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Source: Zoological Science, 32(1) : 77-87

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zs140186

ZOOLOGICAL SCIENCE **32**: 77–87 (2015)

Distribution of *Tolypeutes* Illiger, 1811 (Xenarthra: Cingulata) with Comments on Its Biogeography and Conservation

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This study reviews the data available on the distribution of three-banded armadillos of the genus *Tolypeutes*, identifying potential geographic barriers and evaluating possible biogeographic processes that may account for the present-day distribution of the species and its conservation status. The database was derived from published records, interviews, and voucher specimens, over a timescale ranging from the fossil record to specimens collected in 2013. A total of 236 localities were recorded, with 68 attributed to *Tolypeutes matacus* and 168 to *Tolypeutes tricinctus*. The vegetation within the range of the genus is predominantly a xerophytic mosaic of grassland, savannas, open woodland, and xeric thorn forest. The marine transgressions of the Miocene and the uplifting of the Brazilian Shield may have contributed to the vicariant separation of the ancestral populations of *T. matacus*, to the west and south, and *T. tricinctus*, to the north and east. The three-banded armadillo is possibly one of the most threatened of Brazilian mammals, considering the low number of recent records and the fact that it is hunted intensively throughout its range.

Key words: Dasypodidae, three-banded armadillo, Caatinga, dry forest, hunting pressure

INTRODUCTION

Tolypeutes Illiger, 1811 is one of the few genera of Cingulata that are distributed primarily in the dry forests of South America. Two species are currently recognized (Wetzel, 1985), the Brazilian three-banded armadillo, *Tolypeutes tricinctus* (Linnaeus, 1758) and the southern three-banded armadillo, *Tolypeutes matacus* (Desmarest, 1804). *T. tricinctus* is the only cingulate endemic to Brazil, occurring mainly in the semi-arid scrub forests and savannas of the northeastern and central regions of the country, while *T. matacus* is found in western Brazil, Bolivia, Paraguay, and northern and central Argentina (Wetzel et al., 2007).

Marcgrave (1648) first described aspects of the morphology and behavior of *T. tricinctus*. Despite this early record, this species is one of the least studied armadillos (Santos et al., 1994; Oliveira, 1995; Superina et al., 2014), and the few available publications either refer to occasional encounters (Marini-Filho and Guimarães, 2010), or are distributional notes (Silva and Oren, 1993; Santos et al., 1994; Oliveira, 1995). By contrast, there is a relative wealth of data on the ecology (Bolkovic et al., 1995; Barrientos and Cuellar, 2004), anatomy (Milne et al., 2009) and geographic distribution (Ojeda and Mares, 1989; Mares et al., 1997; Morando and Polop, 1997; Abba and Vizcaino, 2008; Pautasso, 2008) of *T. matacus*.

Based on the available data, Anacleto et al. (2006) modeled the ecological niche of *T. tricinctus*, which they used to define the potential range of this species. More recently, Zimbres et al. (2012) modeled its future distribution in relation to existing protected areas. Until now, however, there has been no systematic mapping of the known localities for *T. tricinctus*, nor any reliable analysis of possible zoogeographic barriers.

Inadequate geographic data can have a negative influence on the development of species conservation and management strategies (Brito, 2004), and more records would permit more accurate ecological niche modeling. *Tolypeutes* populations have declined considerably in recent years, mainly due to hunting pressure (Santos et al., 1994; Barrientos and Cuellar, 2004; Abba and Vizcaino, 2011; Feijó and Langguth, 2013). Despite being classified as Vulnerable (*T. tricinctus*) and Near Threatened (*T. matacus*) by the IUCN (Superina and Abba, 2010; Abba and Superina, 2010), there are few recent data on the distribution of either species or the existence of remnant populations on which to base the definition of priority areas for conservation.

The present study was based on a compilation of the data on the distribution of the two *Tolypeutes* species, with the objective of (i) defining their geographic ranges, (ii) identifying possible geographic or ecological barriers to the dispersal of the species, and (iii) evaluating biogeographic

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doi:10.2108/zs140186

evidence that may account for the present-day distribution of the species.

MATERIALS AND METHODS

A geographical database was compiled for *Tolypeutes* based on published records, museum specimens collected prior to 2013, and interviews with local researchers. In the case of published records, only primary sources were used, which meant that studies such as those of Oliveira et al. (2003), Anacleto et al. (2006), and Zimbres et al. (2012), which were based on the compilation of published data, were not included, although the original sources that these reports cite were.

In the case of *T. matacus*, the distribution of which is relatively well known in comparison with *T. tricinctus*, a number of studies (e.g., Ojeda and Mares, 1989; Morando and Polop, 1997; Pautasso, 2008; Abba and Vizcaino, 2008) are based on the compilation location records. As the primary objective of the present study was to define range limits and possible zoogeographic barriers, marginal records of the occurrence of this species were included in the present analysis.

The records were plotted using the ArcGis 10.2 software (ESRI, 2013) to produce detailed distribution maps based on the geographic coordinates obtained from specimen labels or published records. When exact coordinates of the locality were unavailable, those of the administrative center of the municipality in which the record was obtained were used instead. For the evaluation of the conservation status of *T. tricinctus*, the records for this species were classified in three categories: (i) fossil, (ii) historic (prior to 2000), and (iii) recent.

Tolypeutes specimens were examined in six scientific collections in Brazil and one in Paraguay. In Brazil, the collections are housed at the Zoology Museum of São Paulo University (MZUSP), the National Museum in Rio de Janeiro (MNRJ), the Federal University of Minas Gerais (UFMG) in Belo Horizonte, the Museum of Natural Sciences at the Pontifical Catholic University of Minas Gerais (PUCMG), also in Belo Horizonte, Brasilia University (UNB), and the Federal University of Paraiba in João Pessoa (UFPB). In Paraguay, the National Museum of Natural History (MNHNP) in Asunción was consulted.

