



Nota

ARMORED INVADERS IN PATAGONIA: RECENT SOUTHWARD DISPERSION OF ARMADILLOS (CINGULATA, DASYPODIDAE)

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ABSTRACT. Patagonia, south of 40° S, is currently inhabited by *Chaetophractus villosus* and *Zaedyus pichiy*. In order to reconstruct the Late Pleistocene-Holocene history of these armadillos in southern South America, we compiled and discussed data from zooarcheological sites, notes from naturalists and travellers, museum specimens, and field data. We found that both species experienced significant range expansion southwards. Based on the obtained evidence we concluded that: (a) Southern Patagonia was mainly free of armadillos during the Late Pleistocene-Early Holocene; (b) in the last 10 ky *Z. pichiy* progressively invaded southern Patagonia from the north, down to the Santa Cruz River (~50° S); at the same time, *C. villosus* colonized the northern portion of Patagonia north of Chubut River (~44° S); (c) during the last century, *Z. pichiy* surpassed the Santa Cruz River barrier while *C. villosus* colonized all Patagonian territories to reach the Magellan Strait and finally was introduced in Tierra del Fuego. Although these armadillos have metabolic, dietary and behavioral adaptations to cold and dry habitats that possibly helped them to extend its range southwards, we propose that the observed distributional changes of the last century were triggered mainly by anthropogenic causes.

RESUMEN. Invasores acorazados en Patagonia: dispersión austral reciente de armadillos (Cingulata, Dasypodidae). Patagonia, al sur de los 40° S, está actualmente habitada por *Chaetophractus villosus* y *Zaedyus pichiy*. Con el objeto de reconstruir la historia de estos armadillos en la porción austral de América del Sur durante el Pleistoceno tardío-Holoceno, compilamos y discutimos datos de registros zooarqueológicos, observaciones de naturalistas y viajeros, especímenes de museos y datos de campo. Encontramos que ambas especies experimentaron una considerable expansión de su distribución hacia el sur. De acuerdo a la evidencia obtenida concluimos que: (a) Patagonia austral estuvo básicamente libre de armadillos durante el Pleistoceno tardío-Holoceno temprano; (b) durante los últimos 10 ka, *Z. pichiy* invadió progresivamente el sur de la Patagonia desde el norte alcanzando el río Santa Cruz (~50° S); al mismo tiempo *C. villosus* colonizó la porción norte de Patagonia llegando al norte del río Chubut (~44° S); (c) durante el siglo pasado *Z. pichiy* superó la barrera impuesta por el río Santa Cruz mientras que *C. villosus* colonizó todo el territorio patagónico hasta alcanzar el estrecho de Magallanes y finalmente fue introducido en Tierra del Fuego. Aunque estas especies de armadillos tienen adaptaciones metabólicas, de dieta y de comportamiento a los ambientes fríos y secos que posiblemente

les ayudaron a extender su área de distribución hacia el sur, proponemos que los cambios distribucionales de la última centuria fueron gatillados principalmente por causas antrópicas.

Key words: *Chaetophractus*. Holocene. Human impact. Pleistocene. *Zaedyus*.

Palabras clave: *Chaetophractus*. Holoceno. Impacto del hombre. Pleistoceno. *Zaedyus*.

Armadillos (Cingulata, Dasypodidae) are typical components of Neotropical faunas at least since the upper Paleocene (Bergqvist et al., 2004). Clearly associated with warm or temperate climates (e.g., McNab, 1980, 1985), their living diversity encompasses 9 genera and 21 species that decrease in number from lower to high latitudes (Wetzel et al., 2008). Patagonia (defined here as the portion of the subcontinent south of Colorado river) is currently inhabited by 2 species of the subfamily Euphractinae: *Zaedyus pichiy* (Desmarest, 1804), that reaches the northern border of the Magellan Strait, and *Chaetophractus villosus* (Desmarest, 1804), that is also found further south on Tierra del Fuego island (Poljak et al., 2007; Abba et al., 2012; Superina and Abba, 2014).

