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Research on armadillos: a review and prospectus

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A detailed analysis of 1,039 scientific studies of extant armadillos (Xenarthra: Cingulata, Dasypodidae) published in the last 25 years (1989–2013) revealed substantial biases in coverage, including taxonomically, the locales where field studies were conducted, and in the topics investigated. Examination of the number of other publications that cited each paper revealed that 470 (45%) papers had been cited no more than 10 times, 249 (24%) had never been cited, and 112 (11%) were not even found in the Google Scholar database. The most heavily cited papers were molecular phylogenetic analyses that often used tissues from one or more species of armadillo but were not about the animals per se. Thus, it appears that research on armadillos is plagued by numerous gaps in coverage and is not reaching a wide audience. These data indicate obvious opportunities for future research. In addition, recent findings suggest that even relatively well-studied phenomena may require reexamination. Here, we review recent advances in the study of armadillos and highlight promising areas for future work. One critical need is for a thorough systematic revision of Dasypodidae to be completed. This will make it possible to prioritize those species and populations most in need of study. Additionally, more long-term field studies of populations of marked individuals are required. Although there are many important and interesting questions waiting to be answered, the small number of researchers currently conducting studies of armadillos, particularly in the wild, means that progress will be slow.

Un análisis detallado de 1.039 estudios científicos sobre armadillos actuales (Xenarthra: Cingulata, Dasypodidae), que fueron publicados en los últimos 25 años (1989–2013), mostró que existen considerables sesgos en la cobertura, incluyendo la taxonomía, los lugares donde se realizaron los estudios de campo, y en los temas estudiados. El análisis de la cantidad de otros trabajos que citaron las publicaciones de armadillos mostró que 470 (45%) de los artículos fueron citado no más de 10 veces, 249 (24%) nunca habían sido citado y 112 (11%) ni siquiera fueron encontrado en la base de datos de Google Scholar. Las publicaciones citadas con mayor frecuencia describían análisis filogenéticos moleculares que generalmente utilizaban tejidos de una o más especies de armadillos, pero no trataban de los armadillos per se. Pareciera, entonces, que la investigación en armadillos está plagada de numerosos vacíos en la cobertura y no está alcanzando una amplia audiencia. Estos datos indican claras oportunidades para futuras investigaciones. Adicionalmente, recientes hallazgos sugieren que incluso las peculiaridades relativamente bien estudiadas podrían requerir de análisis adicionales. En este trabajo revisamos recientes avances en el estudio de los armadillos y resaltamos áreas prometedoras para futuras investigaciones. Una de las necesidades críticas es el desarrollo de una detallada revisión sistemática de los Dasypodidae que permitirá priorizar las especies y poblaciones con mayor necesidad de investigación. Adicionalmente, se requieren de estudios a largo plazo que involucren poblaciones de individuos marcados. Si bien existen muchas preguntas importantes e interesantes que esperan ser respondidas, el reducido número de investigadores que actualmente desarrollan estudios sobre armadillos, especialmente a campo, parece prever que será un proceso lento.

Key words: armadillos, citations, Dasypodidae, literature review, publications, research

Within Xenarthra, the order Cingulata consists of those taxa exhibiting some form of armored carapace (Gaudin and McDonald 2008; Wetzel et al. 2008). Representatives include such oddities as the extinct glyptodonts and pampatheres (Edmund 1985; Fernicola et al. 2008). Nowadays, the only remaining members of Cingulata are the 21 currently recognized species of armadillos in the family Dasypodidae (Table 1; see also Abba and Superina 2010). All available evidence indicates armadillos (and all xenarthrans) evolved in South America (Carlini et al. 1997; Murphy et al. 2007; O'Leary et al. 2013); most extant species occupy portions of Central and South America (Table 1; Abba and Superina 2010), with the one exception being the 9-banded armadillo (*Dasypus novemcinctus*), which is found from northern Argentina to the southern United States (Loughry and McDonough 2013a).

In addition to their conspicuous carapace, armadillos share other features. Like all xenarthrans, they have exceptionally low metabolic rates (McNab 1985), which may contribute to their relatively poor thermoregulatory abilities. Diets emphasize invertebrate prey (Redford 1985). The majority of species are active at night, and many dig burrows to which they return during the day. Reproduction is usually seasonal, with females of most species producing a single litter each year. Aside from the pichi (*Zaedyus pichiy*), all species seem to be active year round. Except during the breeding season, social interactions are rare; populations of most species appear to be low-density, consisting of widely scattered individuals that are relatively solitary and asocial (review in Loughry and McDonough 2013a).