These data are complemented by interviews with 26 Brazilian researchers who are currently working in the field within the known distribution of the three-banded armadillos, or who have worked in this area in the recent past. Each researcher was asked if he or she had encountered *Tolypeutes* during fieldwork, and when positive answers were obtained, the identification of the species was confirmed based on photographs or verbal descriptions provided by the interviewees. The geographic coordinates for the locality of the encounter were recorded as for the other records, and included in the database for mapping and analysis.

RESULTS AND DISCUSSION

Geographic distribution

A total of 236 *Tolypeutes* localities were considered for the present study (Fig. 1). The localities are distributed mainly within the dry zone of South America, between latitudes 4° S and 42° S, which encompasses grasslands, savannas, open woodlands, and xeric thorn forest. The two species are distributed allopatrically, with their ranges being separated by a gap of some 1000 kilometers in central Brazil, which coincides with the headwaters of the Paraná River basin to the south, and the Tocantins-Araguaia, to the north.

The geographic distribution of *Tolypeutes matacus* was defined based on 66 marginal localities in western Brazil, southern Bolivia, northern Paraguay, and Argentina (Table 1), primarily in the Chaco dry forests of Bolivia and Paraguay,

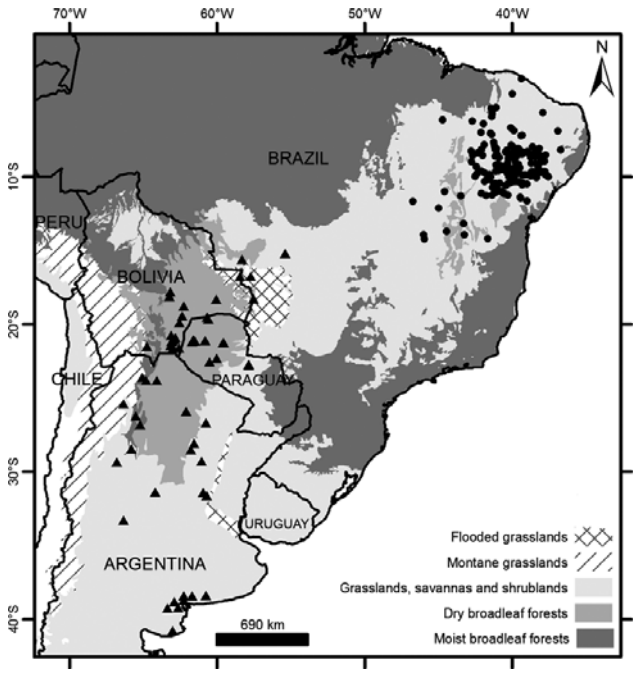

Fig. 1. Localities recorded for *Tolypeutes tricinctus* (circles) and *Tolypeutes matacus* (triangles) in the present study in relation to the principal types of vegetation found in South America.

and the Pampas grasslands of Argentina. The distribution of the species is delimited to the north by the Amazon Forest and to the west by the Andes, while the Paraguay and Araguaia river systems appear to be important barriers to the east (Fig. 2). The original distribution of this species extended as far south as Carmen de Patagones (42° S) at Bahía Blanca, in the Argentine province of Buenos Aires.

The geographic distribution of *T. matacus* presented here includes all historic records. Abba and Vizcaino (2011) concluded that this species is locally extinct from some areas, such as Buenos Aires province, where the most recent record was obtained in 1926. In this case, the current southern limit of the species' range would appear to be between 33° and 34° S, coinciding with the provinces of Mendoza and San Luis, in western Argentina. This local extinction was probably the result of intensive hunting pressure and habitat loss within the region surrounding the Argentinian capital.

A number of well-defined geographic barriers delimit the distribution of *T. matacus* further north. The Paraguay River forms the eastern limit of the species, and is characterized by distinct topography and vegetation types on its two margins (Frutos and Van Den Bussche, 2002). The Chaco biome lies to the west of the Paraguay River, and is characterized by xerophytic vegetation, formed by a mosaic of grassland, savannas, open woodlands, and xeric thorn forest (Willig et al., 2000), while to the east, the vegetation is primarily subtropical humid forest, mixed with plains, grassland, and marshes (Myers, 1982; Willig et al., 2000; Frutos and Van Den Bussche, 2002). While this eastern zone is prone to flooding during the rainy season, the Chaco is semiarid throughout the year. Krumbiegel (1940) confirmed that *T. matacus* occurs only in dry habitats, and is never found in marshy environments, and also that it occurs pre-

Table 1. Marginal localities in which the occurrence of *Tolypeutes matacus* has been confirmed.

