

Diagnosis and redescription of *Panochthus subintermedius* Castellanos (Xenarthra, Glyptodontia) from the Ensenadan (early-middle Pleistocene) of Buenos Aires (Argentina)

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Abstract *Panochthus subintermedius* was originally named by Castellanos in 1933, without any diagnosis and no type material designated. In 1936, he briefly described and designated a holotype for this species (MACN-Pv 5130) and subsequently, in 1942, completed the description, but a diagnosis was still lacking. Some authors have considered this species as *nomen nudum*, but others have accepted its validity since 1942. In this contribution we propose that Castellanos's 1936 paper is the valid name-establishing publication for this species. The holotype includes a large portion of dorsal carapace, the caudal tube, and remains of postcranial skeleton, belonging to a single specimen from the Ensenadan Stage/Age (early-middle Pleistocene) of Buenos Aires, Argentina. In contrast to the original description, new observations of the holotype reveal that the superficial surface of the dorsal carapace osteoderms is ornamented with small polygonal figures without a principal one. This ornamentation differs from that of *P. intermedius* Lydekker (the only species accepted up to now for the Ensenadan), with a central figure in most of its osteoderms. The caudal tube of *P. subintermedius* differs from those of the Bonaerian-Lujanian species

(middle late Pleistocene–early Holocene), in having a sharper distal end, one apical dorsal figure, and a higher number of central figures along the entire dorsal surface. No caudal tube associated with the carapace of *P. intermedius* is known. Accordingly, *P. subintermedius* can be clearly distinguished from other Panochthini species by a unique combination of carapace and caudal tube characters. This new combination of characters provides more information on this taxon and other species of Panochthini for future studies in the interrelationships of Glyptodontia.

Keywords Glyptodontia · Panochthini · *Panochthus* · Ensenadan · Argentina · South America

Kurzfassung 1933 benannte Castellanos *Panochthus subintermedius* ohne eine Diagnose zu machen oder Typusmaterial festzulegen. Im Jahr 1936 folgten vom selben Autor eine kurze Beschreibung und die Definition des Holotypus (MACN-Pv 5130). Später, im Jahre 1942, schloss Castellanos die Beschreibung ab ohne eine Diagnose zu stellen. Einige Autoren betrachten diese Art als *nomen nudum*, während andere ihre Gültigkeit seit 1942 akzeptieren. In diesem Beitrag plädieren wir dafür, die Gültigkeit der Artbezeichnung Castellanos (1936) anzuerkennen. Der Holotypus umfasst einen großen Teil des dorsalen Panzers, der kaudalen Knochenscheide und einige Postcranialelemente von einem einzigen Exemplar aus der Ensenada-Stufe (frühes Mittel-Pleistozän) von Buenos Aires (Argentinien). Im Gegensatz zu der ursprünglichen Beschreibung weisen neue Beobachtungen am Holotypus kleine Polygone ohne Zentralstruktur auf den Osteodermen an der dorsalen Oberfläche des Panzers auf. Diese Ornamentierung unterscheidet sich von *P. intermedius* (LYDEKKER), die bis heute einzige bekannte Art aus dem Ensenadan, indem diese eine Zentralstruktur in den meisten

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Osteodermen aufweist. Die kaudalen Knochenscheiden von *P. subintermedius* und der Bonaerium-Lujanium Art (mittleres Spät-Pleistozän/früheres Holozän) unterschieden sich (d. h. ein spitzes distales Ende, eine apikale dorsale Struktur und eine höhere Anzahl von zentralen Strukturen über die gesamte Dorsalfläche). Der Panzer von *P. intermedius* ist mit keiner kaudalen Knochenscheide verbunden. Zusammenfassend lässt sich feststellen, dass *P. subintermedius* aus dem Ensenadium durch eine einzigartige Kombination von Merkmalen des Panzers und der kaudalen Knochenscheide gekennzeichnet ist. Diese neue Kombination von Merkmalen liefert weitere Informationen zu diesem Taxon und zu anderen Arten der Panochthini für zukünftige Studien der Verwandtschaftsverhältnisse der Glyptodontia.

Schlüsselwörter Glyptodontia · Panochthini · *Panochthus* · Enseadan · Argentinien · Südamerika

Introduction

One of the most informative characters allowing the differentiation among glyptodont genera and species has been the morphology and ornamentation of the osteoderms of the dorsal carapace (Owen 1845; Nodot 1856; Burmeister 1864; Ameghino 1889) and the caudal tube (Burmeister 1864; Ameghino 1889). Ameghino (1889), Castellanos (1959), Hoffstetter (1958), and Paula Couto (1979) were the first authors to realize a systematic analysis based in characters of the caudal tube and carapace. Recently, other authors (Zurita et al. 2005; Fernicola 2008; Zurita et al. 2009) have based their systematic works solely on cranial characters; however, it is important to incorporate the available information from the ornamentation of the dorsal carapace and caudal tube into such analyses. In this context, it becomes necessary to define the most important characters of these regions for the different genera and species.