With European colonization of the Americas, reports about armadillos began to appear, with early notable contributions by Belon (1588), D'Abbeville (1614), Piso and Marcgrave (1648), and Jonstonus (1660). The unusual appearance of armadillos apparently inspired considerable interest and curiosity. For example, Capanna (2009) reported that armadillos were depicted more than any other animal from the New World in zoological works of the 17th century. The unique attributes of armadillos have continued to spark interest in modern times. Some well-known examples include the famous ability of 3-banded armadillos (*Tolypeutes*) to roll into a ball when threatened, the occurrence of polyembryony in armadillos of the genus *Dasypus*, whereby females produce litters of genetically identical offspring via one or more divisions of a single fertilized egg each time they reproduce (the only vertebrates known to do so—Galbreath 1985), and the fact that 9-banded

Table 1.—A phylogenetically organized list of the 21 currently recognized species of armadillos, estimated size of geographic range, and the countries they are found in. Data updated from IUCN (2014). The number of publications produced between 1989 and 2013 that were based on studies conducted within each country is given parenthetically. Note that a single publication can address more than 1 species.

Taxon	Extent of range (km^2)	Countries of occurrence (number of publications)
Chlamyphorinae		
Calyptophractus retusus	272,000	Argentina (3), Bolivia (4), Paraguay (0)
Chlamyphorus truncatus	405,000	Argentina (13)
Dasypodinae		
Dasypus hybridus	1,420,000	Argentina (36), Brazil (6), Paraguay (0), Uruguay (3)
D. kappleri	6,000,000	Bolivia (0), Brazil (2), Colombia (1), Ecuador (0), French Guiana (2), Guyana (0), Peru (0), Surinam (0), Venezuela (0)
D. novemcinctus	19,100,000	Argentina (18), Bélize (5), Bolivia (17), Brazil (107), Colombia (13), Costa Rica (3), Ecuador (3), El Salvador (1), French Guiana (6), Grenada (0), Guatemala (1), Guyana (0), Mexico (27), Nicaragua (0), Panama (1), Paraguay (5), Peru (2), Surinam (0), Trinidad/Tobago (1), United States (209), Uruguay (1), Venezuela (1)
D. pilosus	53,000	Peru (1)
D. sabanicola	445,000	Colombia (0), Venezuela (1)
D. septemcinctus	5,870,000	Argentina (4), Bolivia (0), Brazil (21), Paraguay (1)
D. yepesi	22,000	Argentina (2)
Euphractinae		
Chaetophractus nationi	383,000	Argentina (1), Bolivia (7), Chile (1), Peru (1)
C. vellerosus	1,320,000	Argentina (45), Bolivia (13), Paraguay (0)
C. villosus	2,525,000	Argentina (93), Bolivia (12), Chile (2), Paraguay (0)
Euphractus sexcinctus	7,930,000	Argentina (18), Bolivia (13), Brazil (72), Paraguay (5), Surinam (0), Uruguay (1)
Zaedyus pichiy	1,300,000	Argentina (41), Chile (0)
Tolypeutinae		
Cabassous centralis	780,000	Bélize (0), Colombia (6), Costa Rica (1), Ecuador (0), El Salvador (0), Guatemala (1), Mexico (4), Nicaragua (0), Panama (0), Venezuela (0)
C. chacoensis	479,000	Argentina (9), Paraguay (0)
C. tatouay	2,500,000	Argentina (1), Brazil (15), Paraguay (2), Uruguay (2)
C. unicinctus	9,920,000	Bolivia (1), Brazil (18), Colombia (1), Ecuador (0), French Guiana (0), Guyana (0), Paraguay (1), Peru (0), Surinam (0), Venezuela (0)
Priodontes maximus	9,750,000	Argentina (17), Bolivia (3), Brazil (25), Colombia (0), Ecuador (1), French Guiana (0), Guyana (1), Paraguay (2), Peru (0), Surinam (0), Venezuela (0)
Tolypeutes matacus	1,200,000	Argentina (21), Bolivia (16), Brazil (4), Paraguay (1)
T. tricinctus	937,000	Brazil (19)

armadillos are the only species besides humans known to naturally contract leprosy (Truman 2005, 2008).

