

Using Paleoclimate and the Fossil Record to Explain Past and Present Distributions of Armadillos (*Xenarthra*, *Dasypodidae*)

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Abstract Numerous climatic fluctuations occurred during the Cenozoic (last 66 Ma BP); some of them were drastic (e.g., during the Eocene-Oligocene boundary) while others were more gradual (e.g., late Tertiary cooling), but both have deep effect on the biotas. Armadillos are exclusively from the Americas; they have an old evolutionary history in South America and faunal replacement and/or local extinctions were detected, linked with climatic fluctuations. The global cooling of the late Eocene - early Oligocene coincides with a well-documented faunal turnover of Dasypodinae by Euphractinae in Patagonia. During cold and arid periods of the Quaternary, Euphractinae and Tolypeutinae moved more than once to the eastern Pampean Region, and Dasypodinae moved northward to central Brazil or even further north to the Guyana Region. During interglacial periods some armadillos went extinct locally and/or moved to Patagonia (*Zaedyus*), central Argentina (*Tolypeutes matacus*, *Chaetophractus vellerosus*), or from the north to Mesopotamia and the Pampean Region (*Dasyops*). Since the end of the Pleistocene/early Holocene, human activity has strongly impacted armadillo populations. Currently, the eastern Pampean Region (Argentina) is characterized by the presence of the couple *C. villosus* - *D. hybridus* (probably established since the late Holocene), but during the Pleistocene was *Z. pichiy* - *T. matacus* while *Z. pichiy* - *C. villosus* characterized early-middle Holocene. This work serves as evidence that paleozoological studies can be used to assess responses of biological systems to large scale perturbations and is the basis for studying future species distribu-

tions, in order to identify species in danger of extinction and establish management actions.

Keywords America · Biogeography · Holocene · Mammalia · Pleistocene · Quaternary

Introduction

Armadillos are the only extant Cingulata (*Xenarthra*, *Dasypodidae*), mammals characterized by bony shielded regions that protect their head, body, and tail. The body carapace of cingulates consists of three regions (scapular and pelvic shields separated by movable bands), all of which are composed of small bones known as osteoderms. The morphology and ornamentation of the dorsal surface of an osteoderm has great taxonomic value, which is especially useful for identifying isolated remains found in paleontological and/or archaeological contexts (see Vizcaíno et al. 1995; Soibelzon et al. 2010, 2013, 2015, Soibelzon and Leon 2017; Loponte and Acosta 2012; Ciancio et al. 2013). As a result, cingulates have a good fossil record, particularly compared to other xenarthrans (Gaudin and Croft 2015).

All extant armadillos have traditionally been included in a single family, Dasypodidae (and so they will be considered in this paper), but recent molecular studies aim to divide them into two families, Dasypodidae and Chlamyphoridae, the former containing a single extant subfamily (Dasypodinae: long-nosed, nine- and seven-banded armadillos) and the latter comprising three subfamilies (Chlamyphorinae: fairy armadillos; Euphractinae: hairy, dwarf, and six-banded armadillos; and Tolypeutinae: naked-tailed, giant, and three-banded armadillos) (Gibb et al. 2016; Mitchell et al. 2016). Armadillos have been found exclusively in the Americas, from tropical forest to cold-open grasslands, and comprise approximately 20 extant species (approximately 67% of living xenarthrans). Their

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physiological characteristics (e.g., low basal rates of metabolism and body temperature, high thermal conductance, and the possibly of entering torpor; McNab 1980) largely determine their distribution, and they are more diverse in tropical regions than temperate ones (Fig. 1). Their oldest fossil record comes from the São José de Itaboraí Basin, Brazil and was referred to the early Eocene or latest Paleocene (Bergqvist et al. 2004) but the temporal assignation is under discussion (Gaudin and Croft 2015). In North America, they have been recorded since near the Plio-Pleistocene boundary (USA, Blancan, ca. 2.4 Ma BP; Castro 2015) when the formation of the Isthmus of Panama between the Americas favored terrestrial faunal displacement (this phenomenon is known as “Great American Biotic Interchange” or “GABI”; see details in Cione et al. 2015; O’Dea et al. 2016).

The aim of this study is to analyze the distribution of armadillos during the Cenozoic with emphasis in the Quaternary records, and its relationship with paleoclimates.