Within Glyptodontia, the tribe Panochthini (Castellanos 1927) is known from Upper Pliocene to Pleistocene strata from southern South America, including Argentina, Uruguay, Bolivia (Tonni et al. 2009), and Brazil (Porpino and Bergqvist 2002; Porpino 2009). The species of the tribe Panochthini differ from the other glyptodonts by the presence in most of the dorsal carapace of osteoderms with only small polygonal figures on the superficial surface and, in some sections of the carapace, one central figure. The caudal tube is characterized by its large size, depressed shape, terminal figures at its distal end, lateral figures on the lateral side, and marginal and central figures on the dorsal and ventral surfaces (see Castellanos 1925b, 1942). The surrounding area of these figures is covered by small polygonal figures similar to those present in the carapace osteoderms.

Panochthus is a very important genus within Panochthini because it represents the last lineage of this tribe and also the largest size. The latest revision of the genus *Panochthus* (Burmeister 1866) was carried out by Castellanos (1942), who considered nine valid species, including six previously known taxa: *P. intermedius* (Lydekker 1894), *P. subintermedius* Castellanos, *P. frenzelianus* (Ameghino 1889), *P. morenoi* (Ameghino 1881), *P. vogti* (Ameghino 1889), *P. tuberculatus* (Owen 1845), and three new species: *P. rusconii*, *P. oliveira-roxoi*, and *P. greslebini*, the latter two from Brazil. He also stated that *Panochthus bullifer* (Burmeister 1870–1874) represented a different genus, *Propanochthus* (Castellanos 1925a). Later, two new species from Brazil were defined: *Panochthus rochai* (Paula Couto 1954) and *P. jaguaribensis* (Moreira 1965). Moreira (1971) and Porpino and Bergqvist (2002) synonymized *P. oliveira-roxoi* and *P. rochai* with *P. greslebini*, in a revision of Brazilian panochthines. However, the taxonomic status of *P. jaguaribensis* is debatable, therefore Moreira (1971) proposed the exclusion of this species from *Panochthus* and transferred it a new genus, *Parapanochthus*. However, Porpino and Bergqvist (2002) returned this species to genus *Panochthus*, but this assignment is still controversial (Porpino 2009). Within all species of *Panochthus*, only one was differentiated by cranial characters (*Panochthus vogti* Ameghino, see the section “Materials and methods”), from *P. frenzelianus* and *P. tuberculatus*. In contrast, the last two and the remaining species are recognized by characters of the osteoderms from the dorsal carapace and the caudal tube.

No exhaustive revisions of the group have been made since the work of Castellanos (1942). However, the species *P. vogti*, *P. rusconii*, and *P. subintermedius* have not been mentioned in different faunal lists from southern South America for the Ensenadan (early-middle Pleistocene)–Lujanian (late Pleistocene–early Holocene) interval (Cione and Tonni 2005, and references therein). Only *P. intermedius* has been cited for the Ensenadan, although Castellanos (1933) mentioned a new species, *P. subintermedius*, without providing figures or a formal description. Afterwards, Castellanos (1936: 24–25 pp.), provided a brief differential description in a footnote: “...difiere del *P. intermedius* en lo que respecta a la coraza en que las figuritas centrales de las placas son más pequeñas y el número de filas más reducido y limitado a las zonas marginales” (“...differ from *P. intermedius* with respect to the carapace because the central figures of the osteoderms are smaller in size and have fewer rows and limited to the marginal zones”). Moreover, he designated the holotype (MACN-Pv 5130) and mentioned that he would describe the latter in detail in another work, which was eventually published in 1942.

The aim of this contribution is to provide a formal diagnosis and redescription of the holotype of *Panochthus subintermedius*, and to discuss which year should be

considered as the valid name-establishing date for this species. In addition, we analyze its biostratigraphic implications and provide some characters from the ornamentation of the carapace and caudal tube that should be incorporated into future phylogenetic analyses of glyptodonts.

Materials and methods

The fossil specimens studied are housed in the following institutions: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Sección Paleontología Vertebrados, Buenos Aires, Argentina (MACN-Pv); Museo de La Plata, División Paleontología Vertebrados, La Plata, Buenos Aires, Argentina (MLP); Museo Universitario Florentino y Carlos Ameghino, Rosario, Santa Fé, Argentina (MUFyCA); Divisão de Geologia e Mineralogia, Colección de mamíferos fósiles, del Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil (DGM-M); Muséum National d’Histoire Naturelle, colección Pampeén, Paris, France (MNHN-PAM); American Museum of Natural History, New York, NY, USA (AMNH).

An exhaustive comparative examination of taxonomically informative characters of the carapace and caudal tube of several specimens (including the holotypes of the *Panochthus* species) was made (see [Appendix](#)). Regarding the type specimens, DGM-M 1 (*Panochthus greslebini*) and AMNH 11243–11245 (*Panochthus frenzelianus*) were compared through photographs taken specifically for this analysis. The holotype of *P. vogti* could not be examined and may possibly be housed in the National Museum of Geneva (Switzerland) (Ameghino 1889 and personal inquiry). Ameghino distinguished the species *P. vogti* in 1889 based on cranial characters observed in photographs and indicated that the caudal tube of this new species, although smaller, was very similar to that of *P. tuberculatus*. Accordingly, *P. vogti* may be considered as a valid species on the basis of the cranial characters described by Ameghino (1889), which are not available for comparison in the species studied here.

