pneumatization between MLP 84-IX-2-44 and the Lujanian species of *Panochthus* (*P. tuberculatus*, *P. vogthi* and *P. frenzelianus*). The frontals and nasals are ventrally inclined, but this is not so evident as in *P. tuberculatus*, *P. frenzelianus* and *P. vogthi*. In this sense, in this new material, the angle between the palatal plane and the nasal

area is ca. 50° , whereas in *P. frenzelianus*, *P. vogthi* and *P. tuberculatus* (e.g. MLP 16-38), it is ca. 60° . The nasal openings show the typical morphology of the other species of *Panochthus*, but with some marked differences: the middle lateral notch is not as marked as in *P. tuberculatus*, *P. frenzelianus* and *P. vogthi*.

In frontal view (Fig. 2A), the rostral area is evidently more laterally expanded than in *P. tuberculatus*, *P. frenzelianus* and *P. vogthi* in its distal region (Table 1). In addition, the upper notch of the nasal openings is much more developed than that seen in the other species.

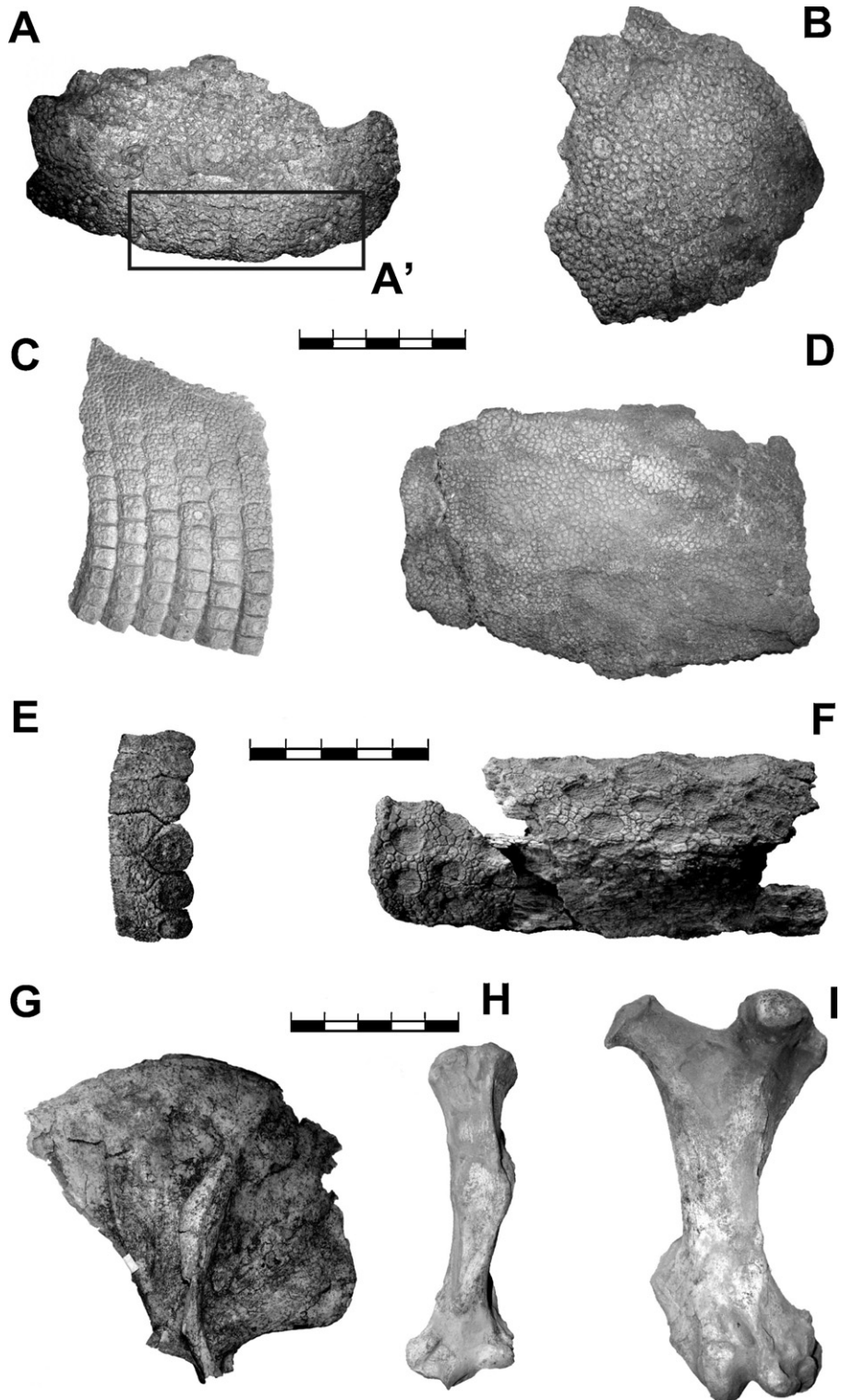


Fig. 3. *P. intermedius* (MHNC-13491). A–D. Dorsal carapace. A–B: antero-dorsal; C: lateral; D: centro-dorsal regions. E–F. Caudal armor. E: caudal ring in dorsal view; F: caudal tube in dorsal view. G. Left scapula in anterior view. H. Left humerus in anterior view. I. Right femur in anterior view. Scale bar: 100 mm.

Fig. 3. *P. intermedius* (MHNC-13491). A–D. Carapace dorsale. Zones A–B: antéro-dorsale; C: latérale; D: centro-dorsale. E–F. Cuirasse caudale. E: anneau caudal en vue dorsale; F: tube caudal en vue dorsale. G. Omoplate gauche en vue antérieure. H. Humérus gauche en vue antérieure. I. Fémur droit en vue antérieure. Échelle: 100 mm.

In dorsal view (Fig. 2C), the well-preserved region is located ahead the orbitals. Its morphology is similar to that of the other species, but is clearly more laterally expanded, especially at its distal portion. As mentioned, the orbitals are posteriorly opened, as in *P. frenzelianus* and the Ensenadan specimen MLP 84-IX-2-44. In occipital view, there are no significant differences with respect to the other species of the genus.