Paleoclimates and Paleogeographic Changes during the Cenozoic

Climatic oscillations occurred repeatedly during the Cenozoic (Fig. 2) and, together with some paleogeographic changes, have had profound effects on biotas. Especially during the early to middle Cenozoic (Paleogene and Neogene periods), xenarthrans experienced a great radiation (Delsuc et al. 2001). The main paleoclimatic conditions and paleogeographic

changes that have strongly influenced their evolution and biogeographic patterns can be summarized as follows: 1- Eocene - Oligocene boundary: the shift from the “Greenhouse” world into the “Icehouse” world (see Goin et al. 2015) and the isolation and separation of South America from Antarctica (which favored the Antarctic Circumpolar Current); 2- Miocene: marine transgressions, epeirogenic uplifting of the central Brazilian shield, Andean orogeny (which produced Patagonian desertification); 3- Quaternary: more than 15 glacial cycles have been detected during the Pleistocene (Rabassa et al. 2005), the three with the greatest development at about 1 Ma, 0.78 Ma, and 26 to 19 ka BP (Great Patagonian Glaciation or GPG, Matuyama/Brunhes Glaciation, and Last Glacial Maximum or LGM, respectively; Soibelzon and Tonni 2009). The LGM ends with colder and arid conditions of the Younger Dryas (ca. 11.7 ka; Broecker et al. 2010) (Fig. 2). The glacial periods were temporarily interrupted by short duration interglacial conditions (e.g., MIS 11, MIS5e) (Cione et al. 2015). During the Holocene (11.7 ka BP until the present day), the climate slowly turned warm, producing deglaciation and sea level rise (Ponce and Rabassa 2012). These processes were drastically interrupted by some episodes such as: the warmer and drier Holocene Thermal Maximum (HTM) or Holocene Climatic Optimum (HCO) during the middle Holocene (between 7 to 5 ka BP in the Southern Hemisphere) (Renssen et al. 2012); and the mid/low-latitude aridification (M-LA) event during the middle-late Holocene boundary (4.2 ka BP). During the last 1000 years, two significant climatic events were recorded: the Medieval Thermal Maximum or MTM (developed during the 800–1200 AD; Broecker 2001) and the Little Ice Age or LIA (between 1550 and 1900 AD) (de Menocal 2001; Tonni 2006; Marcott et al. 2013).

Materials and Methods

In order to analyze the distribution of Dasypodidae during the Quaternary (last 2.6 Ma, Pleistocene and Holocene epochs sensu Cohen et al. 2013), distributional maps were created based on specimens housed in the following paleontological, archaeological, and mastozoological collections: 1-Argentina: Museo de La Plata (La Plata); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires); Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia” (Mar del Plata); 2-Brazil: Coleção de Mamíferos Fósseis do Laboratório de Mastozoologia (Universidade Federal do Estado do Rio de Janeiro); Museu Nacional (Rio de Janeiro); Museu de Ciências Naturais (Pontifícia Universidade Católica de Minas Gerais); 3-USA: American Museum of Natural History (New York); Florida Museum of Natural History (Gainesville); Princeton Collection of Yale Peabody Museum (New Haven); 4-Bolivia: Museo Nacional Paleontológico-Arqueológico de Tarija (Tarija). The database



Fig. 1 Map showing the current distribution of Dasypodidae and species richness (based on IUCN 2016). Climate regionalization taken from Peel et al. (2007)

