Rev. bras. paleontol. 20(1):31-44, Janeiro/Abril 2017
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doi: 10.4072/rbp.2017.1.03

QUATERNARY MAMMALS FROM CENTRAL BRAZIL (SERRA DA BODOQUENA, MATO GROSSO DO SUL) AND COMMENTS ON PALEOBIOGEOGRAPHY AND PALEOENVIRONMENTS

ALESSANDRO MARQUES DE OLIVEIRA
Laboratório de Sistemática e Diversidade, Universidade Federal do ABC, Avenida dos Estados, 5001, Bairro Bangu, 09210-580, Santo André, SP, Brasil. *biolessandro@gmail.com*

BRUNO BECKER-KERBER
Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, Washington Luiz 325 km, 13565-905, São Carlos, SP, Brasil. *bruno.becker92@gmail.com*

LÍVIA MEDEIROS CORDEIRO, RODRIGO BORGHEZAN
Centro de Ciências Biológicas e da Saúde, Universidade Federal do Mato Grosso do Sul, 79070900, Campo Grande, MS, Brasil. liv.biosubt@gmail.com, *rodrigo_borghezan@hotmail.com*

LEONARDO SANTOS AVILLA
Laboratório de Mastozoologia, Universidade Federal do Estado do Rio de Janeiro, Av. Pasteur, 458, Urca, 22290-255, Rio de Janeiro, RJ, Brasil. *leonardo.avilla@gmail.com*

MÍRIAN LIZA ALVES FORANCELLI PACHECO
Departamento de Biologia, Universidade Federal de São Carlos, Campus Sorocaba, Rodovia João Leme dos Santos, km 104, Parque Reserva Fazenda Imperial, 18052-780, Sorocaba, SP, Brasil. *forancelli.ufscar@gmail.com*

CHARLES MORPHY D. SANTOS
Laboratório de Sistemática e Diversidade, Universidade Federal do ABC, Avenida dos Estados, 5001, Bairro Bangu, 09210-580, Santo André, SP, Brasil. *charlesmorphy@gmail.com*

ABSTRACT – Studies regarding Quaternary mammals from the Serra da Bodoquena (South-western Brazil, state of Mato Grosso do Sul) are scarce. In the region, the Fadas Cave has been an important paleontological site. Remnants of Pleistocene fauna were collected along a river channel inside the cave. It is the first record of *Arctotherium*, Scelidotheriinae and Nothrotheriinae in the Serra da Bodoquena. *Smilodon populator*, *Eremotherium laurillardi*, Gomphotheriidae and Glyptodontinae, already known for the region, were also identified. These new occurrences allow us to redefine the paleozoogeographical distribution of some of the aforementioned taxa. Herein we propose the expansion of the range of the Brazilian Intertropical Region, which should include Mato Grosso do Sul and São Paulo. The state of Rio Grande do Sul keeps a greater paleozoogeographical affinity to others temperate zones from Argentina and Uruguay. Taxa associated to open environments indicate the existence of large areas of savannas during the late Pleistocene in the Serra da Bodoquena.

Key words: Brazilian Intertropical Region, Pampean Region, paleozoogeographical zones, Fadas Cave, Quaternary mammals, Serra da Bodoquena.

RESUMO – Os estudos sobre mamíferos quaternários da Serra da Bodoquena (Mato Grosso do Sul) são escassos. Na região, a Gruta das Fadas tem sido um importante sítio paleontológico. Os restos da fauna do Pleistoceno foram coletados ao longo de um canal do rio dentro da caverna. É o primeiro registro de Arctotherium, Scelidotheriinae e Nothrotheriinae na Serra da Bodoquena. Smilodon populator, Eremotherium laurillardi, Gomphotheriidae e Glyptodontinae, já conhecidos pela região, também foram identificados. Estas novas ocorrências nos permitem redefinir a distribuição paleozoogeográfica de alguns dos táxons acima mencionados. Aqui propomos a ampliação da faixa da Região Intertropical Brasileira, que deve incluir Mato Grosso do Sul e São Paulo. O Estado do Rio Grande do Sul mantém uma maior afinidade paleozoogeográfica com outras zonas temperadas da Argentina e do Uruguai. Táxons associados a ambientes abertos indicam a existência de grandes áreas de savanas durante o Pleistoceno final na Serra da Bodoquena.

Palavras-chave: Região Intertropical Brasileira, Região Pampeana, zonas paleozoogeográficas, Gruta das Fadas, mamíferos quaternários, Serra da Bodoquena.

INTRODUCTION

Despite being constantly debated, there are several aspects about South American Pleistocene megafauna (giant mammal fossils with estimated biomass above 1000 kg), especially regarding paleoecology and paleobiogeography, that still need investigation. Frequently, paleoecological and paleoenvironmental approaches take into account the feeding habits based on isotopical and morphological analyses (Bargo & Vizcaíno, 2008; Dantas *et al*., 2013). In Brazil, most of these studies have focused on fossils from North and Northeast regions (Dantas *et al.*, 2013; França *et al.*, 2014). Concerning biogeographical aspects, there are no attempts to correlate or to establish biogeographical affinities among taxa from southwestern Brazil (*e.g*. Mato Grosso and Mato Grosso do Sul) and those from others South American paleozoogeographical zones. Nevertheless, understanding the paleoecological and paleobiogeographical aspects of Quaternary giant mammals can elucidate several questions about their environment and extinction.

In the State of Mato Grosso do Sul (MS), paleontological studies regarding Quaternary mammals are rare (Scheffler *et al.*, 2010). The first mention to Pleistocene mammals in the region was made by Oliveira (1915), based on material collected in Lagoa Seca, 12 km south of the city of Corumbá. In the last 40 years, additional reports on Pleistocene mammal fossils from Mato Grosso do Sul were made by Cunha (1975, 1981), Auler & Boller (1992), Salles *et al*. (2006), Boggiani *et al*. (2009), Perini *et al*. (2009) and Oliveira (2013). However, few of the aforementioned studies deal with biogeographical, paleoecological or paleoenvironmental implications, being restricted to the register of new fossil occurrences.

The present study deals with material from the Serra da Bodoquena, a sustained limestone plateau of the Corumbá Group (Ediacaran), located in the western portion of Mato Grosso do Sul (Figure 1). Caves and sinkholes in the karst plateau of Bodoquena are Quaternary deposits rich in remnants of Pleistocene megafauna and other mammals (Salles *et al*., 2006; Scheffler *et al*., 2010; Oliveira, 2013). Most of the caves occur in dolostones of residual hills in the depression of the Miranda River (Kholer *et al*., 1998).

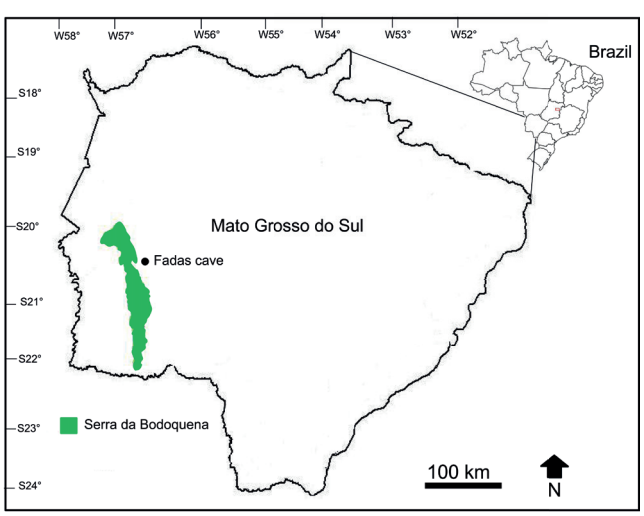

Figure 1. Localization of Fadas cave, Serra da Bodoquena, State of Mato Grosso do Sul, Central Brazil.