The systematic scheme follows Fernicola (2008). The terminology used for the description of the caudal tube was taken from Castellanos (1925a, 1942). The description and terminology for osteoderms follow Hill (2006) and Krmptotic et al. (2009), while the scheme for the different regions of the carapace is based on Porpino (2009) (see [Fig. 1](#)).

Systematic paleontology

Magnorder Xenarthra Cope, 1889
Order Cingulata Illiger, 1811

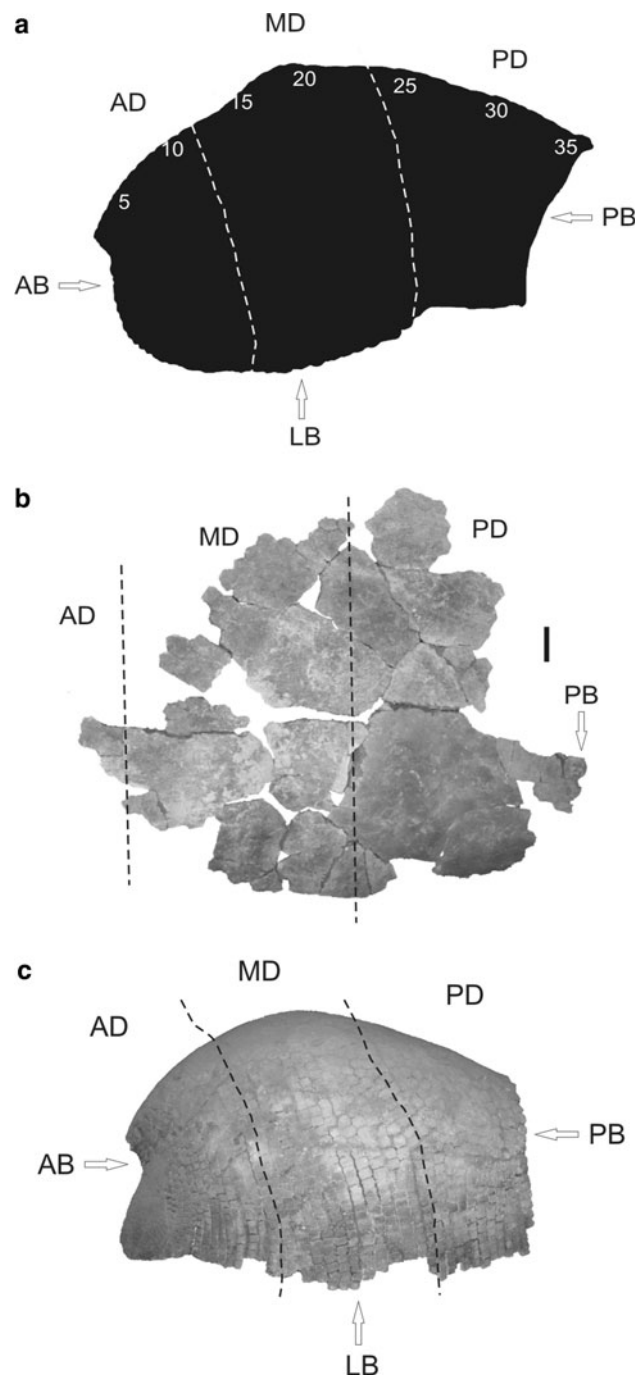


Fig. 1 **a** Schematic representation of the different regions of the glyptodontid carapace. **b** Dorsal view of the carapace of *P. subintermedius* (MACN-Pv 5130). **c** Lateral view of *P. morenoi* (MLP 16-382) and representation of the different regions. AD Anterodorsal region, MD mid-dorsal region, PD posterodorsal region, AB anterior border, LB lateral border, PB posterior border (modified from Porpino 2009)

Suborder Glyptodontia Ameghino, 1889
Infraorder Glyptodontoidei Gray, 1869
Superfamily Gliptodontoidea Gray, 1869
Family Panochthidae Castellanos, 1927
Subfamily Panochthinae Castellanos, 1927

Tribe Panochthini Castellanos, 1927
 Genus *Panochthus* Burmeister, 1866
 Type Species: *Panochthus tuberculatus* Owen, 1845
Panochthus subintermedius Castellanos, 1936
 Figs. 2, 3

Holotype: MACN-Pv 5130. Several carapace fragments corresponding to anterodorsal (two rows only), mid-dorsal, and posterodorsal regions, complete caudal tube fused to last distal ring, proximal fragment of right humerus, fragment of pelvis, and left femur.

Referred material: MUFyCA 342. Distal fragment of the caudal tube.

Geographical and Stratigraphic provenance of the holotype: Ciudad Autónoma de Buenos Aires, Argentina, Ensenadan (early-middle Pleistocene).