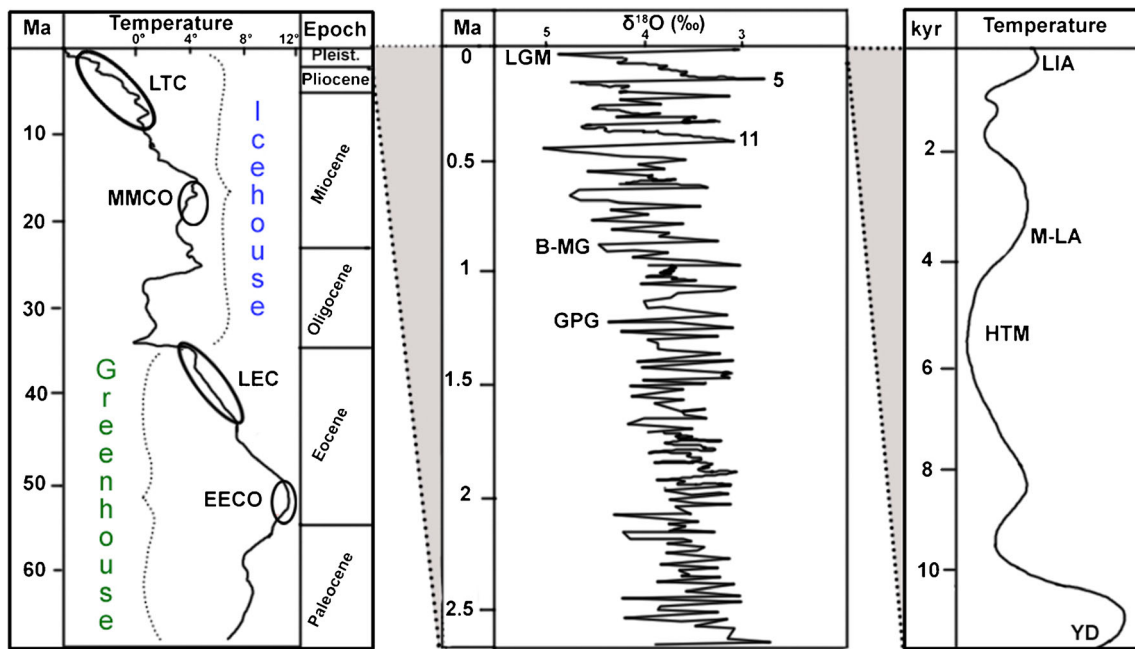


Fig. 2 Time scale for the last 60 Ma BP with main global climatic events mentioned in the text. Redrawn after Zachos et al. 2001 (left and center) and Folland et al. 1990 (right). **B-MG** Matuyama/Brunhes Glaciation, **EECO** Early Eocene Climatic Optimum, **GPG** Great Patagonian Glaciation, **HTM** Holocene Thermal Maximum, **Kyr** Thousand years

before present, **LEC** Late Eocene Cooling, **LGM** Last Glacial Maximum, **LIA** Little Ice Age, **LTC** Late Tertiary Cooling, **Ma** Million years before present, **M-LA** mid/low-latitude aridification, **MMCO** Middle Miocene Climatic Optimum, **Pleist** Pleistocene, **11** and **5** Marine Isotopic Stage

was supplemented with information from FAUNMAP (Graham and Lundelius, 2010), published fossil records in paleontological and archaeological contexts (e.g., Vizcaino et al. 1995; Soibelzon et al. 2006, 2010, 2013, 2015; Soibelzon and León 2017; Loponte and Acosta 2012; Rodriguez-Bualó et al. 2014; Castro 2015; Francia et al. 2015; Ciancio 2016), and new records from recent field investigations in Buenos Aires Province, Argentina (e.g., southern coastal cliffs, San Pedro and Marcos Paz counties). The datasets analyzed during the current study are available in the repository mentioned above and are available from the corresponding author on reasonable request.

The maps of South American species richness and distributional maps were created using IUCN 2016 Red List Spatial Data managed in DIVA-GIS 7.5.0.0.

Abbreviations Institutions, Argentina: **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”; **MLP**, Museo de La Plata; **MMP-S**, Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”; Bolivia: **MUT**, Museo Nacional Paleontológico-Arqueológico de Tarija; France: **MNHN-PAM**, Museum National d’Histoire Naturelle; USA: **YPM PU**, Princeton Collection of Yale Peabody Museum.

B-MG Matuyama/Brunhes Glaciation, **BP** Before Present, **EECO** Early Eocene Climatic Optimum, **GABI** Great American Biotic Interchange, **GPG** Great Patagonian Glaciation, **HTM** Holocene Thermal Maximum, **IUCN** International Union for Conservation of Nature, **Kyr**

Thousand years before present, **LEC** Late Eocene Cooling, **LGM** Last Glacial Maximum, **LIA** Little Ice Age, **LTC** Late Tertiary Cooling, **Ma** Million years before present, **MIS** Marine Isotopic Stage, **M-LA** mid/low-latitude aridification, **MMCO** Middle Miocene Climatic Optimum, **MTM** Medieval Thermal Maximum, **Pleist** Pleistocene, **YD** Younger Dryas.

Results

The family’s oldest fossil record is from Patagonia of Argentina, when tropical to subtropical forest covered southern South America, favored by the prevalent climatic conditions of the Greenhouse phase, especially during Early Eocene Climatic Optimum (Fig. 2) (Ciancio et al. 2013; Ciancio 2016). The beginning of the “Icehouse” phase coincides with the last record of Dasypodinae (a subfamily clearly adapted to tropical - subtropical climates) in Patagonia, and thereafter the family has been recorded during the “Middle Miocene Climatic Optimum” of equatorial South America (Ecuador, Colombia) and late Miocene of Brazil (Castro 2015). The oldest record of a Euphractinae corresponds to the late Eocene of Patagonia (Ciancio et al. 2006), when a great faunal turnover occurred during the Eocene-Oligocene transition, linked with a global cooling (Fig. 2). Thereafter, a great diversity of Euphractinae adapted to temperate climates is recorded (Ciancio 2016). The tolypeutines are poorly represented in

pre-Quaternary times, even though their fossil record includes the late Oligocene of Bolivia and middle Miocene of Colombia (Billet et al. 2011; Ciancio 2016).

The Quaternary records of Dasypodidae in South America show differences in both taxonomic composition and geographical distribution for both fossil and extant species. Members of Dasypodinae, Euphractinae, and Tolypeutinae were recorded (no record of Chlamyphorinae was found) (Table 1).