The Fadas Cave (Figure 1) (20°34'04"S, 56°46'28"W, altitude 336 m) is located in the Campina Settlement, about 10 km from the city of Bodoquena (MS). The cavity has a small entrance, 1.5 m wide and 0.6 m high, which opens into a small chamber with breakdown blocks in the substrate. A cluster of speleothems abruptly contacts the first chamber to a second one, larger, ca. 60 m long and 10 m high at its highest point. Large sandy-clay deposits constitute the substrate. On the left side of the second chamber, two passages lead to a lower conduit through which flows an underground river.

In 2006, the first exploration of the Fadas Cave revealed new Pleistocene mammals, such as ground sloths, gomphotheres, glyptodonts, felines and a single Ursidae specimen (Oliveira, 2013), which were found at the bottom of the river conduit. These findings suggest the paleogeographical and paleoecological importance of Serra da Bodoquena regarding the South American Pleistocene megafauna and others large mammals. The present paper aims to describe these new records of Pleistocene mammal fossils from Fadas Cave, and to comment on their biogeographical significance, as well as to discuss the paleoenvironment of the Serra da Bodoquena during the late Quaternary.

MATERIAL AND METHODS

The fossils were collected on the surface, in gravel banks, and on the riverbed, using snorkeling in deeper sections (1.5 m depth) of the river flowing in Fadas Cave. The specimens were deposited at the Museu de Arqueologia of the Universidade Federal de Mato Grosso do Sul (campus Campo Grande) (labeled PBQ1-23, PBQ1-20, PBQ1-01, PBQ1-22, PBQ1-06, PBQ1-04) and at the Laboratório de Sistemática e Diversidade of the Universidade Federal do ABC (campus Santo André) (labeled PBQ2-1, PBQ2-2, PBQ2-3, PBQ2-4).

In order to establish a clearer taxonomical correlation among Mato Grosso do Sul and other South American paleozoogeographical zones, we made a cluster analysis. Such procedure took into account the occurrence of extinct Quaternary mammals above 50 kg in the Mato Grosso do Sul, Brazilian Intertropical region, São Paulo, Rio Grande do Sul, Uruguay, Mesopotamian region, North central Argentina, South of Bolivia, Paraguay and Pampean region. In Table 1, we present a matrix of presence (1) and absence (0) of taxa in South American paleozoogeographical zones, identified to species level, based on Prado & Alberdi (1999), Bond *et al*. (2001), Alberdi & Prado (2004), Carlini *et al*. (2004), Noriega *et al*. (2004), Zurita *et al*. (2004, 2007, 2011), Soibelzon *et al*. (2005, 2012), Salles *et al*. (2006), Pitana & Ribeiro (2007), Scherer *et al*. (2007), Scheffler *et al*. (2010), Pitana (2011), Miño-Boilini (2012), Silva *et al*. (2012), Zurita *et al*. (2012), Lopes (2013), Díaz *et al*. (2014), Lobo *et al*. (2015), Varela & Fariña (2016), McAfee (2016), Missagia *et al*. (2016), and

Table 1. Matrix of presence/absence of taxa in South American paleozoogeopgraphical zones. The list include only extinct Quaternary mammals above 50 kg weigh. **Abbreviations: SP**, São Paulo; **RS**, Rio Grande do Sul; **BIR**, Brazilian Intertropical Region; **PR**, Pampean region; **MS**, Mato Grosso do Sul; **NCA/SB/P**, North central Argentina, South of Bolivia and Paraguay; **MR**, Mesopotamian Region.

Taxa	SP	RS	BIR	PR	MS	NCA/SB/P	MR
Arctotherium wingei	0	1	1	0	0	1	0
Arctotherium bonariense	0	0	0	1	0	0	0
Arctotherium vetustum	0	0	0	1	0	0	1
Arctotherium angustidens	0	0	0	1	0	1	0
Arctotherium tarijensis	0	0	0	1	0	1	0
Smilodon populator	1	1	1	1	1	1	1
Toxodon gracilis	0	0	0	1	0	0	1
Toxodon platensis	1	1	1	1	1	1	1
Cuvieronius hyodon	0	0	0	0	0	1	0
Notiomastodon platensis	1	1	1	1	1	1	1
Eutatus seguini	0	0	0	1	0	0	0
Holmesina paulacoutoi	0	1	1	1	0	1	1
Holmesina majus	0	1	1	0	0	0	0
Pampatherium typum	0	0	0	1	0	1	0
Pampatherium humboldti	0	1	1	0	1	0	0
Propraopus sulcatus	0	1	1	0	0	0	0
Propraopus magnus	1	0	1	0	0	0	0
Propraopus grandis	0	1	0	1	0	1	1
Sclerocalyptus ornatus	0	0	0	1	0	1	0
Doedicurus clavicaudatus	0	1	0	1	0	0	0
Panochthus tuberculatus	0	1	0	0	0	1	1
Neuryurus rudis	0	1	0	0	0	0	0
Glyptodon munizi	0	0	0	1	0	0	0
Glyptodon elongatus	0	0	0	1	0	1	0
Glyptodon reticulatus	1	1	0	1	0	1	1
Glyptodon clavipes	0	1	0	1	0	0	0
Glyptodon perforatus	0	0	0	0	0	0	1
Glyptotherium cylindricum	0	0	1	0	0	0	0
Ocnopus gracilis	1	0	1	0	0	0	0
Ahytherium aureum	1	0	1	0	0	0	0
Eremotherium laurillardi	1	1	1	0	1	0	0
Mylodon darwini	0	1	0	1	0	0	1
Mylodonopsis ibseni	0	0	1	0	1	0	0
Lestodon ortizianus	0	0	0	0	0	0	1
Lestodon armatus	1	1	0	1	0	1	1
Glossotherium lettsomi	0	0	1	1	1	0	0
Glossotherium robustum	0	1	0	1	0	1	0
Scelidodon tarijensis	0	0	0	1	0	1	0
Scelidotherium bravardi	0	0	0	1	0	0	0
Scelidotherium leptocephalum	0	1	0	1	0	1	1
Valgipes bucklandi	0	0	1	0	0	0	0
Catonyx cuvieri	1	1	1	1	0	0	0
Megatherium americanum	0	1	0	1	0	1	1
Nothrotherium maquinense	1	0	1	0	0	0	0
Equus (Amerhippus) neogeus	0	1	1	1	1	1	1
Hippidium devillei	0	0	1	1	0	1	0
Hippidium principale	0	1	1	1	1	0	0
Catagonus stenocephalus	0	1	1	1	0	1	0
Morenelaphus brachyceros	0	0	0	0	0	1	1
Neolicaphrium recens	0	1	0	1	0	0	0
Macrauchenia patachonica	0	1	1	1	0	1	1
Palaeolama major	0	0	1	0	1	0	0
Hemiauchenia paradoxa	0	1	0	1	0	1	1
Lama gracilis	0	1	0	1	0	0	1
Lama guanicoe	0	1	1	1	0	0	1

including the specimens herein identified. The cluster analysis was performed on binary matrix employing the clustering algorithm UPGMA (Average Linkage Clustering; Sokal & Michener, 1958) and the Euclidean similarity index using the software Past 3.14.