COUNTRY/PROVINCE	LOCALITY, MUNICIPALITY	SOURCE/SPECIMEN
ARGENTINA		
Buenos Aires	Bahia Blanca	Garrod (1878)
	Carmen de Patagones	Garrod (1878)
	Mayor Buratovich, Villarino	Abba and Vizcaino (2011)
	Rio Quequén Salado, Tres Arroyos,	Abba and Vizcaino (2011)
	Rio Sauce Grande, 30 km E Napostá, Bahia Blanca	Abba and Vizcaino (2011)
	Napostá, Bahia Blanca	Abba and Vizcaino (2011)
	Villarino	Abba and Vizcaino (2011)
	Adjacent to the Rio Colorado, Villarino	Abba and Vizcaino (2011)
Catamarca	Catamarca	Mares et al. (1997)
Chaco	Avia Terai	Wetzel et al. (2007)
Santiago del Estero	Copo Reserve	Bolkovic et al. (1995)
Cordoba	Cordoba	Morando and Polop (1997)
Jujuy	Arroyo Saladillo, Ledesma	Vizcaíno (1997)
	Finca “La Mauricia” I, Ledesma	Vizcaíno (1997)
	Arroyo Punta de Agua, Santa Bárbara	Vizcaíno (1997)
	El Palmar, Santa Bárbara	Vizcaíno (1997)
	Islas Chicas, Santa Bárbara	Vizcaíno (1997)
	Islas Grandes, Santa Bárbara	Vizcaíno (1997)
	La Quinta, Santa Bárbara	Vizcaíno (1997)
	Lapachal, Santa Bárbara	Vizcaíno (1997)
	Puesto Nuevo, Santa Bárbara	Vizcaíno (1997)
	Real de los Toros, Santa Bárbara	Vizcaíno (1997)
La Rioja	Ávila	Wetzel et al. (2007)
Salta	Molinos	Ojeda and Mares (1989)
	La Estrella	Vizcaíno (1997)
San Luis	San Luis	Sanborn (1930)
Santa Fe	Estancia El Urunday, 9 de Julio	Pautasso (2008)
	Km 442, San Bernardo, 9 de Julio	Pautasso (2008)
	Provincial highway 13 km S of Federal highway 98, 9 de Julio and Vera	Pautasso (2008)
	San Pedro (Ascochingas), La Capital	Pautasso (2008)
	Colegio San José, Monte del Colegio, Las Colonias	Pautasso (2008)
Tucumán	San Miguel de Tucumán	Sanborn (1930)
	San Pedro de Colalao	Mares et al. (1996)
BOLIVIA		
Chuquisaca	4.5 km by road W of Carandayti	Anderson (1997)
	64 km E of Tiquipa	Anderson (1997)
Santa Cruz	29.5 km W of Roboré	Anderson (1997)
	7 km E and 3 km N of Ingeniero Mora	Anderson (1997)
	Candelaria	Brooks et al. (2002)
	Cerro Colorado	Anderson (1997)
	Curuyuqui	Parker et al. (1993)
	Puesto Perforación	Anderson (1997)
	Santa Cruz de la Sierra	Sanborn (1930)
Tarija	Tarija	Sanborn (1930)
	12 km SE of Capirenda	Anderson (1997)
	15 km NE of Capirenda	Anderson (1997)
	Capirenda	Wetzel (1985)
	Estancia Bolívar	Anderson (1997)
	Estancia Caballo Nambia	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
	Palo Marcado	Felten
	Vicinity of Tarija	Grandidier and Neveu-Lemaire (1905, 1908)

Continued.

Table 1. Continued.

COUNTRY/PROVINCE	LOCALITY, MUNICIPALITY	SOURCE/SPECIMEN
BRAZIL		
Mato Grosso	Caicara, Campo do Marco, Mouth of the Rio Jauru	Sanborn (1930)
	Descalvados Ranch, Rio Paraguay	Sanborn (1930)
	Fazenda Acorizal	Wetzel et al. (2007)
Mato Grosso do Sul	Amolar Mountain Ridge	Porfirio et al. (2014)
PARAGUAY		
Boqueron	150 km N Filadelfia on the highway	MNHNP 510
	Depto Boquerón	MNHNP 1655, 1654,
	Estancia San Ramón	MNHNP 1895
	Estancia Toledo	Brooks (1995)
	Teniente Agripino Enciso National Park (TAENP)	MNHNP 3368, 3369
	15 km S administrative center, TAENP	MNHNP 512
	2 km from administrative center, TAENP	MNHNP 511
		MNHNP 514
	PNTAE, 30 km NW casa de control sobra la Transchaco	
		MNHNP 517
Alto Paraguay	Palmar de Las Islas	MNHNP 3367
	Estancia Tres Marias	MNHNP 65293,
		MNHNP 3371
Chaco	Palmar de las Islas/Estancia San José	Brooks (1995)
Presidente Hayes	Puerto Pinasco	Wetzel et al. (2007)
	110 km W Puerto Pinasco	Sanborn (1930)

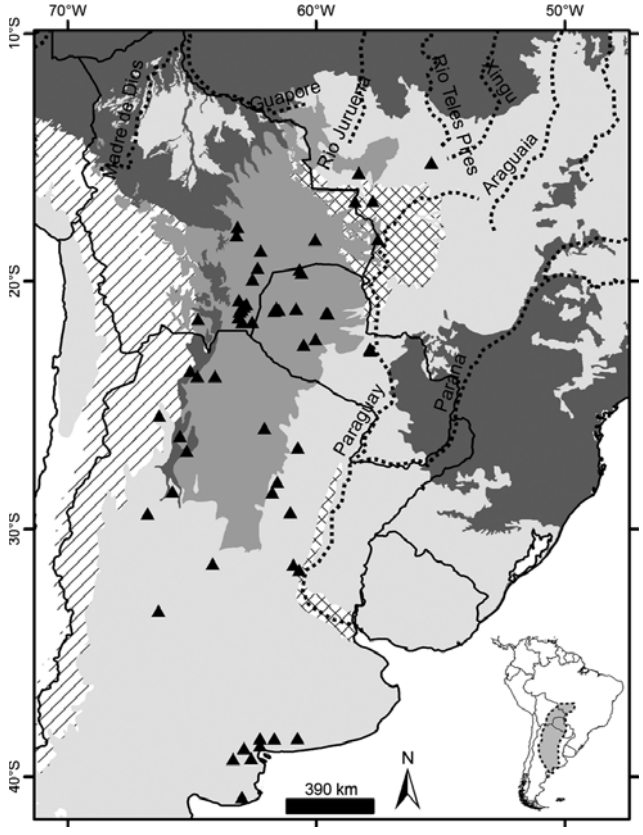

Fig. 2. Details of the distribution of *Tolypeutes matacus* in relation to the principal rivers (dotted lines) and vegetation of South America.

dominantly in lowland areas. In the Andean region, it is confined to savanna-like habitats in the depressions between mountain ranges. This is consistent with the distribution of the species recorded in the present study, between the Andes and areas of humid broadleaf forest.

