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REVIEW

Leprosy in wild armadillos

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Summary Wild nine-banded armadillos (*Dasypus novemcinctus*) in the south central United States are highly endemic natural hosts of *Mycobacterium leprae*. Surveys conducted over the last 30 years on more than 5000 animals confirm that the infection is present among armadillos in Arkansas, Louisiana, Mississippi and Texas. Highest prevalence rates are found among the animals in low-lying alluvial and coastal areas, primarily in Louisiana and Texas. Both animal density and local factors may contribute to the detectability of armadillo leprosy in those regions. Little evidence for *M. leprae* infection is found among armadillos elsewhere in the US range, and only a few reports relate finding the infection among animals in Central or South America. However, the issue has received only scant attention in other countries. Armadillos only recently expanded their range into the US, and leprosy was present in Texas and Louisiana prior to the arrival of armadillos. The ecological relationship between humans and armadillos with *M. leprae* in this region remains unclear. However, infected armadillos constitute a large reservoir of *M. leprae* and they may be a source of infection for some humans in this country, and perhaps in other locations across the animal's range.

Introduction

Other than humans, nine-banded armadillos (*Dasypus novemcinctus*) are the only highly endemic natural hosts of *Mycobacterium leprae*. A leprosy like disease was first reported among wild armadillos in 1975,[1] and by 1983 the sylvan agent had been confirmed to be identical to the *M. leprae* infecting humans.[2] Numerous studies have shown that *M. leprae* is highly prevalent among wild armadillos in parts of Louisiana and Texas, but rare or absent in other locales. The probable origin of the infection, its geographic range, and the risks it might present to humans has been the subject of considerable speculation. This paper reviews our current understanding about the distribution of *M. leprae* infections among wild armadillos and the relative importance of these animals as the only confirmed, large, natural, non-human reservoir of *M. leprae*.

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Natural history

Rudyard Kipling tells that armadillos originated through an effort by hedgehogs and tortoises to flummox jaguars.[3] They are exotic looking, cat-sized animals with short legs and a hard flexible carapace armouring most of their body. Found only in the 'New World', armadillos range throughout South and Central America and into the United States. Members of the mammalian order Xenarthra, the term 'armadillo' is applied across several genera.[4] The 'armadillo' of most importance to leprologists, and the only one present in North America, is *Dasypus novemcinctus* (also known *as* the nine-banded or long-nosed armadillo). In this review, the term 'armadillo' will refer only to the *D. novemcinctus* unless noted otherwise.

Armadillos are not native to the US, but began slowly expanding their range north from Mexico around 1880. They first entered Louisiana in 1926 and had crossed the state to the Mississippi river by 1957. Today, armadillos are found from Argentina to Colorado and through the southeastern US to Florida. They are present on many Caribbean islands and were probably carried there aboard trading ships. Several reports relate private citizens introducing armadillos into the state of Florida, beginning in about 1922. These animals established a second US population, which also slowly expanded its range and merged with the main US group around 1985.[5–7]

Armadillos can occupy a diverse range of ecological habitats, but are usually found in close association with water supplies. Prodigious diggers, armadillos exchange between burrows with impunity. They do not hibernate.[8,9] The main factors limiting their range appear to be a poor tolerance of cold temperatures, and the capacity of the environment to produce sufficient insects and grubs, the mainstays of their otherwise omnivorous diet.[5,7]

In some low-land areas of the US, densities of more than seven armadillos/acre are common,[10] but the animals do not form social communities and are not monogamous. Armadillos are unregulated game in most parts of the US and can be taken as food year round. They are often viewed as pests, except in Texas, where they are the official state small mammal and enjoy some protection. Adult armadillos do not migrate and are relatively sessile. They will not wander outside of their home range for years, unless there is some calamity. Young animals disperse from their birth communities each year to found new habitat, or to compete with aging adults,[11–14] The marked range expansion of armadillos in North America has been associated largely with the diminution of predators, as well as the extraordinary fecundity of the species.[5]

Physiology

Armadillos exhibit a number of interesting traits. As the most abundant Xenarthran, they are of particular interest to comparative and evolutionary biologists.[15–17] To help support those efforts on a molecular level, the Human Genome Consortium recently sequenced the entire *Dasypus novemcinctus* genome. A 2X coverage, containing 75% of the total genomic sequence is already complete and available at the NCBI database (http://www.ncbi.nlm.nih.gov/BLAST/tracemb.html).

Their reproductive cycle has been of special interest because they exhibit both gestational diapause and polyembryony. After fertilization, the armadillo embryo undergoes a 4–5 month period of arrested development prior to implantation, after which it immediately divides to form four identical offspring.[18] The female matures in her second year and can bear quadruplicate offspring through the remainder of her 12-year lifespan. Plasma progesterone concentrations are useful in age stratifying armadillo populations and for assessing their fecundity[10,19] Unfortunately, armadillos reproduce only rarely in captivity, and they must be obtained from the wild for investigative purposes.[20]

Body temperature was the armadillo's main trait that first attracted the attention of leprologists. Even under normal conditions the animal's core temperature is in the 32–35°C range.[21] The hard integument and lack of furry coat probably contribute to their poor thermal maintenance, and a cool temperature can be an effective defense against many parasites and pathogens.[5,22] However, in extending on Shepard's observation that cool temperatures favoured the growth of *M. leprae* in the mouse foot pad,[23] Kirchheimer and Storrs began experimentally infecting armadillos in 1968. By 1971 they had shown that huge quantities of leprosy bacilli could now be made available through armadillos.[24] The animals rapidly became the hosts of choice for *in vivo* propagation of *M. leprae*, and several armadillo colonies were founded around the world. However, while collecting wild armadillos near New Iberia, Louisiana in 1975, Walsh[1] found a systemic mycobacteriosis among some of them that was indistinguishable from the disease caused by *M. leprae*.

