Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

What do we know about armadillos? An analysis of four centuries of knowledge about a group of South American mammals, with emphasis on their conservation

Mariella SUPERINA* *Laboratorio de Endocrinología de la Fauna Silvestre, Instituto de Medicina y Biología Experimental de Cuyo, Centro Científico Tecnológico CONICET Mendoza, Av. Ruiz Leal s/n, Parque Gral. San Martín, Mendoza 5500, Argentina. E-mail: msuperina@mendoza-conicet.gov.ar*
Noralí PAGNUTTI *División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, CONICET, Paseo del Bosque s/n, La Plata 1900, Argentina. E-mail: noralipagnutti@hotmail.com*
Agustín M. ABBA *División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, CONICET, Paseo del Bosque s/n, La Plata 1900, Argentina. E-mail: abbaam@yahoo.com.ar*

Keywords
Cingulata, Dasypodidae, research priorities, threatened species, Xenarthra

*Correspondence author.

Submitted: 21 March 2013
Returned for revision: 18 April 2013
Revision accepted: 16 May 2013
Editor: KH

doi:10.1111/mam.12010

ABSTRACT

1. Basic knowledge on the biology and ecology of a species is fundamental for the realistic assessment of its conservation status and for planning effective conservation strategies. The latest assessment of the 21 extant armadillo species (Xenarthra, Dasypodidae) by the International Union for Conservation of Nature (IUCN) for its Red List of Threatened Species shows that considerable gaps exist in our knowledge of these Neotropical mammals.

2. Our goal was to analyse the existing literature on armadillos to define thematic and regional research priorities that will eventually benefit their conservation.

3. We categorized 3117 publications on extant armadillos published between 1660 and 2011 according to their research topic, species studied, country and publication language.

4. The number of publications per research topic and the number per species were very variable. The nine best-studied species are classed as Least Concern by the IUCN, while three of the four least-studied species are classed as Data Deficient. At least one field study was done in each range country, but over 80% of field research took place in the USA, Brazil, Argentina and Bolivia. Most research was done in the USA on leprosy in *Dasypus novemcinctus*. Most ecological research has been focused on four species, and data on the ecology of Data Deficient and Vulnerable taxa are virtually absent.

5. Field research on armadillos should be intensified to broaden conservation-relevant knowledge. Additional studies in the Guianas, Peru, Ecuador, Colombia, Venezuela and Paraguay are urgently needed to assess the conservation status of armadillos in these regions. Future research should focus on ecology, conservation, population genetics, reproduction and threats. Species priorities should include country endemics, such as *Dasypus pilosus* (Peru), *Tolypeutes tricinctus* (Brazil) and *Dasypus yepesi* and *Chlamyphorus truncatus* (Argentina), as well as other Data Deficient and Vulnerable species, especially *Cabassous centralis* and *Calyptophractus retusus*.

INTRODUCTION

One-quarter of all extant mammal species are classed as Threatened in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Schipper et al. 2008). The rate of species extinction is increasing, and growing pressures on biodiversity indicate that this trend will not be reversed in the near future (Butchart et al. 2010, Hoffmann et al. 2010). Because extinction risk varies depending on the life history, ecology and behaviour of species (Mace et al. 2008), a realistic assessment of the conservation status of a species requires not only knowledge of the threats affecting it but also basic information about its biological traits. Such data are fundamental to the performance of well-planned, strategic conservation actions.

Armadillos (Xenarthra, Dasypodidae) are semi-fossorial mammals that are widely distributed in South America; only one species reaches North America (Wetzel 1985a). They are the only mammals bearing a carapace that consists of osteoderms covered by epidermal scales (Engelmann 1985). Together with sloths (Folivora) and anteaters (Vermilingua) they form the Xenarthra, a monophyletic clade restricted to the Americas, which is considered to be one of the four major clades of placental mammals (Patterson & Pascual 1972, Delsuc et al. 2002, O'Leary et al. 2013). This unique concentration of evolutionary history in the 31 extant species of xenarthrans makes them invaluable for studying the earliest stages of mammalian evolution and reinforces the importance of ensuring their long-term conservation (Aguiar & da Fonseca 2008).

The latest assessment of the conservation status of xenarthrans revealed that fewer than half of the 21 extant armadillo species are currently not facing any risk of extinction (Table 1; Abba & Superina 2010). Four species are classed as Vulnerable in the IUCN Red List of Threatened Species, and four are classed as Near Threatened. The populations of at least seven species are declining (Abba & Superina 2010). However, four armadillo species are categorized as Data Deficient, the population trend of 10 species is unknown, and information on basic topics such as their taxonomy and life history, as well as information on threats to armadillos, seems to be scarce (Abba & Superina 2010). All these facts suggest that considerable gaps exist in our knowledge of the Dasypodidae.

The objective of this study was to analyse the published information on armadillos in order to define research priorities, both thematically and regionally. This will eventually help with the realistic assessment of the conservation status of armadillos and with the design of effective conservation strategies.

METHODS

We based our analysis on the armadillo bibliography database maintained by one of us (MS), which is available online (http://www.xenarthrans.org/bibliography/armadillo). It includes citations retrieved from library catalogues (e.g. Eidgenössische Technische Hochschule Zürich and Universität Zürich, Switzerland; University of Cambridge, UK; University of Chicago, USA) and scientific databases (e.g. Academic Search Premier, Medline, Ovid, WebSPIRS, Thomson's Web of Science, Google Scholar) using the keywords 'armadillo', 'tatou', 'tatú', 'Gürteltier', 'Dasypodidae', 'Cingulata', and the names of all extant genera. Citations were also retrieved from personal bibliographic lists of references obtained from armadillo researchers, from conference proceedings and from the reference lists of over 600 books, book chapters and articles on armadillos.

We included publications on extant species that were published from 1600 to 31 December 2011, and excluded palaeontological and archaeological studies. We also excluded anonymous works.

When possible, we read the entire publication to add the data listed in Tables 2 and 3 to a database created in EndNote X5 (Thomson Reuters, New York, NY, USA). In some cases we retrieved this information only from the abstract or, rarely, from the title. We defined 27 specific research topics and grouped them into 13 general topics (Table 3). If a publication addressed more than one research topic, all topics were listed. For instance, if a phylogenetic study was based on genetic analyses, research topics 'Genetics' and 'Evolution' were both listed. Similarly, if multiple species were addressed in the same publication or a study was done in several countries, all of them were listed. 'Dasypodidae' or 'Xenarthra' were used, respectively, whenever the species could not be determined or a publication was focused on the entire order Cingulata or superorder Xenarthra, such as those by Redford and Eisenberg (1992) and Wetzel (1985b). Such publications were excluded when calculating the number of publications per species. If the publication was not focused on a specific country but on armadillos in North, Central or South America, these terms were used for classification and the publication was excluded from the analyses by country (e.g. de Azara 1923, Krieg 1948). Finally, we used Abba and Superina (2010) to determine the number of extant armadillo species per range country and their threat status according to the IUCN Red List of Threatened Species.

