

A peculiar specimen of *Panochthus* (Xenarthra, Glyptodontidae) from the Eastern Cordillera, Bolivia

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ABSTRACT. *Panochthus* Burmeister is one of the most diversified and widely distributed glyptodonts in the Pleistocene of South America, which includes areas located at high altitudes (>4,000 m a.s.l.). Within the genus, eight species (*P. intermedius* Lydekker, *P. subintermedius* Castellanos, *P. tuberculatus* (Owen), *P. frenzelianus* Ameghino, *P. greslebini* Castellanos, *P. jaguaribensis* Moreira, *P. hipsilis* Zurita, Zamorano, Scillato-Yané, Fidel, Iriondo and Gillette, and *P. florensis* Brambilla, López and Parent) are currently recognized. Here, we report a dorsal carapace (UATF-V n/n) from the Pleistocene of the surroundings of Potosí, Bolivia, that shows some morphological particularities when compared to the carapace of *P. intermedius*, *P. frenzelianus*, *P. subintermedius* and *P. tuberculatus*, including: **a)** its maximum dorso-ventral diameter is at the anterior half, meanwhile in other species is at mid-point (e.g., *Propalaeohoplophorus*) or at posterior half (e.g., *Glyptodon*); **b)** the dorsal profile is different in comparison to other glyptodonts (e.g., *Glyptodon*, *Glyptotherium*, *Neosclerocalyptus*, *Propalaeohoplophorus*); **c)** the ornamentation pattern of the osteoderms shows a central figure surrounded by small polygonal figures along the most exposed surface of the carapace (except for the mid-dorsal region that shows reticular ornamentation pattern), being different from that of the remaining species: of *Panochthus*, in which central figures are limited to the caudal/cephalic and most lateral regions of the carapace. In summary, the combination of characters suggests that it could belong to a new species or, alternatively, to *P. florensis* or *P. jaguaribensis* in which the dorsal carapace is not yet known. The phylogenetic analysis confirms its basal position among *Panochthus* and highlights the importance of these high elevation areas of the Andes in South America in order to understand the complex evolutionary history of glyptodonts.

Keywords: Diversity, Pleistocene, High altitude, South America.

RESUMEN. Un peculiar ejemplar de *Panochthus* (Xenarthra, Glyptodontidae) de la cordillera Oriental, Bolivia. *Panochthus* Burmeister es uno de los gliptodontes más diversificados y ampliamente distribuidos en el Pleistoceno de Sudamérica, incluyendo zonas situadas a gran altura (>4.000 m s.n.m.). Dentro del género, se reconocen actualmente ocho especies (*P. intermedius* Lydekker, *P. subintermedius* Castellanos, *P. tuberculatus* (Owen), *P. frenzelianus* Ameghino, *P. greslebini* Castellanos, *P. jaguaribensis* Moreira, *P. hipsilis* Zurita, Zamorano, Scillato-Yané, Fidel, Iriondo y Gillette, y *P. florensis* Brambilla, López y Parent). Aquí reportamos una coraza dorsal

(UATF-V n/n) procedente del Pleistoceno de los alrededores de Potosí, Bolivia, que muestra algunas particularidades morfológicas respecto a las corazas de *P. intermedius*, *P. frenzelianus*, *P. subintermedius* y *P. tuberculatus*, incluyendo: **a**) máximo diámetro dorso-ventral situado a la altura de la mitad anterior, mientras que en otras especies se encuentra a la altura del punto medio (e.g., *Propalaeohoplophorus*) o de la mitad posterior (e.g., *Glyptodon*); **b**) el perfil dorsal es diferente en comparación con las restantes especies de gliptodontes (e.g., *Glyptodon*, *Glyptotherium*, *Neosclerocalyptus*, *Propalaeohoplophorus*); **c**) el patrón de ornamentación de los osteodermos muestra una figura central rodeada de pequeñas figuras periféricas poligonales a lo largo de la mayor parte de la superficie expuesta de la coraza (excepto en la región medio dorsal que muestra un patrón de ornamentación reticular), el cual es diferente al de las especies restantes, en las que las figuras centrales se limitan a las regiones caudal, cefálica y más lateral de la coraza. En resumen, la combinación de caracteres sugiere que podría pertenecer a una nueva especie o, alternativamente, a *P. floriensis* o *P. jaguaribensis* en las que aún no se conoce la coraza dorsal. El análisis filogenético confirma su posición basal dentro del género *Panochthus*, lo que evidencia la importancia de estas zonas de gran altitud en los Andes de América del Sur para comprender la compleja historia evolutiva de los gliptodontes.

Palabras clave: Diversidad, Pleistoceno, Gran altitud, América del Sur.

1. Introduction

Xenarthra is a particular group of mammals typical of the Neotropical Region; they are widely represented in the South American fossil record, being conspicuous because of their temporal extension (Early Eocene-Recent), and the frequency of their findings (Paula Couto, 1979; Oliveira and Bergqvist, 1998; Bergqvist *et al.*, 2004; Gaudin and Croft, 2015; Delsuc *et al.*, 2016). During most of the Cenozoic they were among the most diversified clades of South America, although their current diversity is quite reduced (Scillato-Yané, 1982; Abba *et al.*, 2012).

Of the two great clades currently recognized, Pilosa and Cingulata; the cingulates achieved the greatest diversification and temporal range. Cingulata has near 220 species distributed in ca. 105 genera known in the fossil record since the Early Eocene (Scillato-Yané, 1980, 1982; McKenna and Bell, 1997), in contrast with the modern diversity, reduced to ca. 21 species (Abba *et al.*, 2012; Feijó *et al.*, 2019).

Within Cingulata, Glyptodontidae is the clade that reached the largest size (Soibelzon *et al.*, 2012). This group is first recorded in the Late Eocene of the Patagonian region of Argentina (Ameghino, 1902; Gaudin and Croft, 2015), and later experienced a diversification and radiation process since the Late Miocene (Fericola, 2008; González-Ruiz *et al.*, 2012; Zurita *et al.*, 2016), probably related to the development of open biomes of grasslands (Delsuc *et al.*, 2004; Carlini and Zurita, 2010; Iglesias *et al.*, 2011; Mitchell *et al.*, 2016).

Glyptodontidae are relatively well known in southern South America since the pioneering studies

of Ameghino (1889), Burmeister (1870-1874) and Scott (1903-1904), among others. However, one of the regions in which their diversity and evolutionary history is least known is that of the Andean and sub-Andean areas of Bolivia and Peru where, traditionally, glyptodonts were only mentioned as part of paleofaunal lists (*i.e.*, Hoffstetter, 1973; Pujos and Salas, 2004).