Detecting *M. leprae* in armadillos

Armadillos exhibit the full spectrum of immunological responses to *M. leprae*, ranging from TT to LL, and can be classified according to the Ridley–Jopling scale with Lepromin.[25,26] The majority of armadillos appear to be multibacillary types. Leprosy progresses very slowly in armadillos, and even laboratory infected animals require 18–24 months of incubation before they succumb to their leprosy. Obviously, nearly all the infected armadillos seen in the wild appear to be adults. There are no gender related differences in susceptibility or disease progress,[27,28] and though armadillos exhibit characteristic nerve involvement, animals in the wild show little evidence of deformity or impairment.[29–31] Such animals may quickly become prey or be easily out-competed in the wild, even though leprosy seems to offer little competitive disadvantage to the population overall.[32]

M. leprae infection in armadillos produces few gross symptoms, and it is not possible to distinguish normal from *M. leprae*-infected animals by their outward appearance. Armadillos manifest a systemic illness that primarily involves the reticuloendothelial tissues.[31,33] Intermittent low level bacteraemia leads to a generalized dissemination of bacilli in the late stages of the infection. No organ system is spared, but cooler body regions tend to exhibit greater involvement. *M. leprae* can be demonstrated in the skin, nodules, lymph nodes, blood or other organ tissues with direct smears, histopathological exam and PCR.[26,28,34]

Multibacillary armadillos also have a strong antibody response to *M. leprae*. Among laboratory infected animals, IgM antibodies to the *M. leprae*-specific PGL-1[35] antigen arise in about a third of the time required for bacilli to become detectable in skin scrapings and ear biopsies.[36,37] The timing of their appearance and general level is highly correlated with the bacterial load in the animal's tissues.[38] First detection is generally associated with a 1 + BI in some RES tissue.[34,39] The levels of PGL-1 IgM increase with increasing bacterial load in the animal and they persist over the course of the disease.[38]

Origin of the infection

The report of a 'leprosy like' disease among wild armadillos was highly controversial, and the enthusiasm of both lay and scientific writers about the subject was unrestrained. Some editorials suggested that a new agent had been discovered that could be useful in modeling human leprosy.[40] Others hailed the report as revealing a new zoonosis and a threat to the public health. No earlier studies had found systemic mycobacteriosis among armadillos, and the report of a sylvan infection was not immediately confirmed by other laboratories.[41] DNA homology studies showed that the sylvan agent actually was *M. leprae*.[2] Skinsnes speculated that sylvan leprosy was newly evolved and that it might have originated through the escape or improper disposal of experimentally infected armadillos at one of the research centers working with armadillos.[42] The accusation polarized the community and trivialized armadillo studies for years. The 'environmental contamination' claim was perpetuated by several groups, and is frequently alluded to even today by uninformed individuals.[28,43–45]

A number of surveys were launched to determine the geographic range of armadillo leprosy. By 1977, Walsh had found 50 *M. leprae*-infected armadillos from among 459 animals sampled at 11 different locations around the state of Louisiana and one in Texas.[46] With such a wide geographical distribution, it seemed unlikely that sylvan leprosy might be a recent phenomenon. However, no evidence of the infection was found among armadillos in Florida, and only one (1/218) *M. leprae*-infected armadillo was found in Mississippi[28,46,47] Kirchheimer examined more than 400 armadillos from various locations in central Texas, Louisiana and Florida, before confirming existence of the disease in a single Louisiana animal[28,43,44,48]. Smith showed that leprosy was highly prevalent (21/451) among armadillos in counties along the Texas coastline and extended towards Mexico.[2,49] However, only one (1/96) infected armadillo was found in Mexico.[50] Eventually, one other infected armadillo was found in Argentina.[51] Otherwise, none (0/536) of the mixed armadillo varieties examined in either Colombia[52] or Paraguay[53] appeared to be infected. The apparent geographical distribution of the infection fueled continued speculation that armadillos had acquired leprosy in the US, perhaps through natural mechanisms,[30] or from contamination of their environment.

The environmental contamination hypothesis was disproved finally in 1985. With the advent of serological screening methods to detect antibodies to the PGL-1 antigen, we examined sera taken from wild armadillos in years predating the animal's use in leprosy research to determine the time frame that armadillos might have acquired *M. leprae*.[36] Collected by Roth[54] in 1960–1964 as part of a survey for leptospires in Louisiana wildlife, the sera had been stored frozen at Louisiana State University for 25 years prior to our study. We found that 17/182 sera reacted specifically with PGL-1, indicating that *M. leprae* must have been enzootic among armadillos at least by 1961. Armadillo leprosy could not have originated through any possible accidental contamination of the environment on the part of leprosy researchers, who only started working with armadillos in 1968/[36] Therefore, it must have evolved by natural means and armadillos could have acquired the infection in any number of different locations or repeated the event many times over the years.