The Dasypodinae are recorded since the early Pleistocene by the extinct genus *Propraopus* and since the late Pleistocene by *Dasyypus* in Argentina, Bolivia, and Brazil (Tonni et al. 2009; Soibelzon et al. 2010; Castro 2015). During the Holocene, *Dasyypus* was registered in some archaeological contexts of Argentina and Brazil (see Vizcaíno et al. 1995; Mazzanti and Quintana 2001; Soibelzon et al. 2013, and the bibliography cited therein).

The Euphractinae are represented since the early Pleistocene in the Pampean Region by the extant genus

Zaedyus and *Chaetophractus* (Fig. 3a, b) and the extinct *Eutatus pasquali* (Holotype MMPS-171, late Pliocene-early Pleistocene) and *E. seguini* (Holotype MNHN-PAM 273, late Pleistocene) (Křmpotic et al. 2009b). *Chaetophractus villosus* is also recorded in the Pleistocene of the Tarija Valley in Bolivia (MACN 1612, YPM PU 16612 and MUT-128; Rodríguez-Bualó et al. 2014). Finally, *Euphractus* is registered since the late Pleistocene of Argentina (northeastern Corrientes Province, Francia et al. 2015) and Brazil (Minas Gerais State, Bahia State, Tocantins; Soibelzon et al. 2015). Therefore, the Quaternary record of Euphractinae includes the early Holocene of Brazil (*Euphractus*, Ceará State), middle and late Holocene of Pampean Region (*Chaetophractus* and *Zaedyus*), and late Holocene of Uruguay (*Chaetophractus*, *Eutatus*; Ubilla et al. 2017). Its record in the middle Pleistocene of the Pampean Region (MLP 69-VIII-9-5) and in the late Holocene of Córdoba Province has been questioned (Soibelzon et al. 2010, 2013).

Table 1 Fossil record and geographic distribution of extant and extinct armadillos in South America. A Argentina, B Bolivia, Be Belize, Br Brazil, C Colombia, Ch Chile, CR Costa Rica, E Early, Ec Ecuador, ES

El Salvador, G Guyana, GF Guyana Francesa, Gu Guatemala, H Honduras, L late, M Middle, Mx México, N Nicaragua, Pa Panamá, P Paraguay, Pe Perú, S Surinam, V Venezuela

Species	Pleistocene	Holocene	Present
Euphractinae			
<i>Chaetophractus villosus</i>	A (E,M, L); B, U (L)	A (E, M, L); U (E)	A, B, P
<i>Chaetophractus vellerosus</i>	A (E-M)	A (L)	A, B, Ch
<i>Euphractus sexcinctus</i>	A and Br (L)	Br (L)	A, B, Br, P, U
<i>Zaedyus pichiy</i>	A (E-M)	A (E, M, L)	A
† <i>Eutatus pasquali</i>	A (L-M)	-	-
† <i>Eutatus seguini</i>	A (M-L)	A, U (E)	-
Dasypodinae			
<i>Dasyypus hybridus</i>	A (L)	A (E, M, L)	A, Br, U
<i>Dasyypus novemcinctus</i>	A, B, Br and U (L)	Br (E)	A to USA
<i>Dasyypus septemcinctus</i>	-	-	A, B, Br, P
<i>Dasyypus kappleri</i>	-	-	B, Br, C, Ec, G, GF, Pe, S, V
<i>Dasyypus sabanicola</i>	V (L)	-	C, V
<i>Dasyypus mazzai</i>	-	-	A
† <i>Dasyypus punctatus</i>	Br (L)	Br (E)	-
<i>Cryptophractus pilosus</i>	-	-	Pe
† <i>Propraopus sulcatus</i>	A (E-M, L); U (L)	B, Br, E, U, V	-
Chlamyphorinae			
<i>Chlamyphorus truncatus</i>	-	-	A
<i>Calyptophractus retusus</i>	-	-	A, B, P
Tolypeutinae			
<i>Tolypeutes matacus</i>	A (E-M, L)	A (M, L)	A, B, Br, P
<i>Tolypeutes tricinctus</i>	Br (L)	-	Br
<i>Cabassous tatouay</i>	-	-	A, Br, P, U
<i>Cabassous chacoensis</i>	-	-	A, P
<i>Cabassous unicinctus</i>	-	-	B, Br, C, Ec, G, GF, P, Pe, S, V
<i>Cabassous centralis</i>	-	-	Be, C, CR, Ec, ES, Gu, H, Mx, N, Pa, V
<i>Priodontes maximus</i>	-	-	A, B, Br, C, Ec, G, GF, P, Pe, S, V