In occlusal view, only the M1-M4 of the right side and the M1 of the left side are preserved. M1 shows a more complex morphology than that of MLP 84-IX-2-44, in which this molariform is simple, with no evidence of lobulation. In fact, MLP 84-IX-2-44 shows clear imbrications among the M1-M3, which do not exist in any of the other known species of *Panochthus*. In this sense, this M1 of this new specimen is similar to that of *P. tuberculatus*, although not as anterior-posteriorly elongated. M2 shows a more evident trilobation. The anterior and posterior margins of the first and last lobes, respectively, are straight and located in an angle of ca. 85° with respect to the anterior-posterior axis of the palate; in contrast, in *P. tuberculatus*, the anterior and posterior margins are located at an angle of 65° and are nearly convex; in MLP 84-IX-2-44, M2 is similar to M1 of this new specimen. M3 and M4 are similar to those of *P. tuberculatus* and MLP 84-IX-2-44, but differ mainly in their third lobe, where there are two evident notches placed in the labial and posterior margins, which are absent in *P. tuberculatus* and MLP 84-IX-2-44.

2.2.2. Cephalic armor

This structure is 328 mm long and 340 mm wide (Fig. 2D). Its general morphology is similar to that of the other species of *Panochthus*, but with some interesting differences. In lateral view, the cephalic armor shows a clear convex morphology, much more pronounced than in the Lujanian species, because this structure extends both to the frontal and occipital regions. The osteoderms that compose this cephalic armor are larger than those of *P. tuberculatus*, *P. frenzelianus* and *P. vogthi*. In addition, each central figure in these species is surrounded by several rows (up to five) of peripheral figures, whereas in the specimen from Bolivia there are only one or two rows of peripheral figures surrounding each central figure. Clearly, this is correlated with the ornamentation pattern observed in the dorsal carapace, which preserves a rosette pattern in some regions.

2.2.3. Mandible

The mandible resembles those of the other recognized species of the genus (Fig. 2E–F), and is similar in size to that of *P. tuberculatus* (Table 1). Among m1-m3, it is possible to observe some imbrications that are not present in any of the other species of the genus. m1 is similar to that of *P. tuberculatus*, but somewhat less lobulated; m2 is more anterior-posteriorly elongated, with a lower degree of lobulation, especially in its lingual side; m3 and m4 are similar to those of *P. tuberculatus*, with the anterior margin of the first lobule slightly straighter (Fig. 2F). The remaining molariforms (m4–m8) are almost identical to those of *P. tuberculatus*.