More recently, the finding of new specimens allowed a better knowledge of these large armored herbivores, especially those of the Pleistocene. Zurita *et al.* (2011) reported the first record of *Panochthus intermedius* Lydekker, 1895 from the middle Pleistocene out of the current territory of Argentina, near Cochabamba, Bolivia. Later on, Zurita *et al.* (2017) recognized the first glyptodont species exclusive from the current territory of Bolivia, *Panochthus hipsilis* Zurita, Zamorano, Scillato-Yané, Fidel, Iriondo and Gillette, 2017, which in turn is one of the fossils of Xenarthra found at the highest altitude, ca. 4,500 m a.s.l., together with the Glyptodontinae *Glyptodon jatunkhirkhi* Cuadrelli, Zurita, Toriño, Miño-Boilini, Perea, Luna, Gillette and Medina, 2020. More recently, Zamorano and Almonte (2018) reported the first record of the genus *Panochthus* Burmeister, 1866 from Peru (ca. 3,800 m a.s.l.) (Zamorano and Oliva, 2020).

Thus, only two genera of the South American Quaternary have been recorded over 2,500 m a.s.l., *Glyptodon* Owen, 1839 and *Panochthus* (Zurita *et al.*, 2017; Cuadrelli *et al.*, 2019; Zamorano and Oliva, 2020), which are also those genera with the widespread latitudinal distribution (Zurita *et al.*, 2009; Porpino *et al.*, 2010; Zamorano *et al.*, 2014; Cuadrelli *et al.*, 2020).

In this contribution, a dorsal carapace referred to *Panochthus* sp., from the Pleistocene of the Cordillera Oriental of Bolivia, near Potosí, is described and compared. It has a particular combination of characters. A phylogenetic analysis is performed in order to test its location within the genus and its relationships with the other species.

2. Materials and methods

The specimen here described belongs to the Vertebrate Paleontology Collections, “Universidad Autónoma Tomás Frías”, Potosí, Bolivia. The list of characters and character states are indicated in the Appendix 1. The materials used for comparison and phylogenetic analysis (Appendix 2) include the holotypes and most complete materials assigned to the different species of *Panochthus* and *Propanochthus* Castellanos, 1925 (see Burmeister, 1874). For chronological purposes, we follow the International Chronostratigraphic Chart¹ (Cohen et al., 2013; International Commission on Stratigraphy, 2020).

The biostratigraphic scheme is that of Flynn and Swischer (1995) and Cione and Tonni (1999, 2005; see also Cione et al., 2015). Anatomic terminology for descriptions and comparisons follows Porpino et al. (2014), Zamorano et al. (2014) and Zurita et al. (2017). Systematics follows Zamorano and Brandoni (2013), Zamorano (2012, 2019), Zamorano and Almonte (2018), Zamorano et al. (2014) and Zurita et al. (2017). Linear measurements are in millimeters (mm).

Description of the phylogenetic analysis: The material here studied (UATF-V n/n) was included in a cladistic analysis modified from that of Zurita et al. (2017) in order to analyze its phylogenetic location. The analysis includes 19 taxa (*Pamphaterium humboldtii* Lund, 1839; *Propalaeohoplorus australis* Ameghino, 1887; *Glyptodon reticulatus* Owen, 1845; *Boreostemma acostae* Villarroel, 1983; *Plohophorus figuratus* Ameghino, 1887; *Pseudoplohophorus absolutus* Perea, 2005; *Stromaphorus compressidens* Moreno and Mercerat, 1891; *Phlyctaenophyga ameghini* (Ameghino, 1889); *Hoplophorus euphractus* Lund, 1839; *Neosclerocalyptus ornatus* Paula Couto, 1957; *Nopachtus coagmentatus* Ameghino, 1888; *N. cabrerai* Zamorano et al., 2011; *Propanochthus bullifer* Burmeister 1870-1874; *Panochthus intermedius* Lydekker, 1895; *P. tuberculatus*

Owen 1845; *P. subintermedius* Castellanos 1937; *P. greslebini* Castellanos, 1941; *P. hipsilis* Zurita et al., 2017 and UATF-V n/n, including 43 morphological characters. The selected characters include a diversity of features of the skull (1-12), dentition (13-15), humerus (16), dorsal carapace (17-35) and caudal tube (36-43). Thirty of them are binary and 13 are multistate (non-additive), and all of them are equally weighted. Character states that could not be coded because of the lack of material appear as “?” and those inapplicable were coded as “-”. The taxa *Panochthus jaguaribensis* Moreira, 1965 and *P. frenzelianus* Ameghino, 1889 were excluded from the analysis because of their poor representation. The matrix (Appendix 2) was developed through the software Mesquite, 3.10 version program (Maddison and Maddison, 2018²). The analyses were carried out by exhaustive search, through the option “Implicit Enumeration” with the TNT program (Tree analysis using New Technology) version 1.1 (Goloboff et al., 2008³). The analysis support was estimated through absolute and relative Bremer (4 suboptimal), and Jackknife (100 replications). Character list and matrix are available in Appendices 1 and 2, respectively.

Institutional abbreviations: **AMNH:** American Museum of Natural History, New York, USA; **MUFyCA:** Museo Universitario Florentino y Carlos Ameghino, **CTES-PZ,** Colecciones Paleontológicas de la Universidad Nacional del Nordeste “Rafael Hersbt” Corrientes, Argentina”, Universidad Nacional de Rosario, Rosario, Argentina; **MACN-Pv:** Colección Nacional de Paleontología de vertebrados del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MCA:** Museo de Ciencias Naturales “Carlos Ameghino”, Mercedes, Buenos Aires, Argentina; **MLF:** Museo de Ciencias Naturales Florentino Ameghino, Las Flores, Buenos Aires, Argentina; **MLP:** División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina; **MHNC:** Museo de Historia Natural de Cochabamba “Alcide d’Orbigny”, Bolivia; **MHNS:** Museo de Historia Natural de Sucre, Sucre, Bolivia; **MNPA-V:** Museo Nacional Paleontológico-Arqueológico, Tarija, Bolivia (colección vertebrados); **MPAC:** Museo Paleontológico Real de San Carlos “Armando Calcaterra”, Colonia, Uruguay; **MPH:** Museo Municipal “Punta Hermengo”, Miramar, Buenos Aires, Argentina; **MURB:** Museo Universitario “Ricardo Bohorquez”, Potosí, Bolivia;

¹ International Commission on Stratigraphy. 2020. International Chronostratigraphic Chart. www.stratigraphy.org. (Last visit 14-03-22).

² Maddison, W.P.; Maddison, D.R. 2018. Mesquite: a modular system for evolutionary analysis. Version 3.04. <http://mesquiteproject.org>. (Last visit: 18-03-22).

³ Goloboff, P.A.; Farris, J.S.; Nixon, K. 2008. TNT: tree analysis using new technology, version 1.1 (Willi Hennig Society Edition). Program and documentation available at <http://www.zmuc.dk/public/phylogeny/tnt>. (Last visit 18-03-2022).

UATF: Universidad Autónoma “Tomás Frías,” Potosí, Bolivia; **USNM:** National Museum of Natural History, Smithsonian Institution.