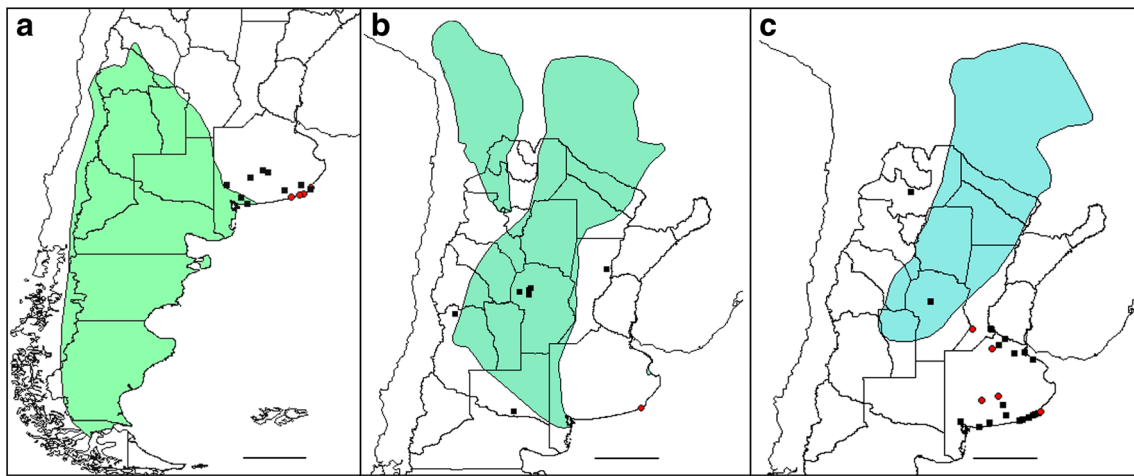


Fig. 3 Maps showing current distributions of the armadillos *Zaedyus pichiy* (a), *Chaetophractus vellerosus* (b), and *Tolypeutes matacus* (c), and their fossil records during the Pleistocene (red dots) and Holocene (black squares). Scale bar = 400 km

The Tolypeutinae are represented by the genus *Tolypeutes* from the early Pleistocene to late Holocene in numerous paleontological and archaeological sites of the northern and southern Pampean Region (Soibelzon et al. 2010, 2017; Beilinson et al. 2015) (Fig. 3c). The provenance of specimen MLP 69-IX-9-1 from “the sub-Andean Tertiary” of Salta is dubious. Deschamps et al. (2003) mentioned their presence during the LIA in Buenos Aires Province. In Brazil, there are a few records assigned to *Tolypeutes tricinctus* in the late Pleistocene of the states of Bahia, Ceará, Rio Grande do Norte, and Sergipe (Feijó et al. 2015).

Discussion

Pre-Quaternary records of armadillos shows faunal replacements during the Eocene-Oligocene boundary, biogeographic connections between Pampean Region and northwest Argentina during late Miocene, and displacements or local extinctions during the Pleistocene and Holocene.

The Quaternary is characterized by climatic oscillations, with a prevalence of cold and arid conditions alternating with warm events of short duration, some of them humid (Tonni et al. 1999). Given that every taxon inhabits certain areas with characteristic climatic attributes, changes in those attributes can have two outcomes for a taxon: local extinction or displacement to an area where the variables have not changed (Lyman 2006). Following Vivo and Carmignoto (2004), the colder and more arid glacial Pleistocene favored the development of grasslands and steppes in southern South America, open forests and savannas in the central Brazil and Central America (Fig. 4a), and xeric scrub and open wooded vegetation in eastern USA. On the other hand, interglacial periods (of short duration) were warm and wet and forced the development of evergreen forest in tropical-subtropical America and temperate paleoenvironments in southern South America (Fig. 4b).

The Dasypodidae have a wide geographic range in America, but their greatest diversity is in tropical-subtropical climates of central South America (Fig. 1). They are adapted to different climatic conditions, and analysis of their past and current distributional records reveals geographic displacements (Fig. 3).

The Dasypodinae (commonly known as “mulitas” or “long-nosed armadillos”) are currently distributed along the Neotropical and Andean biogeographic regions (sensu Morrone 2006); only *Dasypus novemcinctus* has a distribution that extends into southern North America (Taulman and Robbins 2014). The extant genus *Dasypus* has been recorded in South America since the late Pleistocene, with a continuous distribution during the Holocene of the Pampean and Mesopotamia regions (Vizcaíno et al. 1995; Tonni 2003; Soibelzon et al. 2010, 2013; Abba and Vizcaíno 2011; Loponte and Acosta 2012). Strikingly, the oldest record of the genus corresponds to *D. bellus* in the late Pliocene-early Pleistocene of North America (Southeast USA and Mexico; Graham and Lundelius 2010), a species that became extinct in the late Pleistocene (Castro 2015). Apparently, the extant species *D. novemcinctus* reinvaded southern USA around 600 years ago and continues its expansion to the northeast (Humphrey 1974; Shapiro et al. 2015; Taulman and Robbins 2014). The distribution of *D. bellus* resembles the current range of *D. novemcinctus*, but the former probably had greater cold tolerance during the Quaternary (Feng et al. 2016). Several authors have proposed that cold and drought cause death in *D. novemcinctus* (Kalmbach 1944; Fitch et al. 1952; McDonough and Loughry 1997).

