Epidemiology and Infection

www.cambridge.org/hyg

Short Paper

Cite this article: Fernández-González AM, López-Pérez AM, Herrera-Mares A, Chaves A, Ramírez-Corona F and Suzán G (2025). Bartonella tracing in wild rodents in northwestern Mexico. Epidemiology and Infection, 153, e42, 1–6 https://doi.org/10.1017/S0950268825000238

Received: 11 September 2024 Revised: 10 January 2025 Accepted: 30 January 2025

Keywords:

Bartonella; rodent; Mexico; Chihuahua; Baja California

Corresponding author:

Gerardo Suzán; Email: gerardosuz@gmail.com

© The Author(s), 2025. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.



Bartonella tracing in wild rodents in northwestern Mexico

Adriana M. Fernández-González¹, Andrés M. López-Pérez², Angel Herrera-Mares¹, Andrea Chaves^{3,4}, Fabiola Ramírez-Corona⁵ and Gerardo Suzán¹

¹Departamento de Etología, Fauna Silvestre y Animales de Laboratorio, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Ciudad de México, México; ²Red de Biología y Conservación de Vertebrados, Instituto de Ecología A.C., Veracruz, México; ³Centro Nacional de Innovaciones Biotecnológicas (CENIBiot), CeNAT-CONARE, San José, Costa Rica; ⁴Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica and ⁵Taller de Sistemática y Biogeografía, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México

Abstract

Bartonella is a widely distributed Gram-negative bacterium that includes species that are capable of causing illness in humans. Rodents represent one of the main reservoirs of zoonotic pathogens, and monitoring their populations can provide valuable insights into human health. We conducted a surveillance study of rodents from two north-western states of Mexico (Baja California and Chihuahua) to investigate the prevalence and genetic diversity of Bartonella by polymerase chain reaction (PCR) amplification and sequencing of the citrate synthase (gltA) gene. A total of 586 rodents belonging to 28 species were captured, and 408 were tested for Bartonella spp. The overall Bartonella spp. prevalence was 39.71%. The prevalence found in Chihuahua was higher (42.80%) than in Baja California (32.52%), and rodents such as Neotoma albigula, Neotoma mexicana, Peromyscus boylii, and Chaetodipus baileyi had the highest prevalence. The gltA sequences revealed seven genetic variants, some of which were obtained from *Peromyscus* and *Dipodomys* rodents and were associated with *Bartonella* species of human health concern, such as B. grahamii and B. vinsonii subsp. arupensis. In addition, a sequence obtained from a *Peromyscus maniculatus* was clustered with *Candidatus* Bartonella rudakovii, a previously unreported association. This study provides valuable data and new insight into the Bartonella-hosts interactions in rodent species in north-western Mexico.

Introduction

Bartonella is a genus of Gram-negative bacteria with an affinity for erythrocytes and endothelial cells of various hosts, including agents of emerging or re-emerging infectious diseases [1]. These bacteria are widely distributed around the world and parasitize a wide range of mammals, including rodents and humans [2, 3]. Currently, 45 species of Bartonella are recognized, of which at least ten are associated with human illness [4]. The extensive range of hosts that are parasitized by this bacterium and its remarkable richness can be attributed in part, to the transmission route, which is through numerous ectoparasitic vectors (fleas, lice, sand flies, among others) [5]. Furthermore, the high degree of adaptation exhibited by Bartonella to its reservoir hosts facilitates prolonged intraerythrocytic bacteremia and persistent infection of endothelial cells, thereby enabling these reservoir hosts to serve as foci of infection [1, 6].

The order Rodentia is the most abundant and diverse of mammals and has a great richness of Bartonella species [7, 8]. Ectoparasitic vectors, such as fleas, play an important role in the Bartonella-rodent cycle. Fleas are capable of moving between hosts and feeding on them, which provides the opportunity for *Bartonella* spp. to infect different hosts and fleas. This may explain the great richness and diversity of *Bartonella* found in rodents and their fleas [7, 9]. In addition to this, the order Rodentia shows a strong association between specific Bartonella species and certain rodent hosts. For example, specificity has been reported for Bartonella washoensis in sciurid rodents [10] and between Bartonella vinsonii subsp. arupensis and rodents of the genus Peromyscus in the United States and Mexico [11, 12]. Specificity has also been observed between Bartonella and fleas. For example, fleas of the species Oropsylla hirsuta which are specific to Sciuridae such as Cynomys ludovicianus are also infected by B. washoensis, and fleas of the genus Orchopeas which parasitize rodents of the genus Peromyscus are also infected by B. vinsonii subsp. arupensis [9, 13]. However, studies indicate that infection by more than one species or subspecies of Bartonella is possible in rodents and fleas. A longitudinal study in Georgia found multiple genogroups isolated from individual blood samples obtained from Sigmodon hispidus rodents, which occurred in 21% of the blood samples obtained; and another study conducted in Israel with Xenopsylla ramesis fleas and wild rodents indicates a co-infection of two different strains of Bartonella in Meriones crassus and Gerbillus nanus rodents [14, 15]. Regarding fleas, a study on

