Forum communication

How Marine Isotope Stage 3 (MIS3) is reflected in northern Mesopotamia faunal assemblage of Argentina: The Xenarthra Cingulata case

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ABSTRACT

MIS 3 (60–25 ka) corresponds to a long interstadial episode considered generally warmer than MIS 2 and 4, and including numerous and abrupt Dansgaard–Oeschger and Heinrich events, sometimes brief but very intense. The materials studied here, coming from the Late Pleistocene exposures in central-north Mesopotamia (Corrientes province, Argentina, Toropí/Yupoí Fm., MIS 3; *ca.* 52–36 ka), is characterized by the presence of a large and complex vertebrate assemblage, being the Cingulata (Xenarthra) one of the most frequently represented taxa. In this work we provide an updated list of cingulates from Corrientes province, referrable to the Late Pleistocene, after performing new collections in the area and revising previous determinations. This includes: a) Dasypodidae: *Propraopus sulcatus* Lund, *Euphractus* aff. *Euphractus sexcinctus* Linnaeus; *Chaetophractus villosus* (Desmarest); b) Pampatheriidae: *Holmesina paulacoutoi* (Cartelle-Guerra and Mahecha-Bohorquez), *Pampatherium* sp., *Pampatherium typum* Ameghino; c) Glyptodontidae: *Panochthus tuberculatus* (Owen), *Panochthus* sp., *Glyptodon reticulatus* Owen, *Glyptodon* sp., *Neosclerocalyptus paskoensis* (Zurita), *Neosclerocalyptus* cf. *N. paskoensis* (Zurita), *Neosclerocalyptus* sp. The paleoenvironmental context that may be inferred from the palaeofaunal, particularly from the diversity of cingulates in the Quaternary of Corrientes province, is characterized by alternating cold arid or semiarid pulses and warmer humid ones. Generating new evidence related to MIS 3. Even though the taxa recorded are not new, the relative occurrence of each one shows evident differences with those in other areas. Using this information, the diversity of cingulates is compared to that of Late Pleistocene faunas described for sediments from areas currently located in the provinces of Formosa and Buenos Aires (Argentina), northern Uruguay and southern Brazil. Lastly, palaeoclimatic and palaeobiogeographic aspects that may be inferred from the study of this assemblage are discussed in the context of the MIS 3.

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1. Introduction

In recent years, systematic studies of Pleistocene vertebrates in Argentina have expanded considerably, with the publication of new records of faunal associations in some new areas of the country (see, among others, Carlini et al., 2003; Zurita et al., 2004, 2009a; Noriega et al., 2004; Ferrero et al., 2007; Ferrero, 2009; Ferrero and Noriega, 2009). In the Mesopotamian region, the first analyses of Quaternary paleofaunas were those of Herbst and Álvarez (1972, 1977, 1974), while the most recent publications correspond to Herbst and Santa Cruz (1985, 1999), Scillato-Yané et al. (1998, 2002), Noriega et al. (2001, 2004), Zurita and Lutz (2002), Carlini et al. (2003, 2004, 2008), Gasparini and Zurita (2005), Ferrero and Noriega (2007), Ferrero et al. (2007), Ferrero (2009) and Zurita and Ferrero (2009); among others. More specifically, in Corrientes province, particularly in the Pleistocene outcrops in the surroundings of Arroyo Toropí (Bella Vista Department) and in the locality of Lavalle (Lavalle Department) (Fig. 1), abundant and diverse vertebrates with reliable stratigraphic and geographical provenance have been collected during the past ten years, with the record of Xenarthra Cingulata particularly diverse and abundant (Francia, 2014).
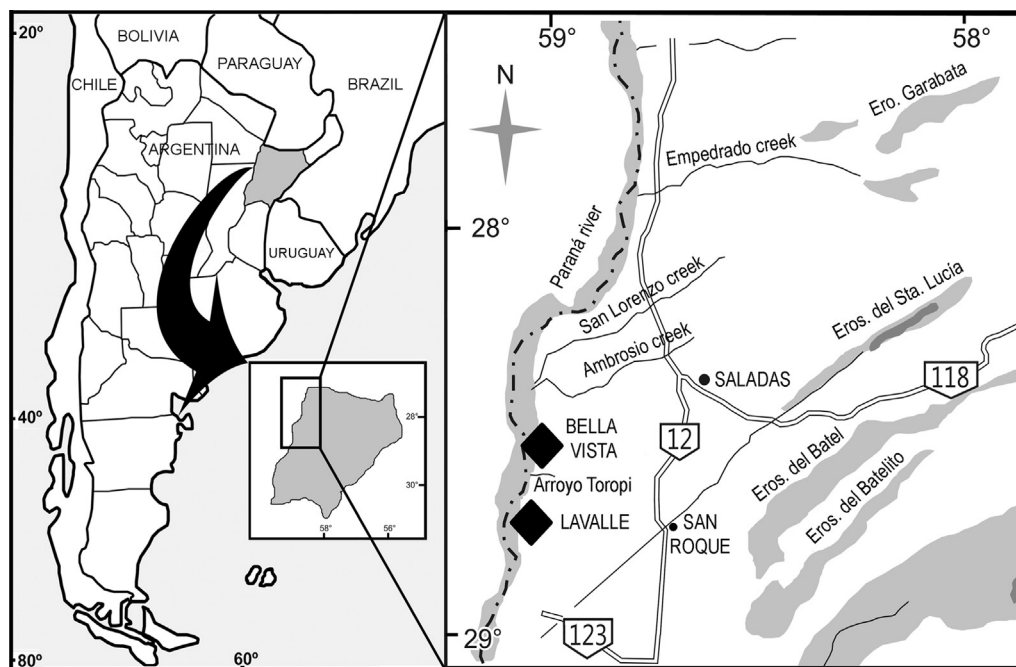
Fig. 1. Map showing the geographical location where the studied fossils were collected.

The Cingulata are characterized by having their bodies covered and protected by numerous osteoderms attached to each other forming a cephalic shield, a dorsal carapace and a caudal sheath. The morphology of these osteoderms (and of the structures they constitute) are the basis for the characters used to generate the classification of fossil forms, because they are the most frequent elements in the fossil record (Soibelzon et al., 2010). Classically, the following groups are recognized within this clade: Glyptodontidae, Pampatheriidae, Peltephilidae, Palaeopeltidae, and Dasypodidae. Thus, the latest records of palaeopeltids and peltephilids correspond to the Late Oligocene and Late Miocene, respectively, while the most recent representatives of pampatheriids and glyptodontids are recorded in the Late Pleistocene and early Holocene; dasypodids are the only family with living representatives (Scillato-Yané, 1980; Carlini and Scillato-Yané, 1999; Soibelzon et al., 2010).

Given that the comparative study of the past (in diverse lapses) and present distribution of certain vertebrate groups may provide information related to climate changes that have taken place throughout geologic time (Lundelius, 1983; Carlini and Tonni, 2000), the Xenarthra are a good example of the influence exerted by climate−environmental changes on their diversity and chorology (see Carlini et al., 2008; Soibelzon et al., 2010).

In this context, and based on the remarkable diversity of cingulates recovered from Late Pleistocene deposits in Corrientes province, which temporarily correspond to MIS3, this work has the following goals: a) present and update the record of Cingulata (Xenarthra); b) compare its diversity with cingulate faunas described for the Late Pleistocene−Early Holocene of the following areas: Formosa province (Río Bermejo Fm., see Rodríguez-Bualó et al., 2009; Zurita et al., 2009a, 2014), Buenos Aires province (Luján Fm., see Tonni and Fidalgo, 1978; Tonni et al., 1999; Cione et al., 2003, 2009), northwestern Uruguay (Sopas Fm., see Ubilla et al., 2004, 2009) and southern Brazil (Touro Passo Fm., see Bombin, 1976; Kerber and Oliveira, 2008; Oliveira and Kerber, 2009; Oliveira and Pereira, 2009; Kerber et al., 2011); and c) analyze palaeoclimatic and palaeobiogeographic aspects associated

to the diversity of Cingulata spanning a particularly interesting lapse (MIS 3; *ca.* 60−25 ka) in a complex climate−environmental scenario.