Given these fascinating features, one might expect that armadillos have been subject to intense and extensive scientific scrutiny. A recent review by Superina et al. (2014) suggested otherwise. They examined over 350 years (1660–2011) of publications about armadillos and found several troubling trends. Prominent among these was a substantial taxonomic bias, with publications about 9-banded armadillos dominating the literature (1,337 of 3,117 publications, 42.9%); the species in second place (*Chaetophractus villosus*) had just 312 publications (10.0%), and only 3 other species (*C. vellerosus*, *D. hybridus*, and *Euphractus sexcinctus*) exceeded 100 publications. Superina et al. (2014) also documented significant geographic biases in where studies were conducted, as well as in the topics examined. For example, although 9-banded armadillos have colonized the southern United States in just the last 200 years (Humphrey 1974; Taulman and Robbins 1996), 83.4% of all publications about this species (1,115 out of 1,337) were based on studies conducted in the United States. Studies that took place in more ancient parts of the vast range of *D. novemcinctus* were quite scarce. Further, fully 40% of all papers about *D. novemcinctus* (541 out of 1,337) were concerned with leprosy, with most of these involving laboratory investigations. Just 17% of all publications from the United States (190 of 1,115) involved field studies. Although not quantified, another problem with many studies (of all species) was small sample sizes, prompting questions about the generality of the findings.

These data indicate major gaps in our knowledge of armadillos. Some species are virtually unknown to science, while studies of better-known species have usually been geographically restricted to a small portion of the total range, and have focused on a limited number of topics. Thus, it would seem that there are abundant opportunities for mammalogists to make important contributions to our understanding of armadillos. But is the situation changing? Perhaps inclusion of so many publications from the past obscured positive trends in current work. To examine this question, we updated and repeated the bibliographic analyses of Superina et al. (2014) to generate a detailed picture of papers published in the last 25 years (1989–2013). Here, we use this data, in conjunction with that of Superina et al. (2014), to compare recent and long-term publication trends. Unlike Superina et al. (2014), we also obtained data on the number of other scientific publications that cited each paper in an attempt to assess the impact each publication has had within the scientific community. Overall, our findings reinforce many of the patterns identified by Superina et al. (2014) and suggest that improving our knowledge and appreciation of armadillos as research subjects remains an elusive goal.

Materials and Methods

We followed the methods described in Superina et al. (2014). Briefly, we used the bibliographic data set maintained by one of us (Superina 2014) in Endnote X5 (Thomson Reuters 2011) and updated it by querying multiple databases of scientific publications (e.g., Academic Search Premier, Medline, Ovid, WebSPIRS, Thomson's Web of Science, Google Scholar) using the key words "armadillo," "tatou," "tatú," "Gürteltier," "Dasypodidae," "Cingulata," and the names of all extant genera. We included journal articles, books, book chapters, theses and dissertations, and technical reports on extant species that were published between 1 January 1989 and 31 December 2013. We excluded paleontological and archaeological studies, as well as abstracts from scientific congresses and anonymous works. In total, we identified 1,039 publications, 163 of which were published since the previous analyses by Superina et al. (2014).

All publications were classified by publication type, year, species studied, country where the study was carried out, environment in which the study was carried out (laboratory, field, office, zoo, or a combination of these), language of publication, whether armadillos were the main object of study, and general and specific research topics (Table 2; for a detailed description, see Superina et al. 2014). Google Scholar was used to obtain the number of other scientific publications that cited each paper, despite the potential problems with this database (Bohannon 2014), because it included more publications on armadillos than the alternative we tested (Scopus).

We quantified the number of publications by country, species, and research topic using the corresponding search terms in Endnote. The statistical software R (R Development Core Team 2012) was used to perform correlation analyses between numbers of citations and area of distribution of the species (extent of occurrence according to IUCN 2014), number of publications per species, and number of publications per research topic.

Results

General features of recent publications.—Our sample of 1,039 publications represents 33.3% of all works that have been published on armadillos since 1660. A breakdown of our sample by publication type shows that 896 (86%) were journal articles, 69 (7%) book chapters, 17 (1.5%) books, 52 (5%) undergraduate or master's theses or doctoral dissertations, and 5 (0.5%) technical reports. Armadillos were the main topic in 49% of all publications and played a secondary role in the remainder—i.e., they were mentioned in one of the chapters or sections of general books or articles on mammals. Numbers of total publications, as well as those in which armadillos were the main topic, fluctuated from year to year, but there was no obvious long-term trend (Supporting Information S1).

Field and laboratory studies of armadillos were about equally common over the past 25 years, accounting for 33% and 36.8%, respectively, of all publications (Supporting Information S2). English was the predominant language of publication (78% of all publications); the proportion of publications in Spanish and Portuguese, the official languages in most countries where armadillos are found, was 15% and 6%, respectively.