Geographic distribution of armadillo leprosy

Seeking mainly to confirm the presence or absence of disease in distant locales, early workers sampled small numbers of armadillos at random locations and often reported disparate prevalence rates. The size and structure of animal populations vary in different environments, and can influence the observable prevalence of disease. Louisiana is a low-land area at the mouth of the Mississippi river. Among its most prominent features are the alluvial swamps and bottoms associated with the Mississippi, Red and Atchafalaya rivers, and the generally similar low prairies and marshes that form the coastal margin and extend on through southern Texas. This region juxtaposes mixed pine and deciduous forests that are easily identified in geologic soil maps and satellite images of the region.[55] A representative drawing of the region on a county basis is shown in Figure 1.

There is a large reservoir of *M. leprae* among wild armadillos in this low-land region. By 1986, investigators had described at least 136 armadillos with histopathologically detectable *M. leprae* in their ear tissues among some 3500 animals sampled mainly in the low-land areas of Louisiana and Texas[2,28,56] A systematic survey among 565 animals spanning four locations in this area between north Louisiana and Corpus Christi, Texas, confirmed the average 3.8% histopathological prevalence rate reported by others, and showed that about 16% of the armadillos populating the area also had detectable IgM antibodies to PGL-1. Repeated observations at the same location where Roth[54] had taken armadillos in the 1960–1964 survey, showed a steady maintenance of the infection from year to year, and confirmed that the prevalence rate had not changed significantly over the ensuing 30-year period.[10] *M. leprae* is intensely transmitted among armadillos in this region. In one location, the incidence density estimate based on PGL-1 IgM seroconversion was 3.5 cases/1000 animal days.[57] The antibody positive animals are almost entirely in the adult cohort. Using

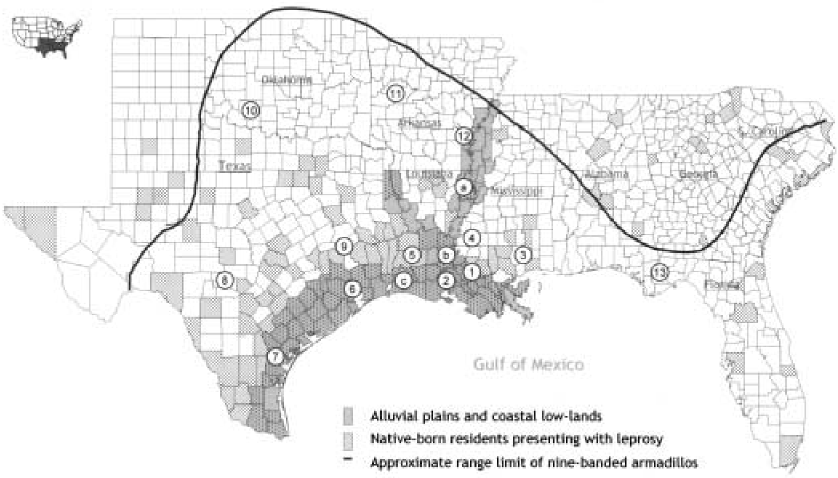

Figure 1. Map of southeastern United States by county. *Insert* shows general location in country. Dark line illustrates the northern range of armadillos in the US. *Grey* counties are part of the alluvial and coastal low-lands. *Stippled* counties have had native-born residents presenting with leprosy. Numbers identify general locations where armadillos have been surveyed. All locations are approximate: 1 = Carville, Louisiana; 2 = New Iberia, Louisiana; 3 = Picayune, Mississippi and area nearby Kentwood, Louisiana; 4 = Woodville Mississippi and Louisiana parishes; 5 = Leesville, Louisiana; 6 = Houston, Texas; 7 = Corpus Christi, Texas and Welder Wildlife Refuge; 8 = Luckenbach, Texas; 9 = area of College Station and Palestine, Texas; 10 = Lawton, Oklahoma, Wichita Mountains National Wildlife Refuge; 11 = Clarksville, Arkansas; 12 = Desha County, Arhkansas; 13 = Tallahassee, Florida and St Marks National Wildlife Refuge; A,B,C = Louisiana locations for systematic survey of armadillos for *M. leprae*, a = Tensas River National Wildlife Refuge, b = East Atchafalaya Management Area, c = Lacassine National Wildlife Refuge.

plasma progesterone concentrations to age stratify the populations showed that the age adjusted antibody prevalence rate remained reliably consistent between the different locations, and nearly a third of all the adult armadillos surveyed appeared to harbour *M. leprae*.[10] Therefore, *M. leprae* infection is really quite common among armadillos in these low-land areas; and steady maintenance of high rates of disease over a very large geographic area suggests that they have harboured *M. leprae* for many generations.