2. Geological setting, stratigraphy and chronology

Herbst (1969, 1971), in his stratigraphic scheme of Corrientes province, was the first to recognize and describe a unit that he named Yupoí Formation, chronologically assigning it to the Later "Entrerriense" and Middle "Mesopotamiense" of Castellanos (1965). This interpretation was later supported by Álvarez (1974), who also recognized the presence of Yupoí Fm. in typical, well-developed form, along the coast of the Paraná river and the coast of other internal rivers and creeks, from Ituzaingó (Ituzaingó Department) to Esquina (Esquina Department). Some years later, Herbst and Álvarez (1977) subdivided Yupoí Fm. into two formational units: Toropí Fm. (formerly lower section of Herbst, 1971) and Yupoí Fm. (formerly upper section of Herbst, 1971). In addition, they assigned Ensenadan and Lujanian mammal ages (*sensu* Pascual et al., 1965) respectively, to these units, acknowledging that the fossils recorded were not sufficient to allow a more precise chronological assignation. Herbst and Santa Cruz (1985, 1999), maintaining the view of Herbst and Álvarez (1977), considered them as independent lithostratigraphic units, attributing undoubtedly (*sic*) an Ensenadan (Early−Middle Pleistocene) age to Toropí Fm. and a Lujanian (Middle−Late Pleistocene) age to Yupoí Fm. (*sensu* Pascual et al., 1965).

More recently, Iriondo (1996) and Iriondo et al. (1998), on the basis of lithology and mineralogic composition, considered that they do not correspond to different formational units, but rather to a single unit, which they named Toropí/Yupoí Fm. These authors also remarked that this formation is correlated with Hernandarias Fm., which would stratigraphically placed it in the Middle Pleistocene. On the other hand, Scillato-Yané et al. (1998) applying greater stratigraphic discrimination, refer to the two units described by Herbst and Álvarez (1977) as: Lower unit (Toropí Fm.) and Upper unit (Yupoí Fm.). They also propose, based on remains

collected by them, that this sequence spans a period that corresponds to the Lujanian *s.l.* (*sensu* Cione and Tonni, 1995). Later, Noriega et al. (2000) report that Orgeira (*pers. comm.* 1998 to E.P.T) performed a magnetostraphigraphic analysis of the sequence under study (unpublished), and determined that the assemblage has normal polarity, assigning it with high probability to the Brunhes magnetic polarity zone (C1n), and confirming that the base of the sequence is younger than 0.78 Ma.

Iriondo (2010) considered that the age of the Toropí/Yupoí Fm. is referrable to the Late Pleistocene, and also mentioned that it is a wetland deposits fill, accumulated on belts left by the Paraná river. This author also remarks that this unit does not outcrop in the east of Corrientes province (i.e. the coasts of Uruguay river and interior water courses), as established by Herbst and Álvarez (1977) and Herbst and Santa Cruz (1985, 1999). At those sectors of the Uruguay river, the exposed unit corresponds actually to Tapebicuá Fm. (Iriondo and Kröling, 2008), originated from marsh and alluvial deposits, and which overlies Yapeyú Fm. Our own observations agree with Iriondo and Kröhling's (2008) interpretation.

Numerical dates have been obtained that allow better temporal constraining of the studied sequence. OSL dating in the area of Arroyo Toropí yielded ages between *ca.* 52 ka (Lower member) and 36 ka (Upper member) for the Toropí/Yupoí sequence (Francia et al., 2012a; Francia, 2014).

3. Materials and methods

Fossil specimens from the collection of the Facultad de Ciencias Exactas y Naturales y Agrimensura (Universidad Nacional del Nordeste, Corrientes, Argentina) were studied. This included both materials from the earliest collections as well as all those obtained by field work in the last fifteen years; in addition, we also analyzed materials from the same locality currently deposited in the División Paleontología de Vertebrados del Museo de La Plata. Previously published works that represent the earliest general contributions about faunas from the study area (*e.g.* Álvarez, 1974; Zurita and Lutz, 2002; Scillato-Yané et al., 1998; Carlini et al., 2003) were used as reference, and faunal comparisons were made on the basis of descriptions of vertebrate assemblages collected from areas that are geographically close and with similar inferred ages (see Ubilla et al., 2004, 2009; Kerber and Oliveira, 2008; Oliveira and Kerber, 2009; Zurita et al., 2009a). The terminology for the description of osteoderms and caudal sheaths corresponds to Moreira (1971), Croft et al. (2007), Zurita (2007), Krmpotic et al. (2009), Porpino and Bergqvist (2002) and Góis-Lima et al. (2013). The biostratigraphic scheme follows Cione and Tonni (1999, 2005).

Abbreviations: **CTES-PZ**, Colección de la Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste; **MLP**, División Plaeontología de Vertebrtados, Museo de La Plata, Universidad Nacional de La Plata; **OSL**, Optically Stimulated Luminescence; **m**, lower molariform; **M**, upper molariform; **MIS**, Marine Isotope Stage.

4. Systematic paleontology

XENARTHRA Cope, 1889
CINGULATA Illiger, 1811
GLYPTODONTIDAE Gray, 1869
GLYPTODONTINAE Gray, 1869
Glyptodon Owen, 1838
Type species: *Glyptodon clavipes* Owen, 1838.

4.1. Glyptodon reticulatus Owen, 1838

(Fig. 2A)
Referred material − geographic and stratigraphic provenance: See Appendix 1.
Description: the dorsal carapace osteoderms are thick and their exposed surface is rugose. In the antero-dorsal region, toward the lower margin and throughout the posterior region, the osteoderms present the typical rosette pattern, with a larger central figure surrounded by 6–8 peripheral figures. In the central-dorsal region, the central figure is subcircular to irregularly pentagonal or hexagonal, equal in size to the peripheral figures, and the typical rosette appearance is replaced by a reticulate pattern formed by the figures from adjacent osteoderms.

The caudal rings are formed by three rows of osteoderms. In the first ring, the exposed surface of the last-row osteoderms presents a flat figure, which in the remaining rings takes the form of strong conical tuberosities. The remaining osteoderms from the rings are hexa- or pentagonal, flat and with a smooth surface.

Comments: Among the Glyptodontidae, *Glyptodon* has the widest distribution in South America, and is frequently recorded in Argentina from the Ensenadan Stage/Age to the Lujanian Stage/Age (Carlini and Scillato-Yané, 1999; Zurita et al., 2009c). For the Middle Early Pleistocene–Early Holocene lapse, four species are recognized: *Glyptodon reticulatus* Owen, 1838, *G. clavipes* Owen, 1839, *G. elongatus* Burmeister, 1866 and *Glyptodon munizi* Ameghino, 1882 (Soibelzon et al., 2006; Zurita et al., 2009b,c, 2013). According to the reticular pattern of the osteoderms of the central-dorsal region of the carapace, this material is assigned to *Glyptodon reticulatus* (see Ameghino, 1889; Tonni and Berman, 1988; Zurita et al., 2009c).

4.2. Glyptodon sp.

Referred material − geographic and stratigraphic provenance: See Appendix 1.
Comments: The characteristics observed in the dorsal carapace osteoderms allow referring these materials to *Glyptodon* (see Soibelzon et al., 2006; Carlini et al., 2008). However, because isolated osteoderms usually lack characters that allow identification to species level, we propose a genus-level assignation. This genus includes large species with a mainly grazing diet (Fidalgo and Tonni, 1983; Fariña, 1995; Pérez et al., 2000; Vizcaíno et al., 2006).

"HOPLOPHORINAE" Huxley, 1864.
HOPLOPHORINI Huxley, 1864
Panochthus Burmeister, 1864
Type species: *Panochthus tuberculatus* Owen, 1845.