The number of publications for each category listed in Table 2 and for each general and specific research topic listed in Table 3 was quantified by using the corresponding search terms in EndNote. For the publication year, data were retrieved by century until 1800, then by decade.

Table 1. Scientific and common name, size, geographic range and conservation status of the 21 extant armadillo species

Scientific name	Common name	Approximate body mass (kg)	Approximate head–body length (cm)	Geographic range	Conservation status (IUCN)
Cabassous centralis	Northern naked-tailed armadillo	2.0–3.5	34	From S Mexico to NW Ecuador and NW Venezuela	Data Deficient
Cabassous chacoensis	Chacoan naked-tailed armadillo	2.5	30	W Paraguay, central Argentina	Near Threatened
Cabassous tatouay	Greater naked-tailed armadillo	4.8–6.2	46	E and S Brazil, NE Uruguay, NE Argentina, SE Paraguay	Least Concern
Cabassous unicinctus	Southern naked-tailed armadillo	2.9	39	From N South America to S Brazil	Least Concern
Calyptophractus retusus	Greater fairy armadillo	0.13	16	C and SE Bolivia, W Paraguay, N Argentina	Data Deficient
Chaetophractus nationi	Andean hairy armadillo	1.2	27	Bolivia, Chile, Peru, N Argentina	Vulnerable
Chaetophractus vellerosus	Screaming hairy armadillo	0.85	23	Bolivia, Paraguay, Argentina	Least Concern
Chaetophractus villosus	Large hairy armadillo	2.5–3	33	Bolivia, Paraguay, Argentina, Chile	Least Concern
Chlamyphorus truncatus	Pink fairy armadillo	0.12	13	C Argentina	Data Deficient
Dasypus hybridus	Southern long-nosed armadillo	2	30	Argentina, Uruguay, Paraguay, S Brazil	Near Threatened
Dasypus kappleri	Greater long-nosed armadillo	10	54	Colombia, Venezuela, Guianas, E Ecuador, E Peru, W Brazil, N Bolivia	Least Concern
Dasypus novemcinctus	Nine-banded armadillo	3–8	36–57	S United States to N Argentina, Uruguay	Least Concern
Dasypus pilosus	Hairy long-nosed armadillo	2–3	44	SW Andes of Peru	Vulnerable
Dasypus sabanicola	Northern long-nosed armadillo	1.5	29	Llanos of Venezuela and Colombia	Least Concern
Dasypus septemcinctus	Seven-banded armadillo	1.5	27	NE Brazil to Bolivia, Paraguay, N Argentina	Least Concern
Dasypus yepesi	Yunga's lesser long-nosed armadillo	1.5–2	31	NW Argentina	Data Deficient
Euphractus sexcinctus	Six-banded armadillo	3.5–5	45	From S Suriname, E Brazil to Bolivia, Paraguay, Uruguay, N Argentina	Least Concern
Priodontes maximus	Giant armadillo	30–50	90	From N Venezuela, Guianas to Paraguay and N Argentina	Vulnerable
Tolypeutes matacus	Southern three-banded armadillo	1.5	30 (incl. tail)	E Bolivia, SW Brazil, W Paraguay, N Argentina	Near Threatened
Tolypeutes tricinctus	Brazilian three-banded armadillo	1.5	27 (incl. tail)	NE Brazil	Vulnerable
Zaedyus pichiy	Pichi	1	27	Central and S Argentina and Chile	Near Threatened

References: Wetzel (1980, 1985a), Cuarón et al. (1989), Eisenberg (1989), Carrillo and Wong (1992), Vizcaíno (1995), Superina and Aguiar (2006), Canevari and Vaccaro (2007), Abba and Superina (2010), J. P. Luaces, pers. comm., Superina, unpublished data.

Table 2. Information collected from each publication on armadillos

Category	Comments
Publication type	*Subcategories*: journal article, conference proceedings, book chapter, book, thesis, conference paper
Publication year	
First author's country of affiliation	
Relevance of armadillos in the study	*Main:* armadillos were the main object of study. *Secondary*: armadillos were mentioned in the study, but were not the main research object (e.g. description of a parasite infesting armadillos, or leprosy studies using mycobacteria that were cultured in armadillo tissues)
Species studied	'Dasypodidae' was used for general descriptions on armadillos or when the species could not be determined. 'Xenarthra' was used for publications about the entire superorder.
Country where the study was carried out	If the work was done in more than one country, all were listed.
Environment in which the study was carried out	*Subcategories:* laboratory, field, office (e.g. reviews), zoological parks, various (e.g. studies with field and laboratory components)
Language of publication	
Research topic	See Table 3 for details. If more than one topic was addressed in the same study, all of them were listed.

Chi-square (χ^2) tests (Zar 1999) were used to compare numbers of publications per species, per country, per research topic and per environment in which the study was carried out. Frequencies were expected to be evenly distributed among all categories tested. Chi-square tests were also used to compare numbers of publications in proportion to the number of armadillo species present in each country. Chi-square analyses of contingency tables were used to evaluate the differences between the number of publications per research topic and the number per species (contingency table: 21 species × 12 topics) and to evaluate the number of publications per research topic for each category of the IUCN Red List of Threatened Species (contingency table: 4 Red List categories × 12 topics). The expected frequencies were calculated following Zar (1999).

RESULTS

The database contained 3376 publications; 210 were excluded because they described palaeontological or archaeological studies, and 29 because they were anonymous. The number of publications included was thus 3117. Of these, 2414 (77%) were journal articles, 279 (9%) conference papers and abstracts, 191 (6%) book chapters, 148 (5%) books and 85 (3%) undergraduate, master's or doctoral theses. Armadillos were the main topic in less than half (1406) of the publications.

The majority of publications were written in English (2155 publications, 68%). Spanish and Portuguese, the native languages in most range countries, were used in 520 (17%) and 151 (5%) publications, respectively. Less than half of the studies on armadillo conservation were published in Spanish or Portuguese (21 and 5 publications, respectively). Relatively large numbers of publications were in German (184; 6%) and French (101; 3%). The remaining works (46; 1%) were published, in descending order of quantity, in Russian, Italian, Latin, Dutch or Polish.

Almost three-quarters of the first authors were affiliated with institutions in only four countries, namely the USA (1198), Argentina (559), Brazil (327) and the UK (206), while the remaining first authors worked in 43 different countries in Europe, Asia, North America, Africa, Australia and the Middle East. The affiliation could not be determined in 102 cases. Most studies (2822; 91%) were carried out in the first author's country of affiliation.