Index abbreviations: **TL:** antero-posterior length of the dorsal carapace without considering the dorsal curvature; **APLDC:** antero-posterior length of the dorsal carapace along dorsal curvature; **ICDC:** Index of Convexity of the Dorsal Carapace: ratio of the length of the dorsal carapace (in a straight line, without considering curvature) and the length considering the curvature.

Other abbreviations: **L:** tree length; **RI:** retention index; **CI:** consistency index; **MPT:** most parsimonious tree; **Ma:** million years; **m a.s.l.:** meters above sea level.

3. Geographical and geological setting

Mojotorillo (*ca.* 3205 m a.s.l.) is a fossiliferous locality placed in the area between Betanzos and Ckonapaya, north-east of Potosí Department, Bolivia (Fig. 1). It is located in the homonymous basin that regionally belongs to the southern part of the Bloque Andino Oriental (Gubbels *et al.*, 1993; Kley, 1996). The basin is geomorphologically characterized by gullies produced by the strong fluvial erosion of the Jachcha LLulu river that crosses the site from east to west, exposing continental sediments. The lithology of the Mojotorillo basin is composed of Cretaceous sandstones overlain by a sequence of Quaternary sediments assigned to the Pleistocene-Holocene (Aubouin *et al.*, 1965). The general sequence reaches a maximum of *ca.* 20 m thick, and is formed from base to top by brown-yellowish siltstones interbedded with conglomerates with clasts of Paleozoic rocks; followed by levels of brown-reddish claystones and lenses of fine to medium grain sandstones. A horizon of volcanic tuff, more than 1 m thick is exposed 2 m below the top of the stratigraphic sequence (Pinto Yupanqui, 2015). Outcrops are limited to ravines, whose fossiliferous horizons are below and over the tuff level. At the precise point where UATF-V n/n was recovered, the sequence is *ca.* 5 m thick (Fig. 1), and locally represented by an interbedding of brownish massive medium grain sandstones and silty fine grain sandstones, with the occasional development of thin levels of clay. Towards the middle of the sequence, below the UATF-V n/n bearing level, there is interbedded a level of conglomerates.

Along the basin, faunal remains are commonly associated with Pleistocene sediments, including a wide variety of mammals: *Xenarthra* (Glyptodontidae, Mylodontidae and Megatheriidae), *Litopterna* (Macraucheniidae), *Perissodactyla* (Equidae), *Carnivora* (Canidae and Felidae) and *Artiodactyla* (Tayassuidae) (Pinto Yupanqui, 2015). Other records of fossil vertebrates from Pleistocene deposits in the surroundings of Mojotorillo include skull remains of *Myiodon darwini* Owen, 1839 (see Brandoni *et al.*, 2010) and indeterminate tayassuids (Daza and Shockey, 1999; Gasparini *et al.*, 2011).

4. Systematic Paleontology

Magnorder *Xenarthra* Cope, 1889

Order *Cingulata* Illiger, 1811

Suborder *Glyptodontia* Ameghino, 1889

Superfamily *Glyptodontoidea* Gray, 1869

Family *Glyptodontidae* Gray, 1869

Genus *Panochthus* Burmeister, 1866

Type species: *Glyptodon tuberculatus* Owen, 1845

***Panochthus* sp.**

Referred materials: UATF-V n/n, almost complete dorsal carapace (antero-lateral margin, ventral margin and postero-lateral margins reconstructed; cephalic notch and caudal notch partially reconstructed) (Figs. 2 and 3A).

Geographic and stratigraphic provenance: Pleistocene sedimentary deposits of Mojotorillo, Bolivia. *ca.* 51 km northeast from Potosí, Eastern Cordillera, at *ca.* 3,205 m a.s.l. (Fig.1).

Comparative descriptions: *General morphology* (Figs. 2 and 3A). In lateral view, the degree of convexity of the dorsal carapace of UATF-V n/n (ICDC= 1.07; Fig. 3A) is less than that of *P. hipsilis* (ICDC= 0.87; Fig. 3B), *P. intermedius* (ICDC= 0.94; Fig. 3C) and *P. tuberculatus* (ICDC= 0.97; Fig. 3D) (Table 1). The dorsal profile of the dorsal carapace of UATF-V n/n has its maximum height at the level of the anterior region, above the scapular region. From this point toward the cephalic end, the dorsal carapace goes down with an angle of *ca.* 30°, whereas toward the caudal end, the dorsal profile is almost completely horizontal, descending only with an angle of *ca.* 3°. Although in *P. tuberculatus*, *P. intermedius* and *P. hipsilis* the carapace reaches

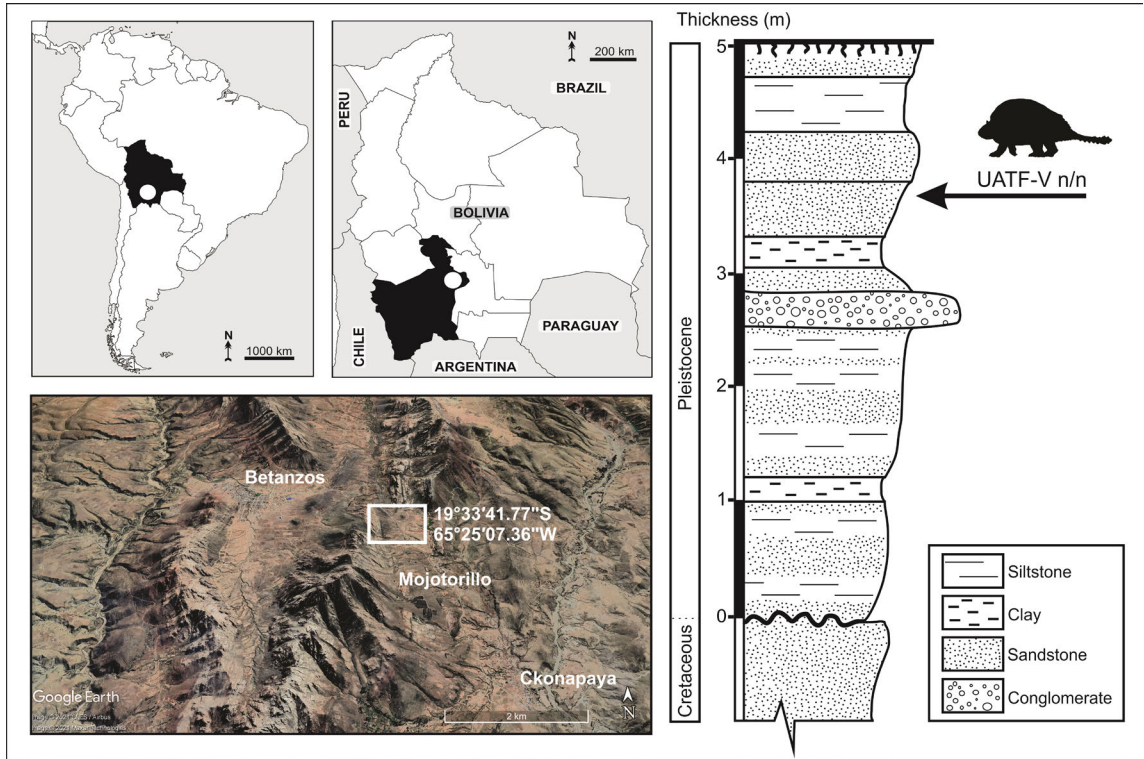


FIG. 1. Geographic (left) and stratigraphic (right) provenance of the remains of *Panochthus* sp. UATF n/n. The rectangle shows the geographic location of the provenance area of the specimen.