4.3. Panochthus tuberculatus (Owen, 1845)

(Fig. 2B)
Referred material − geographic and stratigraphic provenance: See Appendix 1.
Description: the caudal sheath is notably wide in transverse diameter, with a slight antero-posterior concavity. Its cross-section is semicircular proximally and becomes depressed distally as its diameter decreases. In lateral view, it is cylindrical–conical proximally, and strongly depressed with upward longitudinal curvature distally. Laterally it has two asymmetrical rows of lateral figures (L), elliptical in outline, with a conical central tuberosity and numerous radial grooves radiating from the former. The L figures are four on the left side and three on the right side (however, it is difficult to ascertain if that is their total number due to the fragmentary condition of this side). It is important to note that the sheath is broken at its proximal part. L figures are larger distally. Laterally, between
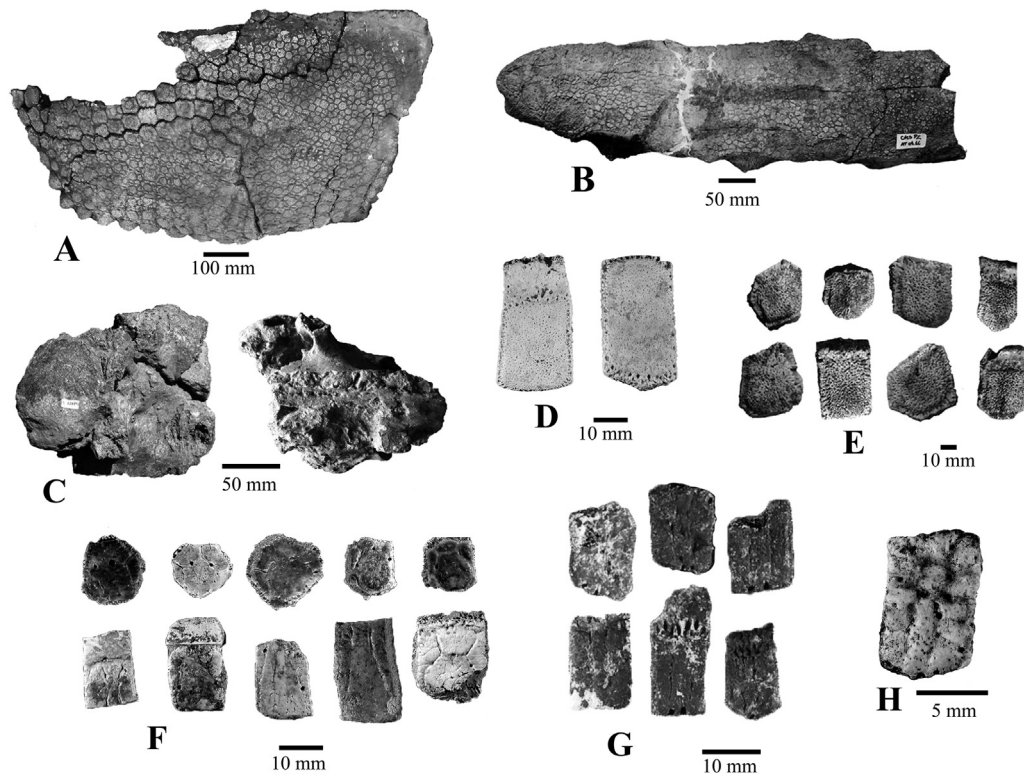
Fig. 2. Diversity of Cingulata in the Late Pleistocene of Corrientes. A, *Glyptodon reticulatus* (CTES-PZ 7334: left lateral portion of dorsal carapace in lateral view) B, *Panochthus tuberculatus* (CTES-PZ 7500: almost complete caudal sheath in dorsal view); C, *Neosclerocalyptus paskoensis* (CTES-PZ 1677: left portion of skull in lateral and occlusal views); D, *Pampatherium typum* (CTES-PZ 7332: one fixed osteoderm and a fragmentary mobile osteoderm from the dorsal carapace); E, *Holmesina paulacoutoi* (CTES-PZ 7495: fixed and mobile osteoderms from the dorsal carapace); F, *Propraopus sulcatus* (CTES-PZ 7511: 13 fixed and mobile osteoderms from the dorsal carapace); G, *Euphractus* aff. *E. sexcinctus* (CTES-PZ 1655: mobile, semimobile and fixed osteoderms); H, *Chaetophractus villosus* (CTES-PZ 7568: one osteoderm from the pelvic shield).

these L figures, there are four pairs of dorsoventral (DV) figures (one dorsal and one ventral), which are subelliptical with rugose surface. The DV/I pair is the most distal and has a dorsal and ventral position, while the remaining DV figures are more lateral. The apex of the sheath is subtriangular and blunt, with a small distal projection between the latero-terminal (T) figures, so that more distally these are separated by three rows of peripheral figures (PF). Dorsally, the apex bears three apical figures (A) subcircular and unequal (A3 posterior, A1 and A2 proximal and symmetrical), while ventrally there is only one rounded figure in a central position. The two T figures are symmetrically aligned, subequal, and dorsally separated from each other, while ventrally they contact each other. With regards to the marginal figures (MF), the distal unpaired MF/1 and MF/2, are dorsally evident. The first of these is located centrally between the A figures and the dorsal figures of the first DV pair, and the second one is more proximal, followed by two asymmetrical longitudinal series (one on each side), close to the margins and dorsal to figures L/I, L/II and L/III (each of them with three, two and one figure, respectively). These MF are few, shallow and with subcircular outline. The central figures (CF) are located on the dorsal surface of the sheath, between the FM; these CF are small, smooth and distributed irregularly. The overall ornamentation of the sheath consists of a reticular pattern of PF, with CF that do not follow a defined pattern.

The dorsal carapace osteoderms are polygonal, showing a clear reticular pattern.

The associated osteoderms correspond mostly to caudal rings, and bear at least two different types of ornamentation. In some cases, two rows can be differentiated: an anterior row of osteoderms whose exposed surface shows a larger, subcircular central

figure surrounded by several rows of small, similar-sized, polygonal peripheral figures, and a posterior row formed by a line of main osteoderms, each of which bears a convex elliptical–circular lump. In other cases, the central figure is missing in the osteoderms of the anterior row, which only presents numerous small similar-sized polygonal figures.

Comments: According to recent phylogenetic hypotheses, *Panochthus* is considered as a monophyletic group and *Hoplophorus euphractus*, as its sister taxon, forming the clade Hoplophorini (Hoplophoridae) (Zamorano and Brandoni, 2013, but see; Porpino et al., 2014).

This genus includes the following species: *Panochthus intermedius* (Lidekker, 1894) and *Panochthus subintermedius* Castellanos, 1936 (Early Pleistocene–Middle Pleistocene); *P. tuberculatus* (Owen, 1845) and *P. frenzelianus* (Ameghino, 1889) (Middle Pleistocene–Late Pleistocene); *P. greslebini* Castellanos, 1942 and *P. jaguaribensis* (Moreira, 1965) only can be referred to the Pleistocene *sensu lato*. These latter two species are interpreted as endemics of the Brazilian Intertropical Region (Zamorano, 2012; Zamorano and Brandoni, 2013; Porpino et al., 2014). With regards to the material analyzed here, most of the characters discussed, both in the caudal sheath and in the dorsal carapace, have been mentioned by Zamorano (2012), Zamorano et al. (2012) and Castellanos (1942) as diagnostic features of *Panochthus tuberculatus*. More precisely, our species-level assignation is based both on the ornamentation pattern and morphology of the caudal sheath, and on the ornamentation of the carapace portions and non associated osteoderms that have been preserved. It is worth noting that some osteoderms belonging to caudal rings present a particular ornamentation pattern that has only been observed in some osteoderms assigned to *Panochthus tuberculatus*.

4.4. Panochthus cf. P. tuberculatus (Owen 1845)

Referred material – Geographic and stratigraphic provenance: See Appendix 1.

Description: the osteoderms from the fragments of dorsal carapace bear on their exposed surface numerous small polygonal figures, forming a reticular pattern.

The caudal rings bear a row of proximal osteoderms, each of them with a convex elliptical–circular lump, and a row of osteoderms bearing on the exposed surface a larger, subcircular central figure surrounded by several rows of small polygonal similar-sized figures. In other cases, the abovementioned central figure is absent and the anterior margin only presents numerous small polygonal figures.

Comments: According to Castellanos (1942), Cruz et al. (2010), Zamorano (2012) and Zamorano et al. (2012) the ornamentation of the carapace is very similar in all the species of *Panochthus*, so that usually neither osteoderms nor isolated carapace fragments can be used to achieve precise species-level determination.

NEOSCLEROCALYPTINI Huxley, 1864.
Neosclerocalyptus Paula Couto, 1957.
Type species: *Glyptodon ornatus* Owen, 1845.

4.5. Neosclerocalyptus paskoensis (Zurita, 2002)

(Fig. 2C)

Referred material – geographic and stratigraphic provenance: See Appendix 1.

Description: In frontal view the skull shows strong pneumatization and lateral expansion of the ossified nasal cartilages (see Zurita et al., 2011b; Fernícola et al., 2012), whose free margins are not curved and are separated from the rest of the skull by a slightly marked narrow slit. Laterally, only the base of the descending process of the maxilla, not very robust, is preserved. In occlusal view, the dental series diverge anteriorly. Only the alveoli of M5, M6 and M7 are present; these are clearly trilobed, condition shared by all the Glyptodontidae.