The studies were done in 60 countries, only 23 of which lie within the area of distribution of the Dasypodidae. The remaining publications were based on laboratory studies, data analyses or reviews performed in an office, or zoo-based research in Europe, Asia, North America and Australia. The range countries accounted for 75% of all publications, but the number of publications varied significantly among countries ($\chi^2 = 14196.04$, d.f. = 20, $P < 0.0001$) and did not reflect the number of species present in a certain country ($\chi^2 = 56066.27$, d.f. = 20, $P < 0.0001$). The vast majority of research was done in the USA, where only one armadillo species is found (Fig. 1).

There was a marked imbalance in numbers of studies performed in different environments ($\chi^2 = 3594.298$, d.f. = 4, $P < 0.0001$). Over 60% of the publications were based on studies performed in a laboratory environment, including the 17% that were related to leprosy research. Field research accounted for less than one-fifth of all studies on armadillos (Fig. 2). At least one field study was done in each range country, but four countries – the USA, Brazil, Argentina and Bolivia – accounted for 82% of all publications based on fieldwork (Fig. 1). Only 55 publications were based on studies performed in zoological parks, 25 of which

Table 3. Number of publications on armadillos per research topic

Research topic	Number of publications	Comments
Health	*1100*	
Leprosy	541	Includes studies in which *Mycobacterium leprae* was cultured in armadillo tissue
Parasitology	215	Descriptions of endo- and ectoparasites of armadillos
Pathologies	188	Includes descriptions of diseases, serological studies, veterinary-medical treatments and studies in which armadillos were used to investigate diseases other than leprosy and Chagas
Chagas	82	Studies in which *Trypanosoma cruzi* was detected in armadillos or in which armadillos were used to perform research on Chagas
Hematology	48	Includes blood cell and plasma studies as well as hematological and serum chemistry parameters
Immunology	26	Includes studies on immunohistochemistry
Anatomy	*600*	
Anatomy	419	Morphological or anatomical descriptions
Histology	107	Microscopy and electron microscopy studies on cells or glands, organ ultrastructure, general histological descriptions
Embryology	74	Includes studies on delayed implantation
Miscellaneous	*391*	
General	308	Includes encyclopaedia articles, catalogues and popular articles that provide general information on armadillos
Methods	47	Articles describing procedures to perform a certain study
Travel reports	36	Reports from naturalists who explored the Americas and mentioned armadillos in their chronicles
Ecology	*351*	
Ecology	182	
Nutrition	72	Descriptions of the diet of wild armadillos
Behaviour	53	
Predators	44	Studies on predators of armadillos
Physiology	*336*	
Physiology	278	Includes biochemical studies
Metabolism	58	Includes studies on thermoregulation, hibernation, sleep
Distribution	*204*	Descriptions of areas of distribution, range expansions; zoogeographical or phylogeographical studies. Includes publications on the impact of climate change on armadillos
Management	*151*	
Use/impact	86	Studies describing how armadillos are used or affected by humans, e.g. by traffic, hunting, alternative medicine or roadkills, without assessing the impact of these activities on the conservation status of the species or suggesting conservation measures to mitigate their potential effect
Captivity	65	Studies describing captive conditions
Reproduction	*128*	Includes descriptions of the morphology of the reproductive system, reproductive hormones, placenta, implantation, reproductive cycles, polyembryony, sex determination, parthenogenesis, gametes, sexual dimorphism, etc.
Genetics	*97*	Includes cytogenetics
Taxonomy	*92*	Includes systematics, descriptions of new species, revisions of museum specimens
Evolution	*61*	Studies on phylogeny, phylogenetic relationships, evolution of specific traits or structures
Conservation	*54*	
Unknown	*3*	The research topic could not be determined

General research topics (italic) may include several specific topics (indented). Topics are listed in order of decreasing number of publications.

were general descriptions of the maintenance (e.g. Flint 1997), nutrition (e.g. Meritt 1977) or pathologies (e.g. Zwart et al. 1989) of captive armadillos.

Publication year spanned from 1660 to 2011; the first mention of armadillos was by Jonstonus (1660). Roughly 500 publications were general descriptions of Dasypodidae or Xenarthra, including 80 of the 100 oldest works. The first two studies on a specific species concerned *Dasypus novemcinctus* (Watson 1765, Frisch 1775), followed by a publication on *Euphractus sexcinctus* (Owen 1831). Substantial increases in the number of publications occurred between 1960 and 1969 and, especially, between 1970 and 1979, when armadillos started to be used in leprosy research; 199 papers were published on this topic in a single decade (Fig. 3). Since then, leprosy has become the most studied topic in armadillo research (Table 3), having been addressed in 15% of all publications and in over one-third of all works in which armadillos play a secondary role.

Thirteen per cent of all publications addressed more than one research topic. The number of publications per research