Analyses of the number of publications that cited papers about armadillos showed that many papers have had minimal impact (Table 2). A total of 112 publications (11%) were not

Table 2.—Total number of publications on armadillos per research topic published between 1989 and 2013, and the number of times they were cited in other papers according to Google Scholar. Note that a single publication can address several research topics. Topics are listed by number of publications. General research topics are indicated in bold, with more specific areas within that topic (if any) listed underneath.

Research topic	Number of publications	Number of times cited	Publications that were never cited	Publications not found in Google Scholar
Health	**308**			
Leprosy	113	1,168	6	19
Pathologies	77	2,007	3	5
Parasitology	69	685	12	3
Chagas	26	731	2	0
Hematology	16	94	0	2
Immunology	7	57	0	0
Ecology	**257**			
Ecology	140	1,201	23	5
Nutrition	48	821	5	4
Predators	38	1,235	2	1
Behavior	31	299	3	0
Physiology	**206**			
Physiology	65	561	3	8
Metabolism	17	237	0	1
Distribution	**124**	2,502	37	15
Anatomy	**150**			
Anatomy	107	1,142	17	8
Histology	32	169	2	1
Embryology	11	278	1	1
Management	**84**			
Use[a]	66	1,169	10	13
Captivity	18	48	3	3
Miscellaneous	**83**			
General	55	1,506	6	15
Methods	28	274	3	3
Genetics	**55**	2,961	6	3
Conservation	**53**	866	12	6
Reproduction	**39**	657	6	3
Evolution	**38**	2,733	3	2
Taxonomy	**16**	917	1	1

[a] Involves impacts of various human activities on armadillos.

found in Google Scholar. The majority of these were papers published in small regional journals from Latin America that were not indexed by Google Scholar. An additional 249 (24%) papers were not cited in other publications, and 470 (45%) were cited ≤ 10 times (Table 2). About half of all publications in Spanish (75 of 156) and Portuguese (31 of 61) were either not found in Google Scholar or have not been cited. Even 16% of publications in English (127 of 807) were never cited, and nearly half of the works in English (381 of 807) were cited ≤ 10 times. The most cited works in all 3 main publication languages were not specifically about armadillos, but publications in which armadillos played a secondary role. Some examples include Eisenberg (1989, cited 1,442 times) and Murphy et al. (2001, cited 1,093 times) in English; Alberico et al. (2000, cited 212 times) and Diaz and Ojeda (2000, cited 167 times) in Spanish; and Machado et al. (1998, cited 154 times) and Cerqueira et al. (1990, cited 52 times) in Portuguese.

Research topics.—In terms of general research topics, the top 3 areas of study over the last 25 years were health, ecology, and physiology (Table 2). As for specific research topics, the single largest number of publications (n = 140) was dedicated to the ecology of armadillos, followed by distributional studies and leprosy (Table 2). Anatomical studies were also quite prevalent (Table 2).

The number of publications about a particular topic was positively correlated with the number of other publications that cited those papers (r = 0.50, P = 0.01). However, the most cited papers by far were those on genetics and evolution even though publications on these topics were not particularly numerous (Table 2). Further, it is worth noting that publications on genetics and evolution often were not about armadillos per se, which considerably distorted the results for the number of citations per species. For instance, 6 publications on genetics (out of 30 papers total) accounted for 80% of citations for *Cabassous unicinctus* (Table 3).

Research species.—The 9-banded armadillo (*D. novemcinctus*) was the most studied species of armadillo with 49% of all works published over the past 25 years dedicated to it (Table 3). However, *D. novemcinctus* was the main topic in just 214 (42%) of these publications (Table 3). Even a focus on armadillos was no guarantee that a particular species was studied in detail. For instance, armadillos were the main topic in 24 of the 30 publications mentioning *C. unicinctus* (Table 3), but only 6 of them dealt exclusively with this species, and of these 5 were descriptions of range extensions and the 6th a description of its karyotype.

Aside from *D. novemcinctus*, only 2 other species (*C. villosus* and *E. sexcinctus*) were the subject of > 100 publications

Table 3.—Publication information for each currently recognized species of armadillo. The total number of publications is provided in each column, with the number of publications where armadillos were the main topic provided parenthetically. Note that a single publication can address several species. Species are listed in order of total number of publications.