The northeastern limits of the distribution of *T. matacus* are less well known, (Anacleto et al., 2006). In Brazil, three historic and one recent record for the species exist (Table 1). Wetzel (1985) added a locality known as "Chavantina das Mortes, Mato Grosso" based on a specimen deposited at the Brazilian National Museum (MN S-10), although we examined this specimen, and confirmed that it belongs to the genus *Dasypus*.

Tolypeutes tricinctus is known from 168 localities in the Brazilian Northeast, including four fossil sites (Table 2, Fig. 3). A majority (n = 85) of these sites were concentrated in the state of Bahia, followed by Pernambuco (38), Piaui (25), Ceara (8), Sergipe (6), Maranhão (2), and Alagoas, Paraiba, Rio Grande do Norte, and Tocantins, all with just one record each. The points were mostly associated with the São Francisco River basin. These sites are located predominantly within the domain of the Caatinga scrub, and some adjacent areas of Cerrado savanna, which suggests a preference for open and/or semi-arid habitats.

The records available to date, however, are limited primarily to the upland areas of northeastern Brazil (Fig. 3); that is, the Borborema plateau, to the northeast (Paraíba and Pernambuco), the mountains of central and western Ceará and the Parnaíba Valley to the west. The Serra Geral de Goiás plateau lies to the southwest and the Espinhaço range to the east. The southern limits of the distribution are still ill-defined, but may coincide approximately with northern Minas Gerais.

Only eight (11.1%) of the 72 records that can be dated accurately were classified as recent. Four (6.25%) of the 64 historic records were collected prior to 1950, and a further six between 1950 and 1989. The other 54 records were collected in the 1990s. It is important to note that all the recent

Table 2. Localities in which the occurrence of *Tolypeutes tricinctus* has been mentioned. *Recent records, †Fossil Record.

STATE	LOCALITY	YEAR	SOURCE	SAMPLES
ALAGOAS	Pedra Pintada	Before 1980	Santos (1993)	Interview
BAHIA	18 km S Amaniú	1990–1991	Santos (1993)	Interview
	20 km Pilão Arcado	1990–1991	Santos (1993)	Interview
	25 km W Monte Santo	Before 1980	Santos (1993)	Interview
	30 km W Andorinhas	Before 1980	Santos (1993)	Interview
	48 km Sento sé	1990–1991	Santos (1993)	Interview
	5 km W de Novo Horizonte	Before 1980	Santos (1993)	Interview
	Alagoinhas	1990–1991	Santos (1993)	Interview
	Amaniú	1990–1991	Santos (1993)	Interview
	Andorinhas	Before 1980	Santos (1993)	Interview
	Barra	1914	This study	MZUSP 3134, 3135, 3136 e 3137
	Barra	1908	This study	MZUSP 2654
	Barreiras	–	Coimbra-Filho (1972)	–
	Batatas	Before 1980	Santos (1993)	Interview
	Bom Jesus da Lapa	1942	This study	MNRJ 4257, 4292 e 9294
	Bom Jesus da Lapa	1961	This study	MNRJ 79723
	Brejo da Caatinga	1990–1991	Santos (1993)	Interview
	Brumado	–	Freitas and Silva (2005)	Photo
	Caldeirãozinho da Serra	Before 1980	Santos (1993)	Interview
	Campo Formoso, near Lagoa Rasa	1990–1991	Marinho-Filho et al. (1997)	Interview
	Canabravinha	1990–1991	Santos (1993)	Interview
	Canché, road between Jeremoabo-Canudos	1990–1991	Santos (1993)	Observation
	Canudos	1988	Santos et al. (1994)	Museum
	Capeado, Serra Vermelha	1990–1991	Santos (1993)	Interview
	Caratacá	Before 1980	Santos (1993)	Interview
	Carnaíba do Sertão	Before 1980	Santos (1993)	Interview
	Casa Nova	Before 1980	Santos (1993)	Interview
	Casa Nova, BR-235 road	Before 1980	Santos (1993)	Interview
	Central	1993	This study	MNRJ 51651 e 61417
	Central	1991	This study	MNRJ 29404
	Coribe, Fazenda Formoso	1988	Silva and Oren (1993)	Observation
	Curaça	Before 1980	Santos (1993)	Interview
	Delfino	1990–1991	Santos (1993)	Interview
	Raso da Catarina Ecological Station	1990–1991	Santos (1993)	Observation
	Euclides da Cunha	1990–1991	Santos (1993)	Interview
	Glória*	2012	This study	Interview
	Gruta dos Brejões	1990–1991	Santos (1993)	Interview
	Igara	Before 1980	Santos (1993)	Interview
	Jaborandi, Jatobá Farm*	2009	Bocchiglieri et al. (2012)	Observation
	Jaborandi, Rio Pratudão Farm	–	Marinho-Filho et al. (1997)	Observation
	Jacobina	1990–1991	Santos (1993)	Observation
	Jeremoabo	Before 1980	Santos (1993)	Interview
	Juazeiro	Before 1980	Santos (1993)	Interview
	Juazeiro	1908	This study	MZUSP 2655, 2656 e 2657
	Juremal	Before 1980	Santos (1993)	Interview
	Lages	1990–1991	Santos (1993)	Interview
	Lagoa	1990–1991	Santos (1993)	Interview
	Monte Santo	Before 1980	Santos (1993)	Interview
	Morro do Chapéu, Chapada Diamantina, Lages*	2004	This study	MNRJ 67911
	Moura	1990–1991	Santos (1993)	Interview
	Mulungú	1990–1991	Santos (1993)	Interview
	Mundo Novo	Before 1980	Santos (1993)	Interview
	Novo Horizonte	Before 1980	Santos (1993)	Interview
	Ouricuri	Before 1980	Santos (1993)	Interview
	Ourolandia	1990–1991	Santos (1993)	Interview
	Palmas de Monte Alto, Fazenda Boa Vista	1991	Silva and Oren (1993)	MPEG 22260
	Paraiso	Before 1980	Santos (1993)	Interview
	Passagem Funda Farm, Raso do Bom Jardim	1990–1991	Santos (1993)	Observation
	Patamuté	Before 1980	Santos (1993)	Interview

Continued.