Since the middle of 19th century, naturalists and travelers have noted that most of the Patagonian territory was inhabited only by *Z. pichiy* while *C. villosus* was restricted to the northern part of this region (Burmeister, 1893; Darwin, 1833; De la Vaux, 2008; Hatcher, 1903). Dennler (1942) and Crespo (1974) were 2 of the few authors that highlighted the widespread absence of *C. villosus* in central and southern Patagonia (see also Cabrera, 1957), although they noted an incipient invasion process throughout the 20th century, an issue also briefly addressed by Atalah (1975) to explain novel records of both armadillos on the Chilean Magellan mainland.

With the aim to contribute to the knowledge of the Late Pleistocene-Holocene history of the armadillos in southern South America we compiled evidence from different sources that clearly documents a very recent invasion (i.e., during the last century) of these animals in Patagonia. Beyond tracking and contextualizing the recorded information, we further advance on the potential factors

that bear on this dispersive process towards high latitudes.

The evidence discussed in this note was retrieved from 3 main sources: (1) Faunal data from archeological sites (Late Pleistocene-Holocene): we compiled published data including recorded taxa, radiocarbon dates and stratigraphical contexts; when it was possible, remains of armadillos were directly inspected by the authors to check their taxonomic identity; (2) notes from naturalists and travelers: we reviewed published diaries and field notes from the entire Patagonian territory during the 19th century retrieving data on recorded armadillos; (3) museum specimens, literature and field data of contemporary records (mainly 20th century): we compiled recorded localities of armadillos housed in the mammal collections of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Buenos Aires) and Museo de Ciencias Naturales de La Plata (MLP; La Plata). In addition we obtained localities of occurrence from 165 contributions including scientific papers, institutional reports, newsletters, etc. Geographical coordinates assigned to each record using a GPS or national and international gazetteers (e.g., National Geographic Institutes of Argentina, NIMA-GeoNET Names Server) were compiled in **Supplementary Material 1** and **2**.

Archaeological records show consistently that during Late Pleistocene-Holocene, southward distribution of *C. villosus* did not extend beyond the latitude of the Chubut River (~44° S), co-occurring with *Z. pichiy*. The latter inhabited almost all of the Patagonian territory, except the southernmost portion, south of Santa Cruz river (~50° S, see **Figs. 1A** and **2A, Supplementary Material 1**). In fact, there are no records of armadillos in key paleonto-