Species	Publications	Citations	Publications that were never cited	Publications not found in Google Scholar
Dasypus novemcinctus	513 (214)	6,465 (2,043)	60 (16)	48 (22)
Chaetophractus villosus	118 (90)	1,034 (787)	14 (11)	13 (12)
Euphractus sexcinctus	117 (55)	1,196 (664)	24 (9)	7 (4)
Chaetophractus vellerosus	63 (41)	511 (252)	12 (8)	3 (3)
Priodontes maximus	58 (42)	735 (599)	11 (6)	9 (7)
Tolypeutes matacus	56 (38)	690 (507)	9 (6)	7 (6)
Zaedyus pichiy	49 (37)	617 (564)	5 (4)	4 (4)
Dasypus hybridus	46 (33)	261 (213)	6 (1)	6 (4)
Cabassous unicinctus	30 (24)	586 (557)	4 (4)	1 (1)
Dasypus septemcinctus	26 (14)	171 (105)	4 (0)	3 (1)
Cabassous tatouay	20 (8)	205 (58)	7 (2)	3 (1)
Tolypeutes tricinctus	20 (14)	142 (138)	5 (1)	1 (1)
Chlamyphorus truncatus	16 (12)	106 (84)	1 (1)	2 (2)
Cabassous centralis	15 (8)	73 (45)	4 (3)	4 (2)
Dasypus kappleri	11 (9)	414 (401)	0 (0)	1 (1)
Chaetophractus nationi	10 (7)	13 (10)	3 (2)	1 (0)
Cabassous chacoensis	9 (9)	47 (47)	2 (2)	1 (1)
Calyptophractus retusus	8 (6)	42 (31)	1 (1)	0 (0)
Dasypus yepesi	2 (2)	28 (28)	0 (0)	0 (0)
Dasypus sabanicola	1 (0)	0 (0)	1 (0)	0 (0)
Dasypus pilosus	1 (0)	3 (0)	0 (0)	0 (0)
Dasypodidae[a]	251 (86)	10,829 (1,757)	24 (12)	30 (12)

[a] Publications discussing armadillos without specifying the species or just mentioning the entire taxon Dasypodidae.

Table 4.—Number of publications per range country (countries where armadillos occur naturally) for papers about armadillos published between 1989 and 2013. The total number of publications is provided as well as the number where armadillos were the main topic of the paper. Countries are listed in order of total number of publications.

Country	Total publications	Number with armadillos as main topic	Country	Total publications	Number with armadillos as main topic
United States	305	153	Ecuador	5	1
Argentina	237	167	Chile	4	3
Brazil	226	82	Peru	4	1
Bolivia	45	23	Venezuela	4	0
Mexico	34	13	Guatemala	2	1
Colombia	22	3	Panama	2	0
Paraguay	11	5	Trinidad & Tobago	2	0
Costa Rica	7	2	El Salvador	1	0
French Guiana	7	3	Guyana	1	1
Uruguay	6	4	Nicaragua	1	1
Belize	5	2	Grenada	0	0

between 1989 and 2013, and for both those species the proportion of works in which they were the main topic was higher than for *D. novemcinctus* (Table 3). In contrast, most other species suffered from neglect by researchers. Seven of 21 species of armadillo were the main topic of < 10 publications, and we could not find a single work published since 1989 in which *D. sabanicola* or *D. pilosus* were the main subject (Table 3). See Supporting Information S3 for a list of the top 3 research topics for each species of armadillo.

Analyses of citations showed that general works on Dasypodidae received a proportionally much higher number of citations than publications involving specific species. While the general works accounted for a total of 10,829 citations, papers on 1 (or just a few) of the 21 extant species were cited 13,338 times (Table 3). Using data from all species, the number of publications that cited each paper was highly correlated with the total number of publications for each species ($r = 0.96$; $P < 0.0000$) as well as with each species' area of distribution ($r = 0.82$; $P < 0.0000$).

Research locations.—The proportion of studies performed in range countries (i.e., those countries where armadillos occur naturally) was 90% between 1989 and 2013 (Table 4). Distribution was the most studied topic in 13 countries, followed by ecology in 11 and use (i.e., impacts from human activities such as traffic or hunting—Superina et al. 2014) in 8 countries (Supporting Information S3). In addition to the data in Table 4, 10% of publications ($n = 109$) were performed in 24 countries where armadillos are not endemic, the most relevant ones being the United Kingdom (18 publications), France (14), and Germany (11). The top 3 research

topics investigated in countries where armadillos are not endemic were leprosy (25.8%), genetics (22.0%), and evolution (12.9%).