The Euphractinae (commonly known as “peludos” or “hairy armadillos”) are currently restricted to the southeast Neotropical region (especially along the “open dry diagonal” of South America, Floresta Atlántica and Pampa, sensu Zanella 2010), Neotropical transition zone, and Andean region (sensu Morrone 2006). The Quaternary record shows

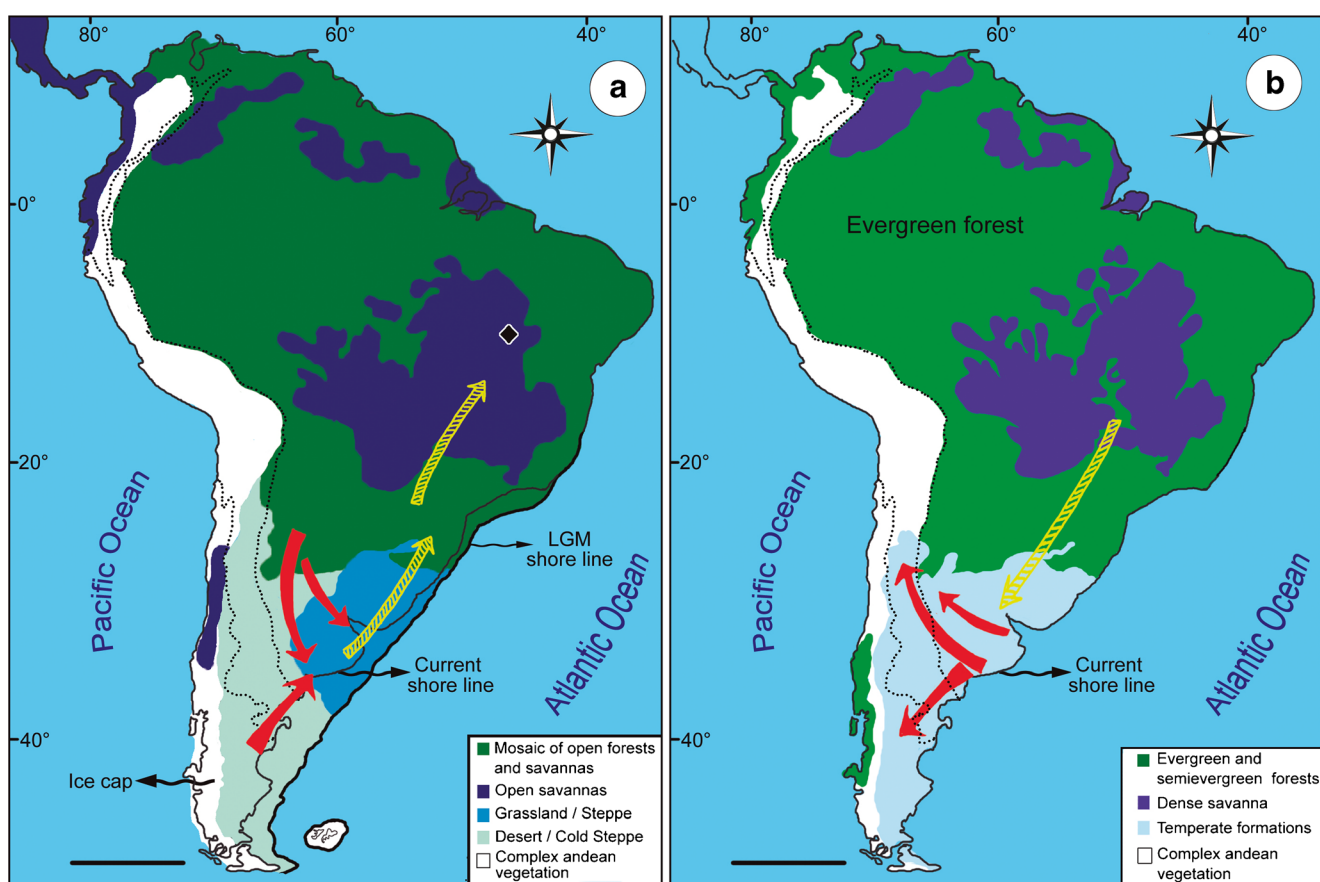


Fig. 4 Map of South America showing major vegetation types and lower sea levels during the Last Glacial Maximum (a) and Holocene Thermal Maximum (b). Redrawn after Vivo and Carmignotto (2004) and Ponce and Rabassa (2012). Solid arrows indicate the displacements of Central and Patagonian fauna (Euphractinae and Tolypeutinae) to the Pampean