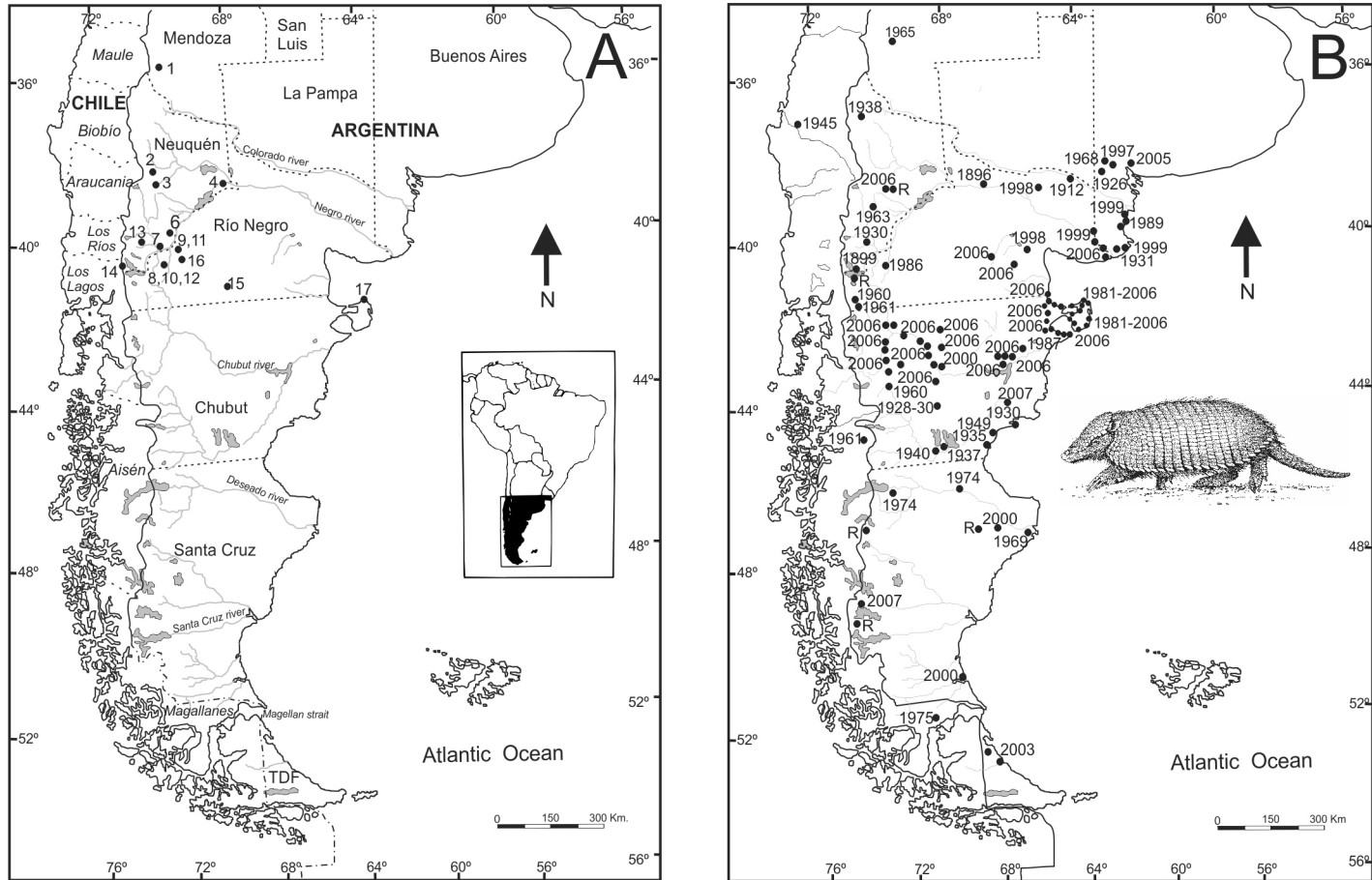


Fig. 1. *Chaetophractus villosus*: archaeological (A) and contemporary (B) records in Patagonia; TDF: Tierra del Fuego province. See Supplementary Material 1 and 2 for data and reference numbers. The schematic figure that illustrates the external aspect of this armadillo was modified from Díaz and Barquez (2002).

logical and archeological sites located between the Santa Cruz River and the northern coast of the Magellan Strait. This is a significant absence considering that these mammals were a common source of proteins for humans when available and, therefore, their remains are frequent in faunal assemblages of archaeological sites (e.g., Mansur et al., 2004; Rindel, 2004; Barberena et al., 2007; Franco et al., 2007).

Data retrieved from notes made by naturalists and travelers, museum specimens, and literature accounted for ca. 120 recording localities of armadillos through Patagonia (Figs. 1B and 2B, see **Supplementary Material 2**). The obtained evidence suggest that until the decade of 1900, *C. villosus* was solely recorded north of Chubut River. By 1930, it was recorded in Chubut province at $\sim 44^\circ$ S; reaching $\sim 45^\circ$ S at the decade of 1940; during the decade of 1970 the species crossed the Deseado River ($\sim 47^\circ$ S) and in 1975 was recorded in southern Chile ($\sim 52^\circ 30'$ S; Atalah, 1975). This species was introduced in Tierra del Fuego in 1982 for aesthetical and feeding purposes (see Poljak et al., 2007).