Examination of works conducted just in range countries showed that the proportion of studies done in Latin America was about twice that of the United States (67% and 33%, respectively). However, much of this was attributable to studies conducted in just 2 countries (Argentina and Brazil). Combined with the United States, these 3 countries accounted for 82% of all publications on armadillos originating in range countries. In contrast, 14 range countries produced < 10 and 2 countries not a single publication on armadillos between 1989 and 2013 (Table 4).

Studies of particular species were not uniformly distributed across range countries. For example, 9-banded armadillos occur in 22 countries (Table 1), yet almost half of the publications about this species originated from a single country, the United States (209 of 421 papers). Conversely, 15 other countries, which constitute much of the range of this species, collectively produced just 30 publications (7.1%). Similar findings were apparent for other species as well (Table 1).

Discussion

Comparison of recent and long-term publication trends.—Generally speaking, our findings echo many of the patterns reported by Superina et al. (2014), which is not too surprising given that many of the same publications were included in both data sets. Nevertheless, a number of differences were found. For example, the proportion of publications based on fieldwork increased from 18% in the period 1660–2011 to 33% in the period 1989–2013, with a corresponding drop in the proportion of publications that were based exclusively on laboratory work (Supporting Information S2). The proportion of mixed studies, i.e., those that combined fieldwork with laboratory analyses, also increased considerably, while works performed in zoos increased slightly (Supporting Information S2).

Undoubtedly connected with the increased emphasis on fieldwork, ecology ranked higher as a general research topic in the recent literature than it did historically (recent = 24.7% of all publications, historic = 11.3%). Conversely, publications about leprosy declined; this topic accounted for 15% of all publications from 1660 to 2011 but was only addressed in 8% of the works analyzed here (Table 2).

English remained the primary language of publication, increasing from 68% of all publications between 1660 and 2011 to 78% for the period 1989–2013. The percentage of publications in Spanish and Portuguese remained stable, but publications in other languages (e.g., German, French, Russian, and Polish) were much less common in the recent literature (< 1% each of all publications).

The proportion of studies performed in range countries increased from 74% in the period 1660–2011 to 90% in 1989–2013. Within range countries, the proportion of works done in Latin America increased from 53% (period 1660–2011) to 67% (period 1989–2013), while studies performed in the United States decreased from 47% to 33%. Comparison of the 3 countries with the most publications (Argentina, Brazil, and the United States) showed that the proportion of works in which armadillos were the main topic remained relatively stable in the United States (153 of 305 [50.2%] in 1989–2013 compared to 516 of 1114 [46.3%] in 1660–2011) and in Argentina (167 of 237 [70.5%] compared to 368 of 575 [64.0%], respectively). In contrast, although there were many recent publications from Brazil, the proportion in which armadillos were the main topic was reduced by almost half from what was found previously (82 of 226 [36.3%] publications in 1989–2013 compared to 256 of 374 [68.4%] in 1660–2011). Instead, in many recent works armadillos played a minor role, such as lists and descriptions of species found in particular areas or as roadkills (e.g., Cáceres et al. 2012; Paes and Povaluk 2012; Weiss and Vianna 2012).

One last trend to mention is the continued dominance of publications about 9-banded armadillos. Superina et al. (2014) found that 36% of publications appearing between 1660 and 2011 were about this species, but this increased to 49% of all works published over the past 25 years (Table 3).

Interpretation of publication trends.—Based on our analyses, it seems reasonable to conclude that taxonomic, geographic, and topic biases continue to persist in publications about armadillos. In addition, data on citation counts indicate that many papers do not have much of an impact. Indeed, an oversimplified summary of our primary findings is that the typical paper about armadillos is written in English and involves a study conducted in the United States of 9-banded armadillos, the results of which will not be widely cited. While there is certainly some truth in this rather negative characterization, our data provide some reasons to be optimistic as well.

On the positive side, the number and diversity of publications we identified suggests knowledge of armadillos is continuing to expand in many areas. A particularly encouraging trend is the increase in the number of publications based on field studies and with an ecological emphasis. Such studies should greatly increase our understanding of armadillos in their natural habitats, but it is important to point out that this only applies to a few species at present. Similar studies are still needed for the majority of species. Likewise, even though the number of ecological studies is on the increase, we found that distributional accounts were the primary topic of research in the majority of range countries, which suggests that we have yet to move beyond basic natural history information in many cases.