Diagnosis: Large species, similar in size to *P. intermedius*. Superficial surface of the osteoderms of the carapace ornamented with polygonal figures without distinct central figure, differing from *P. intermedius* in which this central figure is present in almost all osteoderms from the anterodorsal and posterodorsal regions of the carapace. Osteoderms of penultimate row without central figure in contrast to those of *P. intermedius* and *P. tuberculatus* in which a central figure is present. General shape of the

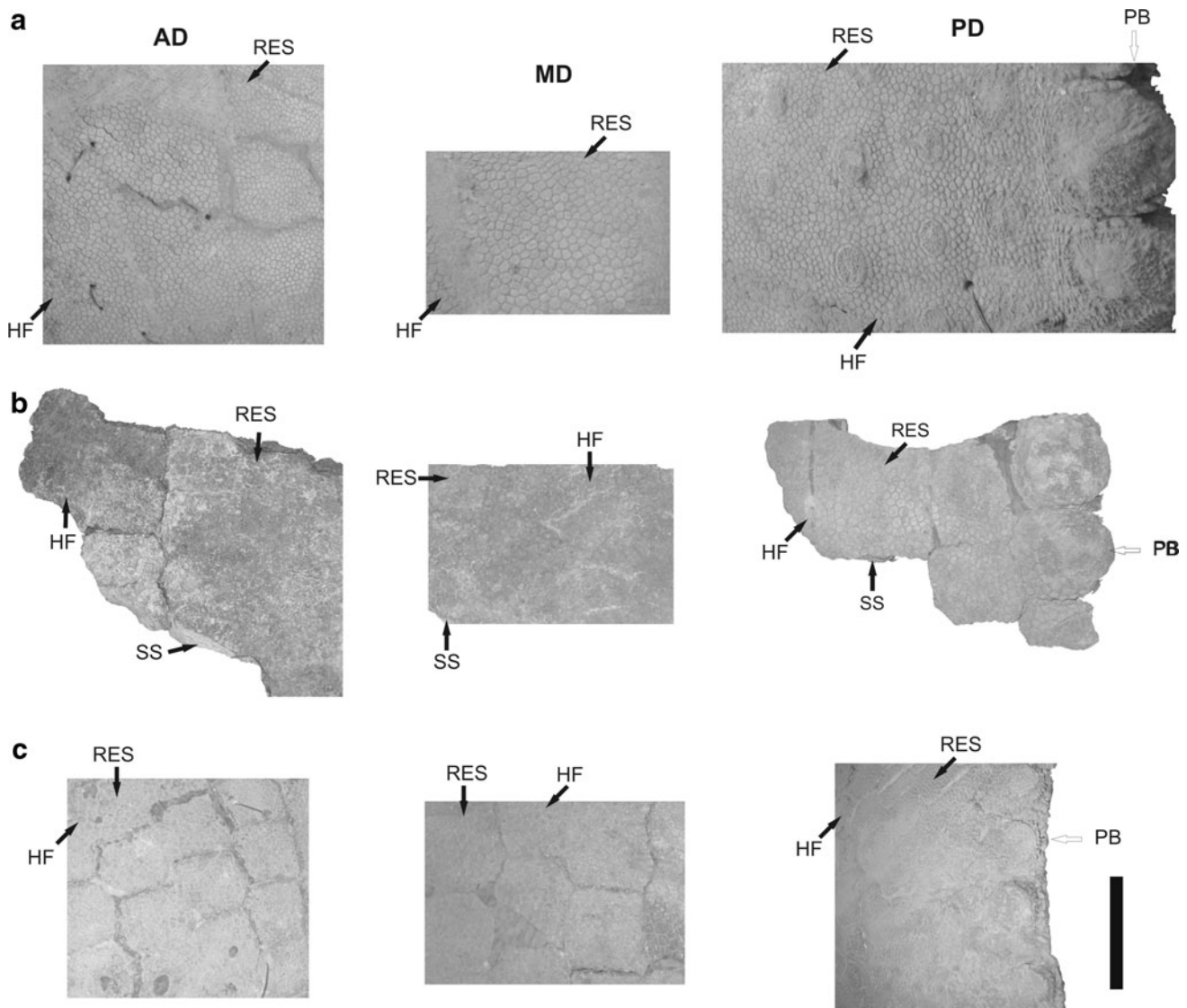


Fig. 2 Comparison of the holotype carapaces of *P. intermedius* (MLP 16-36), *P. subintermedius* (MACN-Pv 5130), and *P. morenoi* (MLP 16-382). Details of the anterodorsal (AD), mid-dorsal (MD), and posterodorsal (PD) regions of **a** *P. intermedius*, **b** *P. subintermedius*,

and **c** *P. morenoi*. HF Hexagonal figure from the superficial osteoderm surface, RES reticulating sulci, SS sutural surface (modified from Hill 2006), other abbreviations as in Fig. 1. Scale: 10 cm