Taxonomical identification followed Cartelle (1992), De Iuliis (1996), Cartelle & De Iullis (1995, 2006), Pereira *et al.* (2012), for *Eremotherium laurillardi*, Brandoni & McDonald (2015) and De Iullis *et al*.(2011) for Nothrotheriinae, Miño-Boilini *et al.* (2014) for *Scelidotheriinae*, Rinderknecht (2000), Zurita *et al*. (2009), Luna & Krapovickas (2011) for *Glyptodontinae*, Paula Couto (1979) and Mothé *et al*. (2012) for Gomphotheriidae, and Cartelle (1998) for *Arctotherium*. The identification of *Smilodon populator* was made after anatomical comparison with material housed at the Natural History Museum of London (cast – specimen no labeled) and at the National Museum of Natural History from Paris (specimen TAR-52).

SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope, 1889
Family MEGATHERIIDAE (Gray, 1821) Owen, 1842

Eremotherium Lund, 1842

Eremotherium laurillardi (Lund, 1842) Cartelle & Bohórquez, 1982
(Figures 2A–C)

Material. PBQ1-23, right astragalus; PBQ2-1, left calcaneum; PBQ2-2, fragment of right mandibular branch.

Description. The right mandibular branch (Figure 2C) is fragmented at the beginning of the second molariform alveoli (MF2). The specimen presents the last molariform (MF4) (measuring 125 mm in length), the third alveoli molariform (MF3), and part of the ascending ramus containing the mandibular foramen. There is a shallow groove between the ascending ramus and the last molariform, typical of the genus *Eremotherium* (Cartelle, 1992; Cartelle & De Iullis, 1995; Pereira *et al*., 2012). As described by Pereira *et al*. (2012) for *Eremotherium laurillardi*, the MF4 of the specimen studied here shows the mesial ridge wider and mesodistally compressed when compared to the distal crest. The pulp cavity occupies about two-thirds of the total size of the tooth, a diagnostic character for *E. laurillardi* according to Cartelle & De Iuliis (2006). The astragalus (Figure 2A) is complete, with few fractures at the edges. Its proximodistal and anteroposterior extensions, measuring 200 and 230 mm, respectively, are within the range of variation presented among

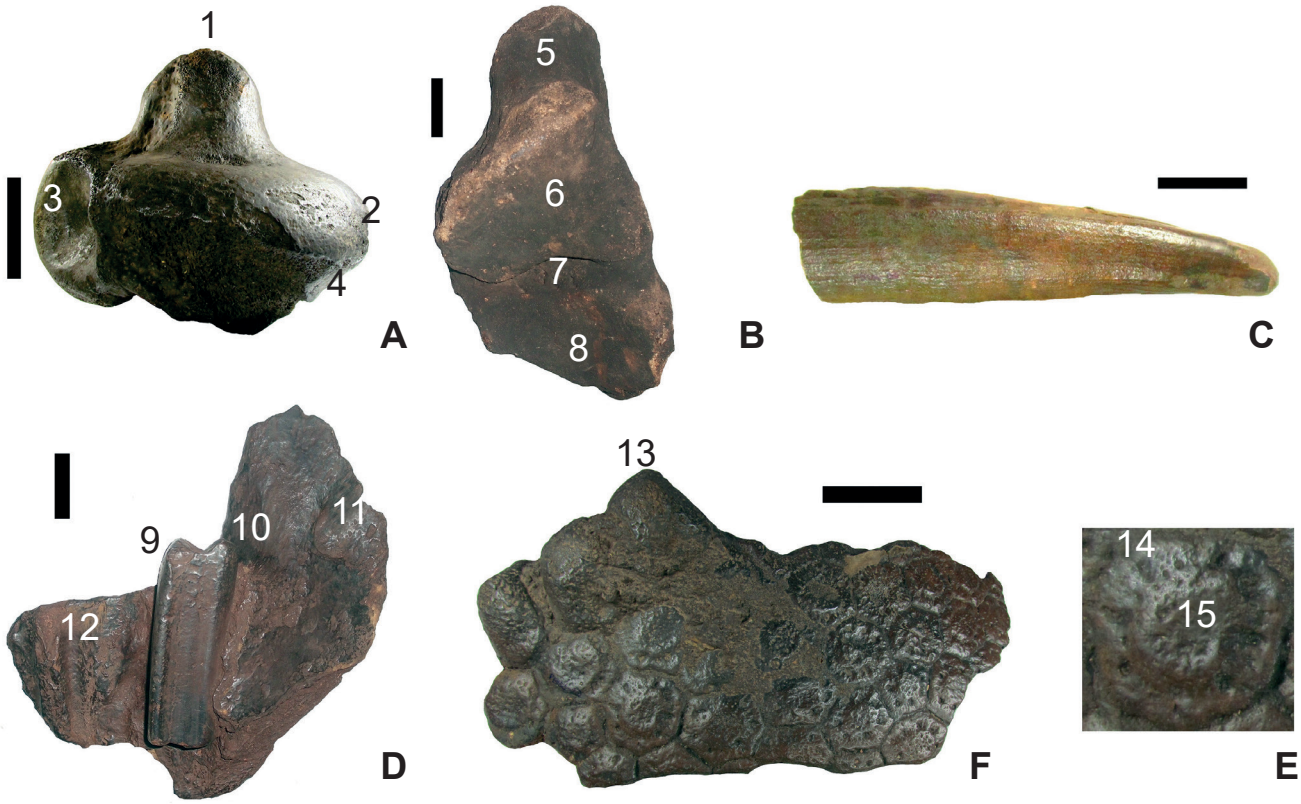

Figure 2. A–C, *Eremotherium laurillardi*. **A**, right astragalus; **B**, right calcaneum; **C**, right mandibular branch. **D**, Gomphoteriidae, part of an incisive tooth. **E–F**, *Glyptodon*, **E,** dorsal portion of the carapace, dorsal view; **F**, detail of osteoderm highlighted. **Abbreviations: 1**, medial trochlea; **2**, lateral trochlea; **3**, articular surface to the navicular; **4**, articular surface to the fibula; **5**, *tuber calcis*; **6**, sustentacular facet; **7**, *sulcus talis*; **8**, ectal facet; **9**, distal crest; **10**, medial crest; **11**, mandibular foramen; **12**, alveoli of third molariform; **13**, lateral osteoderm; **14**, pilose foramen; **15**, central figure. The white arrow indicates downgraded area of central figure. Scale bars: A–C = 50 mm; D–F = 40 mm.

adult megatheriids (De Iuliis, 1996). The medial trochlea is a semi-spherical odontoid process. The lateral trochlea is anteroposteriorly flattened and discoid. Both throcleas form an angle of 90° to each other, indicating a total medium lateral foot rotation. The articular surface to the navicular has a circular concave shape. The calcaneum (Figure 2B) has large sustentacular and ectal facets, each of which measuring 120 x 80 mm, slightly concave and separated by a 20 mm wide *sulcus talis*. The calcaneal tuber is fragmented, with few signs of abrasion on its edges.