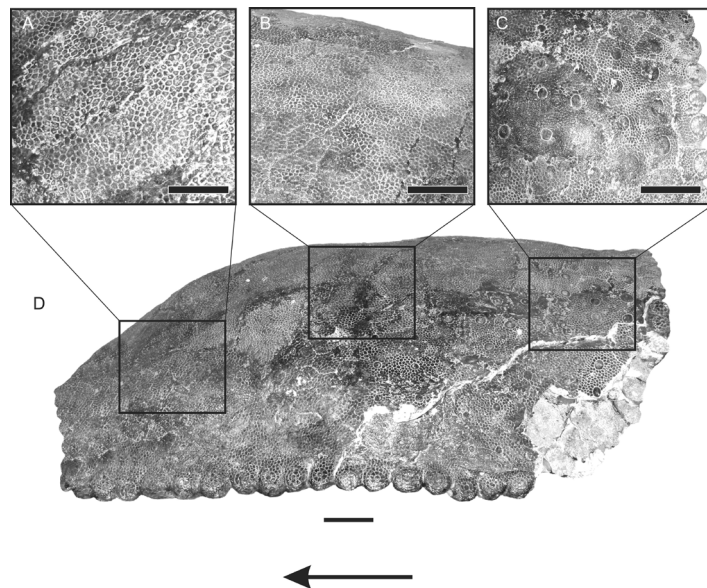


FIG. 2. Dorsal carapace of *Panochthus* sp. UATF n/n (D) scale bar= 100 cm. Detail of the ornamentation pattern of the antero-dorsal region (A); Detail of the ornamentation pattern of the middle-dorsal region (B); Detail of the ornamentation pattern of the postero-dorsal region (C). Scale bar= 15 mm; the black arrow shows a antero-posterior sense.

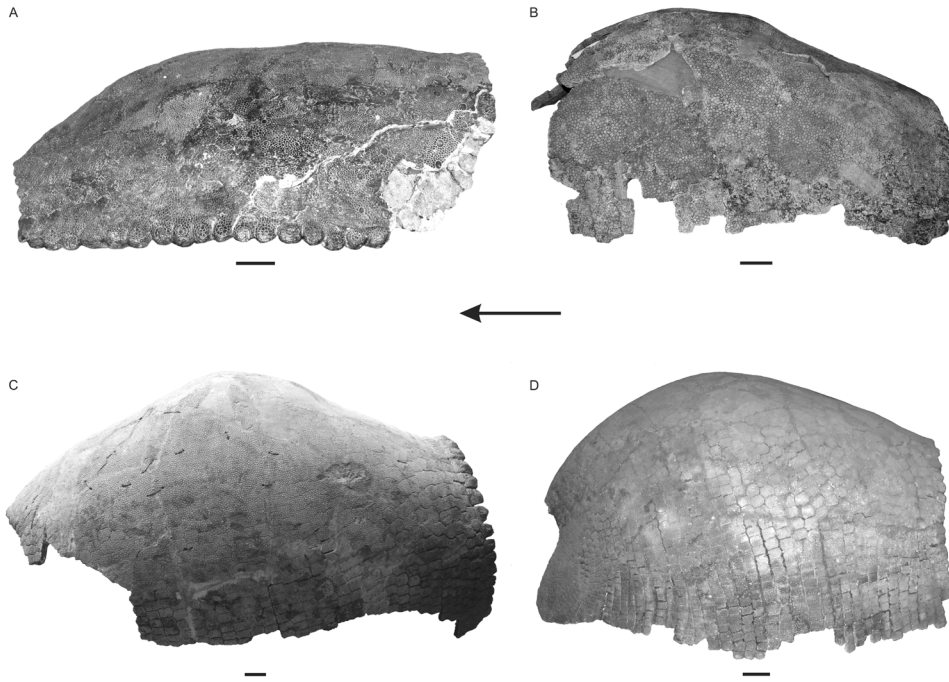


FIG. 3. Lateral view of the dorsal carapaces of *Panochthus* sp. UATF n/n (A); *P. hipsilis* (B); *P. intermedius* (C) and *P. tuberculatus* (D). Scale bar= 100 cm; the black arrow shows an antero-posterior sense.

TABLE 1. CARAPACE MEASUREMENTS IN MILLIMETERS.

Taxa	<i>Panochthus</i> sp.	<i>P. tuberculatus</i>	<i>P. intermedius</i>	<i>P. hipsilis</i>
Specimen number	UATF s/n	MLP 16-29	MHNC 13491	MURB 1906A
APLDC	1,300	1,770	2,030	1,460
TL	1,390	1,720	1,900	1,270
ICDC	1.07	0.97	0.94	0.87

Measurements of the dorsal carapace of *Panochthus* sp., *P. tuberculatus*, *P. intermedius* and *P. hipsilis*. **APLDC**: antero-posterior length of the dorsal carapace along dorsal curvature (expressed in meters); **TL**: antero-posterior length of the dorsal carapace without considering the dorsal curvature (expressed in meters); **ICDC**: Index of Convexity of the Dorsal Carapace: ratio of the length of the dorsal carapace (in a straight line, without considering curvature) and the length considering the curvature.

its maximum height in the same region as in UATF-V n/n; however, the slope towards the caudal end is more marked (*ca.* 10°) in the first three (*P. tuberculatus*, *P. intermedius* and *P. hipsilis*). The dorsal profile of UATF-V n/n differs even more from that corresponding to the carapace of *P. frenzelianus* and *P. intermedius*, since in the latter species the highest point is at the midpoint of the carapace and descends towards both ends (anterior and posterior) with an angle of *ca.* 15°.

Cephalic notch (Fig. 2). It is partially reconstructed, hiding the morphology of osteoderms.

Antero-dorsal region (Fig. 2A). Towards the antero-dorsal region (immediately behind the restored osteoderms that delimit the cephalic notch), a series of osteoderms are visible. They have a central figure, with a smooth and flat to slightly concave surface, which is surrounded by three to five rows of peripheral figures. The series adjacent to the central figure consists of a minimum of 10 polygonal

tubercular figures. In contact with the most distal series, accessory figures can be seen, irregularly distributed and without forming a complete series. The presence of a central figure on the osteoderms of this sector of the carapace is a feature shared only with *P. intermedius*. However, UATF-V n/n differs from this latter species by having between three and five rows of peripheral figures surrounding the central figure, whereas *P. intermedius* has in this region only two or three series rows of peripheral figures. In turn, the exposed surface of the central figure of *P. intermedius* is flat, never concave as in UATF-V n/n.