Comments: the species assignation is based on the condition and morphology of the ossified nasal chamber, a fundamental characteristic of this species due to its extraordinary pneumatization and lateral expansion. This remarkable nasal development has been hypothesized to be related to adaptation to the cold arid/semiarid environments of the Pleistocene (Zurita et al., 2011b; but see; Fernícola et al., 2012). This species is very abundantly recorded in the Pampean region and Central-North Argentina (Carlini et al., 2008; Zurita et al., 2009a and b).

4.6. Neosclerocalyptus cf. N. paskoensis (Zurita, 2002)

Referred material – geographic and stratigraphic provenance: See Appendix 1.

Description: The dorsal carapace osteoderms are thin in transversal section, present a "rosette" ornamentation pattern, with a larger central figure and smaller peripheral figures, and the annular and radial sulci with parabolic shape in transversal section (see Zurita, 2007; Carlini et al., 2008).

The caudal sheath is mainly cylindrical–conical, although somewhat flattened, and its diameter decreases distally; it bears two large oval figures dorsolaterally at its distal end. The ornamentation of the osteoderms that form the caudal sheath is quite similar to that of those from the dorsal carapace. In lateral view, the tube presents numerous oval central figures, surrounded by a row of smaller peripheral figures that may be absent.

The femur is thicker transversally than anteroposteriorly, especially at the proximal epiphysis. The articular surface of the femoral head is subtriangular in outline, and the neck is poorly defined. The greater trochanter surpasses proximally the level of the femoral head, its proximal portion is oblique and rhomboidal in outline. The lesser trochanter, located medially, extends distally as a thick rugose ridge. The third trochanter projects laterally below the middle of the diaphysis as a sub-rectangular lamina, continuous with the lateral epicondyle. At the distal epiphysis, the supra-trochlear fossa is shallow and small in diameter.

The mandible is gracile, with its ascending ramus relatively narrow anteroposteriorly and its anterior margin at the level of m6. Only the tooth series of the left hemimandible is almost complete, with a lobed second molariform and trilobed molariforms m3 to m7 (m8 is fragmented).

Comments: the material is assigned to *Neosclerocalyptus* cf. *N. paskoensis* because the anatomical structures described do not provide characters that would allow positive assignation to the species level. However, this material is closely associated in stratigraphic and geographic terms with a material that is clearly assignable to *N. paskoensis* (CTES-PZ 1677).

4.7. Neosclerocalyptus sp.

Referred material – geographic and stratigraphic provenance: See Appendix 1.

Comments: The stratigraphic record of *Neosclerocalyptus* (= *Sclerocalyptus* Ameghino, 1891) extends from the Early Ensenadan Age/stage to the Lujanian Age/Stage. The geographical distribution of this genus is restricted to southern South America, from the locality Santa Cruz de la Sierra (Bolivia) to Bahía Blanca (Argentina) (Zurita et al., 2011a).

PAMPATHERIIDAE Paula Couto, 1954.
Pampatherium Ameghino, 1891
Type species: *Pampatherium humboldti* (Lund, 1841).

4.8. Pampatherium typum Ameghino, 1891

(Fig. 2D)

Referred material – geographic and stratigraphic provenance: See Appendix 1.

Description: The dorsal carapace osteoderms are mainly flat in transversal section, their exposed surface presents slight relief, the sutures are slightly denticulate, the external surface is finely punctuated, and the lateral margins are thinner than the rest of the osteoderm. The entire marginal area (lateral and posterior) bears a row of foramina (possibly pilliferous follicle foramina) of varied size. The marginal ridges parallel to the articular area between osteoderms on their exposed surface may be from very narrow to indistinguishable (depending on the region of the carapace), and the central longitudinal protuberance is wide and diffuse (very low and blunt in profile, when present), and there is no defined central figure. In the case of osteoderms from mobile bands and of the semimobile osteoderms from the first pelvic band, the transversal depression (intermediate zone between the anterior, unexposed area or cranial portion and posterior exposed area) is poorly developed. The lateral marginal ridge is thicker than in the fixed osteoderms of the scapular shield, and the lateral depressions and central longitudinal protuberance are very undefined. The outline of these osteoderms ranges from hexagonal to subrectangular (depending on their location in the carapace), and their thickness is between 8 and 10 mm.

Comments: In what is currently part of Argentine territory, *Pampatherium* is represented by two species. *Pampatherium typum* is recorded in the Quaternary of Buenos Aires province (Bargo et al., 1986; Tonni et al., 1987); in the Late Pleistocene of Formosa (Zurita et al., 2009a), Entre Ríos (Ferrero and Noriega, 2009) and Corrientes provinces (Scillato-Yané et al., 1998). *Pampatherium humboldtii* is recorded in the Late Pleistocene–Early Holocene of Buenos Aires province (Góis-Lima et al., 2012a) and in the late Pleistocene of Santa Fe province (Góis-Lima, 2013). The assignation at species level is based mainly on the characteristics of the exposed surface of the osteoderms described here. According to Scillato-Yané et al. (2005) and Góis-Lima (2013) the exposed surface of the osteoderms of *Pampatherium typum* is flat and lacks a defined central figure.

The species of *Pampatherium* have been related to colder and arid/semiarid environments with hard-leaved vegetation, compared to the species of *Holmesina* that would have inhabited more humid environments with less abrasive vegetation. *Pampatherium typum* and *P. humboldtii* were probably grazers associated to abrasive vegetation, and *P. typum* was perhaps better adapted to processing resistant vegetation (De Iuliis et al., 2000). In this regard, Scillato-Yané et al. (2005) have proposed more varied environmental conditions for this species.

4.9. Pampatherium sp.

Referred material – geographic and stratigraphic provenance: See Appendix 1.
Comments: On the basis of the comparison of these remains with others belonging to equivalent regions, deposited in diverse paleontological collections, and due to the fragmentary condition of these materials, assignation is made to the genus level only.

Holmesina Simpson, 1930

4.10. Holmesina paulacoutoi (Cartelle Guerra and Bohorquez Mahecha, 1985)

(Fig. 2E)
Referred material – geographic and stratigraphic provenance: See Appendix 1.
Description: The dorsal carapace osteoderms are very large; their exposed surface presents numerous perforations, uniform in size and evenly distributed, with greater diameter compared to other species of the genus (see Scillato-Yané et al., 2005). The fixed osteoderms are thick, with anterior foramina that are few but very large and deep. The marginal area is wide and low, surrounding a protruding longitudinal central area that continues onto the posterior margin. Some osteoderms present a very distinct posterior convexity. The fixed osteoderms are more numerous, between 7.2 and 11.5 mm thick, while mobile osteoderms are 5.7–12 mm thick.

The dental remains are fragmentary. The most complete tooth corresponds to an upper molariform, clearly bilobed, which bears on the labial surface a conspicuous middle groove and anteriorly a small notch. The lingual surface presents two defined grooves; the occlusal surface is flat and with distinct transversal grooves.

Comments: The species in this genus have been characterized by the general morphology of osteoderms and their size (see Scillato-Yané et al., 2005; Góis-Lima, 2013). The fixed osteoderms are thicker, more ornamented and with a more denticulate suture surface than those of any other species of Pampatheriidae (ver Góis-Lima, 2013).

The classically recognized species of *Holmesina* are: *Holmesina occidentalis* (Hoffstetter, 1952) from the Pleistocene of Colombia

and Venezuela, and Late Pleistocene of Ecuador and Peru, somewhat smaller than the other two species; *H. majus* (Lund, 1842) from the Late Pleistocene of Brazil, which is the largest species according to linear measurements of its long bones, and whose osteoderms are somewhat smaller than those of *H. paulacoutoi*, with delicate punctuation and a wide marginal zone; and *H. paulacoutoi* (Cartelle-Guerra and Mahecha-Bohorquez, 1985), known for the Late Pleistocene of Brazil and Argentina, considered as the most robust species, even within all the Pampatheriidae (Scillato-Yané et al., 2005); its osteoderms are very large, with strongly rugose surface, and a wide and low marginal area surrounding an elevated central area. This convexity is sometimes extended posteriorly, a condition considered unique among the Pampatheriidae (Scillato-Yané et al., 2005). Recently, Góis-Lima et al. (2012b), recognized a new species: *Holmesina rondoniensis* from the Rio Madeira Formation, Late Pleistocene–Holocene, Municipality of Vila Nova Mamoré (Rondonia, Brazil), for which no osteoderms are known.

DASYPODIDAE Bonaparte, 1838.
DASYPODINAE Gray, 1821.
Propraopus Ameghino, 1881
Type species: *Propraopus grandis* Ameghino, 1881.