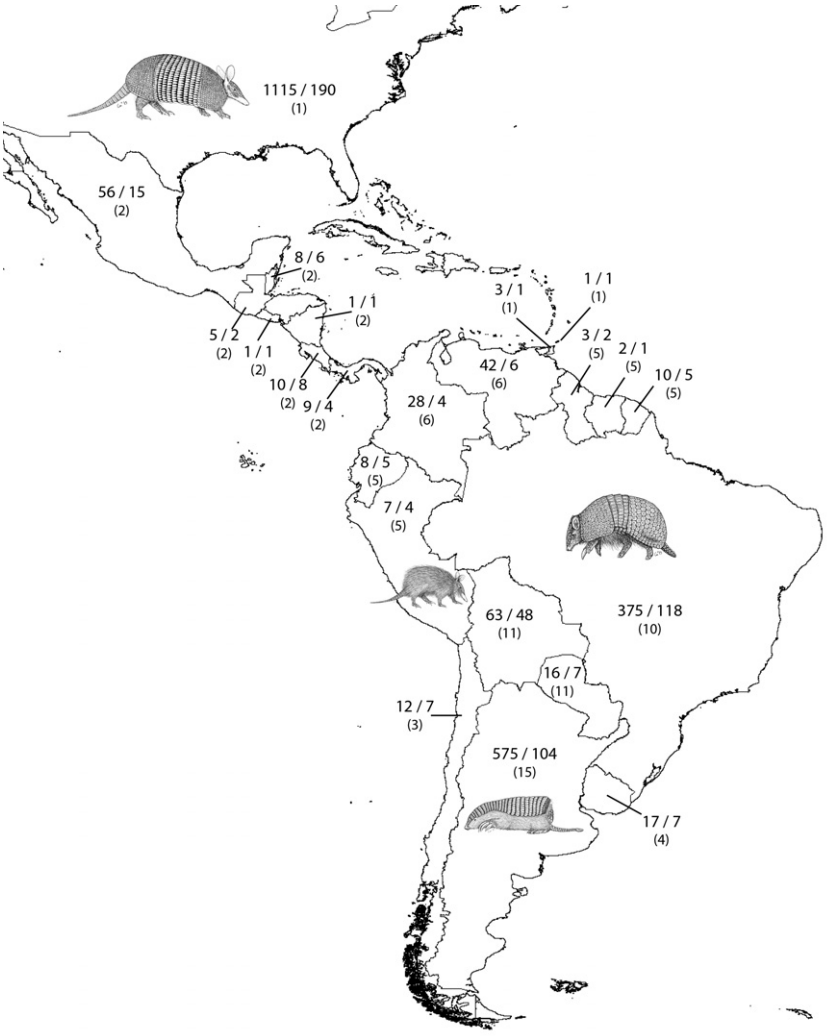

Fig. 1. Map of the range countries of Dasypodidae in North, Central and South America. Numbers for each country indicate the total number of publications/number of publications involving fieldwork. The number of existing armadillo species per country is indicated in parentheses. If a study involved several countries, all of them were counted individually. Publications covering Dasypodidae or Xenarthra in which the species was not given are not shown. Also excluded are publications not covering a specific country but rather relating to armadillos in South America, Central America or North America. Drawings show the most common species, *Dasypus novemcinctus* (USA), and country endemics: *Tolypeutes tricinctus* (Brazil), *Chlamyphorus truncatus* (Argentina) and *Dasypus pilosus* (Peru). Drawings by Luis Pagano.

topic was very heterogeneous ($\chi^2 = 2600.152$, d.f. = 20, $P < 0.0001$); in almost one-fifth of the studies, peculiarities of the anatomy and physiology of armadillos are described, while topics such as behaviour and predators of armadillos are clearly underrepresented (Table 3).

Although the first observations on the ecology of armadillos were published as early as 1830, this research topic only started gaining importance in the 1970s and became even more relevant in the last decade (2000–2011), when 80 out of 546 publications (15%) were dedicated to it. The timing of the slow rise in ecological studies may be explained by the development of ecology as a research discipline in the 1900s (Margalef 1974). Furthermore, it seems to be coupled in time with the spread of *Dasypus novemcinctus* throughout the southeastern USA (Taulman & Robbins 1996). Ecology ranks fourth in the list of general research topics and eighth in the list of specific topics (Table 3).

Fifty-four publications were dedicated to armadillo conservation (Table 3). Over 75% of the publications on

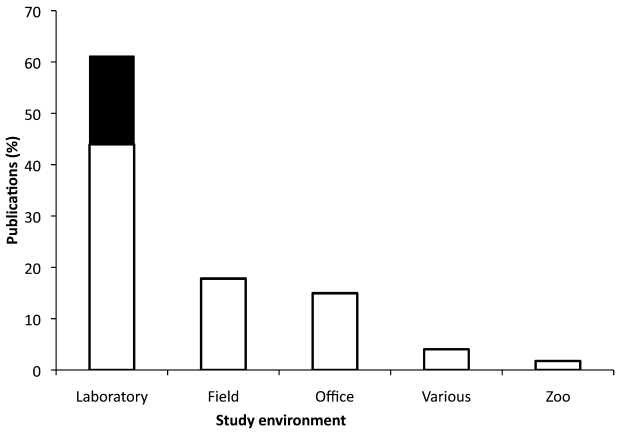

Fig. 2. Percentage of publications carried out in different study environments [the laboratory, the field, the office (e.g. reviews), various environments (e.g. studies with field and laboratory components), and zoological parks]. The black bar indicates publications on leprosy.

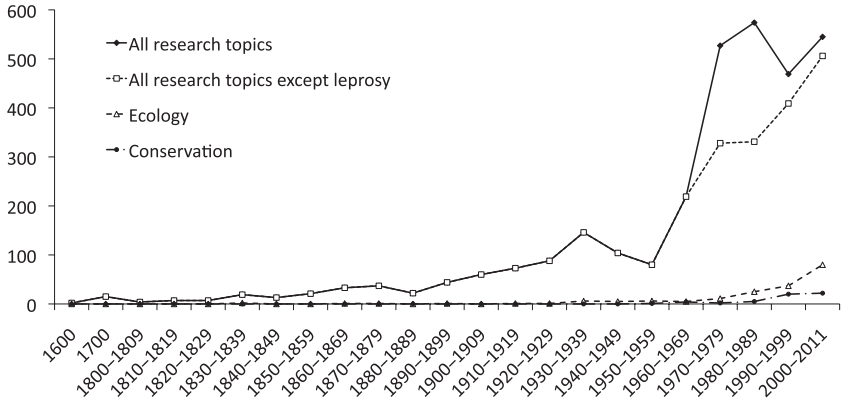

Fig. 3. Numbers of publications on armadillos on all research topics, on all topics except leprosy, on ecology, and on conservation, in each time period (century until 1800, then decade).

this topic were issued after 1990. They represented 4.3% of all works published between 1990 and 1999 and 4.0% of those that appeared between 2000 and 2011 (Fig. 3). The newsletter *Edentata*, which publishes information on different aspects of Xenarthra conservation, was first published in 1994 and seems to have boosted the number of articles on this topic: one-fourth of all publications that were published since its first issue and one-fifth of all available publications on armadillo conservation appeared in *Edentata*.

The number of publications per species was heterogeneous, and some species appeared significantly more frequently than others ($\chi^2 = 13478.37$, d.f. = 20, $P < 0.0001$). Highly significant differences also occurred in the number of publications per Red List category ($\chi^2 = 333.59$, d.f. = 33, $P < 0.0001$). The nine best-known species, the subjects of the highest number of publications (2403), are classed as Least Concern in the IUCN Red List of Threatened Species (Abba & Superina 2010). This includes the nine-banded armadillo *Dasypus novemcinctus*, which is by far the most studied species (Fig. 4) due to its use in leprosy research. Armadillo species classed as Vulnerable were covered in 165, Near Threatened species in 389, and Data Deficient species in 95 publications.