Two prominent concerns uncovered by our analyses are, first, the distinct disparity between the total number of publications that mention armadillos and those in which armadillos were the main topic of the paper (Supporting Information S1). Whether this disparity is more pronounced for armadillos than for other mammals is an open question. Regardless, it seems to us that all too often armadillos were merely components of larger works, as exemplified in distributional accounts and, perhaps most conspicuously, in papers dealing with evolution and genetics. In most cases, these latter publications used samples from one or more species of armadillo as part of larger analyses examining evolutionary relationships among

mammals (e.g., Murphy et al. 2001). While heavily cited and clearly of importance, such papers provide little insight for anyone wishing to know more about armadillos (or any of the other species sampled). However, to be fair, the data generated in these analyses do lay the foundation for future taxon-specific investigations. Second, although we documented an increase in the number of publications originating in the range countries of armadillos, our citation data suggest that many of these are not having much impact, particularly for papers originating in Latin America and written in Spanish or Portuguese. There is probably no easy way to rectify this situation but it does mean that much potentially valuable information is being missed.

Recent findings.—The foregoing bibliographic analyses highlight many areas where more study of armadillos is warranted. However, recent findings indicate that even topics that have been intensively studied in the past may require reexamination. For example, aside from the recognition of *D. yepesi* as a distinct species in the 1990s (Vizcaíno 1995), the taxonomic composition of living cingulates has remained unchanged for decades (Wetzel 1985; Wetzel et al. 2008). Thus, the conventional wisdom that there are 21 extant species of armadillos has gone unchallenged for some time. The situation is changing as several research groups have employed molecular and morphological analyses to reevaluate the taxonomic status of most species (Delsuc et al. 2012; Abba et al. 2015). Their results indicate that the systematics of Dasypodidae requires serious revision. Indeed, at this point, it is difficult to provide a definitive answer to the simple question of how many species of armadillos there are. This is important because, given the substantial taxonomic bias in publications about armadillos documented here and in Superina et al. (2014), there is a pressing need for research efforts directed at lesser-known taxa. However, in order to do this obviously one must first know which taxa actually exist that should be targeted.

Two other examples further highlight the point that our understanding of certain well-known topics may not be as complete as previously assumed. First, the occurrence of polyembryony in long-nosed armadillos of the genus *Dasypus* has been studied for over a century because it is such a unique form of reproduction among vertebrates (Fernandez 1909; Newman and Patterson 1910; review in Loughry and McDonough 2013a). The embryological events that generate polyembryony have been thoroughly documented (Enders 2002) but why long-nosed armadillos reproduce this way in the first place remains unknown. The argument of Galbreath (1985) that polyembryony evolved to increase female reproductive success by by-passing certain reproductive constraints has been accepted uncritically in most subsequent reviews of the subject (Craig et al. 1997; Loughry et al. 1998; Avise 2008). Specifically, Galbreath (1985) proposed that space within the uterine fundus, where the blastocyst sits for a variable length of time prior to implantation, could only accommodate 1 zygote. If so, then the only means for females to produce more offspring would be for a single fertilized egg to divide into multiple embryos after implantation. While this is an appealing hypothesis, Enders (2008) has argued that it fails because there appears to be sufficient space within the uterine fundus for more than 1 blastocyst. Consequently, it may still be true that polyembryony evolved in *Dasypus* armadillos in order to by-pass some constraint that normally limits reproduction to just 1 or 2 offspring (as is the case for all other species of armadillos), but the nature of that constraint remains obscure (Loughry and McDonough 2013a). It is also worth mentioning that, although it is presumed that polyembryony occurs in all *Dasypus* species, it only has been conclusively documented in *D. novemcinctus*. Until data about reproduction in the remaining members of the genus are published, any attempt to explain the evolution of polyembryony in armadillos will by necessity remain incomplete.

Historically, leprosy has been the single most studied topic about armadillos (Superina et al. 2014). There is no doubt that we have learned much about the disease from these largely laboratory-based investigations (review in Truman 2005, 2008). Yet, questions remain, particularly regarding the dynamics, distribution, and consequences of the disease in wild populations. For example, until recently it was thought that infection with *Mycobacterium leprae* (the causative agent in producing leprosy) was restricted geographically (in the United States at least) to populations of 9-banded armadillos located along the west side of the Mississippi River and along the Gulf of Mexico coast from Louisiana to south Texas (Truman 1996). However, new surveys have uncovered infected populations throughout the southern United States, indicating possible rapid and expansive spread of the disease (Loughry et al. 2009). Not only that but also a single genetic strain of *M. leprae* was identified in most infected populations (Truman et al. 2011). This too has changed with new surveys that have found a 2nd strain of *M. leprae* present in at least some populations in Florida (R. Truman, in litt.). Whether the 2 strains have come into contact and, if so, what the dynamics of their interactions are within populations of armadillos remain unknown. More generally, we only have a partial picture of the current geographic distribution of infection, even in the United States. An update will require extensive sampling at many localities, not only in the United States but especially in the remaining portions of the range of *D. novemcinctus* in Central and South America.