2.2.4. Dorsal carapace

Although the dorsal carapace is currently fragmented in numerous associated osteoderms, it was originally discovered almost complete (Fig. 3A–D). Compared with the holotype of *P. intermedius* (MLP 16-36), the morphology of the exposed surface of the osteoderms in the different regions of the dorsal carapace is almost identical, and clearly different from the other species of *Panochthus*, including the other Ensenadan taxon, *P. subintermedius*, whose morphological characterization has been recently improved by Cruz et al. (2010). As in all the species of *Panochthus*, the central-dorsal region shows a clear reticular pattern, composed of small polygonal figures (Fig. 3D). This is different from that observed in *N. coagmentatus* (MLP 16-2) and *N. trouessarti* (MLP 16-117 and MACN 2670), in which the dorsal carapace shows an evident and primitive pattern composed of a central figure generally surrounded by two rows of peripheral figures. In most of the preserved dorsal carapace (posterior-dorsal region) of *P. bullifer* (MACN 1761), it is possible to distinguish a large central figure, generally elevated, surrounded by two rows of peripheral figures.

The central-anterior region of the carapace shows the typical rosette pattern of *P. intermedius* (Fig. 3A, B); in this area, each central figure is surrounded by three to four rows of small peripheral polygonal figures. This represents a character present only in *P. intermedius*. In contrast, in *P. subintermedius*, *P. tuberculatus*, *P. frenzelianus*, and *P. morenoi*, this area does not bear central figures, showing a complete reticular pattern. In addition, the osteoderms that constitute the cephalic notch (Fig. 3A') are almost identical to those observed in *P. intermedius*: each osteoderm has an evident central figure with a very rough surface, surrounded by two rows of peripheral figures at its distal margin and one row at its lateral margin; this is very different from that observed in the Lujanian species (*P. vogthi*, *P. frenzelianus* and *P. tuberculatus*), in which those osteoderms are much smaller and do not bear any central figure, but a clear reticular pattern.

The lateral area of the dorsal carapace (Fig. 3C) is very similar in its general morphology to that of the other species of *Panochthus*, in which the anterior and posterior areas show mobile bands of osteoderms, and thus similar to the Glyptodontidae Propalaeohoplophorinae (*Propalaeohoplophorus* Ameghino and *Eucinepeltus* Ameghino). The most ventral osteoderms present a clearly distinguishable central figure surrounded by small polygonal figures. These central figures become smaller toward the dorsal region, where they completely disappear. This particular structure is visible up to the ninth row of osteoderms, varying according to its location in this lateral area. Although the dorsal carapace of the holotype of *P. intermedius* is not well preserved at this level (because most of the osteoderms are missing), in some of the most ventral osteoderms it is possible to observe the presence of a central figure, showing the same morphology observed in this new specimen of Bolivia. This is clearly different from *P. bullifer* and *Nopachtus*, in which the central figures may be located even in the dorsal region of the carapace.

In the Lujanian species of *Panochthus* (*P. tuberculatus*, *P. morenoi* and *P. frenzelianus*), the complete carapace shows a clear reticular pattern, whereas in the other Ensenadan species (*P. subintermedius*) the osteoderms have only a central figure in the posterior region of the carapace (Cruz et al., 2010). The postero-dorsal region of the dorsal carapace is not preserved in this new Cochabamba material.

2.2.5. Caudal armor

2.2.5.1. Caudal rings. There are three preserved partial caudal rings, which do not show any significant differences with respect to the other species of the genus (Fig. 3E). Each caudal ring is formed by two rows of osteoderms. The proximal ones (which articulate with the next row) present three or four sides and the articular portion is clearly thinner than the distal half; the exposed surface of those osteoderms shows a reticular pattern. The distal row is composed of osteoderms showing five sides; the exposed surface of each osteoderm shows a distal central figure, which is surrounded by one or two rows of peripheral figures, which are more developed in its proximal side. This particular morphology resembles that of Glyptodontidae Glyptatelinae.