Table 2. Continued.

STATE	LOCALITY	YEAR	SOURCE	SAMPLES
	Paulo Afonso	Before 1980	Santos (1993)	Interview
	Pedra Vermelha	1990–1991	Santos (1993)	Interview
	Piçarrão	1990–1991	Santos (1993)	Interview
	Pilão Arcado	1990–1991	Santos (1993)	Observation
	Pinhão	Before 1980	Santos (1993)	Interview
	Poço de Fora	1990–1991	Santos (1993)	Interview
	Poeiras, 18 km W Andorinhas	Before 1980	Santos (1993)	Interview
	Quarenta, 13 km W Santa Brígida	Before 1980	Santos (1993)	Interview
	Raso da Catarina	1984	This study	UFPB 752
	Remanso	Before 1980	Santos (1993)	Interview
	Retirolândia	Before 1980	Santos (1993)	Interview
	Riacho	1990–1991	Santos (1993)	Interview
	Riacho do Sobrado	Before 1980	Santos (1993)	Interview
	Salitre, 30 km W Juazeiro	Before 1980	Santos (1993)	Interview
	Santa Brigida	Before 1980	Santos (1993)	Interview
	Santa Brígida, road Paulo Afonso-Jeremoabo	Before 1980	Santos (1993)	Interview
	Santa Rita de Cássia	1958	This study	MZUSP 8576
	Senhor do Bonfim	Before 1980	Santos (1993)	Interview
	Sento Sé	1990–1991	Santos (1993)	Interview
	Sento Sé*	2012	This study	UFPB 6871
	Serra Branca Farm, Jeremoabo-Canudos road	1990–1991	Santos (1993)	Observation
	Serra da Babilonia	1990–1991	Santos (1993)	Interview
	Serra da Borracha	1990–1991	Santos (1993)	Interview
	Serra da Canabrava	Before 1980	Santos (1993)	Interview
	Serra das Trairas	1990–1991	Santos (1993)	Interview
	Serrinha	Before 1980	Santos (1993)	Interview
	Sobradinho	1990–1991	Santos (1993)	Interview
	Tiquara	1990–1991	Santos (1993)	Interview
	Toca dos Ossos, Ourolândia†	–	Auler et al. (2006)	Fossil
	Umburanas	1990–1991	Santos (1993)	Interview
	Valente	Before 1980	Santos (1993)	Interview
	Vila do Pilar	Before 1980	Santos (1993)	Interview
	Povoado Barrinha, road Juazeiro-Jaguariba	Before 1980	Santos (1993)	Interview
CEARÁ	Alto Jaguaribe	1958	Coimbra-Filho (1972)	Observation
	Assaré	Before 1980	Santos (1993)	Interview
	Crato	–	Moojen (1943)	–
	Juazeiro do Norte	Before 1980	Santos (1993)	Interview
	Santa Quitéria	–	This study	Interview
	São Nicolau, near Aiuaba	Before 1980	Santos (1993)	Interview
	Natural tank at Jirau, Itapipoca†	–	Araújo-Júnior et al. (2013)	Fossil
	Serra dos Cariris Velhos	–	This study	MNRJ 1503
MARANHÃO	Mirador State Park	–	Oliveira (1995)	Interview
	São Miguel	–	Oliveira et al. (2007)	Observation
PARAIBA	Santa Luzia	–	This study	Interview
PERNAMBUCO	12 km N Cachoeira do Roberto	Before 1980	Santos (1993)	Interview
	12 km Rajada, BR-407 road	Before 1980	Santos (1993)	Interview
	18 km Santa Maria da Boa Vista, BR-428 road	1990–1991	Santos (1993)	Interview
	20 km Petrolandia	Before 1980	Santos (1993)	Interview
	9 km Jacaré, road between Parnamirim-Veneza	Before 1980	Santos (1993)	Interview
	Afrânio	Before 1980	Santos (1993)	Interview
	Airi	1990–1991	Santos (1993)	Interview
	Barro do Silva	Before 1980	Santos (1993)	Interview
	Bom Nome, BR-232 road	Before 1980	Santos (1993)	Interview
	BR-426 road, 15 km Cabrobó	1990–1991	Santos (1993)	Interview
	Caatinga do Inferno, 9 km Terra Nova	Before 1980	Santos (1993)	Interview
	Cabrobó	1990–1991	Santos (1993)	Interview
	Cachoeira do Roberto	Before 1980	Santos (1993)	Interview
	Carqueja	1990–1991	Santos (1993)	Interview
	Conceição das Crioulas	Before 1980	Santos (1993)	Interview
	Cruz de Malta	Before 1980	Santos (1993)	Interview
	Serra Negra Biological Station	Before 1980	Santos (1993)	Interview
	Floresta	1990–1991	Santos (1993)	Interview

Continued.

Table 2. Continued.