Remarks. Usually, three species of *Eremotherium* were recognized as valid species: *E. laurillardi* (from Brazil), *E. rusconii* (from Central America and Northeastern South America) and *E. mirabile* (from the United States of America) (Porta, 1961; Edmund 1965; Bocquentin, 1979; Polaco-Ramos, 1981). Later, Cartelle & De Iuliis (1995) synonymized these three species as *E. laurillardi*. These authors observed a wide variation in morphology and size among the specimens of *E. laurillardi*, which may bias the identification of Megatheriidae. Recently, Faure *et al*. (2014) sustained the hypothesis of *E. rusconii* as a valid species based on the description of two mandibles, which these authors interpreted one as belonging to a young individual of *E. rusconii* and the other to an adult of *E. laurillardi*. However, after studying 944 molariform teeth, Cartelle *et al*. (2015) showed that *E. rusconii* is more likely to be a junior synonym and that the morphological differences represent intraspecific variations of *E. laurillardi*. It is possible that *E. laurillardi* was distributed throughout Brazil during the Pleistocene (Cartelle & Bohorquez, 1982; De Iuliis & Cartelle, 1999). *E. laurillardi* was first recorded to Mato Grosso do Sul by Ayub *et al*. (1996). Carbon isotope analyses have shown a generalist diet for *E. laurillardi* in the Brazilian Intertropical Region, suggesting that the species was associated with both open areas and forests (Dantas *et al*., 2013a; França *et al*., 2014).

Family MYLODONTIDAE Gill, 1872
Subfamily SCELIDOTHERIINAE Ameghino, 1904
(Figures 3A–D)

Material. PBQ1-01, left humerus.

Description. Humerus (Figures 3A–D) 480 mm length, with straight and semi-cylindrical shaft, shorter and more robust compared to other mylodontids, such as *Catonyx cuvieri* and *Valgipes buckland*. The deltoid and pectoral ridges are not evident in cranial view and there is no intermediate ridge. At the proximal epiphysis, the humeral head is less prominent and limited by the greater and lesser tubercles; the lateromedial diameter is approximately 160 mm. The distal epiphysis is lateromedially expanded, about 225 mm in width, and anteroposteriorly flattened. The entepicondylar foramen is present, and its entepicondylar bar is horizontally oriented.

Remarks. Among the mylodontids recorded in Brazil, *Glossotherium*, *Lestodon* and *Catonyx cuvieri* do not have an entepicondylar foramen. *Valgipes buckland* presents the entepicondylar bar obliquely arranged. The species *Scelidodon tarijensis*, unknown from Brazil, has a more developed deltoid crest in comparison to the specimen here described. The morphology of our specimen is suggestive, but not conclusive: identifying the material to species level demands some cranial bone elements absent here. Nonetheless, positioning the specimen in the subfamily Scelidotheriinae seems reliable. Miño-Boilini *et al*. (2014) recognized the existence of two species of this genus, *Scelidotherium leptocephalum* and *Scelidotherium bravardi*. *S. leptocephalum* is restricted to the Bonaerense-Lujanense of the Pampean Region and to the Lujanense of the Argentinian provinces of Córdoba, Santa Fe, Corrientes, Salta and Formosa. *S. bravardi* is known for Ensenadan Age deposits, near the cities of Buenos Aires, La Plata and Mar del Plata, and for the Pleistocene of Villa Larca, in the Argentinian province of San Luis. The specimen here described is the first record of Scelidotheriinae to Mato Grosso do Sul state. Species of this subfamily were probably adapted to both dry/cold and hot/humid environments (Cione & Tonni, 1995; Carlini *et al*., 2004, 2008; Ferrero & Noriega, 2009; Tonni, 2009), with great ecological tolerance (Miño-Boilini, 2012).

Family NOTHROTHERIIDAE Ameghino, 1920
Subfamily NOTHROTHERIINAE Ameghino, 1920
(Figures 3E–H)

Material. PBQ2-3, left femur; PBQ2-4, right femur.

Description. Both femurs (Figures 3E–H) are complete and have 430 mm in length. They are wide and anteroposteriorly flattened, with the distal portion lightly broader than the proximal one. At the proximal epiphysis, the femoral head is prominent but the neck is reduced and the fovea is fully inserted in the *caput*. The greater trochanter is prominent, with a discrete proximal projection. The lesser trochanter is not prominent, being more medially projected in PBQ2-4 than in PBQ2-3, forming a triangular protuberance. A deep trochanteric fossa is present. Distally, the third trochanter is connected to the lateral epicondyle forming a continuous surface. At the distal epiphysis, the medial and lateral condyles are asymmetric (80 and 60 mm respectively), and separated by the intercondylar notch. The patellar trochlea has a concave surface and it is not connected to the medial and lateral condyles. The lateral epicondyle is anteriorly projected.

Remarks. Brandoni & McDonald (2015) described a similar specimen of Nothrotheriinae from the Pleistocene of Argentina (MACN Pv 14148 and MACN Pv 14149), placing it as a *Nothrotheriops* unidentified species or as *Nothropus carcarensis* (which was described based only on a partial mandible). The specimens from Serra da Bodoquena (Figure 3) have a set of characters that strongly suggests their identification as a species of the genus *Nothrotheriops* (*e.g.* shape and position of the greater trochanter; development of the lesser trochanter; connection between the third trochanter and the lateral epicondyle, and the size). However, the lack of specific diagnostic characters led us to identify the specimens PBQ2-3 and PBQ2-4 as an undetermined Nothrotheriinae, based on the same features listed by Brandoni & McDonald (2015). Nothrotheres are known