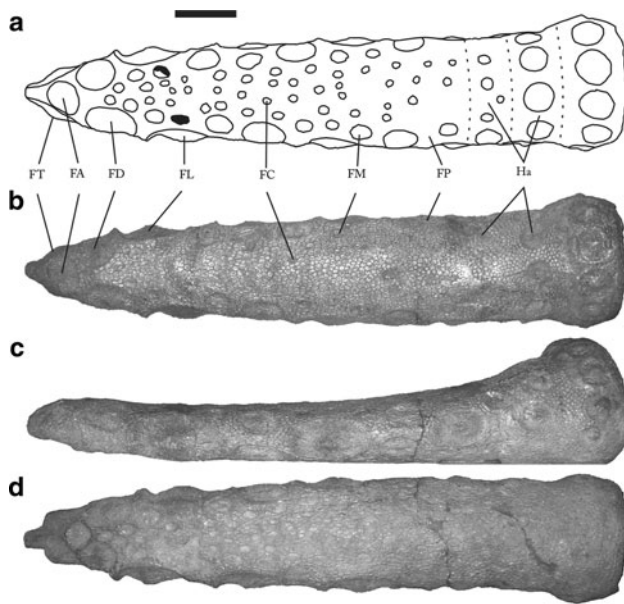


Fig. 3 Caudal tube of *P. subintermedius* (MACN-Pv 5130). **a** Schematic representation of dorsal view. *FT* Terminal figure, *FA* apical figure, *FD* dorsal figure of the dorsoventral pair, *FL* lateral figure, *FC* central figure, *FM* marginal figure, *FP* polygonal figure, *Ha* annular row (the black circles indicate reconstructed sections). **b** Dorsal view. **c** Right lateral view. **d** Ventral view. Scale 10 cm

carapace similar to that of *P. tuberculatus*; in both species, the mid-dorsal outline of the carapace presents a horizontally elongated S-shape in lateral view, different from the convex dorsal outline of the carapace in *P. intermedius*, *P. morenoi*, and *P. frenzelianus*. Caudal tube with a strongly sharpened tip, differing from the less sharp morphology of *P. greslebini* and *P. rusconii*, and the blunt tip of *P. tuberculatus*, *P. morenoi*, and *P. frenzelianus*; dorsal surface of tube with one apical figure at its distal end, between the first pair of dorsoventral figures, a character shared only with *P. greslebini*; central figures distributed over entire dorsal surface, differing from *P. tuberculatus*, *P. morenoi*, and *P. rusconii* in which central figures are restricted to the distal region of the tube; terminal figures separated in dorsal view and united in ventral view, in contrast to *P. frenzelianus* in which the terminal figures are separated on both surfaces.

Comparative description

Carapace (Figs. 1, 2) A large portion of the carapace from specimen MACN-Pv 5130 is preserved, from the last row of the anterodorsal region to the posterior border, but all lateral margins are missing. The general shape of the carapace is similar to that of *P. tuberculatus*, and both species present a characteristic concave-convex outline (oblong S-shape) at the anterior section of the mid-dorsal region. This convexity corresponds to the rise of the

sacrolumbar crest and of the transversal crest developed by the superior part of the iliac bones. This carapace morphology contrasts with those of *P. intermedius*, *P. morenoi*, and *P. frenzelianus* in which the carapace presents a convex dorsal outline.

Most of the osteoderms are fused so that their limits are not visible on the superficial surface, but the sutures are evident on the deep surface. The osteoderms (except those from the posterior border) present several polygonal figures of similar size, each of them flat or slightly depressed at the center, without central figure (see Fig. 2). In contrast, Castellanos's (1942: 492) original description stated: "Su escultura externa se caracteriza por presentar en cada placa figuras centrales, como en *Panochthus intermedius* Lyd., pero se diferencian de las de éste porque son de menores dimensiones y la zona de la coraza que ofrecen estas figuras es más reducida. Por consiguiente, resulta una transición entre el *Panochthus intermedius* y los *P. frenzelianus* y *P. tuberculatus*, estos dos últimos con la ornamentación de sus caparazones muy semejante" ("the external sculpture is characterized by a central figure in each plate, such as in *P. intermedius* Lyd., but smaller and in a more restricted region of the carapace. Consequently, this morphology is a transition between *Panochthus intermedius* and that of *P. frenzelianus* and *P. tuberculatus*, the last two with very similar carapace ornamentation"). The carapaces of the holotypes of *P. intermedius* and *P. subintermedius* differ in that, in the former, the osteoderms of the anterodorsal and posterodorsal regions have a clearly distinguishable central figure, whereas in *P. subintermedius* no central figure is present in the last anterodorsal row or in the posterodorsal region. These areas present only small polygonal figures; a central figure is only present in the posterior border of the carapace.