Middle-dorsal region (Fig. 2B). As in all species of *Panochthus*, in UATF-V n/n all the osteoderms of this region have a reticular ornamentation pattern, in which no central figure can be distinguished; most of them are isodiametric, although some of them may have slightly different proportions.

Postero-dorsal region (Fig. 2C). In UATF-V n/n, osteoderms of this region have a “rosette” ornamentation pattern, as in *P. intermedius* and *Propanochthus bullifer* Burmeister, 1874. The central figure is circular or sub-circular, with a flat and smooth surface, unlike in *Pr. bullifer* or *P. intermedius*. In *Pr. bullifer*, the central figures are strongly convex and rugose, whereas in *P. intermedius*, they are flat (some of them slightly depressed) and rugose. In UATF-V n/n, the central figures are surrounded by four to six series of peripheral figures; whereas in *P. intermedius* there are up to seven series surrounding the central figure, and only up to five series in *Pr. bullifer*. In UATF-V n/n the diameter of the central figures increases antero-posteriorly, as in *P. intermedius* and *Pr. bullifer*; however, the diameter of the peripheral figures decreases proportionally antero-posteriorly while increasing in number.

Caudal notch (Fig. 2). Most osteoderms of the caudal notch are reconstructed; however, it can be seen that the original osteoderms have almost straight proximal and lateral margins, while the distal margin is semicircular, entirely occupied by a broad central figure, circular to sub-circular and rugose surface. Six or seven incomplete series of isometric peripheral figures surround this central figure on the lateral and proximal margins. The most proximal series to the central figure has up to 11 or 12 peripheral figures. The relative diameter of the figures of each series diminishes toward the

margins of the osteoderm (the peripheral figures of the proximal series are almost twice the diameter of the more distal series). This morphology is similar to that observed in *Propanochthus bullifer* and in most species of *Panochthus*, except for *P. frenzelianus*, in which the osteoderms of the caudal notch have no central figure, but are formed by tubercular, blunt and cylindrical figures.

Antero-lateral region. Osteoderms that delimit the margin of this region of the dorsal carapace are mostly reconstructed. However, subsequent osteoderms have an ornamentation pattern similar to those of the mid-dorsal region (Fig. 2B), forming a reticular pattern, but with a shorter relative diameter. This condition is shared with the remaining species of the genus (e.g., Porpino et al., 2010).

Middle-lateral region. Osteoderms that limit the ventral margin of this region are mostly reconstructed. Original osteoderms show that the exposed surface of the most anterior area of this region shows a reticular pattern with ca. 17 polygonal and tubercular figures in each osteoderm, whereas the most posterior osteoderms have a flat and smooth central figure, similar to the remaining species of the genus and *Pr. bullifer*. In UATF-V n/n, these central figures occupy a central position of the osteoderm, and are surrounded by four to six series of polygonal peripheral figures.

Postero-lateral region. Approximately 60% of the ventral area of this region is missing, but the preserved portions show that ornamentation of the most dorsal osteoderms does not differ significantly from the osteoderms of the most posterior area of the middle-lateral region, i.e., central figure surrounded by four or six series of peripheral figures.

5. Phylogenetic results

One MPT was obtained from the phylogenetic analysis, with the following characteristics: L=77, CI=0.65, RI=0.74 (Fig. 4). The clade *Glyptodon reticulatus* + *Boreostemma acostae* (9[0]; 11[0]; 15[0]; 33[1]) behaves as the sister group of the remaining Glyptodontidae analyzed. These latter are related to each other through the following synapomorphies: 1[1]; 30[0]; 32[0], being *Propalaeohoplophorus australis* the taxon with the highest number of plesiomorphic characters. In this context, synapomorphies 6[0]; 9[2]; 28[1]; 35[1] associate the remaining species, which, in turn, are distributed into two major lineages.

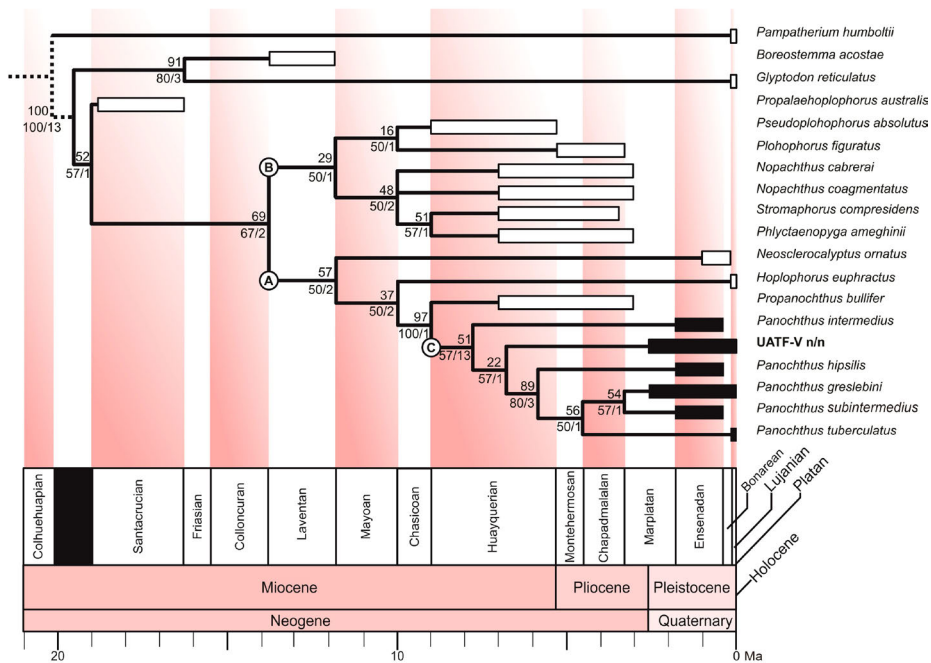


FIG. 4. Most parsimonious tree (MPT). Length= 77 steps; consistency index (CI)= 0.65; retention index (RI)= 0.74. Numbers above nodes correspond to Jackknife values; numbers below nodes correspond to relative (left) and absolute (right) Bremer support.

The first one, **node A** (synapomorphies 1[2]; 5[1]; 8[1]; 33[1]; 37[1]), is formed by *Neosclerocalyptus ornatus*, *Hoplophorus euphractus*, *Propanochthus bullifer*, *Panochthus intermedius*, *P. hipsilis*, *P. tuberculatus*, *P. greslebini*, *P. subintermedius*, and UATF-V n/n. In this group, *N. ornatus* occupies a basal position, whereas *H. euphractus* is the sister taxon of the remaining species of the **node A**. The analyzed members of the genus *Panochthus* form a monophyletic group together with UATF-V n/n and *Propanochthus bullifer*, supported by the synapomorphies 25[1]; 27[2]; 31[1]; 38[1]; 41[1] and 42[2], being *Pr. bullifer* the member with the most plesiomorphic characters. In turn, *Panochthus intermedius* is the sister taxon of the remaining *Panochthus* spp. (**node C**; 10[1]), while UATF-V n/n is related to the other representatives of the genus through the synapomorphies 19[1]; 21[2]; 22[2]; 23[2] and 29[1]. The **node B** (synapomorphies 12[2]; 33[0]; 36[2]) includes *Pseudoplohophorus absolutus* + *Plohophorus figuratus* (16[1]) on the one hand, and relates *Nopachthus coagmentatus*, *N. cabrerai*, paraphyletically with the clade *Phlyctaenopyga*

ameghiini + *Stromaphorus compressidens* (23[0]) on the other hand.