In historical times *Z. pichiy* was cited as living at around 50° S near Lago Viedma, Santa Cruz province (Burmeister, 1893). However, at the beginning of 20th century Hatcher (1903:116) clearly stated that “In such places they are [*Z. pichiy*] fairly abundant north of the Santa Cruz River, but we never observed a specimen south of that stream, nor after careful enquiries could I discover that they had ever been seen by others in the region lying south of this river.” Around 1970 the species was detected in Magallanes, Chile, $\sim 53^\circ$ S (Texera, 1973).

All compiled sources suggest that the colonization of armadillos in southern Patagonia took place in the last century. *Z. pichiy*, a species with several adaptations to cold and dry habitats (Superina and Abba, 2014 and the references therein) that was already widely distributed in northern and central Patagonia during the Holocene, may have surpassed to the south of the Santa Cruz River ($\sim 50^\circ$ S) during the 20th century, occupying a territory of ca. 40 000 km² previously free of armadillos (Fig. 2B). The case of *C. villosus* is astonishing; in the last century this armadillo expanded its

distribution across an area of ca. 300 000 km² south to the Chubut River ($\sim 44^\circ$ S; Fig. 1B).

Molecular evidence shows that *C. villosus* has not genetic population structure in Patagonia, suggesting that the species dispersed to the south from the Pampean Region in a single wave (Poljak et al., 2010). To the contrary, preliminary data on *Zaedyus* from Patagonia—based on sequences of the cytochrome b—reveals a large degree of variation that can be associated to a more ancient history in the region (M. Gabrielli, unpubl. data). The absence of *C. villosus* from most of the Patagonian region and, more in general, the absence of armadillos south of Santa Cruz River, can be linked with the glacial history of the region during the Plio-Pleistocene (Rabassa, 2008; Rabassa et al., 2011). The hypothesis that armadillos were extirpated from part of Patagonia due the hostile climatic conditions associated to glacial advances and that subsequently failed in recolonizing a territory mainly crossed by west-east rivers, deserves a closed inspection.

As a working hypothesis, we suggest that recent range expansion of *C. villosus* and *Z. pichiy* was favored by anthropogenic causes. During the last 2 centuries human activities in Patagonia deeply modified regional environmental conditions by increasing the productivity of soils due to livestock and agriculture and by building structures such as roads, bridges and oil pipelines. Livestock and agriculture provided large amounts of organic matter, favoring the development of soil macro invertebrates, key elements in the diet of these armadillos (Redford, 1985; Abba, 2008; Cuéllar, 2008; Superina et al., 2009). Dead cattle are a direct and important source of protein for *C. villosus*, and an indirect source for both armadillos species due to the development of arthropod fauna associated with carcasses. In addition, roads, bridges and oil pipelines facilitate wildlife dispersion, making it possible to overcome barriers like rivers (insuperable for Euphractinae armadillos), changing soil physical conditions such as temperature (Poljak et al., 2007) and increasing the soil invertebrate biomass. In the last 80 years, ca. 31 959 km of roads were built in southern Argentina with a notorious development since 1960 (see <http://www.e-asfalto.com/>