4.11. Propraopus sulcatus (Lund, 1842)

(Fig. 2F)
Referred material – geographic and stratigraphic provenance: See Appendix 1.
Description: The fixed osteoderms are hexagonal or pentagonal, 4–7 mm thick. The exposed surface is ornamented, presenting a convex central figure, quite large (diameter 8–10 mm) polygonal and smooth, with several very small foramina scattered on its surface. This main figure is surrounded by up to six peripheral figures, three of which are always located along its anterior margin. The peripheral figures present incomplete circular outline, smooth convex surface, and are separated from each other (and from the central figure) by well-defined sulci. The sulcus around the central figure bears one to five (generally three) deep foramina in its anterior portion, and in some cases, several small foramina in its posterior portion.

The mobile osteoderms are incomplete and thus their total length cannot be measured; they have rectangular outline, up to 14 mm wide with an anterior unadorned portion forming the cranial portion (which probably represented almost half of the total length of the osteoderm) and a posterior ornamented portion, separated by a transversal depressed area. The exposed surface of the ornamented portion bears two longitudinal sulci that begin close to each other at the transversal depressed area and diverge posteriorly, ending at the posterior angles. The area comprised between these sulci forms a subtriangular figure, flanked by two smaller inverted triangles with a series of shallow transversal grooves. Each longitudinal sulcus bears up to four large foramina and several small pores, and the posterior margin bears one or two pilliferous follicle foramina opening toward the rear.

Comments: *Propraopus* is characterized by its wide latitudinal and altitudinal distribution in South America, from sea level at middle latitudes in Argentina, to 2800 masl in Ecuador (Castro et al., 2013). *Propraopus* is known from the Pleistocene of Argentina, Uruguay, Brasil, Bolivia, Ecuador and Venezuela (Hoffstetter, 1958; Scillato-Yané, 1980; Marshall et al., 1984; Scillato-Yané et al., 1995; Cione and Tonni, 2005; Castro et al., 2013). Some of the nominal species described for *Propraopus* have been challenged by diverse authors (*e.g. P. magnus, P. grandis* and

P. sulcatus; see Hoffstetter, 1952; Paula-Couto, 1979; Scillato-Yané, 1982; Castro et al., 2013), although others support the validity of *P. grandis* and *P. sulcatus* (see Oliveira and Pereira, 2009). Recently, Castro et al. (2013) proposed the synonymy of *P. sulcatus* and *P. grandis*, with *P. sulcatus* being the valid name by priority.

The species-level assignation of the remains studied here is based mainly on the morphology and size of the osteoderms (*e.g.* location, number and characteristics of the pilliferous follicle foramina in carapace osteoderms; see Castro et al., 2013).

EUPHRACTINAE Winge, 1923.
EUPHRACTINI Winge, 1923
Euphractus Wagler, 1830
Type species: *Euphractus sexcinctus*

4.12. *Euphractus aff. E. sexcinctus Linnaeus, 1758*

(Fig. 2G)

Referred material – geographic and stratigraphic provenance: See Appendix 1.

Description: The mobile and semimobile osteoderms from the pelvic shield are rectangular in outline; their exposed surface presents an anterior, unadorned portion (cranial portion, not exposed) and a posterior ornamented portion (exposed) with two longitudinal rows of perforations (arranged along a slight sulcus) delimiting a central figure that is completely flat and with no lateral deviation. The lateral figures are also flat and undivided, and the pilliferous follicle foramina are very scarce. Two very conspicuous pilliferous follicle foramina can be observed on the posterior margin, always in a row behind the main central figure. The fixed osteoderms are quadrangular in outline, with an entirely flat central figure surrounded by equally flat peripheral figures, and with pilliferous follicle foramina arranged similarly to those found in the exposed area of the mobile osteoderms.

Comments: *Euphractus* has a distinctly tropical and subtropical distribution (Scillato-Yané, 1982; Wetzel, 1985), supposedly with records since the Ensenadan (Early–Middle Pleistocene) of the Pampean region (Scillato-Yané, 1982; Carlini and Scillato-Yané, 1999; Cione et al., 1999), although according to Soibelzon et al. (2010), the materials referred to that age lack reliable provenance data. *Euphractus sexcinctus* is currently distributed in Bolivia, Brazil, Uruguay, Suriname, Paraguay and north Argentina (Redford and Wetzel, 1985); it is characteristic of open areas and humid tree savannas (Welker, 1975; Scillato-Yané, 1982).

Although the assignation was based on the presence of features (as well as measurements) of the carapace osteoderms that are characteristic of *E. sexcinctus* (see Scillato-Yané, 1982), it is worth noting that the number and size of pilliferous follicle foramina in both fixed and mobile osteoderms of this material differ from those from corresponding regions of the carapace of the extant species.

Chaetophractus Fitzinger, 1871
Type species: *Chaetophractus villosus* (Desmarest 1804) Fitzinger 1871.

4.13. *Chaetophractus villosus (Desmarest 1804) Fitzinger 1871.*

(Fig. 2H)

Referred material – geographic and stratigraphic provenance: See Appendix 1.

Description: the exposed osteoderm surface bears an elongated main figure surrounded anteriorly and laterally by smaller peripheral figures. The main figure covers the posterior two thirds of the osteoderm and is surrounded by small foramina that correspond to opening of glandular spaces (see Krmpotic et al., 2009). The main figure is flanked on each side by three lateral peripheral figures arranged in an antero-posterior line, and anteriorly by four anterior peripheral figures that occupy its anterior and antero-lateral margins. There is also an additional anterior figure surrounded by these anterior figures and located on the midline before the main figure. The posterior margin of the osteoderm bears four small pilliferous follicle foramina.

Comments: *Chaetophractus* species usually inhabit open areas, and are well adapted to semidesertic conditions (Nowak, 1991). On the other hand, among the Dasypodidae of Argentina, *C. villosus* is the species with widest distribution, occurring in a variety of environments with diverse climates and food resources (Gardner et al., 2005). However, its known current distribution does not include the Argentinian Mesopotamia (Parera, 2002; Abba and Vizcaíno, 2008), although it has been cited, with doubts, for Entre Ríos province (see Bárquez, 2006).

From the rectangular shape of the osteoderm, it may be inferred that it belongs to the pelvic shield, and from the orientation of the main figure (inclined toward the left) that it corresponds to an osteoderm belonging to the lateral region of the dorsal carapace. On the other hand, the presence of two anterior rows of peripheral figures is characteristic and exclusive of the pelvic shield osteoderms of *C. villosus* (Scillato-Yané, 1982). The osteoderms of the three living *Chaetophractus* species are morphologically similar; however, because of its size (osteoderms from homologous zones of *Chaetophractus vellerosus* and *Chaetophractus nationi* are approximately 20% smaller than those of *C. villosus*) and for presenting one or two additional peripheral figures anterior to the main figure, it is assigned to *C. villosus* (see Francia and Ciancio, 2013).

5. Discussion

During the last glacial period, intense climate fluctuations (in the scale of thousands of years) have been documented and the deep polar ice cores provide reference records commonly employed in global correlation of past climate events (EPICA Community Members, 2006; Jouzel et al., 2007). These sudden and unexpected climate change, known as the Heinrich (cold) and Dansgaard–Oeschger (temperate–warm) events, are mainly characteristic of MIS 3 (*ca.* 60 to 25 ka) which corresponds to a long interstadial period considered generally warmer than MIS 2 and 4 (Walker, 2005; Siddall et al., 2008; Van Meerbeeck et al., 2009; Buiron et al., 2012; Rabassa, 2013).

The succession of Dansgaard–Oeschger events were first identified in Greenland ice cores and associated to variations of the Atlantic meridional overturning circulation (EPICA Community Members, 2006). These abrupt events have a smooth and lagged counterpart in water stable isotopes from Antarctic ice cores (Hessler et al., 2011; Buiron et al., 2012). A systematic one-to-one correspondence has been established between stadial and interstadial transitions in Greenland and Antarctic, and the amplitude of the Antarctic warm events is found to be linearly dependent on the duration of the concurrent stadial in the North, suggesting that they all result from a similar reduction in the meridional overturning circulation (EPICA Community Members, 2006; Buiron et al., 2012). Van Meerbeeck et al. (2009), based on modelings, cited conditions for MIS 3 that were warmer than the ones in the Last Glacial Maximum (*ca.* 24 ka), with development of ice sheets and convection cycles similar to current ones.