6. Discussion

The comparative study carried out in this work indicates that the dorsal carapace UATF-V n/n has a combination of characters typical of the genus *Panochthus*, i.e., dorsal carapace with thick osteoderms polygonal in outline, with small, isodiametric, polygonal tubercles, forming a reticular pattern on the mid-dorsal region; or, in “rosette” in other regions, with a flat and smooth central figure, never elevated as in *Propanochthus*, *Nopachthus*, or *Phlyctaenopyga* (Porpino *et al.*, 2010; Zamorano *et al.*, 2014). In turn, UATF-V n/n has its own characteristics in the carapace, different from the other *Panochthus* species in which this structure is known. Among them, the dorsal profile (i.e., maximum height at the level of the anterior region, with a slope *ca.* 30° from this point to the cephalic end, and posterior profile from the maximum height almost horizontal) and the ornamentation pattern of the osteoderms of the antero-dorsal, postero-dorsal

and postero-lateral regions and posterior area of the middle-lateral region (*i.e.*, distinguishable central figure, flat, smooth and sub-circular, surrounded by up to five series of peripheral figures) (Fig. 2). This combination of characters suggests that UATF-V n/n may represent a new species of *Panochthus*. However, it has to be noted that, up to date, the dorsal carapace of some species, such as *P. jaguaribensis* and *P. floresiensis* is still unknown, preventing a rigorous comparison between these taxa and UATF-V n/n.

From a phylogenetic standpoint (Fig. 4), the analysis here developed confirms the monophyly of the genus *Panochthus* (**node C**), thus corroborating the proposal of Zamorano and Brandoni (2013) (see Zamorano *et al.*, 2014; Zurita *et al.*, 2017). Likewise, five synapomorphies (*i.e.*, 19[1]; 21 [2]; 22[2]; 23[2] and 29[1]) support the inclusion of UATF-V n/n in this genus, occupying a basal position within the lineage *Propanochthus* + *Panochthus* (although with more derived characters than *Pr. bullifer* and *P. intermedius*). This basal position of UATF-V n/n results similar to that obtained by Cuadrelli *et al.* (2020) for another sub-andean glyptodont, *G. jatunkhirkhi*, in which this latter appears as sister group of *G. reticulatus* + *G. munizi*. Thus, taxa from high areas belonging to different lineages (*i.e.*, *G. jatunkhirkhi* and *P. hipsilis*) consistently show basal phylogenetic positions relative to lowland Pleistocene taxa of both genera, *Glyptodon* and *Panochthus* (Zurita *et al.*, 2017; Cuadrelli *et al.*, 2020).

These results support the ideas posed, in a precladistic context, by Castellanos (1942), suggesting that the presence of a single evolutionary lineage characterized by the progressive change of ornamentation of osteoderms of the dorsal carapace, from the most plesiomorphic condition of a “rosette” pattern (central figures surrounded by one or more series of peripheral figures, such as *Propanochthus*), up to the most apomorphic condition, with a “reticular” pattern (osteoderms with only isodiametric figures, without distinguishable central figures, such as most regions of the carapace of *Panochthus*) (Zamorano, 2012; Zurita *et al.*, 2017). On the other hand, the phylogenetic distribution of the representatives of the genus *Panochthus*, together with related taxa, is also in agreement with the last proposal of Zurita *et al.* (2017) for this clade, in which *Pr. bullifer* forms the sister group of *Panochthus* (Fig. 4).

From a paleobiogeographic point of view, Cuadrelli *et al.* (2020) suggested an early dichotomic

radiation of Glyptodontidae, with two lineages: one of northern origin, with a wide latitudinal distribution and low specific diversity (*i.e.*, Glyptodontinae) and another one of southern origin (not yet formally named), with more restricted latitudinal distribution but higher specific diversity (*i.e.*, the remaining representatives of Glyptodontidae). Within this last radiation, geographically more restricted (“southern radiation”), *Panochthus* represents the clade with the largest latitudinal distribution, with records in Argentina (Chaco-Pampean, Mesopotamic, sub-Andean and Patagonian regions), Uruguay; Brazil (southeast and northeast) Paraguay (southeast), Bolivia (central and south), and Peru (southeast). In this scenario, the southernmost limit belongs to the locality of Fitz Roy, Deseado Department, Santa Cruz Province, Argentina (*P. tuberculatus*, 47°01' S 67°14' W, Tauber and Palacios, 2007), whereas the records of northeastern Brazil represent its northern limit (*P. greslebini* and *P. jaguaribensis*, 05°11' S 39°17' W; Porpino *et al.*, 2014).

From a paleoecological perspective, the records of *Panochthus* are commonly associated with the presence of *Glyptodon* (*e.g.*, Duarte, 1997; Porpino *et al.*, 2004; Oliveira *et al.*, 2010; Gasparini *et al.*, 2016). In this sense, in low-land regions (*i.e.*, Argentina, Uruguay and south of Brazil) the presence of both genera (*Glyptodon* and *Panochthus*) are commonly related to open or semi-open grasslands and semi-forested environments, under wide range of different paleoclimatic conditions, at least for the late Pleistocene (Gasparini *et al.*, 2016; Krapovickas and Tauber, 2016; Ferrero *et al.*, 2017; Ubilla *et al.*, 2017).

In turn, the records of *Panochthus* in the intertropical region (*i.e.*, northeastern Brazil) corresponds to *P. greslebini* and *P. jaguaribensis* (the latter species considered endemic to this region), however the holotypes of these species have no stratigraphic provenance and can only be assigned to the Pleistocene *sensu lato* (Porpino *et al.*, 2014; Zamorano *et al.*, 2014). Although this situation difficult determining the type of environment inhabited by these species, the presence of *Panochthus* in this intertropical region, together with *Glyptotherium* and *Pachyarmatherium*, indicates a variety of ecological niches (Oliveira *et al.*, 2010), linked to dense vegetation and high humidity that characterized the northeastern Brazil during the Pleistocene (Vivo and Camingnotto, 2004; Cione *et al.*, 2009; Zamorano *et al.*, 2014). In this sense, the presence of

Panochthus in northeastern Brazil could be explained by the movement of these glyptodonts through arid corridors, grasslands or savannas (Scillato-Yané *et al.*, 1995; Zamorano *et al.*, 2014) following, for example, the eastern route proposed by Prado *et al.* (2003) to explain the dispersal of *Stegomastodon* (= *Notiomastodon* Cabrera, 1929) in South America, or it could indicate that the endemic species of *Panochthus* in this region (*P. jaguaribensis*) was adapted to more humid conditions compared to the remaining species of *Panochthus*.