STATE	LOCALITY	YEAR	SOURCE	SAMPLES
	Ibimirim	Before 1980	Santos (1993)	Interview
	Inajá	Before 1980	Santos (1993)	Interview
	Itacurubá, BR-316 road	Before 1980	Santos (1993)	Interview
	Jacaré	Before 1980	Santos (1993)	Interview
	Jutaí	1990–1991	Santos (1993)	Interview
	Lagoa Grande, Sítio do Meio	1990	Valle (2007)	Photo
	Ouricuri	Before 1980	Santos (1993)	Interview
	Parnamirim	Before 1980	Santos (1993)	Interview
	Petrolândia	1990–1991	Santos (1993)	Interview
	Petrolina	Before 1980	Santos (1993)	Interview
	Poção	–	Moojen (1943)	–
	Quixaba	Before 1980	Santos (1993)	Interview
	Raso do Porco	1990–1991	Santos (1993)	Interview
	Riacho do Navio, near Varjota	1990–1991	Santos (1993)	Observation
	Santa Maria da Boa Vista	1990–1991	Santos (1993)	Observation
	Santa Ria Farm, 12 km Cruz de Malta	Before 1980	Santos (1993)	Interview
	Tacaratú	Before 1980	Santos (1993)	Interview
	Tanque Farm, 14 km Lagoa Grande, BR-428 road	Before 1980	Santos (1993)	Interview
	Terra Nova, road between Cabrobó-Parnamrim	Before 1980	Santos (1993)	Interview
	Urinamã	Before 1980	Santos (1993)	Interview
PIAUI	26 km N São João do Piauí	Before 1980	Santos (1993)	Observation
	28 km SW São João do Piauí	1990–1991	Santos (1993)	Observation
	36 km Simplício Mendes	1990–1991	Santos (1993)	Interview
	43 km Jaicos	Before 1980	Santos (1993)	Interview
	Acauã	Before 1980	Santos (1993)	Interview
	Brejo do Piauí*	2010	This study	MNRJ 63501
	Brejo Grande	Before 1980	Santos (1993)	Interview
	Buritis dos Montes, Serra da Ibiapaba	Before 1980	Santos (1993)	Interview
	Cacimbinhas, 15 km SE Picos	Before 1980	Santos (1993)	Interview
	Canto Verde, National Park Serra das Confusões*	2002	This study	MZUSP 35269
	Coqueiros	Before 1980	Santos (1993)	Interview
	Dirceu Arcoverde	Before 1980	Santos (1993)	Interview
	Jacobina, BR-404 road	Before 1980	Santos (1993)	Interview
	Jenipapeiro	Before 1980	Santos (1993)	Interview
	Novo Oriente	1990–1991	Santos (1993)	Interview
	Oeiras	Before 1980	Santos (1993)	Interview
	Paulistana	Before 1980	Santos (1993)	Interview
	Picos	Before 1980	Santos (1993)	Interview
	Regeneração	1990–1991	Santos (1993)	Interview
	road between Castelo do Piauí-São Miguel do Tapaio	Before 1980	Santos (1993)	Interview
	São João do Piauí	Before 1980	Santos (1993)	Interview
	São Miguel do Tapuio	Before 1980	Santos (1993)	Interview
	São Raimundo Nonato	Before 1980	Santos (1993)	Interview
	São Raimundo Nonato, Serra da Capivara National Park*	2012	This study	MNRJ 63480 and Interview
	Simplicio Mendes	Before 1980	Santos (1993)	Interview
	Várzea Grande	1990–1991	Santos (1993)	Interview
RIO GRANDE DO NORTE	Lajedo Soledade, Apodi†	–	Porpino et al., 2004	Fossil
SERGIPE	6 km S Monte Alegre	Before 1980	Santos (1993)	Interview
	Campim Grosso	Before 1980	Santos (1993)	Interview
	Canindé de São Francisco	Before 1980	Santos (1993)	Interview
	Curituba	Before 1980	Santos (1993)	Interview
	São José Farm, Poço Redondo†	–	França et al. (2011)	Fossil
	Lagoa Redonda	Before 1980	Santos (1993)	Interview
TOCANTINS	Dianópolis*	2010	This study	Photo

records were collected in a relatively small portion of the species' range, in the central and southwestern extreme (Fig. 3).

The geographic distribution of *T. tricinctus* is even less well defined than that of *T. matacus*. The distribution map is characterized by the concentration of a large number of localities in the center of the species' distribution, but extensive lacunas in peripheral areas, impeding a more conclusive interpretation of possible barriers to dispersal. Despite these shortcomings, it is possible to infer the existence of