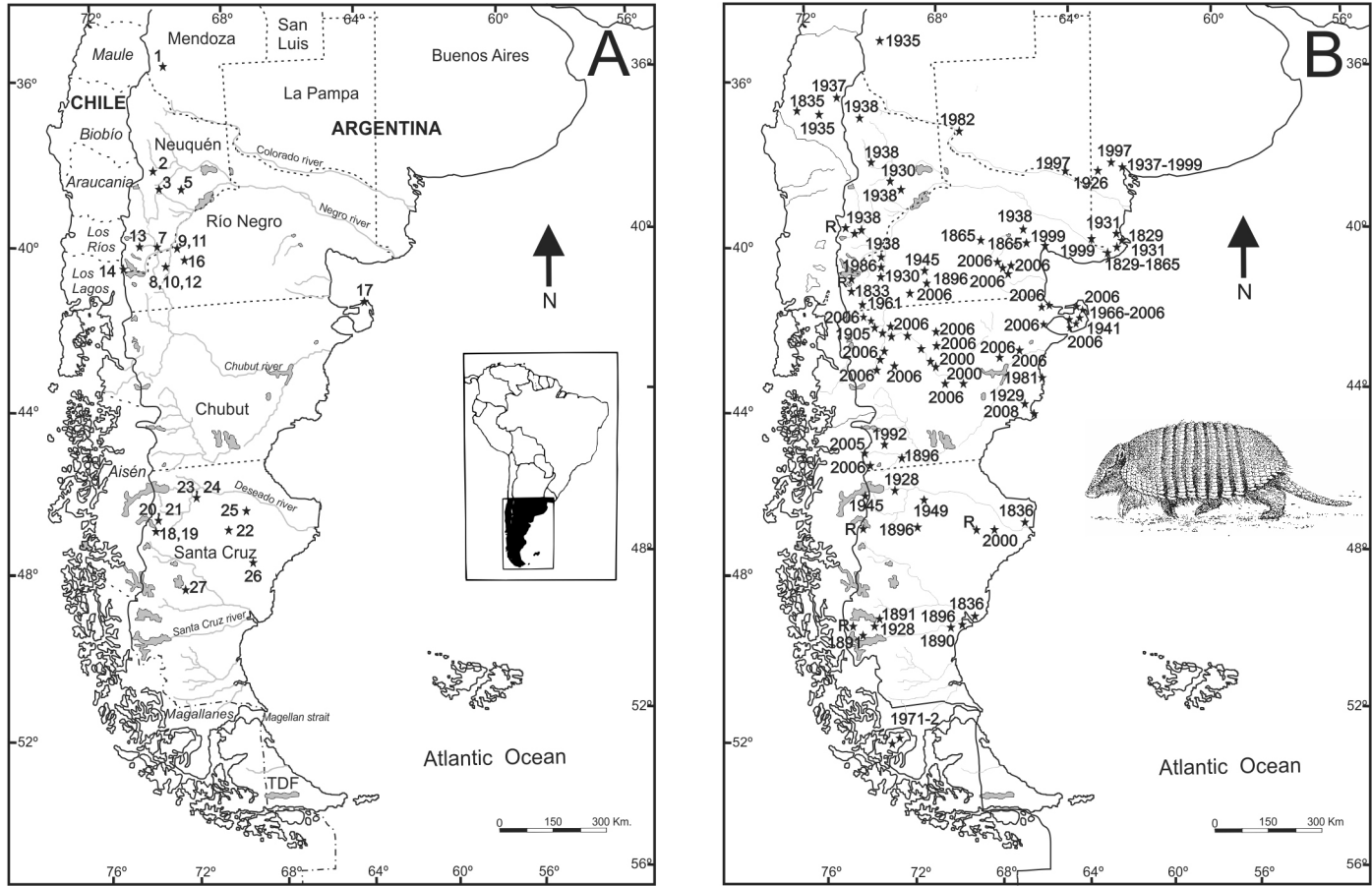


Fig. 2. *Zaedyus pichiy*: archaeological (A) and contemporary (B) records in Patagonia; TDF: Tierra del Fuego province. See Supplementary Material 1 and 2 for data and reference numbers. The schematic figure that illustrates the external aspect of this armadillo was modified from Parera and Erize (2002).

redvialarg/redvial.htm). This expansion probably allowed armadillos to overcome natural barriers and presented many opportunities for translocations (see Poljak et al., 2007). Within this context, we suggest that armadillos were capable to establish their populations into areas with adverse climatic conditions as those of southern Patagonia due its omnivorous diet (see Superina et al., 2009), fossorial habits and thermoregulatory strategies.