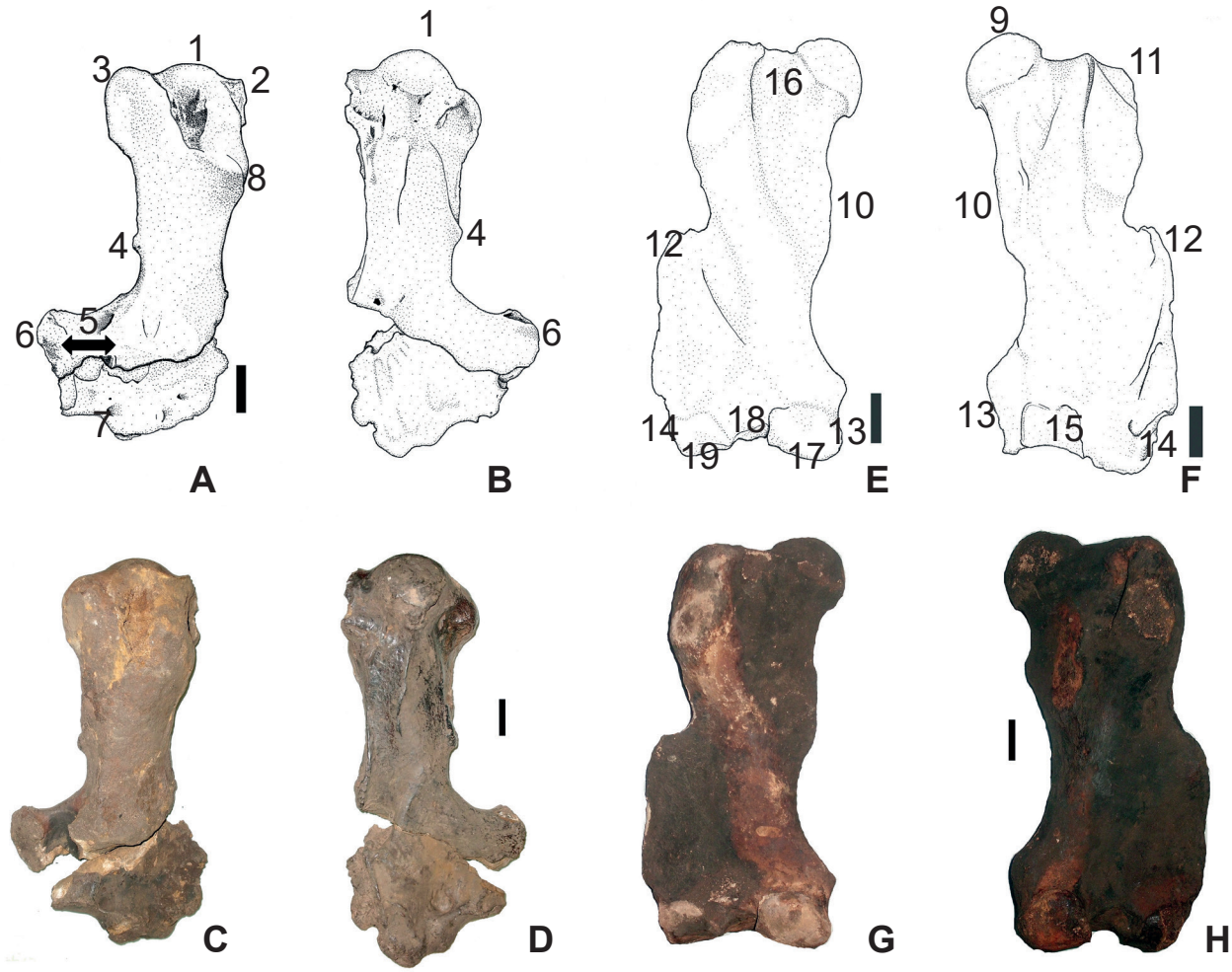

Figure 3. A–D, Scelidotheriinae, left humerus in anterior (**A**, **C**) and posterior (**B**, **D**) views. **E–H**, Nothrotheriinae, left femur in posterior (**E**, **G**) and anterior (**F**) views; right femur in anterior view (**H**). **Abbreviations: 1**, humeral head; **2**, lesser tubercle; **3**, greater tubercle; **4**, pectoral crest; **5**, entepicondylar foramen; **6**, medial epicondyle; **7**, trochlea; **8**, deltoid crest; **9**, femoral head; **10**, lesser trochanter; **11**, major trochanter; **12**, third trochanter; **13**, medial epicondyle; **14**, lateral epicondyle; **15**, patella surface; **16**, trochanteric fossa; **17**, medial condyle; **18**, intercondylar fossa; **19**, lateral condyle. Arrow indicates entepicondylar bar. Scale bars = 40 mm.

from the first half of the Miocene until the Pleistocene (De Iullis *et al*., 2011). They have been placed in the family Megalonychidae (McDonald & Muizon, 2002) or among the Megatheriidae (Paula Couto, 1979; Patterson *et al*., 1992). However, nothrotheres are considerably distinct from Megatheriidae and Megalonychidae. Hence, we place the Nothrotheriinae here identified in the family Nothrotheriidae (cf. Gaudin & De Iullis, 1999; Muizon *et al*., 2004).This is the first record of a nothrothere for Central Brazil – Brazilian nothrotheres were previously known only for the states of São Paulo, Minas Gerais, Bahia and Ceará (Lund, 1839; Cartelle & Fonseca, 1983; Cartelle, 2000; Ghilardi *et al*., 2011). In South America, Quaternary nothrotheres are included in two genera: *Nothrotherium* (found mainly in Brazil) and *Nothropus* (Argentina).The genus *Nothrotheriops* is unknown for South American Quaternary deposits, being recorded only in North America (Brandoni & McDonald, 2015). In general, species of Nothrotheriinae were inhabitants of open environments, browsing on a variety of xerophytic vegetation (Thompson *et al*., 1980; Ghilardi *et al.*, 2011). Although there are several evidences that support an opportunistic browsing or mixed feeding strategy for *Nothrotheriops shastensis* (Poinar *et al.*, 1998; Hofreiter *et al.,* 2000), Green (2009) found a more abrasive diet based on a dental microwear analysis, which could be explained by the consume of grasses.

Family GLYPTODONTIDAE Gray, 1869
Subfamily GLYPTODONTINAE Burmeister, 1879
(Figures 2E–F)

Material. PBQ1-22, fragments of carapace.
Description. 33 osteoderms (Figures 2E–F) were recovered and analyzed. Three are lateral cone-shaped osteoderms. The other osteoderms have irregular, pentagonal or hexagonal shape, with a circular central figure, surrounded by poorly

defined peripheral figures that are much smaller than the central one. Such peripheral figures vary in number from 7 to 8 (the number of peripheral figures varies from 6 to 8 in *Glyptodon* and from 7 to 13 in *Glyptotherium*, and the overlap often leads to misidentification) and are separated by a piliferous foramen, which also varies in number from 7 to 8. The sulci separating the peripheral figures, as well as the central sulcus, are very shallow, almost imperceptible. The central figure appears circular and higher in relation to the peripheral, but due to the degree of abrasion of the material, it is difficult to observe such a feature. In the central area of the central figure, there is a slight downgrade, typical of juvenile specimens of glyptodonts, including *Glyptodon* (Luna & Krapovickas, 2011; Gillette *et al*., 2016). The diameter of each osteoderm varies from 30 to 40 mm.

Remarks. At the Pliocene/Pleistocene boundary, glyptodonts were widely distributed in South America, from Argentina to Venezuela. Glyptodontidae is represented by approximately 67 genera (Fernicola, 2008), with *Glyptodon* being the most documented in Brazil. Previous authors suggested that the Brazilian Intertropical Region was inhabited by *Glyptotherium*, while *Glyptodon* would have been restricted to Southern Brazil (Oliveira *et al*., 2010). In the state of the Mato Grosso do Sul, the genus *Glyptodon* was previously recorded by Salles *et al*. (2006) and Ayub *et al*. (1996) at the city of Jardim. In general, the glyptodonts are considered grazers adapted to open environments (Bargo *et al*., 2006).