Armadillos are more difficult to acquire outside low-land areas, and most surveys in non-low-land regions have had to rely on samples from ‘road-killed’ animals[58] or commercial trappers. However, numerous results show that *M. leprae* infection is significantly less common among armadillos in those locales. No infected armadillos have been reported from among nearly 1000 animals examined in Florida,[28,38,44] and, similarly, we found no evidence of the infection (0/67) among armadillos taken near the other end of their range around Lawton, Oklahoma (Table 1). In Texas, one infected armadillo was reported from around College Station[59] and Walsh found one (1/61) infected armadillo among a group taken near Palestine, Texas in 1977.[46] Otherwise, no evidence for leprosy has been reported among 427 armadillos sampled more than 100 k from the Texas coastal margin,[28,43,60,61] including (0/86) a group of animals from near Luckenbach, Texas that also was screened serologically (Table 1). A large survey of ear tissues taken from 853 road-killed armadillos in Alabama, Arkansas, Florida, Georgia and Mississippi also failed to find any histopathological evidence for *M. leprae* infection in those areas.[62] Walsh too reported no evidence for *M. leprae* (0/178) among armadillos taken near Picayune, Mississippi.[46] Otherwise, one armadillo (1/40) with histopathologically detectable bacilli in its ear tissues was found near Natchez,[47] and we

Table 1. Additional wild armadillos examined for naturally acquired leprosy at the NHDP

Country	State	City	Number sampled	Number PGL-1 IgM+[a]	Number histopath+[b]
Argentina	Corrientes	Mercedes	83	2	0
Grenada		St George’s	25	0	0
United States	Arkansas	Clarksville	102	0	0
		Desha County	42	9	ND
	Florida	Sarasota	26	0	0
		St Mark’s NWR	37	0	0
		Tallahassee	142	0	0
	Louisiana	Kentwood	145	9	2
		Deritter	13	1	1
		Felecianas	135	3	0
		Atchafalaya[c]	550	85	16
		Tensas NWR[c]	77	18	5
		Lacassine NWR[c]	78	16	1
	Mississippi	Woodville	54	1	0
	Oklahoma	Lawton	67	0	0
	Texas	Luckenbach	86	0	0
		Corpus Christi	35	6	2

Armadillos were acquired by local trappers at various locations and examined for evidence of infection with *M. leprae*.

[a] ELISA positive for IgM antibodies for PGL-1.

[b] Histopathological examination of ear tissues detected acid fast bacilli in dermal nerves.

[c] Values recorded for comparison purposes, prevalence previously reported Truman *et al.*[10] and Paige *et al.*[57].

ND = not done; NWR = National Wildlife Refuge.

captured one (1/54) PGL-1 IgM positive armadillos near Woodville, Mississippi (Table 1). In addition, we found serological evidence for the infection (9/42) among armadillos in the eastern Arkansas low-lands around Desha county, but armadillos in western Arkansas near Clarksville appear to be free (0/67) of *M. leprae* (Table 1). *M. leprae* infection is found among Louisiana armadillos outside the low-land area, but the prevalence appears to be less. We captured one (1/12) PGL-1 IgM positive armadillos near Deritter, three (3/135) in the Feliciana parishes and nine (9/145) near Kentwood, Louisiana (Table 1).

The distribution of the infection among armadillos does not seem to be influenced by local variations in susceptibility or disease type. Laboratory studies with armadillos from all these locations show that they are susceptible to experimental infection with *M. leprae* and tend to react similarly to Lepromin-A. The low-land areas appear to favour both the number of armadillos and a high prevalence of infection. Animal density may play some role in the observed prevalence of disease, but measures indexing animal crowding are more reliable and systematic studies outside the low-land region are needed to address the issue.[10]

There have been few contemporary studies on armadillos from outside the US. Pena found 2/83 PGL-1 IgM positive armadillos in northern Argentina (Table 1), but was unable to demonstrate presence of *M. leprae* in the tissues examined (unpublished observation). We found no evidence for the infection (0/25) among armadillos on the island of Grenada in the Caribbean (Table 1). However, Deps recently reported finding 5/14 Brazilian armadillos sampled near Vitoria to be positive by PCR for *M. leprae* in their blood.[63,64] Her results await confirmation, but armadillo leprosy is likely to be more common in other countries than is currently recognized.

Clearly, armadillos in parts of Louisiana and Texas are a large natural reservoir of *M. leprae*. Between the two states, there are more than 60,000 square miles of these low-land habitats where we find a high prevalence of sylvan leprosy. If armadillos utilize even 1% of that space at a density of just one or two animals per acre, then there are likely more than 100,000 *M. leprae* infected armadillos in Louisiana and Texas. The size of this reservoir alone suggests that armadillos may contribute to some cases of human infection, but the impact that they have had on human health in the region has been difficult to discern.

Association with humans

Most cases of leprosy in the US arise among immigrants from endemic countries or nationals who may have acquired their disease while living abroad. However, there is persistent autochthonous transmission of the infection in Texas and Louisiana that gives rise to 30–40 cases each year among native citizens.[65–67] The county of residence of those native-born cases, as derived from the National Hansen's Disease Registry (NHDP, Baton Rouge, LA), shows a clustering within areas bordering the western crescent of the Gulf of Mexico (Figure 1).