As was discussed by different authors, most armadillo distributions are limited by climatic conditions, and the major constraints are the periods when feeding is difficult due to freezing (Humphrey, 1974; McNab, 1980, 1985; Taulman and Robbins, 1996). Global warming in the 20th century changed the Patagonian weather conditions, including the reduction of the freezing days (Villalba et al., 2005). This climatic scenario, coupled with the previously mentioned anthropogenic disturbances during the last 200 years, allowed the expansion of the armadillos to the south. This process could have been similar to that described by Taulman and Robbins (1996) for *Dasyopus novemcinctus* in the southern regions of the United States. They proposed 2 combined dispersal processes: "neighborhood" diffusion or dispersal of pioneers along the advancing front of a contiguous population, and "hierarchical" diffusion, i.e., the dispersal of pioneers from propagules that have been introduced into new territories. This last process is evident and well documented in the case of the invasion of Tierra del Fuego Island by *C. villosus* (Poljak et al., 2007).

Based on the compiled data, the average speed of distribution range expansion of armadillos in Patagonia was at least of 13 km/year for *C. villosus* (1300 km in 100 years) and 5 km/year in the case of *Z. pichiy* (400 km in 80 years). The invasion rate of *C. villosus* is similar to the historic mean of 10.3 km/year reported for *D. novemcinctus* in the Northern Hemisphere (Taulman and Robbins, 1996). There are other examples of mammals (European wild rabbit [*Oryctolagus cuniculus*], European hare [*Lepus europaeus*], American mink [*Neovison vison*], American beaver [*Castor canadensis*], Muskrat [*Ondatra zibethicus*], Grey fox [*Lycalopex gymnocercus*])

that have invaded the Patagonian territory or surrounding areas (see Bonino and Soriguer, 2009; Fasola et al., 2011; Jaksic et al., 2002). In general, the values of range expansion rates for exotic mammals vary between 3.1 to 20 km/year, encompassing those reported in this paper for both *C. villosus* and *Z. pichiy*.

Against a generalized pristine perception of the Patagonian fauna, our knowledge of current mammal distribution, coupled with the fossil record of the last centuries and the observations made by travelers suggest a more complex scenario of recent mammal expansions and retractions. Some of these processes are relatively well documented and seem to be linked to human disturbances in the context of a general trend towards more arid and temperate conditions over the Patagonian ecosystems. These include the local regional extinctions of some micromamal species (e.g., *Lestodelphys halli*, *Tympanoctomys kirchnerorum*) and the expansion and population increment of others (e.g., *Calomys musculinus*, *Oligoryzomys longicaudatus*; Pardiñas et al., 2012; Pardiñas and Teta, 2013; De Tommaso et al., 2014; Teta et al., 2014). In turn, our knowledge about the recent changes on medium-sized mammals in Patagonia, although early highlighted (e.g., Dennler, 1942; Crespo, 1974), is still incipient and needed of detailed studies. For example, we do not know the chronologies and mechanisms that triggered the apparent expansion of *Lycalopex culpaeus* (Canidae) from western Andean areas to the steppes at the east, or *Galictis cuja* (Mustelidae) from north to south, as had been reported by Dennler (1942) over the basis of scattered and anecdotic observations. As a gain from this, a more complete picture of the recent changes in mammal distributions could help to understand changes in the ecosystemic functions and ecological interactions as well as to establish accurate management and conservation plans.

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SUPPLEMENTARY MATERIAL ONLINE

Suppl. Mat. 1. Zooarcheological records for *Chaetophractus villosus* and *Zaedyus pichiy* in Patagonia. http://www.sarem.org.ar/wp-content/uploads/2014/12/SAREM_MastNeotrop_21-2_Abba-sup1.doc

Suppl. Mat. 2. Records for *Chaetophractus villosus* and *Zaedyus pichiy* in Patagonia based on observations made by naturalist and travelers, museum specimens, and general literature. http://www.sarem.org.ar/wp-content/uploads/2014/12/SAREM_MastNeotrop_21-2_Abba-sup2.doc