Order PROBOSCIDEA Illiger, 1811
Family GOMPHOTHERIIDAE Hay, 1922
(Figure 2D)

Material. PBQ1-06, incisor fragment of juvenile individual.
Description. Incisor fragmented (Figure 2D) in the middle portion, 200 mm length, with longitudinal bands of enamel.
Remarks. Gomphotheres are well documented in South America (Argentina, Brazil, Chile, Colombia, Ecuador, Paraguay, Peru, Uruguay and Venezuela) from Ensenadense to Lujanense (Prado *et al*., 2001), with a single species found in Brazil, *Notiomastodon platensis* (Mothé *et al*., 2012). Due to the absence of diagnostic features on the studied specimen, we have decided to not assign a specified taxonomical classification beyond Gomphotheriidae. Based on stable isotopes analysis, Dantas *et al*. (2013) attributed a generalist diet to Brazilian gomphotheres (*N. platensis*). This would indicate that the species had a high ecological flexibility, being able to live in open areas as well as in forests. However, França *et al.* (2014) stated that *N. platensis* could not modify its diet in a short period of time, which would expose them to local extinction or force them to migrate if the environment abruptly changed.

Order CARNIVORA Bowdich, 1821
Family FELIDAE Gray, 1821

Smilodon Lund, 1842

Smilodon populator Lund, 1842
(Figures 4A–D)

Material. PBQ1-21, right humerus with part of the epiphyses fragmented.
Description. Right humerus (Figures 4A–D), 400 mm length. At the proximal epiphysis, portions of the greater tubercle, lesser tubercle and the humeral head are fragmented. The shaft is sub-triangular in cross section, with distal portion thinner than the proximal one. The deltoid crest is poorly developed compared to extant big cats (*Panthera tigris* and *Panthera leo*). Distal epiphysis has medial-lateral extent of 125 mm, and is fragmented in the medial epicondyle. Entepicondylar foramen is present and entepicondylar bar is obliquely oriented. In anterior view, the radial fossa is shallow, and the capitulum and the mediodistally directed trochlea are highly developed. In posterior view, the olecranon fossa is deep and the lateral supracondylar ridge is well developed. The aforementioned features are diagnostic for *Smilodon populator*, the single saber toothed-tiger recorded to Brazil.
Remarks. *Smilodon populator* had occurred in the Pampean Region (PR) in Argentina, Southern Chile (Prieto *et al*., 2010), Peru (Shockey *et al*., 2009), Uruguay, Ecuador, Brazil, Bolivia and Venezuela (Rincón, 2006). In Brazil, fossils of this feline have been found in the states of Minas Gerais (Piló & Neves, 2003), Paraíba (Correa *et al*., 2012), Ceará (Gomide *et al*., 1987; Bergqvist *et al*., 1997), Goiás (Gomide *et al*., 1987), Bahia (Lessa *et al*., 1998), Rio Grande do Sul (Lessa *et al*., 1998), Rio Grande do Norte (Lessa *et al*., 1998; Porpino *et al*., 2004), Piauí (Guérin *et al*., 1996; Faure & Guérin, 2014), Pernambuco (Silva *et al*., 2003), Sergipe (Dantas, 2012), São Paulo (Castro & Langer, 2008; Ghilardi *et al*., 2011) and Mato Grosso do Sul (Salles *et al*., 2006; Perini *et al*., 2009). The classification of the genus *Smilodon* is controversial. Some authors claim there was a single species in the Americas (Paula Couto, 1979; Berta, 1987; Lessa *et al*., 1998; Cartelle & De Iuliis, 2006), whereas others recognize two species (Kurtén & Werdelin, 1990; Christiansen, 2012). Bocherens *et al.* (2016) suggested that *S. populator* predominantly hunted prey in open environments, behaving as a social predator. However, ecomorphological studies have indicated that these great felines were also adapted to forests (Meloro *et al*., 2013).

Family URSIDAE Gray, 1825

Arctotherium Bravard, 1857
(Figures 4E–H)

Material. PBQ1-04, distal epiphysis of left humerus with part of a shaft.
Description. Distal epiphysis of left humerus (Figures 4E–H), 200 mm length. The humeral shaft is cylindrical. The distal epiphysis is wide with 120 mm medial-lateral extent. The medial condyle is greater than the lateral one, mediodistally directed. Entepicondylar foramen is arranged on the medial face; entepicondylar bar is obliquely arranged and the trochlear fossa is quite broad. The abrasion marks on

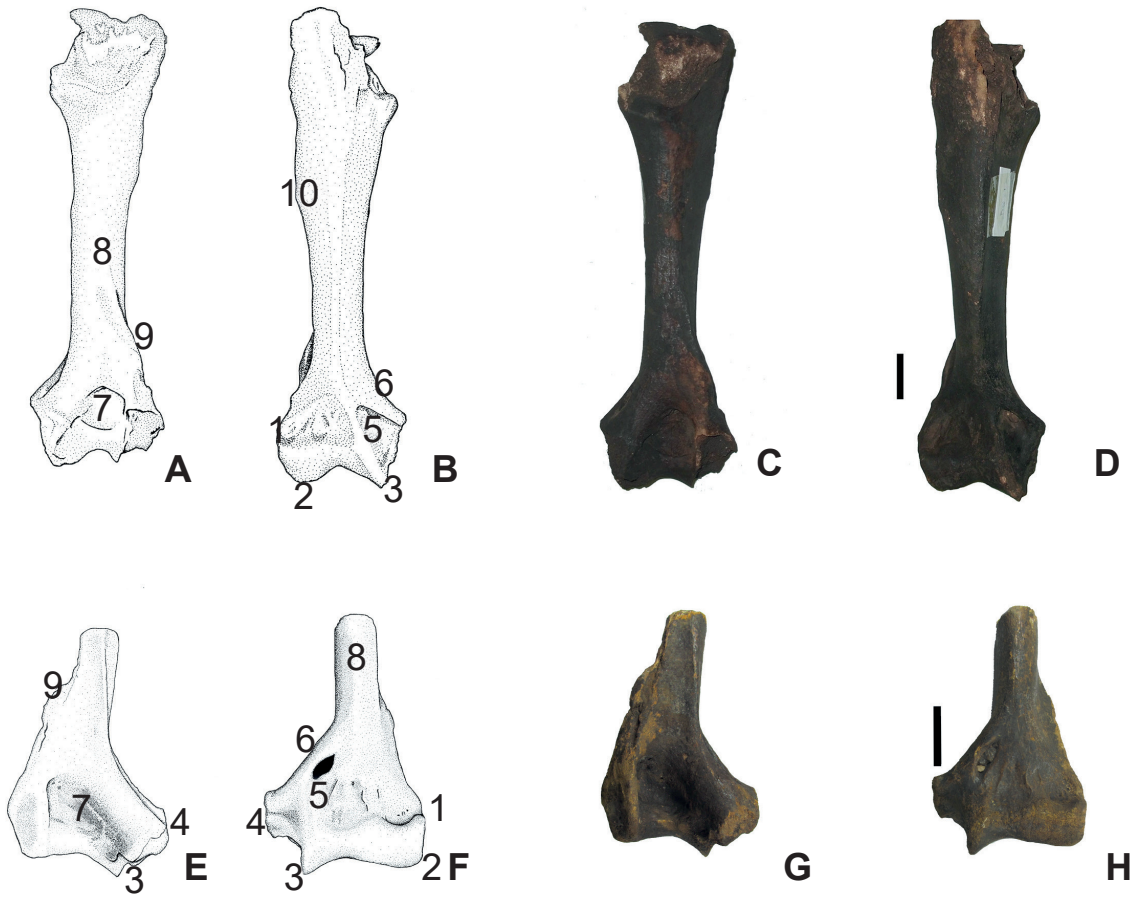

Figure 4. A–D, *Smilodon populator*, right humerus in posterior (**A**, **C**) and anterior (**B**, **D**) views. **E–H**, *Arctotherium* sp., distal epiphysis of left humerus in anterior (**F**, **H**) and posterior (**E**, **G**) views. **Abbreviations: 1**, lateral epicondyle; **2**, *capitulum*; **3**, trochlea; **4**, medial epicondyle; **5**, entepicondylar foramen; **6**, entepicondylar bar; **7**, olecranon fossa; **8**, shaft; **9**, lateral supracondylar crest; **10**, deltoid crest; **11**, humeral head; **12**, greater tubercle. Scale bars = 40 mm.