Published case reports relate development of leprosy among at least 13 individuals from Louisiana or Texas who had no known exposure to *M. leprae*, other than perhaps their contact with the organism through armadillos. Though casual exposure also was implicated, these people generally reported extensive direct contact with armadillos, such as handling the animals, or preparing and consuming their flesh.[68–71] However, in an early case-control study with 19 native-born patients in Louisiana, Filice found no association between contact with armadillos and the presence of leprosy in humans. Both cases and controls reported no difference in the nature or frequency of their contact with the animals.[72]

Exposure to armadillos is quite common in this region. About half of all the leprosy cases attending a Houston clinic acknowledged some direct or indirect exposure to the animals.[73] In another case-control study among Mexican born patients attending health clinics in Los Angeles, Thomas found a significantly increased risk for leprosy among cases who reported a history of contact with armadillos in Mexico.[74] Unfortunately, the geographical distribution and prevalence of leprosy among Mexican armadillos has not been described, and it is uncertain if the risk attributed in this study relates to contact with *M. leprae* through armadillos or might have been associable with other factors.

Definitive conclusions about zoonotic transmission of leprosy may come only with establishment of suitable molecular strain typing systems. Recent analysis based on single nucleotide polymorphisms (SNP) predicts that leprosy was carried to North America by European immigrants and African slaves. Armadillos too are relatively recent arrivals to the area. The SNP strain-type seen among armadillos matches that of the human settlers to the region,[75] and the animals must have acquired *M. leprae* from humans at some point in time. Both humans and armadillos have established a persistent focus of infection in the US region lining the western Gulf of Mexico. Deciphering the factors which underlie the relationship between humans and armadillos to *M. leprae* in this region could provide significant new insights into leprosy transmission.

Conclusions

Nine-banded armadillos in parts of the southern United States are known to harbour *M. leprae* and they represent a large natural reservoir for infection. It is unclear where or when the animals might first have acquired *M. leprae*. However, the infection appears to have evolved by natural means and armadillos today support intense transmission of *M. leprae* in their communities. The disease is most common among armadillos in low-land habitats and may be rare or absent elsewhere. Few studies have addressed its occurrence among armadillos outside the US. Animal densities and local topographical or environmental circumstances may influence detection of the disease in some locales. However, it seems unlikely that the infection would be confined wholly to a single nidus in the US and the issue merits investigation elsewhere in the armadillo range.

Leprosy remains rare in the US, while exposure to armadillos is common. The impact that infected armadillos have on human health is difficult to discern. Colonists, slaves and armadillos were all relatively recent arrivals to this region, but both the humans and animals now show similarities in the geographical distribution of their infections. Understanding the ecological relationship of humans and armadillos with *M. leprae* in this region may come only with establishment of more suitable molecular strain-typing methods. Additional studies with these animals could benefit our basic understanding of leprosy transmission. Presently, armadillos should be viewed as a potential source of infection for our citizens.

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References

1. Walsh GP, Storrs EE, Burchfield HP *et al.* Leprosy like disease occurring naturally in armadillos. *J. Reticuloendothel Soc*, 1975; **18**: 347–351.
2. Smith JH, Folse DS, Long EG *et al.* Leprosy in wild armadillos dasypus novemcinctus of the texas gulf coast USA epidemiology and mycobacteriology. *J Reticuloendothel Soc*, 1983; **34**: 75–88.
3. Kipling RR. *The beginning of the armadilloe* McMillan, New York 1982.
4. Hall ER. *The mammals of North America* Wiley, New York 1981, pp. 1–690.
5. Talmage RV, Buchannan GD. *The armadillo (Dasypus novemcinctus): a review of its natural history, ecology, anatomy and reproductive physiology*. The Rice Institute Monograph in Biology XLI(2), Houston, 1954, pp. 1–135.
6. Smith LL and Doughtty RW. The amazing armadillo: geography of a folk critter. University of Texas Press, Austin, 1984, pp. 1–134.
7. McDonough CM, McPhee SA, Loughry WJ. Growth rates of juvenile nine-banded armadillos. *Southwestern Naturalist*, 1998; **43**: 462–468.
8. McDonough CM, Loughry WJ. Influences on vigilance in nine-banded armadillos. *Ethology*, 1995; **100**: 50–60.
9. Loughry WJ, McDonough CM. Spatial patterns in a population of nine-banded armadillos (*Dasypus novemcinctus*). *Amer Mid Natural*, 1998; **140**: 161–169.
10. Truman RW, Kumaresan JA, McDonough CM *et al.* Seasonal and spatial trends in the detectability of leprosy in wild armadillos. *Epidemiol Infect*, 1991; **106**: 549–560.
11. McDonough C. Determinants of aggression in nine-banded armadillos. *J Mammal*, 1994; **75**: 189–198.
12. McDonough C. Pairing behavior of the nine-banded armadillo (*Dasypus novemcinctus*). *Amer Mid Natural*, 1997; **138**: 290–298.
13. Loughry WJ, Dwyer GM, McDonough CM. Behavioral interactions between juvenile nine-banded armadillos (*Dasypus novemcinctus*) in staged encounters. *Amer Mid Natural*, 1998; **139**: 125–132.
14. McDonough CM. Social organization of nine-banded armadillos (*Dasypus novemcinctus*) in a Riparian Habitat. *Amer Mid Natural*, 2000; **144**: 139–151.
15. Delsuc F, Scally M, Madsen O *et al.* Molecular phylogeny of living xenarthrans and the impact of character and taxon sampling on the placental tree rooting. *Molec Biol Evol*, 2002; **19**: 1656–1671.
16. Waddell PJ, Cao Y, Hauf J, Hasegawa M. Using novel phylogenetic methods to evaluate mammalian mtDNA, including amino acid-invariant sites-LogDet plus site stripping, to detect internal conflicts in the data, with special reference to the positions of hedgehog, armadillo, and elephant. *Syst Biol*, 1999; **48**: 31–53.
17. Churakov G, Smit AF, Brosius J, Schmitz J. A novel abundant family of retroposed elements (DAS-SINEs) in the nine-banded armadillo (*Dasypus novemcinctus*). *Mol Biol Evol*, 2005; **22**: 886–893.
18. Enders AC. The reproductive cycle of the nine-banded armadillo (*Dasypus novemcinctus*). *Symp Zool Soc Lond*, 1966; **15**: 295–310.
19. Peppler RD, Hossler FE, Stone SC. Determination of reproductive maturity in the female nine-banded armadillo *Dasypus novemcinctus*. *J Reprod Fertil*, 1986; **76**: 141–146.
20. Job CK, Sanchez RM, Kirchheimer WF, Hastings RC. Attempts to breed the nine-banded armadillo *Dasypus novemcinctus* in captivity a preliminary report. *Int J Lepr Other Mycobact Dis*, 1984; **52**: 362–364.
21. Storrs EE. Growing points in leprosy research. I. The armadillo as an experimental model for the study of human leprosy. *Lepr Rev*, 1974; **45**: 8–14.
22. Burns TA, Waldrip EB. Body temperature and electro cardiographic data for the nine-banded armadillo *Dasypus-Novemcinctus*. *J Mammal*, 1971; **52**: 472–477.
23. Shepard CC. The experimental disease that follows the injection of human leprosy bacilli into footpads of mice. *J Exp Med*, 1960; **112**: 445–454.
24. Kirchheimer WF, Storrs EE. 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. *Int J Lepr Other Mycobact Dis*, 1971; **39**: 693–702.
25. Job CK, Kirchheimer WF, Sanchez RM. Variable lepromin response to *Mycobacterium leprae* in resistant armadillos. *Int J Lepr Other Mycobact Dis*, 1983; **51**: 347–353.