Region; upward diagonal fill arrow indicates the displacement of the Dasypodinae to the north. Dotted line: limits between Neotropical Region, South America transition zone, and Andean Region (sensu Morrone 2006). Black diamond: Aurora do Tocantins (see text). Scale bar = 1000 km

the presence of *Zaedyus* and *Chaetophractus vellerosus* (Fig. 3a, b) in the southeast Pampean Region (Soibelzon et al. 2006; Soibelzon and León 2017; Carlini et al. 2016), which went extinct locally, probably when interglacial conditions prevailed. A relictual population of *C. vellerosus* currently inhabits the area of Bahía Samborombón, (Buenos Aires Province); this disjunct distribution has been explained as a relic of a more extensive paleodistribution that included the entirety of the current territory of Buenos Aires Province (Soibelzon et al. 2007; Carlini et al. 2016). Phylogeographic studies performed by Poljak (2009) indicated that the ancestral haplotype of the species is located in central Argentina (Tucumán province) and the derived ones in Samborombón Bay. *Chaetophractus villosus* has one of the widest distributions in Argentina, excluding only Mesopotamia and the Puna of Argentina; its range could be extended due to the expansion of agricultural frontiers (Abba and Vizcaíno 2011). Following Carlini and Scillato-Yané (1999), its fossil record dates back to the Chapadmalalan Age (late Pliocene), while Cione et al. (2015) referred it at most to the Marplatán Age (late Pliocene-early Pleistocene). Pleistocene records include

Bolivia (Tarija Valley; Rodríguez-Bualó et al., 2014), Argentina (Buenos Aires and Corrientes provinces; Soibelzon et al. 2010; Francia and Ciancio 2013; Francia et al. 2015), and Uruguay (Sopas Formation, late Pleistocene; Ubilla and Marinez 2016; Ubilla et al. 2017), and numerous archaeological sites document its presence during the Holocene (Vizcaíno et al. 1995; Loponte and Acosta 2012; Soibelzon and León 2017). Poljak et al. (2010), based on molecular markers, suggested an ancestral lineage in the Pampean Region with a later dispersion to Patagonia after the retraction of the Pleistocene glaciers (Fig. 4b). Finally, in recent times, humans introduced the species in the southernmost province of Argentina (Tierra del Fuego; Poljak et al. 2007). The last member of Euphractinae recorded during the Quaternary is *Euphractus*. Following Carlini and Scillato-Yané (1999), it has been recorded since the Ensenadan Age (early Pleistocene) based on some specimens with dubious geographic and/or stratigraphic provenance (e.g., MLP 69-VIII-9-5). For this reason, its biochron has been restricted to the late Pleistocene of Brazil (Soibelzon et al. 2015) and Argentina (Francia et al. 2015; Gasparini et al. 2016) to Recent.

Finally, eutatines, which are recorded since the late Eocene of Patagonia, are the most hairy armadillos, probably in connection with the adaptation to colder climates (Krmptoc et al. 2009a; Scillato-Yané et al. 2010). Quaternary records are restricted to *Eutatus pascuali* (early to middle Pleistocene) and *E. seguini* (middle Pleistocene to early Holocene) distributed only in Argentina and Uruguay.

The Tolypeutinae (commonly known as “mataco bola” or “southern three-banded armadillo”) are currently restricted to warm-temperate climates in desert or semi-desert regions (Feijó et al. 2015). In Argentina, the Quaternary records corresponds to *Tolypeutes matacus*, which has been recorded from the early Pleistocene to late Holocene (including during the LIA) in numerous localities of the Pampean Region (with the exception of the specimen from Salta mentioned above) where it is currently absent, up to 800 km outside its current distribution (Fig. 3c). In Brazil, only a few records attributed to *T. tricinctus* are known. Following Feijó et al. (2015), its allopatric distribution could be explained as vicariant, linked to Miocene marine transgressions and uplift of the Brazilian Shield.