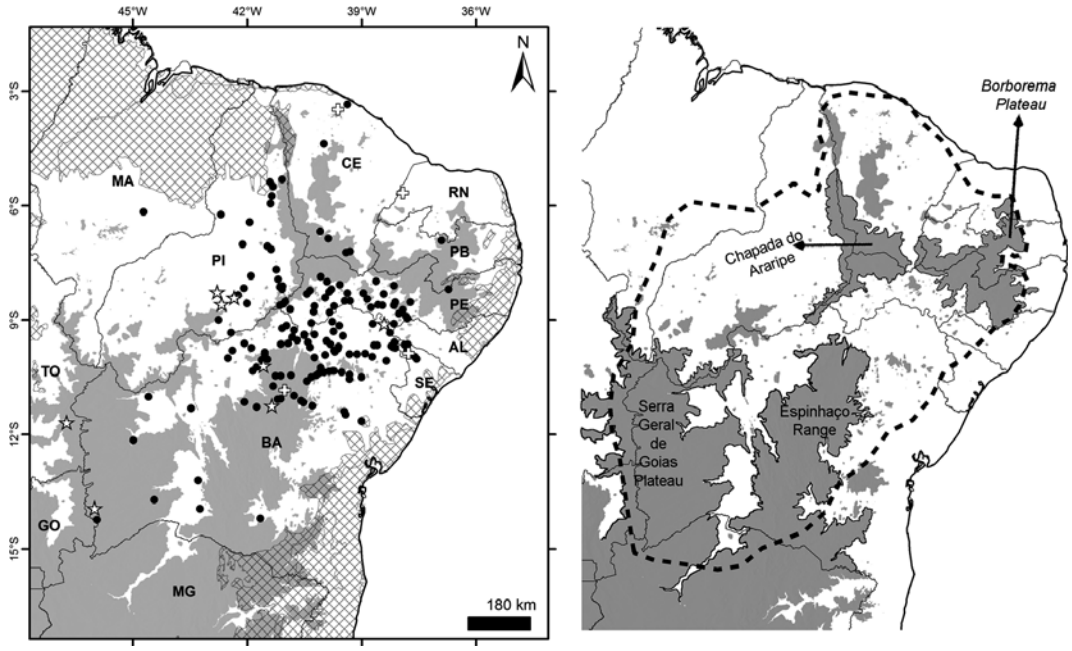

Fig. 3. Details of the distribution of *Tolypeutes tricinctus* in northeastern Brazil. Left Localities in relation to moist broadleaf forests (grid) and upland areas (gray). Crosses mark fossil finds, circles represent historic records (pre-2000), and stars show recent records (since 2000). Right: Potential distribution of *T. tricinctus* with upland areas of northeastern Brazil. Brazilian states: AL = Alagoas; BA = Bahia; CE = Ceará; MA = Maranhão; MG = Minas Gerais; PB = Paraíba; PE = Pernambuco; PI = Piauí; RN = Rio Grande do Norte; SE = Sergipe; TO = Tocantins.

probable barriers to dispersal. The available records indicate that *T. tricinctus* is distributed on both plains and upland areas, in contrast with the pattern found in *T. matacus*. The areas to the southwest and northeast of the range of *T. tricinctus* correspond to two major upland areas, Serra Geral de Goiás and the Borborema highlands, respectively (Fig. 3). To the east, the range is limited by the Atlantic Forest biome, and to the west, by the Amazon forest, although the southern limit remains unclear, and the apparent absence of the species south of the southern limit of the Caatinga in northern Minas Gerais may be the result of sampling deficiencies.

While Marcgrave (1648) referred to this armadillo as a common animal, geographic lacunae have long been known, and even when specimens are available, their localities may not be known (Sanborn, 1930). While 168 localities were identified in the present study, the vast majority (138) were obtained from an unpublished masters dissertation (Santos, 1993), although the occurrence of *T. tricinctus* was confirmed directly at only eight of these localities (see Table 2), while all the other points were identified only from interviews. Excluding these indirect records and the fossils, only 27 (16%) localities have been recorded reliably over the past 104 years (Table 2).

The Brazilian Caatinga has traditionally been considered to be a biome of low mammalian diversity and endemism (Mares et al., 1981; Willig and Mares, 1989), attracting little interest from researchers (Brito et al., 2009). Over the past decade, however, the number of mammal species known to occur in the Caatinga has almost doubled (Carmignotto et al., 2012), stimulating new interest, although most of this research has focused on either the mesic cloud forest enclaves (*brejos de altitude*) or transition zones with neighboring biomes (Oliveira et al., 2003; Carmignotto et al., 2012; Feijó and Langguth, 2013). Areas of typical Caatinga, the thorn scrub of the arid central portions of this biome, where *T. tricinctus* occurs, have still been poorly surveyed. These sampling problems may be exacerbated by the ongoing extinction of local populations.

Conservation of *Tolypeutes tricinctus*

The armadillos of the genus *Tolypeutes* are unique among the cingulates in having hard, articulated armor and the ability to roll up completely into a ball, protecting the ventral portion of the body. This makes the digging of burrow – the strategy used by other armadillos to escape their predators – unnecessary (Marcgrave, 1648; Sanborn, 1930; Smith, 2007; Deem et al., 2009), but also renders the three-banded armadillo extremely vulnerable to human hunters throughout its range (Silva and Oren, 1993; Santos et al., 1994; Marinho-Filho et al., 1997; Noss et al., 2003; Feijó and Langguth, 2013).

These animals have been hunted intensively as a source of food since the early colonization of South America in the seventeenth century (Marcgrave, 1648; Azara, 1801; Santos et al., 1994; Bolkovic et al., 1995; Noss et al., 2003; Smith, 2007; Papavero et al., 2009). The fat of *T. tricinctus* is also used by many populations as a remedy for asthma, diarrhea, headaches, inflammations, and earache (Alves and Rosa, 2007), which also contributes to the exploitation of the species. In addition to this hunting pressure, the habitats occupied by these armadillos, especially *T. tricinctus*, have suffered extensive anthropogenic impacts, which may be especially intense in the semi-arid Caatinga, due to the intrinsic characteristics of this biome (Leal et al., 2005).

The lack of recent records from many areas—including most of the northern and eastern extremes of the range—suggests that the species may now be locally extinct from a large proportion of its original geographic distribution. From a conservation perspective, there is clearly an urgent need for more detailed data on the current distribution of the species, and in particular, the occurrence of remnant populations appropriate for conservation management.

The ecology of *T. tricinctus* is also poorly known, which further compounds the problems for the conservation of the species. While the ecology of *T. matacus* may be better

understood, there appear to be important differences between species which limit the potential for extrapolation. As well as being more widespread than *T. tricinctus*, for example, *T. matacus* appears to be relatively abundant in some areas (Bolkovic et al., 1995; Noss et al., 2003; Barrientos and Cuellar, 2004). However, the species has also suffered local extinction, such as that observed in the province of Buenos Aires (Abba and Vizcaino, 2011).