[26] Job CK, Sanchez RM, Hastings RC. Manifestations of experimental leprosy in the armadillo Dasypus novemcinctus. *Am J Trop Med. Hyg*, 1985; **34**: 151–161.
[27] Truman RW, Sanchez RM. Armadillos: Models for leprosy. *Lab Animal*, 1993; **22**: 28–32.
[28] Walsh GP, Meyers WM, Binford CH. Naturally acquired leprosy in the nine-banded armadillo: a decade of experience 1975–1985. *J Leukoc Biol*, 1986; **40**: 645–656.
[29] Folse DS, Smith JH. Leprosy in wild armadillos dasypus novemcinctus on the texas gulf coast USA anatomic pathology. *J Reticuloendothel Soc*, 1983; **34**: 341–358.
[30] Meyers WM, Walsh GP, Binford CH *et al.* Indigenous leprosy in nine-banded armadillos. *The armadillo as an experimental model in biomedical research.* Pan American Health Organization, Washington, DC., 1978, pp. 67–72.
[31] Binford CH, Meyers WM, Walsh GP *et al.* Naturally acquired leprosy like disease in the nine-banded armadillo *Dasypus-Novemcinctus*. histopathologic and microbiologic studies of tissues. *J Reticuloendothel Soc*, 1977; **22**: 377–388.
[32] Scholl DA, Truman RW. Mathematical simulation model of leprosy transmission in a population of free ranging nine-banded armadillos. *J Computational Medicine*, 1996; **2**: 184–191.
[33] Binford CH, Storrs EE, Walsh GP. Disseminated infection in the nine-banded armadillo (*Dasypus novemcinctus*) resulting from inoculation with *M. leprae*. Observations made on 15 animals studied at autopsy. *Int J Lepr Other Mycobact Dis*, 1976; **44**: 80–83.
[34] Job CK, Drain V, Williams DL *et al.* Comparison of PCR techniques with other methods for detection of M. leprae in tissues of wild armadillos. *Lepr Rev*, 1991; **62**: 362–373.
[35] Hunter SW, Fujiwara T, Brennan PJ. Structure and antigenicity of the major specific glyco lipid antigen of *Mycobacterium-leprae*. *J Biol Chem*, 1982; **257**: 15072–15078.
[36] Truman RW, Shannon EJ, Hagstad HV *et al.* Evaluation of the origin of Mycobacterium leprae infections in the wild armadillo, Dasypus novemcinctus. *Am J Trop Med Hyg*, 1986; **35**: 588–593.
[37] Truman RW, Job CK, Hastings RC. Antibodies to the phenolic glycolipid-1 antigen for epidemiologic investigations of enzootic leprosy in armadillos (*Dasypus novemcinctus*). *Lepr Rev*, 1990; **61**: 19–24.
[38] Truman RW, Morales MJ, Shannon EJ, Hastings RC. Evaluation of monitoring antibodies to PGL-1 in armadillos experimentally infected with M. leprae. *Int J Lepr Other Mycobact Dis*, 1986; **54**: 556–559.
[39] Job CK, Drain V, Truman RW *et al.* Early infection with *M. leprae* and antibodies to phenolic glycolipid-I in the nine-banded armadillo. *Ind J Lepr*, 1990; **62**: 193–201.
[40] Weiser RS. Natural leprosy like disease in armadillos: a boon to leprosy research. *J Reticuloendothel Soc*, 1975; **18**: 315–316.
[41] Kirchheimer WFaSRM. Carville Hospital researchers find no sign of mycobacteriosis in 141 feral armadillos studied. *Pub Hlth Repts*, 1976; **91**: 481.
[42] Skinsnes OK. Leprosy in wild armadillos. *Int J Lepr Other Mycobact Dis*, 1976; **443**: 376–377.
[43] Kirchheimer WF. Occurrence of *Mycobacterium leprae* in nature. *Lepr India*, 1977; **49**: 44–47.
[44] Kirchheimer WF, Sanchez RM. Examination of North American armadillos for mycobacteriosis. *Lepr Ind*, 1978; **50**: 156–160.
[45] Kirchheimer WF. Examination of North American armadillos for mycobacteriosis – a further report. *Lepr Ind*, 1979; **51**: 60–64.
[46] Walsh GP, Storrs EE, Meyers W, Binford CH. Naturally acquired leprosy like disease in the nine-banded armadillo *Dasypus Novemcinctus*: recent epizootiologic findings. *J Reticuloendothel Soc*, 1977; **22**: 363–368.
[47] Fox MD, Anderson DC, Kaufman AF. Leprosy like disease in a wild armadillo – Mississippi. *Leprosy Scientific Memoranda*, 1977; **L865**: 5.
[48] Kirchheimer WF, Sanchez RM. Leprosy in the wild. *Leprosy Scientific Memoranda*, 1978; **L-966**: 5.
[49] Smith JH, File SK, Nagy BA *et al.* Leprosy like disease of wild armadillos in french acadiana louisiana USA. *J Reticuloendothel Soc*, 1978; **24**: 705–720.
[50] Amezcua ME, Escobar-Gutierrez A, Storrs EE *et al.* Wild Mexican armadillo with leprosy like infection [letter]. *Int J Lepr Other Mycobact Dis*, 1984; **52**: 254–255.
[51] Martinez AR, Resoagli EH, de Millan SG *et al.* Lepra salvje en dasypus novemcinctus (linneo 1758). *Arch Argent Dermat*, 1984; **34**: 21–30.
[52] Munoz-Rivas G. Notes on granulomatosis in armadillos innoculated with *M. leprae*. *The Armadillo as an experimental model in Biomedical Research*. Pan American Health Organization, Washington DD., 1978, pp. 99–102.
[53] Innami S. The study of the armadillo in Paraguay. Pan American Health Organization, Washington DD., 1978, pp. 89–95.
[54] Roth EE, Greer B, Moore M *et al.* Serologic analysis of two related leprostospiral serotypes isolated in Louisiana. *Zoonoses Res*, 1964; **3**: 31–38.
[55] Kniffen FB, Hillard SB, *Louisiana: its land and people*. Louisiana State University Press, Baton Rouge 1988.
[56] Job CK, Harris EB, Allen JL, Hastings RC. A random survey of leprosy in wild nine-banded armadillos in louisiana USA. *Int J Lepr Other Mycobact Dis*, 1986; **54**: 453–457.