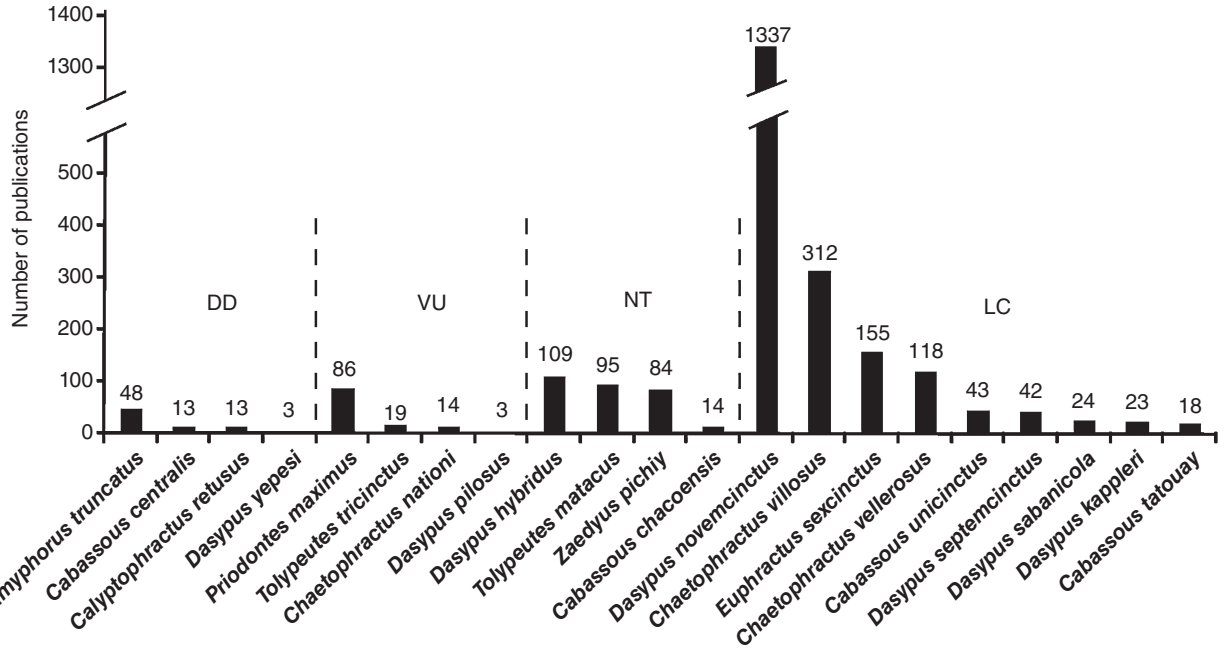

Fig. 4. Number of publications per species, grouped by conservation status according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Within each group, species are listed in order of decreasing number of publications. Publications involving the entire taxon Dasypodidae or Xenarthra are excluded from this analysis. DD, Data Deficient; VU, Vulnerable; NT, Near Threatened; LC, Least Concern.

Table 4. Numbers of publications addressing general research topics for armadillo species classed as Vulnerable or Data Deficient in the IUCN Red List of Threatened Species (Abba & Superina 2010)

	Vulnerable*				Data Deficient*			
General research topic	*Chaetophractus nationi*	*Dasypus pilosus*	*Priodontes maximus*	*Tolypeutes tricinctus*	*Cabassous centralis*	*Calyptophractus retusus*	*Chlamyphorus truncatus*	*Dasypus yepesi*
Distribution	3	1	23	10	6	4	9	2
Ecology	1	0	23	8	1	1	4	1
Anatomy	0	0	10	1	1	2	16	0
Miscellaneous	1	2	13	2	1	3	10	0
Conservation	2	0	9	3	0	1	4	0
Physiology	4	0	7	0	4	0	4	0
Management	4	0	8	0	0	1	2	0
Health	0	0	6	1	3	0	3	0
Genetics	1	0	7	1	0	0	2	0
Taxonomy	1	0	2	1	1	4	1	1
Evolution	0	0	7	1	0	0	1	0
Reproduction	1	0	1	0	0	0	3	0
Number of general research topics	9	2	12	9	7	7	12	3
Total publications	14	3	86	19	13	13	48	3
Publications addressing more than one general research topic	3	0	25	8	3	2	8	1

General research topics are explained in Table 3 and listed here in order of decreasing numbers of publications. Publications can address more than one research topic, and general works focusing on the entire order Cingulata or superorder Xenarthra were excluded from this analysis.
*Conservation status according to the IUCN Red List of Threatened Species (Abba & Superina 2010).

Three of the four least-studied armadillo species are considered Data Deficient, and the remaining one is classed as Vulnerable (Fig. 4). *Priodontes maximus* is the most studied species of the four armadillos classed as Vulnerable. A total of 86 publications dedicated to this species cover research topics belonging to all 12 categories (Table 4). *Dasypus pilosus* lies at the other end of the scale: only one publication reports on its distribution, and two describe general aspects of the species (Table 4). The amount of information available on Data Deficient armadillo species varies from 48 publications addressing 12 different general research topics in *Chlamyphorus truncatus* to three publications on three topics (distribution, ecology and taxonomic status) in *Dasypus yepesi* (Table 4).

DISCUSSION

From the standpoint of species conservation, the situation is not as bleak as depicted by Amori and Gippoliti (2000), who did not find any papers on Xenarthra conservation in their analysis of publications in the four major conservation journals. Still, it is far from ideal, as only 54 out of 3117 publications were dedicated to conservation issues. Armadillo conservation did not seem to be relevant until the 1950s, when Lagiglia (1956) raised concern about the conservation of *Chlamyphorus truncatus*.

The predominance of English as the publication language for articles on conservation and on other research topics is a cause for concern. Politicians and decision-makers in non-English-speaking countries with armadillo populations often have little or no knowledge of English and very limited access to international scientific journals (Ceballos et al. 2009). This makes it difficult to apply scientific knowledge about armadillos to conservation policies. Similarly, it is difficult for members of the general public to understand the importance of armadillo conservation if information is not available in their native language. Ideally, research results should be published in English to ensure their dissemination among the scientific community, while an easily understandable summary of the conclusions should be made available to policy-makers and the general public in their native language.

Basic data on biology, ecology and threats are essential prerequisites for the realistic assessment of the conservation status of a species (Mace et al. 2008) and for the development of effective conservation strategies. The peculiar appearance of armadillos and their variety of unusual physiological features (among other traits) have driven a wealth of studies on armadillos. In particular, understanding the physiological traits of a species helps researchers to evaluate its potential to cope with environmental changes, such as climate change, one of the most important threats

to species conservation (Hayward 2011). It has been postulated that the distribution of armadillos is limited by their low basal metabolic rates and high thermal conductance (McNab 1980). It is therefore surprising that we could not find a single publication in which the authors discussed the potential impact of global climate change on the distribution or chances of long-term survival of armadillos. Furthermore, with the exception of *Zaedyus pichiy* (Superina & Boily 2007), there are no publications on the specific physiological adaptations of armadillos inhabiting extreme habitats, such as *Chaetophractus nationi* (high altitudes) or *Chaetophractus vellerosus*, *Chlamyphorus truncatus* and *Calyptophractus retusus* (xeric environments).