Bolkovic et al. (1995) recorded an insectivorous-generalist diet for *T. matacus*, which appears to feed primarily on beetle larvae, but consumes a larger proportion of ants and termites during the dry season, and of fruit during the rainy season. By contrast, *T. tricinctus* appears to be a more specialized insectivore, feeding preferentially on termites and ants (Guimarães, 1997). These ecological differences are reflected in the interspecific variation in cranial and dental morphology. The cranium of *T. tricinctus* is comparatively lightly built, and the teeth are much less robust than those of *T. matacus*. These features may represent adaptations for a more specialist diet in *T. tricinctus*, which could further reinforce its vulnerability to anthropogenic impacts, in particular in comparison with *T. matacus*.

The review of the evidence presented in this study indicates that the current situation of the species may be very critical. In fact, it seems likely that *T. tricinctus* is one of the most endangered mammal species in Brazil, given that its occurrence was only confirmed at eight sites, and it continues to suffer intense hunting pressure and habitat loss. The species is known to occur in six protected areas: the Serra da Capivara and Serra das Confusões national parks in Piaui, the Chapada Diamantina National Park and the Raso da Catarina Ecological Station in Bahia, the Serra Negra Biological Station in Pernambuco, and Mirador State Park in Maranhao, which together cover a total area of almost 17,000 km², although this represents only 2% of the Caatinga biome. Based on niche modeling, Zimbres et al. (2012) concluded that the species was not adequately protected, given that less than 10% of its original range encompasses some kind of protected area, and highlighted the urgent need for the creation of new conservation units in the Caatinga, especially within the species' range. The administration and management of existing protected areas must also be reinforced (but see Torres et al., 2009).

Biogeography

The paleoenvironments of the Tertiary played an important role in the evolutionary history of the South American xenarthrans (Delsuc et al., 2004, 2012). During this period, the most important events in South America were the marine transgressions into much of the Chaco and the Paraná River basin (Hérnandes et al., 2005), and the epirogenic uplifting of the central Brazilian shield, which resulted in a landscape of extensive plateaus separated by major depressions (Coli, 2005) and the deepening of some river basins (Werneck, 2011).

No reliable estimates of the divergence time of the two *Tolypeutes* species are available, although Delsuc et al. (2012) recently published a molecular phylogeny which indicated that the subfamily Tolypeutinae [(*Cabassous* + *Tolypeutes*) *Priodontes*] arose sometime after the Eocene-Oligocene transition, and that *Tolypeutes* diverged from *Cabassous* at the beginning of the Miocene, which means that the two *Tolypeutes* would have separated at some time from the Miocene onwards.

The allopatric distribution of the two *Tolypeutes* species suggests an evolutionary history similar to that proposed by Delsuc et al. (2012) for *Calyptophractus-Chlamyphorus*, in which the marine transgressions of the Miocene are suggested to have acted as a vicariant mechanism separating the ancestral population of *T. matacus*, to the west, from that of *T. tricinctus*, to the east, which would have subsequently evolved in isolation. These transgressions may have played a profound role in the diversification of many widely-distributed taxa within the dry zone of South America (Pascoal and Jaureguizar, 1990; Coli, 2005) and is related to the emergence of new life styles, such as fossoriality (Galewsky et al., 2005; Delsuc et al., 2012). The uplifting of the Brazilian Shield at the end of the Tertiary may also have contributed to this process. Coli (2005) concluded that this was the decisive factor in the diversification of the herpetofauna of the dry zone of South America, by creating distinct environments within a limited geographic space.

The combination of these processes had a profound effect on the hydrographic basins of this region, in particular those of the Paraná and Tocantins-Araguaia rivers, contributing to the differentiation of environments in central Brazil, including those considered to be Cerrado refuges (Coli, 2005; Werneck, 2011). These same river basins could have been crucial to the isolation of the ancestral populations of the present-day *Tolypeutes* species. However, a more conclusive analysis of this process would require a systematic phylogeographic study supported by molecular markers for the estimation of divergence times.

CONCLUSION

The geographic distribution of *T. matacus* is better known than of *T. tricinctus*. While *T. matacus* has suffered local extinction at some sites, a number of populations are known to persist, primarily in the Chaco of Paraguay and Bolivia. However, the northeastern portion of the distribution of the species is poorly sampled, and requires verification, especially in the lowland areas of open habitat, such as those found in the Brazilian state of Mato Grosso. The records of *T. tricinctus* are concentrated in the central portion of its known range, with few data from marginal areas, which impede the reliable definition of barriers to dispersal, reinforcing the need for new surveys in keys states, such as Piauí, Maranhão, Tocantins, and southern Bahia. It will also be important to revisit the sites of historic records for the collection of confirmatory data. Given the available evidence, the establishment of new protected areas for the Brazilian three-banded armadillo may be essential for the survival of this species, which may be one of the most endangered mammals found in Brazil.

ACKNOWLEDGMENTS

We are grateful to the curators of the scientific collections visited during the present study – Mario de Vivo (MZUSP), João Alves de Oliveira (MN), Fernando A. Perini (UFMG), Claudia Guimarães Costa (PUCMG), Jader Marinho-Filho (UNB), Pedro Cordeiro Estrela (UFPB), and Isabel Gamarra de Fox (MNHCP), as well as the interviewees for providing valuable complementary information,

Marília Marques Guimarães Marini for help with references, and two anonymous reviewers for their helpful comments on previous drafts of this paper. We would also like to thank CAPES (AF, BATPC, GSTG, PAR) for graduate stipends and CNPq for research fellowships to SFF and AL.

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(Received August 4, 2014 / Accepted October 11, 2014)