[57] Paige CF, Scholl DT, Truman RW. Prevalence and incidence density of *Mycobacterium leprae* and *Trypanosoma cruzi* infections within a population of wild nine-banded armadillos. *Am J Trop Med Hyg*, 2002; **67**: 528–532.
[58] Loughry W, McDonough C. Are road kills valid indicators of armadillo population structure?. *Am Midl Natural*, 1996; **135**: 53–59.
[59] Anderson M. Leprosy in an armadillo from Texas. *Leprosy Scientific Memorandum*, 1978; **L-967**: 5.
[60] Wilson GT, Horton P, Stevens WC, Shake RE. Absence of leprosy like disease in the nine-banded armadillo dasypus-novemcinctus in and around taylor county texas USA. *Tex J Sci*, 1984; **36**: 73–79.
[61] Clark KA, Kim SH, Boening LF *et al.* Leprosy in armadillos (*Dasypus novemcinctus*) from Texas. *J Wildl Dis*, 1987; **23**: 220–224.
[62] Howerth EW, Stallknecht DE, Davidson WR, Wentworth EJ. Survey for leprosy in nine-banded armadillos (Dasypus novemcinctus) from the southeastern United States. *J Wildl Dis*, 1990; **26**: 112–115.
[63] Deps PD, Santos AR, Yamashita-Tomimori J. Detection of *Mycobacterium leprae* DNA by PCR in blood sample from nine-banded armadillo: preliminary results. *Int J Lepr Other Mycobact Dis*, 2002; **70**: 34–35.
[64] Deps PD, Michalany NS, Tomimori-Yamashita J. False positive reaction of the immunohistochemistry technique using anti-BCG polyclonal antibodies to identify *Mycobacterium leprae* in wild nine-banded armadillos. *Int J Lepr Other Mycobact Dis*, 2004; **72**: 327–330.
[65] Enna CD, Jackson RR, Trautman JR, Sturdivant M. Leprosy in the United States. *Pub Hlth Repts*, 1979; **93**: 468–473.
[66] Neill MA, Hightower AW, Broome CV. Leprosy in the United States, 1971–1981. *J Infect Dis*, 1985; **152**: 1064–1069.
[67] Joseph BZ, Yoder LJ, Jacobson RR. Hansen's disease in native-born citizens of the United States. *Pub Hlth Repts*, 1985; **100**: 666–671.
[68] Lumpkin LR 3rd, Cox GF, Wolf JE Jr. Leprosy in five armadillo handlers. *J Am Acad Dermatol*, 1983; **9**: 899–903.
[69] Lumpkin LR 3rd, Cox GF, Wolf JE Jr. Leprosy in armadillo handlers. *J Am Acad Dermatol*, 1984; **10**: 1073.
[70] West BC, Todd JR, Lary CH *et al.* Leprosy in six isolated residents of northern Louisiana. Time-clustered cases in an essentially nonendemic area. *Arch Intern Med*, 1988; **148**: 1187–1192.
[71] Freiberger HG, Fudenberg H. An appetite for armadillo. *Hospital Practice*, 1981; **16**: 137.
[72] Filice GA, Greenberg RN, Fraser DW. Lack of observed association between armadillo contact and leprosy in humans. *Am J Trop Med Hyg*, 1977; **26**: 137–139.
[73] Bruce S, Schroeder TL, Ellner K *et al.* Armadillo exposure and Hansen's disease: an epidemiologic survey in southern Texas. *J Am Acad Dermatol*, 2000; **43**: 223–228.
[74] Thomas DA, Mines JS, Mack TM *et al.* Armadillo exposure among Mexican-born patients with lepromatous leprosy. *J Infect Dis*, 1987; **156**: 990–993.
[75] Monot M, Honore N, Garnier T *et al.* On the origin of leprosy. *Science* 2005; **308**: 1040–1042.