The ranking of research topics by papers published is led by leprosy, the focus of over 500 publications (Table 3), which make up the bulk of works in which armadillos play a secondary role. Of these, some studies (e.g. Loughry et al. 2009, Morgan & Loughry 2009) have been focused on the ecological impact of this disease for wild armadillo populations. The discovery by Kirchheimer and Storrs (1971) that *Dasypus novemcinctus* can be infected with *Mycobacterium leprae* experimentally led to a substantial increase in publications on armadillos in the 1970s (Fig. 3). The need to maintain and breed *Dasypus novemcinctus* in a laboratory environment to investigate this disease has also led to multiple studies on other topics, such as reproduction (reviewed in Peppler 2008), immunology (e.g. Ulrich 1978) and haematology (e.g. D'Addamio et al. 1978). The fact that 40% of publications appearing between 1970 and 1980 addressed armadillos in general or species other than *Dasypus novemcinctus* strongly suggests that leprosy brought the taxon as a whole to the attention of the scientific community.

Ecology ranks fourth in our analysis of research topics (Table 3), but only four species classed as Least Concern in the IUCN Red List of Threatened Species (*Dasypus novemcinctus*, *Chaetophractus villosus*, *Chaetophractus. vellerosus*, *Euphractus sexcinctus*) account for two-thirds of all publications on this topic. Studies on the ecology of the Data Deficient and Vulnerable armadillo species are virtually absent, with the notable exception of *Priodontes maximus* (Table 4). Long-term studies of different armadillo species are urgently needed to increase understanding of population dynamics and trends and to allow the estimation of population growth rates, as information on these topics is only available for *Dasypus novemcinctus* (McDonough et al. 2007, McDonough & Loughry 2008, Loughry et al. 2013) and *Chaetophractus vellerosus* (Abba et al. 2011). Similarly, data on the population genetics of armadillos are limited to *Dasypus novemcinctus* (Prodöhl et al. 2008), although such information is fundamental for the assessment of the extinction risk of a species (Frankham 2005).

Our analysis reveals that, with the exception of *Dasypus novemcinctus,* information on the reproductive strategies of most species is still scarce or even non-existent. Because the survival of a species is inevitably tied to its ability to reproduce, data on its reproductive cycle are paramount when deciding how best to manage it (Dixson et al. 2003). The substantial differences in reproductive strategies of armadillos require that each species be studied individually. For instance, several researchers have investigated the peculiar reproductive strategy of *Dasypus novemcinctus*, which includes polyembryony and delayed implantation (Peppler 2008). It is generally assumed that polyembryony is common to all species of the genus *Dasypus,* although the reproduction of *Dasypus kappleri*, *Dasypus yepesi* and *Dasypus pilosus* has never been studied.

In the context of species conservation, it is worrying that less than 20% of the publications were based on field studies. Armadillos are difficult to study in the wild due to their semi-fossorial, solitary habits and low population densities, which may explain – at least in part – why so few field studies have been performed on this taxon. Population studies are further complicated by the fact that armadillos cannot be captured with commercial traps. For instance, da Silva and Henriques (2009) used Havahart traps over 9205 trap-nights in a study on the population ecology of *Dasypus septemcinctus* and reported a capture success rate of 0.23%.

Although it is clear that laboratory studies and office-based analyses can provide important information, it is difficult to develop effective conservation strategies if the threats affecting a species are not assessed in the field. Virtually all armadillo species are affected by hunting (Abba & Superina 2010), but the harvest levels and trends remain to be studied. Similarly, habitat degradation and fragmentation is thought to affect at least 17 species (Abba & Superina 2010), but the scarcity of field studies does not allow an assessment of the impact of these threats on armadillo populations.

The example of the USA, home to a single armadillo species, clearly shows that the number of field-based publications does not necessarily reflect the number of species present in a certain country. However, three of the four countries in which the largest numbers of field studies were produced are inhabited by 10 or more armadillo species (the fourth being the USA). The notable exception to this pattern is Paraguay, which is home to 11 species but has only hosted seven field-based publications.

An analysis of the number of field-based publications in range countries that contain fewer than 10 armadillo species reveals worrying numbers. For instance, the five countries inhabited by five species each produced one to five field-based publications (Fig. 1). The largest range countries – the USA, Brazil and Argentina – had the highest number of field-based publications, but this relationship did not hold true for others, such as Peru and Colombia, which have a larger area than Bolivia. Intensifying research on armadillos

in the Guianas, Peru, Ecuador, Colombia and Venezuela should thus be a priority.

The preponderance of publications from the USA and on *Dasypus novemcinctus* is probably also related to other factors, such as funding availability. While, in 2008, the investment made by the USA in research and development was 2.79% of its gross domestic product, Latin America and Caribbean countries invested a mere 0.65% (Anonymous 2012a). Logistical problems in performing fieldwork in remote areas of the Neotropics may also explain the low number of studies on armadillos in certain countries, such as the Guianas (Fig. 1). It is, of course, easier to investigate an abundant and wide-ranging species (e.g. *Dasypus novemcinctus*) than a habitat specialist with a restricted range (e.g. *Dasypus pilosus,* which only lives in subtropical forests in the Peruvian Andes). Such differences are invariably reflected in the number of studies performed on each species as well as in each country.

Zoo-based research could provide valuable data on armadillo biology for conservation planning, especially if it is performed on endangered taxa. However, few of the zoo-based research publications addressed topics relevant to conservation issues, and since the most frequently kept armadillos are those that are most common in the wild (Anonymous 2012b), zoo-based studies often fail to provide useful information for developing *in situ* conservation strategies.

Some armadillo species classed as Least Concern in the IUCN Red List of Threatened Species have received more attention from the research community than others. Nevertheless, the abundance of publications on *Dasypus novemcinctus* does not mean that it is thoroughly understood. As pointed out by McDonough and Loughry (2008), observations of *Dasypus novemcinctus* in the USA are not necessarily representative of what occurs in populations from South or Central America, where very few data are available on the ecology of this species. Other species classed as Least Concern, such as *Cabassous tatouay* and *Dasypus kappleri*, have been the focus of only a few studies (Fig. 4), and more research on them is needed to ensure that their conservation status has been correctly assessed.

It is, however, more pressing to intensify field studies on the four species classed as Data Deficient (Fig. 4). The extremely low number of publications on *Cabassous centralis*, *Calyptophractus retusus* and *Dasypus yepesi* confirms that insufficient information is available to assess their conservation status. *Dasypus yepesi* was only recently described (Vizcaíno 1995), which may explain the lack of field data, but it is difficult to understand why only 13 publications are available on *Cabassous centralis*, a species that occurs in 11 countries in Central and South America. Although *Chlamyphorus truncatus* has been the subject of 48 publications, 16 deal with its anatomy, and 10 are general descriptions that do not provide relevant information for the assessment of its conservation status.