the edges are minimal. All these descriptions are compatible with the specimen IGC-10 attributed to *Arctotherium* by Cartelle (1998).

Remarks. The Ursidae subfamily Tremarctinae was distributed exclusively in the Americas. It probably originated in Central Western North America, reaching South America during the so called "Great American Biotic Interchange", from the late Miocene to the Holocene (Soibelzon *et al*., 2005). In a systematic review of the Tremarctinae, Soibelzon (2004) recognized a single genus (*Arctotherium*) and five species for this group in South America (*A. augustinenses*, *A. wingei*, *A. vetustum*, *A. bonariens*e and *A. tarijense*). *Arctotherium* was recorded in Brazil in the states of Minas Gerais, Ceará, Bahia, Rio Grande do Norte and possibly Rio Grande do Sul (Trajano & Ferrarezi, 1994; Cartelle, 1998; Lessa *et al*., 1998; Soibelzon *et al*., 2005; Porpino *et al*., 2004; Pereira *et al*., 2012). With the occurrences registered in the present paper a new geographical distribution for *Arctotherium* in South America is configured, now including the Brazilian territory of Mato Grosso do Sul. A primarily herbivore diet has been attributed to *A. wingei* (Figueirido & Soibelzon, 2009). According to Soibelzon & Schubert (2011), large guilds of big carnivores would have increased in diversity after the "Great American Biotic Interchange", and smaller species of *Arctotherium* could have changed their diets to herbivory or omnivory in response to competitive pressures with large carnivores. However, our specimen is bigger than other *Arctotherium* specimens previously reported to Brazil. Some authors claim that *Arctotherium* was associated with arid and semi-arid paleoenvironments (Trajano & Ferrarezzi, 1994) and even to cold environments resultant from glacial events during the Late Pleistocene (Lopez *et al*., 2008). If this statement is correct, the distribution of *Arctotherium* may indicate that the Serra da Bodoquena was more arid in that period.

CLUSTER ANALYSIS

The greatest Euclidean Distance Index (EDI) (6,0827625) obtained is between Brazilian Intertropical Region (BIR) and Pampean Region (PR). The lesser EDI (3,6055513) is observed between Mato Grosso do Sul (MS) and São Paulo (SP), and between Rio Grande do Sul (RS) and Uruguay (Uru) (Table 2). The state of the MS, SP and BIR form a group,

Table 2. Euclidian Distance Index among paleozoogeographical zones in South America.

	SP	RS	BIR	PR	MS	NCA/SB/P	MR	Uru
SP	0	5,099019	4,242640	5,916079	3,605551	5,099019	4,690415	4,582575
RS	5,099019	0	4,898979	4,582575	5	4,690415	4,242640	3,605551
BIR	4,242640	4,898979	0	6,082762	3,872983	5,656854	5,656854	5,567764
PR	5,916079	4,582575	6,082762	0	5,830951	4,358898	4,795831	4,690415
MS	3,605551	5	3,872983	5,830951	0	5,196152	4,795831	4,690415
NCA/SB/P	5,099019	4,690415	5,656854	4,358898	5,196152	0	4,242640	4,123105
MR	4,690415	4,242640	5,656854	4,795831	4,795831	4,242640	0	3,872983
Uru	4,582575	3,605551	5,567764	4,690415	4,690415	4,123105	3,872983	0

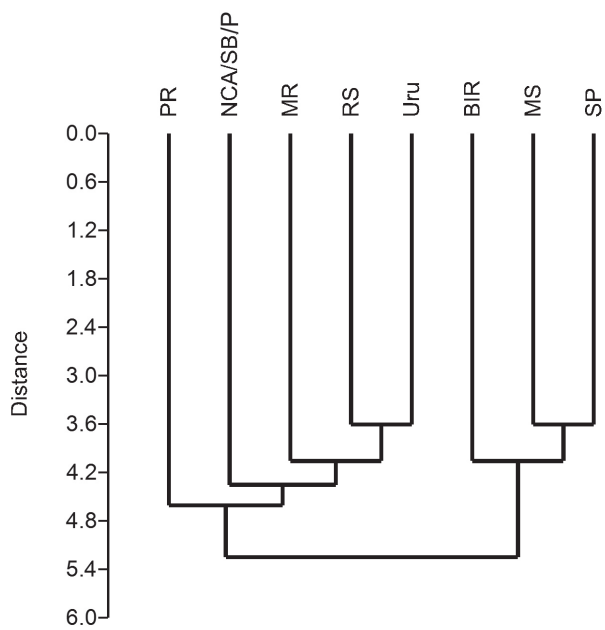

Figure 5. Cluster analysis indicating greater taxonomical affinity among Mato Grosso do Sul (**MS**), São Paulo (**SP**) and the Brazilian Intertropical Region (**BIR**). The state of Rio Grande do Sul (RS) is more similar to Uruguay (**Uru**). The group composed by RS and Uru, Mesopotamian Region (MR), north central Argentina, South of Bolivia and Paraguay (**NCA/SB/P**) share most of their taxa from Pampean Region (**PR**).

whereas RS, Uruguay, North central Argentina, South of Bolivia and Paraguay (NCA/SB/P) and Mesopotamian Region (MR) share greater taxonomical affinity to PR, forming a second group (Figure 5).

PALEOBIOGEOGRAPHY AND PALEOENVIRONMENT

Cartelle (1999) defined the Brazilian Intertropical region (**BIR**) as a paleozoogeographical region especially characterized by the presence of large mammals in savannahs ca. 20,000–10,000 years BP. BIR included the states of Goiás, Minas Gerais, Rio de Janeiro, Espírito Santo, Bahia, Sergipe, Alagoas, Pernambuco, Rio Grande do Norte, Paraiba, Ceará and Piauí. The Pampean region (**PR**) is located in Argentina between 30°–39°S and 57°–66°W, with current climate ranging from temperate to humid subtropical (Prado & Alberdi, 2010). According to Tonni & Figalgo (1978), during Pleistocene the climatic conditions alternated between arid or semi-arid and humid. The predominance of dry and cold climate in the late Pleistocene is suggested by the presence of fossil pollen especially from the Brassicaceae (Quattrocchio *et al*., 2008), and of fossil of extant mammals from Patagonian and Central sub-regions, associated to arid or semi-arid and cold weathers (*Microcavia australis* and *Pediolagus salinicola*) (Tonni, 1981, 1985; Tonni *et al.,* 1992; Prado & Alberdi, 2010).