Recently, however, wild armadillos have been appearing with a naturally occurring form of leprosy. If the disease spreads in the armadillo population, researchers will not be able to use these animals for leprosy studies, since study animals must be completely free of the disease as well as the bacteria that cause it. Mice have also been used to study leprosy, but laboratory conditions, such as temperature, must be carefully controlled in order to sustain the infection in mice.Â The stigma associated with leprosy perished with the discovery that the disease occurs naturally in wild armadillos. Also, in 1950 a Danish pathologist related skeletons from a leprosaria of the twelfth and thirteenth centuries with those of bacterial leprosy. As of 1940 leprosy could be treated with the drug dapsone. Leprosy survey among rural communities and wild armadillos from Amazonas state, Northern Brazil. Mariane Martins AraÃºjo Stefani, Patricia Sammarco RosaÂ Abstract. There is evidence that in southern US, leprosy is a zoonosis infecting wild Dasypus novemcinctus armadillos but the extent of this finding is unknown. This ecological study investigated leprosy in rural communities and in wild armadillos from the Brazilian Amazon. The study area was the MamiÃ¡ Lake of Coari municipality, Amazonas State, Northern region, a hyper endemic leprosy area where residents live on subsistence farming, fishing and armadillo hunting and its meat intake are frequent. Wild nine-banded armadillos (Dasypus novemcinctus) in the south central United States are highly endemic natural hosts of Mycobacterium leprae. Surveys conducted over the last 30 years on more than 5000 animals confirm that the infection is present among armadillos in Arkansas, Louisiana, Mississippi and Texas. Highest prevalence rates are found among the animals in low-lying alluvial and coastal areas, primarily in Louisiana and Texas. Both animal density and local factors may contribute to the detectability of armadillo leprosy in those regions. Little evidence for M. leprae infection is found among armadillos elsewhere in the US range, and only a few reports relate finding the infection among animals in Central or South America. Researchers believe that armadillos actually inherited leprosy from humans approximately 400-500 years ago. Many nine-banded armadillos, the primary species found in the southern United States, host Mycobacterium leprae â€" a microbe that is apparently transmitted from one armadillo to another. The microbe can be passed on to humans when handling or eating infected nine-banded armadillos.Â And the vast majority of armadillos that live in the wild donâ€™t survive long enough to develop a full-blown leprosy infection. Recent Florida Cases Have Raised the Alarm Regarding Leprosy and Armadillos. While leprosy is not a widespread issue in the United States, some recently reported leprosy cases have raised concerns about an increase in the armadillo-leprosy threat. The link between leprosy infections and armadillo contact was established in a 2011 research paper published in the New England Journal of Medicine by a team which includes Scollard. The scientists genotyped strains of leprosy found in three Americans who had never traveled abroad and one wild armadillo, and found they â€œwere essentially identicalâ€. â€œThereâ€™s a fair amount of interaction between armadillos and people,â€ Scollard said. â€œDown here, theyâ€™re common. And in Louisiana, and especially in Texas, people see armadillos in the garden, they keep them as pets, they shoot them and eat them â€" thereâ€™s more interaction with armadillos than you might think.â€