Armadillo species classed as Vulnerable in the IUCN Red List of Threatened Species are represented in varying numbers of publications. Although the giant armadillo *Priodontes maximus* is often mentioned as one of the least-studied species, our analyses suggest that there are 14 even less well-known armadillo species (Fig. 4). Nevertheless, it is clear that knowledge on certain aspects of this taxon is still scarce. *Chaetophractus nationi* is currently classed as Vulnerable, but the lack of significant genetic or morphological differences suggests that it is not a distinct species from *Chaetophractus vellerosus* and should thus be classed as Least Concern (Valverde et al. in prep.).

The fact that only three publications exist on *Dasypus pilosus* raises the question of whether it is indeed correctly assessed or if it should be classed as Data Deficient, as it is hard to believe that sufficient information on populations and threats is available to allow an accurate assessment of its extinction risk. Local researchers should be encouraged to initiate research on this virtually unknown species, which is endemic to Peru. Similarly, *Dasypus yepesi* and *Chlamyphorus truncatus* occur only in Argentina and *Tolypeutes tricinctus* only in Brazil; these species should therefore be a priority for field research in their range countries. *Calyptophractus retusus* occurs in three countries, but it is a habitat endemic that only occurs on loose, sandy soils of the Gran Chaco region (Abba & Superina 2010). Field studies on this cryptic species in Bolivia, Paraguay and Argentina are urgently needed to increase understanding of its ecology and the threats to which it is exposed and to assess its extinction risk.

CONCLUSIONS

We encourage researchers to intensify field research to broaden conservation-relevant knowledge of armadillos. Easily understandable summaries of the conclusions from scientific publications should be made available in the relevant country's native language to increase the probability that scientific knowledge will be translated into effective conservation policies. We propose the following priorities for future armadillo research to assess the conservation status of armadillos realistically and to allow the design of effective conservation strategies:

- Research topics: ecology, conservation, population genetics, reproduction, threats.
- Species: *Dasypus pilosus* (Peru), *Tolypeutes tricinctus* (Brazil), *Dasypus yepesi* and *Chlamyphorus truncatus* (Argentina). Other species classed as Data Deficient or Vulnerable in the IUCN Red List of Threatened Species, especially *Cabassous centralis* and *Calyptophractus retusus*.
- Countries: Guyana, Suriname, French Guiana, Peru, Ecuador, Colombia, Venezuela and Paraguay.

ACKNOWLEDGEMENTS

We thank Luis Pagano (División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina) for providing drawings of the species. Funding was provided by CONICET (PIP 114-201001-00137), Universidad Nacional de La Plata and Agencia Nacional de Promoción Científica y Tecnológica (PICT 2010-1412 and PICT 2010-0276).

REFERENCES

Abba AM, Superina M (2010) The 2009/2010 armadillo Red List assessment. *Edentata* 11: 135–184.

Abba AM, Cassini GH, Cassini MH, Vizcaíno SF (2011) Historia natural del piche llorón *Chaetophractus vellerosus* (Mammalia: Xenarthra: Dasypodidae). *Revista Chilena de Historia Natural* 84: 51–64.

Aguiar JM, da Fonseca GAB (2008) Conservation status of the Xenarthra. In: Vizcaíno SF, Loughry WJ (eds) *The Biology of the Xenarthra*, 215–231. University Press of Florida, Gainesville, Florida, USA.

Amori G, Gippoliti S (2000) What do mammalogists want to save? Ten years of mammalian conservation biology. *Biodiversity and Conservation* 9: 785–793.

Anonymous (2012a) *Research and Development Expenditure (% of GDP)*. http://data.worldbank.org/topic/science-and-technology

Anonymous (2012b) *ISIS Species Holdings*. http://www.isis.org

de Azara F (1923) Armadillos. In: de Azara F (ed.) *Viajes por la América Meridional*, 267–279. Editorial Calpe, Buenos Aires, Argentina.

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA et al. (2010) Global biodiversity: indicators of recent declines. *Science* 328: 1164–1168.

Canevari M, Vaccaro O (2007) *Guía de Mamíferos del Sur de América del Sur*. Literature of Latin America, Buenos Aires, Argentina.

Carrillo EJ, Wong GR (1992) Registro y medidas de restos de un *Cabassous centralis* (Edentata: Dasypodidae) en el Parque Nacional Manuel Antonio, Quepos, Costa Rica. *Brenesia* 38: 153–154.

Ceballos G, Vale MM, Bonacic C, Calvo-Alvarado J, List R, Bynum N, Medellín RA, Simonetti JA, Rodríguez JP (2009) Conservation challenges for the Austral and Neotropical America section. *Conservation Biology* 23: 811–817.

Cuarón AD, March IJ, Rockstroh PM (1989) A second armadillo (*Cabassous centralis*) for the faunas of Guatemala and Mexico. *Journal of Mammalogy* 70: 870–871.

D'Addamio GH, Walsh GP, Harris L, Borne R, Derouen MS (1978) Hematologic parameters for wild and captive nine-banded armadillos (*Dasypus novemcinctus*). *Laboratory Animal Science* 28: 607–610.

Delsuc F, Scally M, Madsen O, Stanhope MJ, de Jong WW, Catzeflis FM, Springer MS, Douzery EJP (2002) Molecular phylogeny of living xenarthrans and the impact of character and taxon sampling on the placental tree rooting. *Molecular Biology and Evolution* 19: 1656–1671.

Dixson A, Harvey N, Patton M, Setchell J (2003) Behaviour and reproduction. In: Holt WV, Pickard AR, Rodger JC, Wildt DE (eds) *Reproductive Science and Integrated Conservation*, 24–41. Cambridge University Press, Cambridge, UK.

Eisenberg JF (1989) *Mammals of the Neotropics, Volume 1. The Northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana*. University of Chicago Press, Chicago, Illinois, USA.

Engelmann GF (1985) The phylogeny of the Xenarthra. In: Montgomery GG (ed.) *The Evolution and Ecology of Armadillos, Sloths and Vermilinguas*, 51–64. Smithsonian Institution Press, Washington, DC, USA.

Flint MP (1997) Zoo standards for keeping xenarthrans (edentates) in captivity. In: Shoemaker A (ed.) *American Zoo and Aquarium Association Minimum Husbandry Guidelines for Mammals*, 15–24. American Zoo and Aquarium Association, Bethesda, Maryland, USA.

Frankham R (2005) Genetics and extinction. *Biological Conservation* 126: 131–140.