Based on fossils from the Upper Ribeira speleological deposits, Ghilardi *et al*. (2011) considered the states of São Paulo and Southern Brazil as the transition area between the BIR and PR. According to them, this transition area encompassed a combination of megafauna species recurrent in both BIR and PR, with greater taxonomical affinity to BIR. Carlini *et al*. (2004) considered four paleozoogeographical zones in Southern portion of South America (Figure 6): (i) North central Argentina, South of Bolivia and Paraguay (NCA/SB/P); (ii) Mesopotamian region (MR); (iii) Rio Grande do Sul and Uruguay (RS/Uru); (iv) Pampean region. However, these authors noted high taxonomical similarity between NCA/SB/P and PR; whereas the MR and RS/Uru would share taxa from both PR and BIR. The taxonomical affinities between Paraguay and PR have been noticed by Carlini & Tonni (2000), Souberlich & Uchoa (2013) and Diaz *et al*. (2014) as well.

The cluster analysis (Figure 5) performed herein shows that Mato Grosso do Sul has greater taxonomical affinity to São Paulo, and both share the most of taxa from BIR. This result corroborates Ghilardi *et al*. (2011) who proposed a greater taxonomical similarity between the state of São Paulo and BIR, relative to PR. Therefore it is suggested herein an expansion of BIR, which should include Mato Grosso do Sul (Figure 6). Additionally our results confirm partially Carlini *et al*. (2004), who hypothesized greater taxonomical affinity: (i) between Rio Grande do Sul and Uruguay (composing a single area); (ii) between the Mesopotamian region and that area constituted by Rio Grande do Sul and Uruguay. However, the EDI is lesser between NCA/BS/P and Uruguay; and between NCA/SB/P and MR. Therefore, the hypothesis of greater taxonomical affinity between NCA/SB/P and PR is not clear.

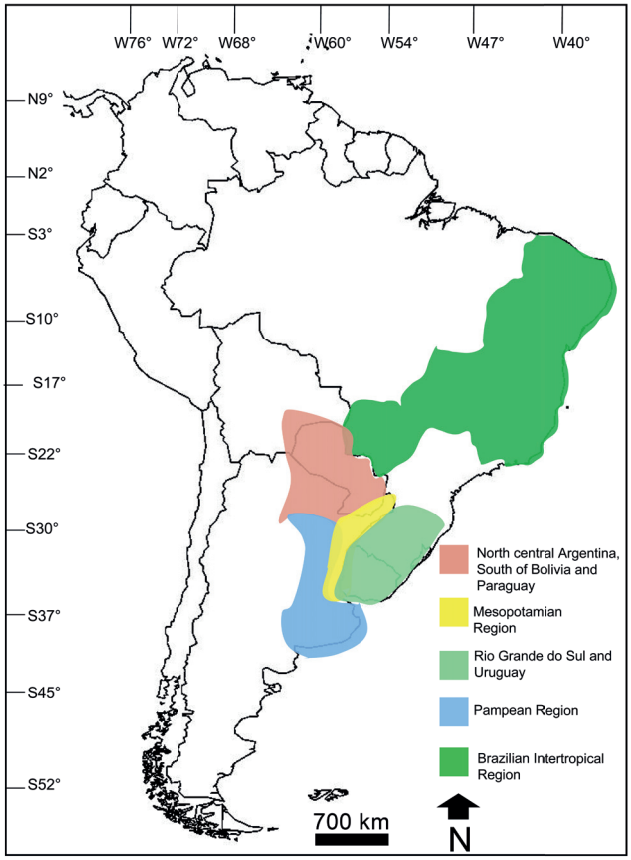

Figure 6. Paleozoogeographical zones in South America during the late Pleistocene.

As Prado *et al*. (1987) claimed, at the late Pleistocene, the PR probably had much lower winter temperatures than today's average, which led to the dispersion of some species towards the North. In this context, it is likely that species from PR (*e.g. Scelidotherium*, *Megatherium*, *Lestodon armatus* and *Glyptodon*) dispersed to warmer areas, reaching Paraguay, South of Bolivia, North Argentina, Southern Brazil, São Paulo and Mato Grosso do Sul.

As mentioned by Ghilardi *et al*. (2011), the presence of taxa from temperate region in the state of São Paulo can indicate that this region and Southern Brazil formed a transitional zone between temperate and intertropical regions. In this context, some authors have mentioned, doubtfully, the presence of *Megatherium* and *Glyptodon* in Mato Grosso do Sul (Scheffler, 2006; Salles *et al*., 2006). If this assertion is confirmed, Mato Grosso do Sul could be included in the transitional zone.

The occurrence of taxa associated with different paleoenvironmental contexts led us to hypothesize that Serra da Bodoquena would be marked by large areas of grasslands and forest fragments or spots, and lower temperatures than the current ones (between 20° and 22° Celsius in average) during the late Pleistocene. This assumption can be compared to other paleoclimate data from Central Brazil, which indicates drier environmental conditions from 22,000–11,500 years BP, followed by an increase in humidity in the last 7,000 years (Salgado-Labouriau *et al*., 1997; Barberi *et al*., 2000). Drier conditions during the late Pleistocene have also been inferred for regions adjacent to the Serra da Bodoquena, like the Pantanal, specifically in the alluvial fan of the Taquari River (Soares *et al*., 2003).

CONCLUSIONS

The present paper is the first attempt to correlate the Pleistocene fauna from Serra da Bodoquena to other South American paleozoogeographical regions. Our data strongly suggest that species of the genus *Arctotherium*, a third species of Scelidotheriinae unidentified and a second species of the Nothrotheriinae was distributed throughout the Western portion of the State of Mato Grosso do Sul during the Pleistocene.

The result of cluster analysis reinforces the hypothesis that the State of Mato Grosso do Sul took part of Brazilian Intertropical region. Likely the State of São Paulo served as a transitional zone contacting Northern, Northeastern and Southern regions of South America. However, the same it is not clear for Mato Grosso do Sul, which the presence of taxa from Pampean region need to be confirmed. The state of Rio Grande do Sul keeps greater similarity to North central Argentina, South of Bolivia, Paraguay, Mesopotamian region, Pampean region and Uruguay than to Brazilian Intertropical region. Additionally, a greater paleozoogeographical affinity between Rio Grande do Sul and Uruguay is corroborated.

Paleoenvironmental inferences from the identified taxa indicate drier scenarios with larger areas of open vegetation in the Pleistocene/Holocene transition when compared to the current characterization of Serra da Bodoquena. Future studies, including the analysis of stable isotopes and absolute dating, should be made in order to offer a more complete picture of the paleoenvironmental aspects of this region.

ACKNOWLEDGEMENTS

We are grateful to Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), to M. Domingues, to G.R. Martins (Museu de Arqueologia, Universidade Federal de Mato Grosso do Sul). We also thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support. Finally we thank the reviewers for criticisms and suggestions in an early version of this manuscript.

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Received in September, 2016; accepted in March, 2017.