Regarding to high elevation areas, the representatives of *Panochthus* from Bolivia include: (1) an incomplete skull and almost complete dorsal carapace (MURB 1906A/1906B) holotype of *P. hipsilis*, and a caudal tube (MHNS 8) assigned to *P. hipsilis*, from the surroundings of Potosí (Bolivia), at ca. 4,000 m a.s.l.; (2) an isolate osteoderm (MUSM-s / n) referable to *Panochthus* sp., from Desaguadero (Peru) at ~3,800 m a.s.l. (found very close to the limit with Bolivia); (3) an almost complete dorsal carapace (UATF-V n/n) here assigned to *Panochthus* sp., from the surroundings of Potosí (Bolivia), at ca. 3,205 m a.s.l.; (4) an almost complete specimen (MHNC-13491) assigned to *P. intermedius*, from near Cochabamba (Bolivia), at ca. 2,600 m a.s.l.; (5) one osteoderm and fragments of a caudal tube (MNPA-V 006598) assigned to *Panochthus* sp., from the Tarija Valley (Bolivia), at ca. 1,870 m a.s.l. (Zamorano and Almonte, 2018; Zamorano and Oliva, 2020). In this sense, these five records of *Panochthus*, together with the large diversity of herbivores and mega-herbivores (*i.e.*, Glyptodontidae, Gomphotheriidae, Megatheriidae, Toxodontidae) from the Andean region of central Bolivia and southern Peru, may be likely related to the “Minchin paleolakes system”, a huge system of water bodies located in the Andean Altiplano, that would have increased the primary productivity of these ecosystems during the Pleistocene (Sánchez-Saldías and Fariña, 2014). Specifically, the locality of Mojotorillo has provided several remains belonging to large (*i.e.*, Equidae and Carnivora) and megamammals (*i.e.*, Xenarthra and Litopterna) (Pinto Yupanqui, 2015), including this particular specimen of *Panochthus*. Although we cannot confirm the co-occurrence of this palaeofauna, the restricted stratigraphical level from which most of them were recovered, suggests that these fauna could have lived in a very short geological time. If so, this could support the idea

that mountainous areas developed a large vegetal diversity supporting a high faunal variety, both with significant levels of endemism (Wardle, 1991; Rogers and Walker, 2005; Burke 2007; Sadler and Bradfield, 2010, among others).

These paleobiogeographic and paleoecologic aspects suggest that the different species of *Panochthus* were likely adapted to a specific environment. This is particularly evident in those taxa that inhabited high-altitude ecosystems in the Eastern Cordillera of Bolivia, associated with high primary productivity and high biodiversity (Wardle, 1991; Roger and Walker, 2005; Burke 2007; Sadler and Bradfield, 2010; Sánchez-Saldías and Fariña, 2014) such as *P. hipsilis* and UATF-V n/n, or those species from the Amazon, related to dense vegetation and high humidity levels, such as *P. jaguaribensis* (Scillato-Yané *et al.*, 1995; Vivo and Camingnotto, 2004; Cione *et al.*, 2009; Zamorano *et al.*, 2014). Both cases contrasting with the Pampean species, commonly associated with temperate savannas and temperate grasslands related to high variation of annual temperature (Ray and Adams, 2001; Vivo and Carmignotto, 2004; Mayle, 2006; Varela *et al.*, 2018), such as *P. frenzelianus*, *P. subintermedius* and *P. florensis* (Zurita *et al.*, 2017; Zamorano *et al.*, 2021).

7. Conclusions

In this work, a new record of *Panochthus* from the Pleistocene of Mojotorillo, Potosí, Bolivia, is reported. This is the second most complete specimen recovered in the high Andes of Bolivia. The specimen here described is assigned to *Panochthus* sp. because it shares some features with the other species of the genus (*i.e.*, osteoderms of the mid-dorsal region with a reticular pattern); however, it has also features not yet described for any other species of *Panochthus* from which the dorsal carapace is known (*i.e.*, distinguishable central figure in the osteoderms of most regions of the dorsal carapace). The existence of three species (*P. greslebini*, *P. jaguaribensis* and *P. florensis*) in which the dorsal carapace is not yet known prevents confirming that it is a new taxon.

Phylogenetically, UATF-V n/n has five synapomorphies allowing its inclusion within the genus *Panochthus*, occupying a basal position within the obtained cladogram, as sister group of all *Panochthus* spp. but *P. intermedius*.

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Appendix 1

List of features and feature state

1. Presence of a notch in the margins of the narial aperture (in lateral view): (0) absent; (1) present.
2. Position of the roof of the skull respects the upper edge of the orbit: ratio between the height of the skull roof (over the upper edge of the orbit) and the height of the orbit: (0) lower than 0.25; (1) between 0.26 and 0.33; (2) greater than 0.34.
3. Development of the postorbital process: (0) uncomplete; (1) complete.
4. Angle between the palatal plane and the plane of the rostral area: (0) lower than 45°; greater than 46°.
5. Outline of the orbital notch in lateral view: (0) dorso-ventrally elongated; (1) subcircular.
6. Length of the skull: ratio between the length of the skull and the height of the skull (regardless of the descendant process of the zygomatic arch): (0) great than 1.5; (1) less than 1.4.
7. Size of the temporal fossa: ratio between the antero-posterior length of the temporal fossa and the antero-posterior length of the orbit: (0) more than 2.5 times the antero-posterior length of the orbit; (1) nearly 2 times the antero-posterior length of the orbit.
8. Relation between the dorsoventral diameter of the zygomatic arch below the temporal fossa and the dorsoventral diameter below the orbital fossa: (0) similar; (1) different.
9. Orientation of the zygomatic arch (in lateral view): (0) oblique; (1) horizontal.
10. Cross section of the occipital condyles: (0) subcircular; (1) subelliptic; (2) nearly squared.
11. Orientation of the external nostrils: (0) anterior; (1) antero-ventral.
12. Ratio between labial-lingual axis and anterior-posterior axis of the Mf1: (0) minor or equal to 75%; (1) major to 75%.
13. Start of the trilobulation of the molariforms: (0) Mf1; (1) Mf2; (2) Mf3; (4) Mf4.
14. Imbrication of the molariforms: (0) imbricated; (1) no imbricated.
15. Premaxilar teeth: (0) absent; (1) present.
16. Entepicondilar foramen: (0) absent; (1) present.
17. Highest point of the dorsal carapace: (0) at the central region; (1) at the anterior region; (2) at posterior region; (3) convexity not evident.
18. Presence of mobile bandes: (0) absent; (1) present.
19. Pattern of ornamentation of the osteoderms of the middle-dorsal region of the dorsal carapace: (0) rosette pattern; (1) reticular pattern.
20. Presence of a central figure in the osteoderms of the anterior region: (0) with a central figure; (1) without a central figure.
21. Ornamentation of the osteoderms of the posterior region: (0) with a convex central figure; (1) with a flat central figure; (2) with a reticular pattern.
22. Disposition of the small figures of the osteoderms of the anterior region: (0) with a central figure surrounded by 4-7 rows of peripheral small figures; (1) with a central figure surrounded by 1-3 rows of peripheral small figures; (2) in a complete reticular pattern.
23. Disposition of the small figures of the osteoderms of the posterior region: (0) with central figure surrounded by 4-7 rows of peripheral small figure; (1) with central figure surrounded by 1-3 rows of peripheral; (2) in a complete reticular pattern.
24. Number of small figures in the first row of the osteoderms of the anterior region: (0) more than 12 peripheral small figures; (1) less than 12 peripheral small figures; (2) conforming a complete reticular pattern.
25. Number of small figures in the first row of the osteoderms of the posterior region: (0) more than 10 peripheral small figures; (1) less than 10 peripheral small figures; (2) conforming a complete reticular pattern.