Frisch JL (1775) *Das Natur-System der vierfüssigen Thiere in Tabellen, darinnen alle Ordnungen, Geschlechte und Arten, nicht nur mit bestimmenden Benennungen, sondern beygesetzten unterscheidenden Kennzeichen angezeigt werden zum Nutzen der erwachsenen Schuljugend*. Christian Friedrich Günther, Glogau, Prussia.

Hayward MW (2011) Using the IUCN Red List to determine effective conservation strategies. *Biodiversity and Conservation* 20: 2563–2573.

Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SHM et al. (2010) The impact of conservation on the status of the world's vertebrates. *Science* 330: 1503–1509.

Jonstonus J (1660) *Historiae Naturalis de Quadrupedibus*. I.I. Schipper, Amsterdam, the Netherlands.

Kirchheimer WF, Storrs EE (1971) Attempts to establish the armadillo (*Dasypus novemcinctus* Linn.) as a model for the study of leprosy. I. Report of lepromatoid leprosy in an experimentally infected armadillo. *International Journal of Leprosy* 39: 693–702.

Krieg H (1948) *Zwischen Anden und Atlantik*. Carl Hanser Verlag, München, Germany.

Lagiglia HA (1956) Nota sobre la retrocesión y conservación del *Chlamyphorus truncatus* Harl. dentro de la fauna mendozina. *Revista Científica de Investigación, Museo de Historia Natural San Rafael, Mendoza* 1: 33–34.

Loughry WJ, Truman RW, McDonough CM, Tilak M, Garnier S, Delsuc F (2009) Is leprosy spreading among nine-banded armadillos in the southeastern United States? *Journal of Wildlife Diseases* 45: 144–152.

Loughry WJ, Perez-Heydrich C, McDonough CM, Oli MK (2013) Population ecology of the nine-banded armadillo in Florida. *Journal of Mammalogy* 94: 408–416.

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland EJ, Stuart SN (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology* 22: 1424–1442.

Margalef R (1974) *Ecología*. Ediciones Omega, S.A., Barcelona, Spain.

McDonough CM, Loughry WJ (2008) Behavioral ecology of armadillos. In: Vizcaíno SF, Loughry WJ (eds) *The Biology of the Xenarthra*, 281–293. University Press of Florida, Gainesville, Florida, USA.

McDonough CM, Lockhart JM, Loughry WJ (2007) Population dynamics of nine-banded armadillos: insights from a removal experiment. *Southeastern Naturalist* 6: 381–392.

McNab BK (1980) Energetics and the limits to a temperate distribution in armadillos. *Journal of Mammalogy* 61: 606–627.

Meritt DA Jr (1977) Edentate nutrition. In: Rechcigl M (ed.) *CRC Handbook Series in Nutrition and Food* Vol. 1, 541–547. CRC Press, Cleveland, Ohio, USA.

Morgan RE, Loughry WJ (2009) Consequences of exposure to leprosy in a population of wild nine-banded armadillos. *Journal of Mammalogy* 90: 1363–1369.

O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP et al. (2013) The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339: 662–667.

Owen R (1831) On the anatomy of the weasel-headed armadillo (*Dasypus sexcinctus*, Linn.). *Proceedings of the Zoological Society of London* 1: 154–157.

Patterson B, Pascual RR (1972) The fossil mammal fauna of South America. In: Keast A, Erk FC, Glass B (eds) *Evolution, Mammals, and Southern Continents*, 247–309. State University of New York Press, Albany, New York, USA.

Peppler RD (2008) Reproductive biology of the nine-banded armadillo. In: Vizcaíno SF, Loughry WJ (eds) *The Biology of the Xenarthra*, 151–159. University Press of Florida, Gainesville, Florida, USA.

Prodöhl PA, Loughry WJ, McDonough CM (2008) Genes and demes. Population genetic analyses of the Xenarthra. In: Vizcaíno SF, Loughry WJ (eds) *The Biology of the Xenarthra*, 205–211. University Press of Florida, Gainesville, Florida, USA.

Redford KH, Eisenberg JF (1992) Order Xenarthra (Edentata): family Dasypodidae. In: Redford KH, Eisenberg JF (eds) *Mammals of the Neotropics, Volume 2: The Southern Cone: Chile, Argentina, Uruguay, Paraguay*, 52–68. The University of Chicago Press, Chicago, Illinois, USA.

Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V et al. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322: 225–230.

da Silva KFM, Henriques RPB (2009) Ecologia de população e área de vida do tatu-mirim (*Dasypus septemcinctus*) em um cerrado no Brasil central. *Edentata* 8–10: 48–53.

Superina M, Aguiar JM (2006) A reference list of common names for the edentates. *Edentata* 7: 33–44.

Superina M, Boily P (2007) Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). *Comparative Biochemistry and Physiology. A, Comparative Physiology* 148: 893–898.

Taulman JF, Robbins LW (1996) Recent range expansion and distributional limits of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. *Journal of Biogeography* 23: 635–648.

Ulrich M (1978) Immunology of the armadillo. In: *The Armadillo as an Experimental Model in Biomedical Research: Proceedings of a Workshop Held at the Pan American Center for Research and Training in Leprosy and Tropical Diseases, Caracas, Venezuela*, 32–37. Pan American Health Organization, Washington, DC, USA.

Vizcaíno SF (1995) Identificación específica de las 'mulitas', género *Dasypus* L. (Mammalia, Dasypodidae), del noroeste argentino. Descripción de una nueva especie. *Mastozoología Neotropical* 2: 5–13.

Watson W (1765) An account of an American armadillo. *The Monthly Review, or, Literary Journal* 33: 446.

Wetzel RM (1980) Revision of the naked-tailed armadillos, genus *Cabassous* McMurtrie. *Annals of Carnegie Museum* 49: 323–357.

Wetzel RM (1985a) Taxonomy and distribution of armadillos, Dasypodidae. In: Montgomery GG (ed.) *The Evolution and Ecology of Armadillos, Sloths and Vermilinguas*, 5–21. Smithsonian Institution Press, Washington, DC, USA.

Wetzel RM (1985b) The identification and distribution of recent Xenarthra (=Edentata). In: Montgomery GG (ed.) *The Evolution and Ecology of Armadillos, Sloths and Vermilinguas*, 23–46. Smithsonian Institution Press, Washington, DC, USA.

Zar JH (1999) *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zwart P, Kaashoek M-J, van der Haage M, Dorrestein GM (1989) Erkrankungen südamerikanischer Säugetiere aus niederländischen Tiergärten. In: Ippen R, Schröder HD (ed.) *Verhandlungsbericht des 31. Internationalen Symposiums über die Erkrankungen der Zoo- und Wildtiere*, 7–14. Akademie-Verlag, Berlin, Germany.