wild mammals and their fleas demonstrated a co-infection with two different strains of *Bartonella* in fleas *Aetheca wagneri* and *Orchopeas leucopus*, collected from *Peromyscus maniculatus* rodents [16]. Therefore, in the *Bartonella*-rodent-flea cycle, some specificity of the bacteria with certain species of fleas and rodents can be observed; however, there is also the possibility of finding co-infection of different species and subspecies of *Bartonella* in rodents and their fleas which could give the opportunity for genetic recombination and thus diversification of this bacterium [17].

In North America, a high prevalence of *Bartonella* has been reported in several rodents. In Kansas, a prevalence of 90.4% was reported in *Onychomys leucogaster* rodents; in Colorado, the prevalence in *P. maniculatus* was 82.4% [11, 18]; in New Mexico, the prevalence in *Neotoma* rodents was 64% [19]; and in northern Mexico, the prevalence of *Bartonella* infection was found to be significantly higher in *Dipodomys merriami* (57%), *Dipodomys spectabilis* (51%), *Onychomys arenicola* (80%), *O. leucogaster* (83%), *Peromyscus leucopus* (50%), and *P. maniculatus* rodents (50%) [12].

The infection caused in humans by different species of *Bartonella* is called bartonellosis and includes several diseases such as cat scratch disease, Oroya fever, or trench fever caused by *Bartonella henselae*, *Bartonella bacilliformis*, and *Bartonella quintana*, respectively. Mortality in humans is generally low; however, the immune status of the patient, the specific *Bartonella* species involved, and the accuracy and timeliness of the treatment are critical factors in preventing fatal outcomes [20]. Although the majority of infections caused in humans are attributed to *Bartonella* species that are not directly associated with rodents (*B. henselae*, *B. quintana*, and *B. bacilliformis*), several rodent-associated *Bartonella* species (*B. elizabethae*, *B. grahamii*, *B. rochalimae*, *B. tamiae*, *B. tribocorum*, *B. vinsonii arupensis*, and *B. washoensis*) compromise human health as they cause clinical manifestations including endocarditis, neuronitis, splenomegaly, fever, and myalgia [7, 20].

In Mexico, the order Rodentia is the most species-rich order of mammals, with 243 species representing eight families. Approximately 112 species have been recorded in north-western Mexico, including the states of Baja California, Sonora, and Chihuahua [21]. The presence of Bartonella DNA has been recently recorded in at least 12 rodent species corresponding to seven genera (Neotoma, Onychomys, Peromyscus, Chaetodipus, Dipodomys, Cynomys, and Xerospermophilus) in the state of Chihuahua [12]. Despite the scarce research in the country, there is an evidence of zoonotic species in rodents and their fleas in north-western Mexico [9, 12, 22]. It is necessary to continue the surveillance of the bacteria in the north-western region, given that north-western Mexico has a high richness of rodents, and there is evidence that some zoonotic species of Bartonella are circulating in rodents and fleas in Chihuahua. Therefore, this study aims to show the prevalence and genetic diversity of Bartonella in wild rodents in two north-western Mexican states, Chihuahua and Baja California.

Materials and methods

Study area, rodent capture, and blood collection

During 2019 and 2021, rodents were captured in Baja California (32°7′13.59″N, 115°15′4.61″W) and Chihuahua (30°39′8.50″N, 108°31′23.76″W). In both states, agricultural activities are practiced, such as intensive and extensive cattle raising and agriculture, which includes different crop types such as onions, wheat, cotton, and chilli.