26. Percentage of the surface of the osteoderms of the posterior region formed by small figures: (0) less than 50%; (1) more than 51%.
 27. Morphology of the central figures of the posterior region versus those of the anterior region of the dorsal carapace: (0) both flat; (1) posterior ones convex, anterior ones flat.
 28. Maximum number of peripheral figures in the osteoderms of the dorsal carapace: (0) up to 12; (1) up to 20; (2) 21 or more.
 29. Peripheral and accessory figures in the osteoderms of the dorsal carapace: (0) one series with accessory figures in the 10% or less of the osteoderms; (1) one series with accessory figures in more of the 10% of the osteoderms.
 30. Pattern of ornamentation of the osteoderms of the posterior-dorsal region of the dorsal carapace: (0) rosette pattern; (1) reticular pattern.
 31. Peripheral figures in the osteoderms forming the caudal opening: (0) lateral and proximal peripheral figures; (1) proximal peripheral figures.
 32. Series of peripheral figures in the osteoderms forming the caudal notch: (0) one serie; (1) two or more series
 33. Morphology of the osteoderms that constitute the margin of the dorsal carapace: (0) tubercular osteoderms absent, or limited to the caudal notch; (1) tubercular osteoderms present along the entire margin of the dorsal carapace.
 34. Peripheral accessory figures of the osteoderms of the dorsal carapace with flat to slightly concave surface: (0) absent; (1) present.
 35. Morphology of the central figure of the osteoderms that limit the caudal notch: (0) circular; (1) oval in lateromedial sense; (2) tubercular.
 36. Morphology of the caudal armor: (0) with rings up to 90% of the caudal armor; (1) with rings up to 60% or less of the caudal armor (caudal tube represent 40% of the total length of the caudal armor).
 37. Form of the distal end of the caudal armor: (0) rounded; (1) pointed; (2) blunt.
 38. Ornamentation of caudal armor versus ornamentation of the dorsal portion of the carapace: (0) different; (0) similar.
 39. Morphology of the central figure of the osteoderms of the most proximal region of the caudal tube: (0) with lateral apollae and central figures in the osteoderms of the dorsal area; (1) with lateral apollae and reticular pattern in the osteoderms of the dorsal area.
 40. Lateral figures of the caudal tube modified in spines: (0) absent; (1) present.
 41. Morphology of the exposed surface of the lateral figures of the caudal tube: (0) smooth surface; (1) rugose surface.
 42. Surface of the caudal tube spines: (0) without spines; (1) flat surface; (2) rugose surface.
- Apendix 2:
Character matrix.

Appendix 2

Character matrix

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
<i>Pampatherium humboldtii</i>	0	0	0	0	0	0	1	0	0	1	0	1	-	1	1	1	-	1	-	0	1	-	-	-	-	-	0	-	-	-	-	-	-	-	-	0	0	0	-	-	-	0
<i>Propalaeohoplophorus australis</i>	0	1	0	0	0	0	1	0	0	1	0	1	3	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	-	-	0
<i>Glyptodon reticulatus</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	1	2	0	0	0	0	-	-	0	
<i>Boreostemma acostae</i>	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	1	2	0	0	0	0	-	-	0
<i>Nopactus coagmentatus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0	?	0	0	?	1	?	0	?	1	0	1	
<i>Nopactus cabrerai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0	?	?	0	?	?	?	?	?	?	?	?	
<i>Propanochthus bullifer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	0	?	0	1	?	2	1	0	0	1	0	1	1	1	2	1	1	1	1	1	2	
<i>Panochthus intermedius</i>	1	2	0	1	0	1	0	1	1	2	1	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	0	2	1	0	0	1	0	1	0	1	?	1	1	1	1	2
<i>Panochthus tuberculatus</i>	1	2	1	1	0	1	0	1	1	2	1	0	1	0	0	1	1	0	1	1	2	2	2	2	2	1	0	2	1	1	0	1	0	1	0	1	2	1	1	1	1	2
<i>Panochthus subintermedius</i>	1	1	0	?	0	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	2	2	2	2	2	1	0	2	1	1	0	1	0	1	0	1	1	1	1	1	1	2
<i>Panochthus greslebini</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	2	2	2	2	2	1	0	2	1	1	0	?	?	1	?	1	1	1	1	1	1	2
<i>Panochthus hipsilis</i>	1	?	1	1	0	1	0	1	?	2	1	0	1	0	0	?	1	0	1	1	1	2	2	2	0	1	0	2	?	1	0	1	0	1	0	?	?	?	?	?	?	?
<i>Plohophorus figuratus</i>	0	1	0	0	0	0	0	0	0	2	0	1	2	0	0	1	1	0	0	0	1	1	1	1	0	0	0	1	1	0	0	?	0	0	?	1	2	0	0	0	0	
<i>Pseudoplohophorus absolutus</i>	0	1	0	0	0	0	0	0	0	2	0	1	2	0	0	1	1	0	0	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1	2	0	0	0	0
<i>Stromaphorus compressidens</i>	0	1	0	0	0	0	0	0	1	2	0	1	2	0	0	?	1	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	?	1	2	0	0	0	0	
<i>Phlyctaenophyga ameghini</i>	0	1	0	0	0	0	0	0	0	2	0	1	2	0	0	?	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1	1	2	0	0	0	0	
<i>Hoplophorus euphractus</i>	0	2	0	0	0	?	0	?	?	2	0	?	?	?	0	?	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	1	0	1	?	1	2	1	0	1	0	1
<i>Neosclerocalyptus ornatus</i>	0	2	0	0	0	1	0	0	1	2	0	1	1	0	0	1	3	0	0	0	1	1	1	1	0	0	0	1	1	0	0	?	0	1	1	1	0	1	0	0	0	
UATF-V s/n	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	1	0	0	1	1	1	0	2	1	0	0	0	1	0	?	?	?	?	?	?	?