The ornamentation of the osteoderms on the posterior border and the penultimate row is another noteworthy character that differs among some species within *Panochthus*. The osteoderms of the penultimate row of *P. subintermedius* do not bear central figures, in contrast to those of *P. intermedius* and *P. tuberculatus* in which a central figure is present. The osteoderms on the posterior border comprise a central figure that is almost the size of the osteoderm. This figure is surrounded by a row of small polygonal figures, and in the anterior region of the osteoderm, also by a second row of peripheral figures. Although only a few osteoderms of the posterior border are preserved, it is possible to observe that this character differs depending on the carapace region: the central figure is smaller closer to the lateral borders, and the rows of polygonal figures increase toward the anterior region. In *P. morenoi* no polygonal figures are distinguishable, only a rugose area surrounds the anterior half of the central figure,

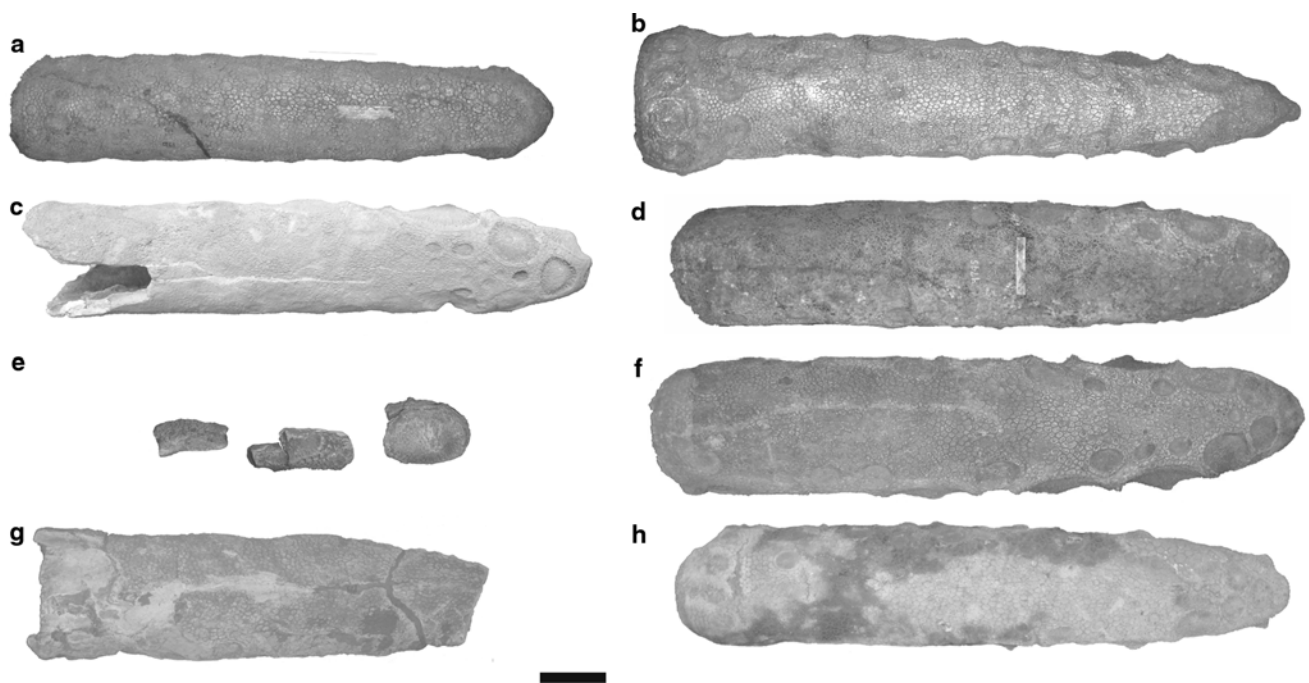


Fig. 4 Dorsal view of the caudal tube of **a** holotype of *Propanochthus bullifer* (MACN-Pv 1761), **b** holotype of *Panochthus subintermedius* (MACN-Pv 5130), **c** holotype of *P. greslebini* (DGM-M 1),

d *P. tuberculatus* (MACN-Pv 1745), **e** holotype of *P. nodotianus* (MNHN-PAM 291), **f** *P. morenoi* (MNHN-PAM ?), **g** *P. sp.* (MLP 16-381), **h** *P. sp.* (MLP 16-32)

and in contrast to Ameghino's (1889) statement, this region differs from the comparable area in *P. tuberculatus*. On the other hand, and in accordance with the description of Ameghino (1889), the posterior border and the penultimate row of *P. frenzelianus* are highly similar to those of *P. subintermedius*. Nevertheless, in the holotype of *P. frenzelianus*, most, if not all, of the osteoderms corresponding to these rows have been reconstructed, and it was not possible to observe them.

Caudal tube (Figs. 3, 4) The caudal tube is 96 cm long, including the last caudal ring, which is fused to the caudal tube (see Table 1 for the rest of the measurements). The proximal opening is almost circular, but the dorsal surface of the caudal tube descends abruptly in the first third of its length and the tube becomes depressed. There are five lateral figures on the right side of the tube, whereas there are only four figures on the left lateral region. This character is similar to the condition in some caudal tubes of *P. tuberculatus* and *P. morenoi*, but other tubes of both species have only four on each side, whereas in *Propanochthus bullifer* there are five figures on each side. These figures are conical tubercles and become larger toward the tip. Between these conical figures, the lateral surface bears small polygonal figures, as in the superficial surface of the osteoderms. At its distal end, the tube presents two terminal figures that are very extended anteroposteriorly

Table 1 Measurements of the caudal tube of *P. subintermedius* (MACN-Pv 5130)

Measurement	Value (mm)
Total length	960.00
Proximal dorsoventral diameter	201.20
Middle dorsoventral diameter (proximal middle of the caudal tube)	80.40
Distal dorsoventral diameter	82.26
Proximal transverse diameter	198.14
Middle transverse diameter	167.26
Distal transverse diameter	12.56

and compressed, making for a sharper apex in contrast to the less sharp morphology of *P. greslebini* and *P. rusconii*, and the blunt tip of *P. frenzelianus*, *P. morenoi*, and *P. tuberculatus*.