Rodent trapping was conducted over two seasons by placing grids of 7×7 Sherman traps (7.6 cm \times 8.9cm \times 22.9 cm; H.B. Sherman Traps, Inc., Tallahassee, FL). Each grid was spaced at least \geq 500m apart. Traps were baited with a mixture of oats and vanilla extract and opened for three consecutive nights. In total, 12 and 18 grids were placed in Baja California and Chihuahua, respectively. The quadrats were distributed in surrounding areas and far from human settlements; most of them were in a mosaic landscape dominated by mesquite shrublands, grassland, and croplands vegetation; and others were placed in oak forest areas.

Once the rodents were captured, they were weighed and sexed, and morphometric measurements were taken for identification using a mammal identification guide [23]. Subsequently, blood samples were obtained from the retro-orbital plexus, placed in cryovials with EDTA, and stored at -70° C. After handling, each rodent was released at the capture site.

Molecular analysis

DNA extraction from rodent blood samples was performed using the DNeasy Blood and Tissue kit (Qiagen®), following the supplier's recommendations. Once the extraction was performed, polymerase chain reaction (PCR) was continued by amplifying 767 bp of the gltA gene using the following primers: CS443f: 5' GCTATGTCTG-CATTCTCTCTCTCTCTATCA 71 3' and CS1210r: 5' GAT-CYTCAATCATTTCTTTCCA 3' [24]. Amplification consisted of a 25 μl final volume mix containing 12.5 μl Top Taq® Master Mix, 5 μl nuclease-free water, 2.5 µl CoralLoad buffer, 2.5 µl DNA, and 1.25 μl (10 μM) of each primer using the following parameters: initial denaturation (2 min 94°C), followed by 45 cycles at 94°C for 30 s, 48°C for 1 min, and 72°C for 1 min, and a final extension of 72°C for 7 min. The PCR products were visualized for amplicons of the expected size by electrophoresis in a 1% agarose gel with ethidium bromide staining. Some amplicons were purified from an agarose gel (1.5%) with the EZ-10 Spin Column DNA Gel Extraction kit (Bio Basic). Subsequently, purification of the remaining PCR products, and sequencing which was performed in both directions, was carried out in Korea by Macrogen. The phylogenetic relationship of our sequences and the reference sequences obtained from GenBank were aligned using MUSCLE in the MEGA 11 program [25]. Using the same program, the phylogenetic tree was reconstructed by maximum likelihood by Tamura 3-parameter method and a bootstrap calculation with 1000 replicates. The visualization and modification of the phylogenetic tree style were carried out at Fig Tree version 1.4.4. The novel sequences were submitted to GenBank (PQ655038-PQ655044).

Results and discussion

Bartonella prevalence

A total of 586 rodents belonging to four families (Cricetidae, Heteromyidae, Muridae, and Sciuridae), 12 genera, and 28 species were captured (Table 1). PCR was performed on 408 rodents (Chihuahua=285 and Baja California= 123) obtaining an overall prevalence of *Bartonella* spp. of 39.71%. The highest prevalence was found in the state of Chihuahua with 42.80%, followed by Baja California with a prevalence of 32.52% (Table 1). Previously, a study conducted in 2014 in the same area in Chihuahua reported a higher prevalence in rodents (50.01%) [12], and later in 2016, a prevalence of 40.4% was found in wild rodent fleas [9]. To our knowledge, our study is the first to report *Bartonella* DNA in wild rodents in Baja

Epidemiology and Infection 3

Table 1. Prevalence of Bartonella spp. in wild rodents from Chihuahua and Baja California