Finally, field studies have failed to uncover any obvious consequences of leprosy infection in wild populations of *D. novemcinctus* (Morgan and Loughry 2009) despite ample evidence of physiological costs documented in the laboratory (review in Truman 2008). In addition, because most field studies of leprosy have involved single surveys for infection prevalence, we have a very limited understanding of how patterns of infection may change over time (Williams and Loughry 2012). Thus, a priority for the future will be to develop detailed longitudinal studies of infected populations that will allow further analyses of the consequences and dynamics of leprosy in wild armadillos. Similar concerns apply to other pathogens and other species of armadillos. For most armadillos, the few publications about pathologies and parasites largely describe the presence or absence of a certain pathogen or its seroprevalence. In most

cases, it remains unknown how pathogens affect their hosts, including how they might influence host behavior, or how they impact population dynamics.

Looking ahead.—We have highlighted a number of areas where, in our opinion, mammalogists can make important contributions to our understanding of armadillos. Such information will be interesting in its own right but will also have broader implications due to the many special features of cingulates (and xenarthrans generally—Superina and Loughry 2015) that make these animals such unique mammals. We conclude by mentioning what we consider to be some of the most pressing, as well as promising, priorities for future study.

Perhaps of most immediate concern will be a systematic revision of Dasypodidae in light of new molecular and morphological data (Delsuc et al. 2012; Abba et al. 2015). With a revised taxonomy in place researchers will be able to identify those species and populations most in need of study, both from a purely scientific standpoint, and for assessment of conservation status. Clearly, a top priority should be to initiate studies of lesser-known taxa that are also most at risk of extinction.

A related point is that, for all species of armadillos, there is an obvious need for more field studies, particularly involving long-term monitoring of populations of marked individuals. Such information is essential in order to address many basic questions in ecology and evolution (Clutton-Brock and Sheldon 2010) and will also be necessary in order to formulate viable management plans for the conservation of imperiled taxa. In addition, investigators will need to think about ways to broaden the appeal of their research to those studying other taxa by employing a more experimental approach, in which studies of armadillos are used to test fundamental, theoretical ideas as opposed to the past emphasis on largely descriptive studies of the natural history of particular species (Loughry and McDonough 2013b). Such an approach has already proven quite successful in studies of the functional morphology of armadillos and other xenarthrans (Vizcaíno et al. 2008) and should be applied more broadly.

We end by noting that, while there are clearly many opportunities for progress to be made on many fronts in the study of armadillos, it is hard to be optimistic about how rapidly advances will come, at least in the short term. This is because, at present, there are very few individuals actively engaged in the study of armadillos, particularly in the wild. For example, the Anteater, Sloth and Armadillo Specialist Group of the International Union for the Conservation of Nature's Species Survival Commission currently has a total of 21 members, but only 6 or 7 of whom could be considered to work primarily on armadillos. Indeed, it is difficult to list more than a handful of field studies that are currently underway. Undoubtedly, there are many reasons for this but the fact remains that unlike many other groups of mammals, armadillos (and all xenarthrans) have not attracted large numbers of researchers. Given this state of affairs, it seems likely that many of the publication patterns we have described largely reflect the contributions of a small group of individuals, probably < 30 in number, whose idiosyncratic preferences have led to emphases on a limited number of topics in a limited number of species, and in a limited number of locales. It is our hope that this paper will go some way toward rectifying this situation, and spur individuals to consider armadillos as important, worthy, and rewarding research subjects.

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Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Temporal changes in the total number of publications on armadillos (solid line) and those in which armadillos were the main topic of the paper (dashed line) for the period 1989–2013.

Supporting Information S2.—Percentage of publications about armadillos classified by the environment in which the study was conducted. Office refers to analyses and reviews that relied on previously collected data; mixed studies were done in a combination of environments. Historic data are for the period 1660–2011 and come from Superina et al. (2014). Recent data are for the period 1989–2013 and come from the present study. Numbers above the columns indicate the number of publications per period and study environment.

Supporting Information S3.—Top 3 research topics (by number of publications) for each species of armadillo and each range country. Species and countries are listed alphabetically. See Tables 3 and 4 for total numbers of publications for each species and country.

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