2.2.5.2. Caudal tube. Only the proximal half of this structure is preserved (Fig. 3F). It is 420 mm long and shows a more primitive morphology than that of the other Lujanian species of *Panochthus*, and is more similar in this sense to *P. bullifer*. The general contour is clearly depressed. The transverse diameter is 100 mm, and the dorso-ventral diameter is 173 mm. This cross-sectional shape is different from *P. tuberculatus*, *P. morenoi* and *P. subintermedius*, in which the proximal part of the caudal tube is almost circular (Table 1). The dorsal surface of the caudal tube bears central figures clearly extended antero-posteriorly and depressed, with a very rugose surface (except the first two rows of the central figures, which are almost circular). Each central figure is surrounded by two rows of peripheral figures. This particular morphology differs from that of the other species of *Panochthus*, in which this dorsal surface shows an evident reticular pattern, similar to that observed in the dorsal area of the dorsal carapace. This primitive condition is present in *P. bullifer*; however, in this species the central figures are more circular, they are not depressed and its exposed surface is almost smooth. The lateral region of the caudal tube is almost identical to that of the other species of *Panochthus*. Compared with the intertropical species of the genus, the caudal tube of *P. jaguaribensis* (IESC 1) is very similar to that of *P. tuberculatus*. In *P. greslebini* (DGM 1), it is possible to observe the presence of some central depressed figures restricted to the distal part of the tube, whereas in this new material from Bolivia these figures reach up to the proximal part of the tube, are somewhat smaller and are separated by a higher number of peripheral figures.

2.2.6. Scapula

The scapula shows the typical morphology observed in *P. tuberculatus*, without significant differences (Burmeister, 1870–1874) (Fig. 3G).

2.2.7. Humerus

Both humeri are preserved. The humerus is more gracile and more dorso-ventrally extended than that of the Lujanian species of *Panochthus* (Table 1) (Fig. 3H). Its general morphology resembles that of *P. vogthi* (Bonaerian and Lujanian Age/Stage of the Pampean region of Argentina) and the one of *P. subintermedius* (Ensenadan Age/Stage of the Northeast of Buenos Aires Province). Unlike *P. tuberculatus* (Lujanian Age/Stage), the “V” deltoid extends two thirds of the total length, whereas in the new specimen it extends half the total length.

2.2.8. Femur

Both femora are preserved. The femur is more dorso-ventrally extended than that of all the species of *Panochthus* in which the femur is known, except *P. subintermedius* (Table 1) (Fig. 3I). In anterior view, the margins diverge slightly towards the proximal end from the maximum constriction of the diaphysis, whereas in *P. subintermedius*, like in all the species of the Lujanian Age/Stage, this divergence is more marked, forming a triangular structure in the proximal half of the femur. The greater trochanter is slightly higher than the femoral head, whereas it always seems to be slightly lower in *P. tuberculatus*, *P. vogthi* and *P. subintermedius*. The lamina that forms the third trochanter with the internal epicondyle is much less expanded than in *P. tuberculatus* and *P. vogthi*; in these two species, the margin of this lamina is everted towards the anterior surface and ends in a tip that protrudes dorsally. The supracondylar fossa is narrower and more extended than in *P. tuberculatus* and *P. vogthi*, in which it is rounded.

3. Discussion

3.1. The Ensenadan Glyptodontidae *Panochthini*

As mentioned, the first record of a *Panochthini* corresponds to *Nopactus* (*N. coagmentatus* and *N. trouessarti*) and *Propanochthus* (*P. bullifer*) from the Late Miocene–Early Pliocene of southern South America (Castellanos, 1942a,b). Afterward, the tribe has been well recorded in Late Pleistocene sediments of southern South America.

The last taxonomic revision includes one genus, *Panochthus* (Porphino and Bergqvist, 2002). *Parapanochthus* Moreira (*P. jaguaribensis*), the other Pleistocene genus, was synonymized by Porphino and Bergqvist (2002). In *Panochthus*, there are two Ensenadan species (see Castellanos, 1942a,b; Cruz et al., 2010), and seven Lujanian species (Ameghino, 1889; Burmeister, 1866; Castellanos, 1942). We suggest that some of these Late Pleistocene taxa, especially those coming from the Pampean region (*P. vogthi* and *P. morenoi*), could be synonymous with *P. tuberculatus*, taking into account their morphological variation. However, a more integral taxonomic revision is needed.