In this scenario, the Late Pleistocene paleofauna exhumed from sediments of the Toropí/Yupoí Formation (Corrientes, north Mesopotamia) is characterized by a combination of taxa that reflects its faunal links with faunas from north Uruguay and south Brazil (quite

possibly, during humid warm pulses), along with others from the Late Pleistocene of the Pampean region (Carlini et al., 2004; Francia et al., 2012b; Francia and Ciancio, 2013; Francia, 2014; among others). In this sense, the paleoenvironmental context that may be inferred from the palaeofaunal and chronological evidences obtained (ca. 52–36 ka), and particularly the diversity of cingulates in the Quaternary of Corrientes province, is characterized by alternating cold arid or semiarid pulses and warmer humid ones. This points to the development of a geographic area with distinct features. For the southern part of the Argentine Mesopotamia, this scenario has also been mentioned for the Late Pleistocene of Entre Ríos province (see, among others, Ferrero, 2009; Ferrero and Noriega, 2009; Zurita and Ferrero, 2009), although with a different taxonomical composition.

Quaternary evidence shows that species exhibit individualistic responses to climate change, whereas vegetation is related to change of the climate (Hodgson et al., 2009 and references therein).

In this context, the occurrence of dynamic and complex palaeoclimatic–environmental conditions during much of the deposition of the fossil-bearing sediments that correspond to Toropí/Yupoí Fm. may have favored the development of a particular faunal aggregate. The latter includes taxa with diverse ecological requirements (e.g. C. villosus vs. Holmesina paulacoutoi; Pampatherium typum vs. Holmesina paulacoutoi; see Fig. 3), that in some cases currently occupy different geographic areas (e.g. Euphractus sexcinctus vs. Dolichotis patagonum; Tayassu pecari vs. D. patagonum; see Fig. 4) and are not even recorded in the current territory of Corrientes province (e.g. C. villosus, Galea spp., Boa constrictor, Panthera onca).

In addition, similar associations have been observed in Late Pleistocene–Early Holocene palaeofaunas of Buenos Aires province (Tonni and Fidalgo, 1978; Tonni et al., 1999; Cione et al., 2003, 2009; Gasparini et al., 2013), west Uruguay (Ubilla, 2004; Ubilla et al., 2004) and south Brazil (Kerber and Oliveira, 2008; Oliveira and
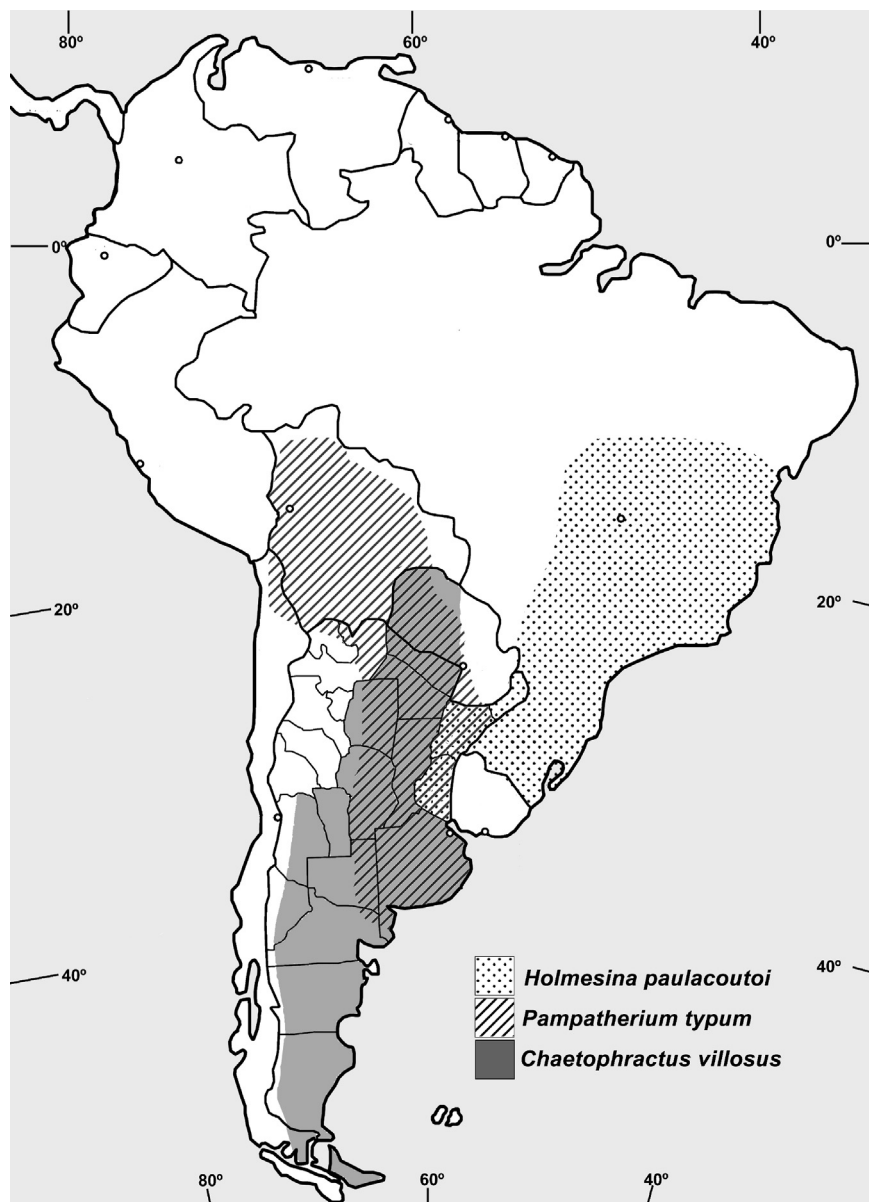

Fig. 3. Map showing the geographical distribution of *Chaetophractus villosus, Holmesina paulacoutoi* and *Pampatherium typum* (see Scillato-Yané et al., 2005; Abba et al., 2012; Francia and Ciancio, 2013).
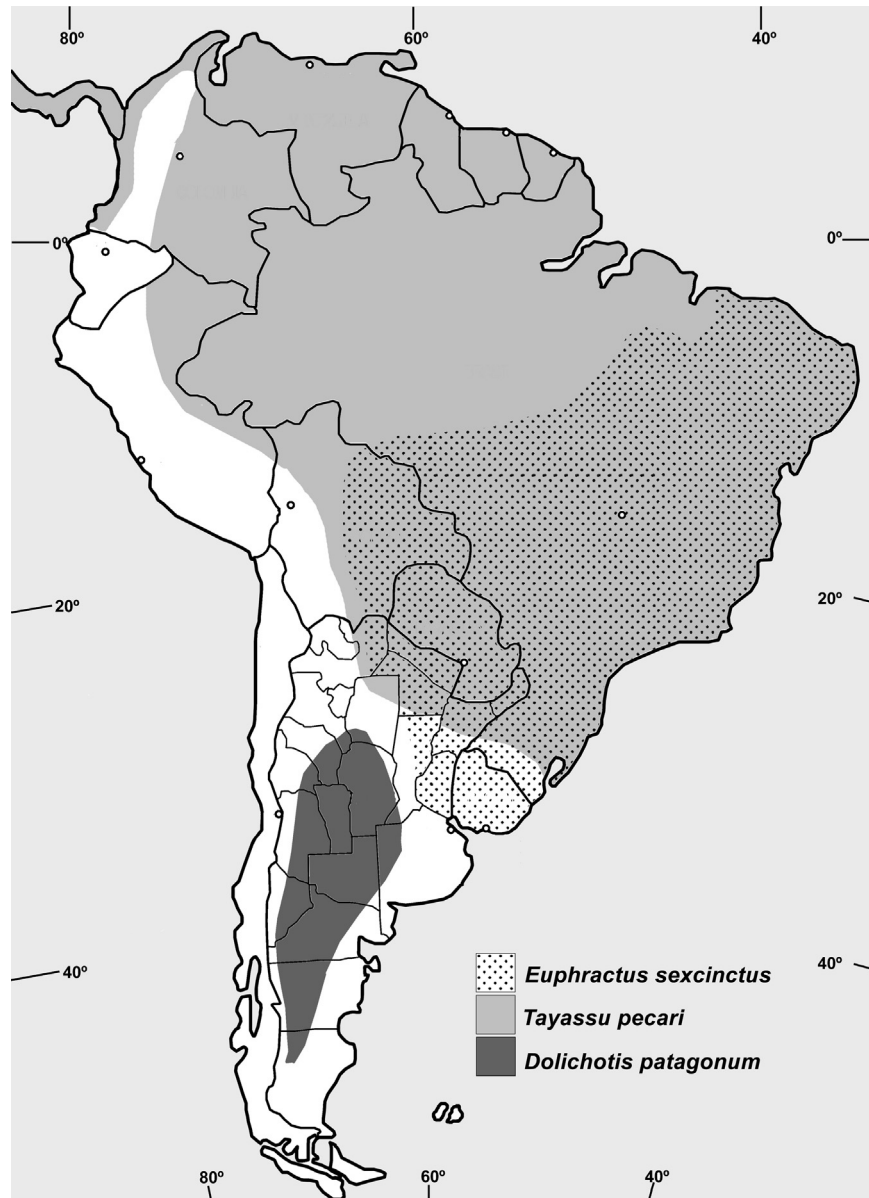
Fig. 4. Map showing the current geographical distribution of *Euphractus sexcinctus*, *Tayassu pecari* and *Dolichotis patagonum* (see Redford and Wetzel, 1985; Redford and Eisenberg, 1992; Gasparini et al., 2006; Abba et al., 2012).