The dorsal surface (Fig. 3a, b) bears one apical figure between both terminal figures, a character shared only with *P. greslebini*, and dorsoventral pairs of figures: five on the left side and four on the right side. Five to eight marginal figures are located between these figures. Finally, the dorsal surface among all these figures is covered by small polygonal figures and numerous central figures without a defined pattern. Of note, the central figures are not arranged in transverse rows as in the

caudal tube of the *Propanochthus bullifer*, but present greater continuity than the ones in the caudal tubes of *Panochthus morenoi*, *P. tuberculatus*, and *P. rusconii* (Figs. 3a, b, 4).

The proximal end presents two annular rows of helicoidal figures; the first one includes four figures similar to those of the dorsoventral pairs. The second row bears only three figures, smaller and similar in shape to the central figures. The ventral surface of the caudal tube does not differ from that of other species; the only major difference is that the terminal figures are adjacent, they touch each other, whereas they are separated in *Propanochthus bullifer* and *Panochthus frenzelianus*.

Results and discussion

Our results highlight two useful carapace characters for distinguishing some species of *Panochthus*: (1) the general shape of the carapace (Figs. 1 and 2) and (2) the presence of the central figure in the superficial ornamentation of the osteoderms from the anterodorsal and posterodorsal regions, and from the penultimate and/or posterior border (Fig. 2). Thus, as a summary of the observations made of different species of panochthines, the following can be concluded. (1) Based on the general shape of the carapace in lateral view, two groups can be distinguished among *Panochthus* species: (a) carapace with oblong S-shape of the mid-dorsal region (*P. subintermedius* and *P. tuberculatus*) (Fig. 1a) and (b) carapace uniformly convex (*P. intermedius*, *P. morenoi*, and *P. frenzelianus*) (Fig. 1c). (2) The osteoderms from *Propanochthus bullifer* (posterodorsal region) and from *Panochthus intermedius* (anterodorsal and posterodorsal region) are easily recognizable because they have a distinct central figure different from the peripheral polygonal figures. In the remaining species for which almost complete carapaces are known, namely *P. subintermedius*, *P. tuberculatus*, *P. morenoi*, and *P. frenzelianus*, the osteoderms only have a central figure in the posterior border of the carapace and/or in the osteoderms from the penultimate row, and in the three or four osteoderms from the lateral borders, in agreement with some previous descriptions (Burmeister 1870–1874; Ameghino 1889, 1895; Castellanos 1942). Nevertheless, this character cannot be evaluated with full certainty because in the case of *P. morenoi* and *P. frenzelianus*, many of the osteoderms in these regions have been restored.

Regarding the characteristics of the caudal tube, some important features that allow distinguishing among the species of *Panochthus* are as follows (Figs. 3, 4): (1) shape of the distal end of the tube, (2) distribution of the central figures on the dorsal surface, (3) number of apical figures,

and probably (4) size. The number of lateral figures on the caudal tube is a more variable character because in some cases, e.g., *P. subintermedius* (MACN-Pv 5130) and *P. morenoi* (MNHN-PAM, unnumbered), each side of the tube has a different number of figures.

The results suggest that the caudal tube of *Panochthus subintermedius* differs from the other species by a combination of characters: strongly sharpened apex, only one apical figure, and central figures irregularly arranged on the entire dorsal surface of the tube. The annular rows of helicoidal figures on the proximal end of the tube and their arrangement should probably be considered as a combination of particular characters rather than as individual exclusive features, as is the case for most tube-related characters.

As previously pointed out, because Castellanos (1933) was the first to mention *Panochthus subintermedius*, some authors have accepted the validity of this species from that publication (Paula Couto 1954; Soilbelzon 2008), others considered it as a *nomen nudum* and accepted its validity as from 1942 (Mones 1986), yet others considered it in 1933–1936 (Castellanos 1942), and finally, some authors informally considered this species as a synonym to *P. intermedius*. Thus, taking into account Article 13 of the International Code of the Zoological Nomenclature (1999) and considering that it was in 1936 that Castellanos provided a brief description and designated the holotype and its repository, we propose the 1936 publication as the one in which the species was named.