Knowledge of the Ensenadan *Panochthini* has been restricted to *P. intermedius* and *P. subintermedius*. In

particular, *P. intermedius* was represented by an almost complete dorsal carapace, which shows a more derived condition than *Nopachtus* and *P. bullifer*, but it is clearly more primitive than the Lujanian taxa, in which the exposed surface of the dorsal carapace is composed of a reticular pattern, without distinguishable central figures (Ameghino, 1889; Burmeister, 1870–1874; Castellanos, 1942a,b). More recently, a partial skull was recovered from La Plata (Buenos Aires province) in sediments assignable to the Ensenadan Age/Stage (Scillato-Yané and Carlini, 1998; Tonni et al., 1999; Zamorano and Scillato-Yané, 2006). On the basis of its stratigraphic origin, this material was tentatively assigned to cf. *P. intermedius*, but because of the discovery that the other Ensenadan species (*P. subintermedius*) is a valid and well characterized taxon (Cruz et al., 2010), the original classification as cf. *P. intermedius* remained highly uncertain (Zamorano, 2009).

The morphological comparisons between this new material from Bolivia and the holotype of *P. intermedius* strongly support the conclusion that both belong to the same species. They share the following characters:

- the particular ornamentation of the anterior-dorsal and lateral regions of the dorsal carapace, which is not present in any of the other known species;
- the morphology of the osteoderms that constitute the cephalic notch. Therefore, the knowledge of *P. intermedius* has been greatly improved.

Further, the comparison with the MLP 84-IX-2-44, tentatively assigned to *P. intermedius*, completely refutes the possibility that this material belongs to this species. The skull is evidently much larger (Table 1) and the molariforms (especially the first two) are markedly different and show a more primitive morphology in MLP 84-IX-2-44. However, they share some primitive characters, such as the absence of a postorbital bar. In this way, we could argue that the skull of MLP 84-IX-2-44 could belong to the other Ensenadan species, *P. subintermedius*, but this is hypothetical. However, this seems to be the most parsimonious hypothesis because both come from the same stratigraphic and geographical provenance (Ensenadan Stage/Age of the eastern sector of Buenos Aires province, Argentina). Nevertheless, new and more complete findings are necessary to test this taxonomic hypothesis.

Compared with the Lujanian taxa, this new specimen shows a general similar morphology, but preserves some primitive characters:

- dorsal carapace retaining a central figure in its lateral and antero-dorsal osteoderms;
- osteoderms of the cephalic armor presenting much fewer peripheral figures than those observed in the Lujanian taxa;
- skull with open postorbital (only preserved in *P. frenzelianus* among the Lujanian species);
- rostral area with a broader transverse diameter, especially in its distal part;

- caudal tube depressed and bearing a central figure on its dorsal surface.

4. Conclusions

The evidence clearly suggests that this new material belongs to *P. intermedius* Lydekker, because it has the unique combination of features that characterize this taxon: the presence of central figures at the anterior-dorsal and lateral regions of the dorsal carapace, and the particular morphology of the osteoderms at the cephalic notch. This set of characters is not present in any other species of *Panochthus*. Therefore, the morphological knowledge of this species has been greatly improved. This exceptional finding represents the most complete Glyptodontidae Panochthini from the Ensenadan Age/Stage (Early-Middle Pleistocene) of South America and one of the most complete Glyptodontidae for this interval of time.

The comparison between this new material and MLP 84-IX-2-44, tentatively assigned to *P. intermedius*, clearly demonstrates that this skull does not belong to this species. Alternatively, it could correspond to the other Ensenadan species, *P. subintermedius*, but further findings are necessary.

Its general morphology shows a more derived condition than the Tertiary taxa *Nopachtus* and *P. bullifer* (Late Miocene-early Pliocene), but preserves some primitive characters not present in late Pleistocene species, especially at dorsal carapace and skull level.

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Appendix A. List of materials analyzed in this article

MLP 16-2 (holotype of *N. coagmentatus*)
 MLP 16-117 (*N. trouessarti*)
 MACN 2670 (*N. trouessarti*)
 MACN 1761 (holotype of *P. bullifer*)
 MLP 16-36 (holotype of *P. intermedius*)
 MACN 5130 (holotype of *P. subintermedius*)
 MLP 16-38 (*P. tuberculatus*)
 MD 08-02 (*P. tuberculatus*)
 MMNP 1000 (*P. tuberculatus*)
 MLP 84-IX-2-44 (*Panochthus* sp.)
 MHNG P-S.E 1.1 (holotype of *P. vogthi*)
 AMNH 11243–11245 (holotype of *P. frenzelianus*)
 IESC 1 (holotype of *P. jaguaribensis*)
 DGM 1 (holotype of *P. greslebinii*)

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