Kerber, 2009). This particular situation has also been recorded in other parts of the world, particularly in the Pleistocene of Australia, North America, Europe and Asia (Lundelius, 1983 and references cited therein). This type of associations were termed "disharmonious" by Semken (1974), referring to faunal assemblages with living taxa that are currently allopatric and have disparate ecological requirements. Lundelius (1983) stated that such "disharmonious" faunas might be explained by Pleistocene climate regimes that are not extant at present.

However, the assemblage of taxa found in a fossil bed (with the abovementioned characteristics) need not necessarily be explained as a "disharmonious" fauna, or by a scenario that would have allowed their past coexistence and which is currently unknown. On the contrary, it is possible to simply assume that such deposits do not preserve a geologic–sedimentologic record of changes. These changes may have been fast enough so that the taxa exhumed from the sediments constitute faunas that appear to be synchronic, when in fact, the apparent coexistence of taxa with different ecological requirements is the result of a temporal synthesis spanning a range of contrasting environments. Thus, the records that constitute these faunas are only a secondarily generated artifact and would reflect an artificial homogenization of records (Tonni et al., 2003). Hodgson et al. (2009) proposed that defining area, quality and aggregation for multiple species simultaneously is not straightforward because the requirements of species vary.

In this sense, the cases of supposed "disharmonious" or "non analogue" assemblages in late continental faunas of Southern South America coincide, at least in part, with MIS3 (ca. 60 to 25 ka), a central period for investigating the classical bipolar expression of the millennial variability over the last glacial period (EPICA Community; Jouzel et al., 2007; Buiron et al., 2012; Veres et al., 2013).

The presence of Quaternary assemblages with remarkable assortments of taxa with different ancestries has been observed in localities where faunal elements have been exhumed from the La

Chumbiada and Guerrero Members of Luján Fm. (ca. 37−13 ka; see Figini et al., 1995; Pomi and Tonni, 2011), and from the Toropí/Yupoí (ca. 52−36 ka), Sopas (ca. 360−43 ka; see Martínez and Ubilla, 2004; Ubilla et al., 2004, 2009) and Touro Passo (ca. 42−11 ka; see Kerber et al., 2011) formations. At this point, differences can be observed in the species represented in all the abovementioned associations, which are in some cases euryoic and in others, stenoic (see Tonni and Fidalgo, 1978). Alberdi et al. (1989) proposed that in

is the most frequently recorded genus (Kerber et al., 2011). Among the Pampatheriidae, cases of sympatry between Holmesina paulacoutoi and Pampatherium typum have also been observed in the Late Pleistocene of central-north Argentina (Rodriguez-Bualó et al., 2009; Zurita et al., 2014), and in Touro Passo Fm. (see Kerber et al., 2011). It should also be mentioned that both at genus and species level, remarkable coincidences exist between the cingulates exhumed from Bermejo Fm. and those from Toropí/Yupoí Fm.

Table 1

Comparative chart of the Cingulata recorded in the Late Pleistocene of Corrientes (Toropí/Yupoí Fm.), Formosa (Río Bermejo Fm.) and Buenos Aires provinces (Luján Fm.), north Uruguay (Sopas Fm.), and south Brazil (Touro Passo Fm.).

Corrientes province (Toropí/Yupoí Fm.)	Formosa province (Bermejo Fm.)[a]	Buenos Aires province (Luján Fm.)[b]	Uruguay (Sopas Fm.)[c]	Brazil (Touro Passo Fm.)[d]
			Dasypus aff. D. novemcinctus	
Propraopus sulcatus		P. sulcatus		P. sulcatus
	Propraopus sp.		Propraopus sp.	Propraopus sp.
		Eutatus seguini		
Chaetophractus villosus		C. villosus		
	Chaetophractus sp.			
		Tolypeutes matacus		
		Dasypus hybridus		
Euphractus aff. E. sexcinctus				
		Zaedyus pichiy		
Holmesina paulacoutoi	H. paulacoutoi			H. paulacoutoi
Pampatherium typum	P. typum	P. typum		P. typum
Pampatherium sp.	Pampatherium sp.			Pampatherium sp.
			P. humboldtii	P. humboldtii
		Doedicurus clavicaudatus		
Neosclerocalyptus paskoensis				
N. cf. N. pasckoensis	N. cf. N. paskoensis			
Neosclerocalyptus sp.	Neosclerocalyptus sp.	Neosclerocalyptus sp.		
Panochthus sp.		Panochthus sp.		Panochthus sp.
Panochthus tuberculatus		P. tuberculatus	P. tuberculatus	P. tuberculatus
			"Clamydotherium"	
Glyptodon sp.	Glyptodon sp.			Glyptodon sp.
Glyptodon reticulatus				G. cf. G. reticulatus
		G. reticulatus		
		G. clavipes	G. clavipes	G. clavipes
		Neothoracophorus depressus		
			Neothoracophorus sp.	
				Neothoracophorus aff. N. elevatus
			Neuryurus rudis	
	Neuryurus sp.			

[a] From Zurita et al. (2009a, 2014), Rodríguez-Bualó et al. (2009).
[b] From Tonni and Fidalgo (1978), Tonni et al. (1999) and Cione et al. (2003, 2009).
[c] From Ubilla et al. (2004).
[d] From Bombin (1976), Kerber and Oliveira (2008), Oliveira and Kerber (2009) and Kerber et al. (2011).

the Late Pleistocene, the central and Patagonian faunas occupied a much larger surface area, including all of the current territory of Buenos Aires province, while Brazilian faunas would have been represented in a narrow area along the Pleistocene coast. Consequently, the lack of records of strong tropical−subtropical ancestry in the Late Pleistocene of Buenos Aires province could be due to the fact that they were restricted to the coastal area, similarly to the present condition (Alberdi et al., 1989).

From a compositional and comparative perspective, regarding the Cingulata exhumed from north Uruguay, south Brazil and Formosa province (Argentina) (see Table 1), it is remarkable that compared with the taxa recorded in Sopas Fm., there are no records of Glyptodontidae Neuryurini in Toropí/Yupoí Fm., but the Doedicurinae are absent from both (see Ubilla et al., 2004). In turn, comparing to the deposits from the south of Brazil (Touro Passo Fm.), in this formation there is a complete absence of Neosclerocalyptus and a shared absence of Doedicurinae, and Glyptodon

6. Conclusions

1. The palaeofauna of Cingulata found in the Late Pleistocene of Corrientes province seems to be restricted and to respond to the particular climate characteristics of MIS 3. Several biogeographic features could be linked to the rise of this complex faunal association during the Late Pleistocene of the northern Argentine Mesopotamia. Among them, it seems possible that a break of the biogeographic connection between the Mesopotamic and Pampean regions (Carlini et al., 2003, 2004), as well as the occurrence of migratory processes occurred (Scillato-Yané, 1982; Carlini et al., 2003, 2004, 2008).

2. The taxonomic revision of the association of Cingulata in the Late Pleistocene of Corrientes province included the following taxa: a) Dasypodidae: *Propraopus sulcatus* Lund, *Euphractus* aff. *E. sexcinctus* Linnaeus, *Chaetophractus villosus* (Desmarest); b) Pampatheriidae: *Pampatherium typum* Ameghino,

Pampatherium sp., *Holmesina paulacoutoi* (Cartelle and Bohórquez); and c) Glyptodontidae: *Panochthus tuberculatus* (Owen), *Panochthus* sp., *Glyptodon reticulatus* Owen, *Glyptodon* sp., *Neosclerocalyptus paskoensis* (Zurita), *Neosclerocalyptus* cf. *N. paskoensis*, *Neosclerocalyptus* sp.