The expansion from central Argentina to the southeast Pampean Region (and vice versa) during glacial/interglacial cycles (*C. vellerosus*, *T. matacus*) was probably across the “Argentinean arid diagonal” (local expression of the “South America transition” zone sensu Morrone 2006) (Fig. 4). This arid diagonal has a long evolutionary history in South America (Monge-Nájera 1996; Iglesias et al. 2011), having its major development in the past and acting as a primary barrier to the dispersal of taxa from northeast to southwest (Bruniard 1982). Additionally, during glacial periods, sea level drops generated more continental conditions than those recorded today in the eastern Pampean Region and allowed armadillos to move to that region, where climatic conditions were probably similar to those prevalent in central Argentina and Patagonia during interglacial cycles. Following Ciancio et al. (2006), during the late Miocene (Chasicuan and Huayquerian stage), biogeographic connections between Pampean Region (Buenos Aires and La Pampa provinces) and northwest Argentina (San Juan and Catamarca provinces) were sustained in the diversity of Euphractini and Eutatini. Likewise, the development of open forests and savannas in lower latitudes allowed the latitudinal expansion of the Dasypodinae *Propraopus* and *Dasypus* to the Guiana Region of Brazil (e.g., Aurora do Tocantins in Brazil, Soibelzon et al. 2015) (Fig. 4a). Then, during interglacial cycles, warm and moist climates favored their expansion to the north, reaching southern USA (Shapiro et al. 2015) and to the south, into evergreen forest of central Brazil (Soibelzon et al. 2015), Mesopotamia, and Humid Chaco of Argentina.

Conclusions

Changes in the fossil record of Dasypodidae can be explained as displacements and/or local extinctions linked to past climate changes. The end of the “Greenhouse” phase and beginning of the “Icehouse” is connected with a faunal turnover of Dasypodinae by Euphractinae in Patagonia.

During cold and arid periods of the Quaternary, Euphractinae and Tolypeutinae moved to the eastern Pampean Region and Dasypodinae moved northward to the central Brazilian shield (*Propraopus*, *Dasypus*; Soibelzon et al. 2015) (Fig. 4a), or even farther north to the Guyana Region. This region could have acted as refuge, as has been proposed for other vertebrates. These geographic displacements surely have occurred more than once, probably during the early Pleistocene coinciding with the Great Patagonian Glaciation, the Brunhes/Matuyama boundary, the Last Glacial Maximum, and throughout the different cold and/or arid phases of the Holocene (i.e., Holocene Thermal Maximum, Little Ice Age) (Fig. 4a; Table 1). During interglacial periods (e.g., MIS 11, MIS 5e, current interglacial), armadillos went extinct locally and/or moved to Patagonia (*Zaedyus*), central Argentina (*Tolypeutes matacus*, *C. vellerosus*), or Mesopotamia and the Pampean Region (*Dasypus*) (Fig. 4b). Similarly, during these periods, some subtropical mammals expanded their distributions to higher latitudes (e.g., *Tapirus* in southeast Buenos Aires Province; Cione et al. 2015).

Taking into account the effects of the climatic and/or environmental perturbations on the organisms (see Walther et al. 2002, among others); and the physiological limitations of armadillos for living in temperate climates (McNab 1980); their presence in the eastern Pampean Region is due to climatic conditions in the past. Currently this area could be characterized by the couple *C. villosus* - *D. hybridus* (Abba and Vizcaíno 2011), probably established since the late Holocene (Tonni et al. 1992). But the characteristic association in the Pleistocene was *Z. pichiy* - *T. matacus* while *Z. pichiy* - *C. villosus* characterized early-middle Holocene (Tonni 1985; Vizcaíno et al. 1995). Today, the former association is recorded approximately 1000 km to the northwest of the Pampean Region (north of San Luis Province). Likewise, glacial conditions during the late Pleistocene and Holocene of Corrientes Province favored the expansion of *C. villosus* to that region, where they are currently absent. This is supported both by paleontological and archaeological records (Tonni 2003; Soibelzon et al. 2010, 2015, 2017; Francia et al. 2015) as well as molecular data (Poljak 2009; Poljak et al. 2010). The presence of *D. hybridus* in the Pampean Region during the LIA could be explained by particular microenvironments with wet conditions, as was proposed for other species (Teta and Medina 2005).

As detailed above, climate has had an important role in the distribution of armadillos but, since the end of the Pleistocene/

early Holocene, human activity has strongly impacted armadillo populations. Archaeological evidence demonstrates the exploitation of armadillos as a food resource and the beginning of the transformation of native forests and grasslands for agricultural purposes by early humans (which entered South America as part of the GABI). Currently, armadillos suffer intensive hunting pressure for the damage caused to livestock by burrows, to prevent disease transmission, and/or for ornamental use (Chamberlain 1980; Feijó et al. 2015; Soibelzon and León 2017).

There is an urgent need for continuing data collection and revision of fossil (zooarchaeologic and paleontologic), historical, and current records of armadillos, in a way to elucidate how current climate change and anthropogenic disturbances will influence the biogeography of armadillos.

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