Finally, there is a general consensus, expressed in faunal lists, to recognize only some of the species of the genus *Panochthus* for southern South America (e.g., *P. intermedius* from the Ensenadan and *P. frenzelianus*, *P. tuberculatus*, and *P. morenoi* from the Bonaerian-Lujanian interval (Scillato-Yané and Carlini 1998; Zamorano 2005; Cione and Tonni 2005, and references therein). Thus, *P. subintermedius* represents a well-characterized species for the *Mesotherium cristatum* Biozone, biostratigraphic base of the Ensenadan (Cione and Tonni 2005; *Tolypeutes pampaeus* Biozone from Cione and Tonni 1995, and references therein), which increases the diversity of glyptodons in sediments from the early-middle Pleistocene of southern South America.

Conclusions

Panochthus subintermedius differs from the remaining species of the genus (*P. intermedius*, *P. tuberculatus*, *P. rusconii*, *P. frenzelianus*, *P. greslebini*, *P. morenoi*, and *P. vogti*) by a unique combination of characters found in the dorsal carapace and caudal tube: the general shape and ornamentation of the carapace are similar to those of

P. tuberculatus, although it is larger and comparable to that of *P. intermedius*; and it lacks central figures in most of the osteoderms. The distal end of the caudal tube of *P. subintermedius* is sharper than in other species, with only one apical figure on the dorsal surface and central figures along the entire dorsal surface.

Panochthus subintermedius (Castellanos 1936) is a valid species according to the International Code of the Zoology Nomenclature (1999). Consequently, two species of *Panochthus* are recorded for the Ensenadan of southern South America: *P. intermedius* and *P. subintermedius*.

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Appendix

Materials

MLP 16-382 *Panochthus morenoi*. Carapace exhibited in the Exhibition Hall of the Museo de La Plata. Geographic provenance: Buenos Aires province. Stratigraphic provenance: Pampean.

MLP 16-36 *Panochthus intermedius*. Holotype. Carapace exhibited in the Exhibition Hall of the Museo de La Plata. Geographic provenance: Ensenada, La Plata, Buenos Aires. Stratigraphic provenance: Ensenadan.

MLP 16-32. *Panochthus* sp. Caudal tube. Geographic provenance: unknown. Stratigraphic provenance: unknown.

MLP 16-381 (ex 125). *Panochthus* sp. Caudal tube. Geographic provenance: Buenos Aires. Stratigraphic provenance: Pampean.

MACN-Pv 1761 *Propanochthus bullifer*. Holotype. Posterior fragment of the carapace and caudal tube (illustrated in Burmeister 1870–1874, Pl XVI: Figs. 3, 4, and 5, and Ameghino 1889, Pl LXV: Figs. 4 and 5). Geographic provenance: Mina Clavero, Sierra Alta, Córdoba. Stratigraphic provenance: lower Pampean.

MACN-Pv 1745. *Panochthus tuberculatus*. Caudal tube (illustrated in Burmeister 1870–1874, Pl XVI: Figs. 1 and 2, and Ameghino 1889, Pl LXVI Figs. 1 and 1a). Geographic provenance: Buenos Aires. Stratigraphic provenance: Pampean.

MACN-Pv 10109 *Panochthus* sp. Caudal tube, humerus, and osteoderms. Geographic provenance: Río Carcarañá, Santa Fe. Stratigraphic provenance: upper Pampean.

MACN-Pv 10108. *Panochthus* sp. Caudal tube. Geographic provenance: Río Carcarañá, Santa Fe. Stratigraphic provenance: upper Pampean.

MACN-Pv 9643. *Panochthus* sp. Fragment of the carapace and caudal tube. Geographic provenance: Buenos Aires. Stratigraphic provenance: upper Pampean.

MACN-Pv 5014. *Panochthus* sp. Distal fragment of the caudal tube. Geographic provenance: unknown. Stratigraphic provenance: Lujanian.

MUFyCA 383. *Panochthus* sp. Caudal tube. Geographic provenance: Barrancas de Pizarro, Río Grande de Nono, Córdoba. Stratigraphic provenance: Pleistocene.

MUFyCA 342. *Panochthus subintermedius*. Caudal tube. Geographic provenance: Río Carcarañá, Córdoba. Stratigraphic provenance: Pleistocene.

MNHN-PAM 291. *Panochthus nodotianus*. Holotype. Fragments of the caudal tube. Geographic provenance: Montevideo, Uruguay. Stratigraphic provenance: Pleistocene.

MNHN-PAM unnumbered. *Panochthus morenoi*. Caudal tube exhibited in the Galerie de Paléontologie at the Muséum National d'Histoire Naturelle (illustrated in Ameghino 1889 Pl LXV, Figs. 1 and 2). Geographic provenance: Argentina. Stratigraphic provenance: Pleistocene.

DGM-M 1. *Panochthus greslebini*. Holotype. Fragment of the carapace and caudal tube. Geographic provenance: Ceará state, Brazil. Stratigraphic provenance: unknown.

AMNH 11243-11245. *Panochthus frenzelianus*. Holotype. Almost complete skeleton, cephalic shield, carapace, and caudal tube exhibited in the Primitive Mammals Hall at the American Museum of the Natural History. Geographic provenance: Buenos Aires province. Stratigraphic provenance: Bonaerian.

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