3. The reanalysis of materials previously assigned to *Tolypeutes* sp. and *Panochthus* cf. *P. intermedius* (Scillato-Yané et al., 1998; Francia et al., 2010) rules out the presence of these taxa in the Late Pleistocene of Corrientes province.

4. Although the taxa recorded are not new, the relative representation of each of them shows evident differences compared to other areas. In the record of Glyptodontinae, *Glyptodon* is clearly the most frequent and represents over 70% of the findings, followed by *Neosclerocalyptus* (Neosclerocalyptini) and *Panochthus* (Hoplophorini). In this sense, the absence of Doedicurinae and "Hoplophorinae" Neuryurini, with relatively common records in the Pampean region of Argentina, is remarkable.

Acknowledgments

Appendix 1. List of analyzed materials

Glyptodon reticulatus Owen, 1838

CTES-PZ 7334: left lateral portion of dorsal carapace, almost complete; associated carapace osteoderms and caudal sheath rings — Lavalle, Toropí/Yupoí Fm. (Lower Member).

Glyptodon sp.

CTES-PZ 3577: 20 dorsal and marginal osteoderms from the dorsal carapace, CTES-PZ 3578: 4 fragments of vertebrae, CTES-PZ 7509: 20 carapace osteoderms, CTES-PZ 7506: one carapace osteoderm, CTES-PZ 7504: 4 dorsal carapace osteoderms, CTES-PZ 7540: 3 dorsal carapace osteoderms; CTES-PZ 7601: osteoderms — Arroyo Toropí, Bella Vista, Toropí/Yupoí Fm. (Lower Member). CTES-PZ 1590: osteoderm, scaphoid, cuboid, phalanx and proximal femur fragment, CTES-PZ 7507: 3 marginal carapace osteoderms, CTES-PZ 7505: 2 carapace osteoderms, CTES-PZ 7508: lateromarginal carapace osteoderm; CTES-PZ 7542: 4 dorsal carapace osteoderms — Arroyo Toropí, Bella Vista; Toropí/Yupoí Fm. (Upper Member).

Panochthus tuberculatus (Owen, 1845)

CTES-PZ 7500: almost complete caudal sheath, 15 dorsal carapace osteoderms, 8 osteoderms from caudal rings, proximal femur, fragmentary molariform, phalanx and portion of caudal vertebra — Arroyo Toropí, Bella Vista; Toropi/Yupoí Fm. (Upper Member).

Panochthus cf. *P. tuberculatus* (Owen 1845)

CTES-PZ 3573: fragments of a caudal sheath; CTES-PZ 7497: fragmentary osteoderm; CTES-PZ 7498: two dorsal carapace osteoderms — Arroyo Toropí, Bella Vista; Toropi/Yupoí Fm. (Upper Member). CTES-PZ 1597: fragments of dorsal carapace, associated osteoderms and three fragments of vertebrae; CTES-PZ 7382: 6 dorsal carapace osteoderms, from a caudal ring and an ungueal phalanx; CTES-PZ 7496: osteoderm from a caudal ring; CTES-PZ 7365: fragmentary osteoderm; CTES-PZ 7499: caudal sheath fragment — Arroyo Toropí, Bella Vista; Toropi/Yupoí Fm. (Lower Member).

Neosclerocalyptus paskoensis (Zurita, 2002)

CTES-PZ 1677: fragment of left side of skull — Arroyo Toropí, Bella Vista; Toropi/Yupoí Fm. (Lower Member).

Neosclerocalyptus cf. *N. paskoensis* (Zurita, 2002)

CTES-PZ 1593: caudal sheath, associated osteoderms, left femur, left hemimandible with molariforms, fragments of right hemimandible and eight isolated molariforms — Arroyo Toropí, Bella Vista; Toropi/Yupoí Fm. (Lower Member).

Neosclerocalyptus sp.

CTES-PZ 3574: fragment of dorsal carapace, CTES-PZ 3576: fragment of dorsal carapace, CTES-PZ 1688: 12 osteoderms from the dorsal carapace and proximal part of ulna, CTES-PZ 3586: partial caudal sheath, poorly preserved, CTES-PZ 3587: distal portion of caudal sheath, CTES-PZ 7333: fragmentary dorsal carapace osteoderms, CTES-PZ 7469: fragmentary osteoderm, CTES-PZ 7493: fragments of dorsal carapace and remains of undetermined bones, CTES-PZ 7501: 30 dorsal carapace osteoderms and caudal ring, CTES-PZ 7502: fragmentary dorsal carapace osteoderms, CTES-PZ 7503: fragmentary dorsal carapace osteoderms, CTES-PZ 7539: osteoderms from one caudal ring, CTES-PZ 7602: isolated osteoderms, CTES-PZ 7603: osteoderm, CTES-PZ 7604: isolated osteoderms, CTES-PZ 7605: isolated osteoderms — Arroyo Toropí, Bella Vista; Toropi/Yupoí Fm. (Lower Member). MLP 76-IV-23-2: eight dorsal carapace osteoderms — Arroyo Toropí, Bella Vista; Toropi/Yupoí Fm.

Pampatherium typum Ameghino, 1891

CTES-PZ 7332: 11 fixed and mobile osteoderms from the dorsal carapace, CTES-PZ 7517: fragment of mobile osteoderm from the dorsal carapace, CTES-PZ 7518: two complete fixed osteoderms and some fragments, CTES-PZ 7516: fixed and mobile carapace osteoderms and some fragments, CTES-PZ 7466: mobile osteoderm and fragmentary fixed osteoderm from the dorsal carapace, CTES-PZ 7606: fragmentary carapace osteoderm — Arroyo Toropí, Bella Vista, Toropí/Yupoí Fm. (Lower Member). CTES-PZ 7519: fixed dorsal carapace osteoderm — Arroyo Toropí, Bella Vista, Toropí/Yupoí Fm. (Upper Member). CTES-PZ 7372: fragment of mobile osteoderm from the dorsal carapace, CTES-PZ 7373: fixed carapace osteoderm, CTES-PZ 7374: fragment of fixed osteoderm — Lavalle; Toropí/Yupoí Fm. (Lower Member).

Pampatherium sp.

CTES-PZ 7514: fragmentary osteoderm from the dorsal carapace and fused marginal and submarginal osteoderms, CTES-PZ 7515: fragmentary osteoderm, CTES-PZ 7362: fragmentary fixed osteoderm — Arroyo Toropí, Bella Vista; Toropí/Yupoí Fm. (Lower member)

Holmesina paulacoutoi (Cartelle Guerra and Bohorquez Mahecha, 1985)

CTES-PZ 7495: 36 complete osteoderms, both fixed and mobile, from the dorsal carapace, and numerous fragments, remains of molariforms, remains of vertebrae and appendicular elements (left femur, distal portion of tibia–fibula, astragalus, calcaneus, cuboid, navicular, fragmentary entocuneiform, metatarsals III, IV and phalanges) — Arroyo Toropí, Bella Vista; Toropí/Yupoí Fm. (Lower Member).

Propraopus sulcatus (Lund, 1842)

CTES-PZ 7454: 10 osteoderms, fixed, mobile and from the caudal sheath, CTES-PZ 7468: two fixed osteoderms, CTES-PZ 7511: 13 fixed and mobile osteoderms, CTES-PZ 7513: fragmentary osteoderm, CTES-PZ 7607: osteoderm, CTES-PZ 7366: fixed osteoderm — Arroyo Toropí, Bella Vista; Toropí/Yupoí Fm. (lower member). CTES-PZ 7512: 16 fixed osteoderms, CTES-PZ 7541: worn osteoderm — Arroyo Toropí, Bella Vista; Toropí/Yupoí Fm. (Upper member).

Euphractus aff. E. sexcinctus Linnaeus, 1758

CTES-PZ 1655: 15 fixed, mobile and semimobile osteoderms, proximal end of ulna, radius and calcaneus — Arroyo Toropí, Bella Vista; Toropí/Yupoí Fm. (Upper member).
CTES-PZ 7568: 1 pelvic shield osteoderm — Arroyo Toropí, Bella Vista; Toropí/Yupoí Fm. (Lower member).

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