	Chihuahua					Baja California				
Rodent species	С	Α	(+)	(-)	%	С	А	(+)	(-)	%
Baiomys taylori	2	_	-	-	-	0	-	-	-	_
Chaetodipus baileyi	0	-	-	=	=	1	1	1	0	100
Chaetodipus eremicus	2	-	-	=	=	0	=	-	=	=
Chaetodipus hispidus	4	2	1	1	50	0	-	-	-	_
Chaetodipus intermedius	30	18	8	10	44.44	0	-	-	-	-
Chaetodipus penicillatus	6	6	1	5	16.66	65	55	19	36	34.54
Chaetodipus sp.	3	1	0	1	0	0	-	-	-	-
Chaetodipus spinatus	0	-	-	-	-	7	5	1	4	20
Dipodomys merriami	67	44	19	25	43.18	7	2	1	1	50
Dipodomys ordii	8	5	2	3	40	0	-	-	-	_
Dipodomys spectabilis	5	2	1	1	50	0	-	-	-	-
Mus musculus	14	8	1	7	12.5	16	13	4	9	30.76
Neotoma albigula	25	18	13	5	72.22	2	2	1	1	50
Neotoma mexicana	1	1	1	0	100	0	-	-	-	-
Onychomys arenicola	48	32	14	18	43.75	0	-	-	-	-
Onychomys leucogaster	14	11	6	5	54.54	0	-	-	-	-
Perognathus flavus	21	8	2	6	25	0	-	-	-	-
Peromyscus boylii	9	6	6	0	100	0	-	-	-	-
Peromyscus eremicus	31	24	13	11	54.16	14	12	6	6	50
Peromyscus fraterculus	0	-	-	-	-	3	3	1	2	33.33
Peromyscus leucopus	22	20	9	11	45	0	-	-	-	-
Peromyscus maniculatus	79	56	23	33	41.07	33	26	6	20	23.07
Peromyscus sp.	1	-	-	-	-	0	-	-	-	-
Rattus rattus	0	-	-	-	-	2	2	0	2	0
Reithrodontomys fulvescens	27	18	1	17	5.55	0	-	-	-	-
Reithrodontomys megalotis	0	-	-	-	-	3	1	0	1	0
Sigmodon hispidus	7	2	0	2	0	0			_	
Sigmodon ochrognathus	1	1	0	1	0	0			_	
Xerospermophilus spilosoma	3	2	1	1	50	0	-	-	-	-
Xerospermophilus tereticaudus	0	-		-	-	3	1	0	1	0
Total	430	285	122	163	42.80	156	123	40	83	32.52

Note: Capital letters represent total rodents captured (C) and abundance of rodents considered for PCR (A)

California; this provides new information in this state, and together with previous studies conducted in Chihuahua and Sonora with rodents and/or their fleas, we confirm the circulation of this bacterium in the three north-western states of Mexico (Baja California, Sonora, and Chihuahua) that border the United States [9, 12, 22].

We found *Bartonella* spp. in several rodent species (Table 1). In Chihuahua, we found 18 rodent species infected with *Bartonella* of which seven are new records (*Chaetodipus intermedius*, *Mus musculus*, *Neotoma mexicana*, *Perognathus flavus*, *Peromyscus boylii*, *Peromyscus eremicus*, and *Reithrodontomys fulvescens*). The species with the highest prevalence in Chihuahua were *Neotoma albigula* (72.22%), *N. mexicana* (100%), and *P. boylii* (100%) (Table 1). The

high prevalence found in *N. albigula* may be common, as previous studies in the same state and in New Mexico, United States and adjacent to Chihuahua, recorded a high prevalence in this rodent species (75%–100%) [12, 19]. The prevalence we found in *N. mexicana* and *P. boylii* is higher than that reported for these species in the United States, 38.7% and 33.3%, respectively [26, 27]. In Baja California, *Bartonella* DNA was found in nine rodent species, with the highest prevalence being *Chaetodipus baileyi* (100%), followed by *D. merriami* and *N. albigula* (each 50%). The prevalence found in *D. merriami* and *N. albigula* species has been previously reported as moderate to high [12, 19, 28], but caution should be taken with the high prevalence we found in

C. baileyi, since the only captured individual was positive. Therefore, further studies to confirm this observation is necessary.

Phylogenetic analysis

A total of 26 positive PCR products were sequenced, with both forward and reverse sequencing performed on each. Of these, only 18 consensus sequences were successfully recovered. Basic Local Assignment Search Tool (BLAST) analysis yielded similarity and query cover values for eight sequences. These sequences were subsequently deposited in GenBank. Notably, some sequences were identical and thus were deposited with the same accession number (PQ655043, PQ655044), as indicated in the supplementary mater ial table. Seven genetic variants were determined and grouped into three clades (Figure 1). In the first clade (I), there were five variants belonging to the rodents P. boylii (3), P. leucopus (1), D. merriami (1), Peromyscus fraterculus (1), and O. leucogaster (1) (accession numbers: PQ655039-PQ655041, PQ655043, and PQ655044). These variants were associated with the B. vinsonii group that include subspecies that have been categorized as pathogenic (B. vinsonii arupensis and B. vinsonii berkhoffii) [7, 29]. Particularly, the variants belonging to a D. merriami (PQ655041, 595 bp) captured in Chihuahua and a P. fraterculus (PQ655040, 463 bp) from Baja California were grouped with *B. vinsonii arupensis* (AF214557) with 98,90% and 99,14% similarity.

Previously, in the state of Chihuahua, the presence of *B. vinsonii* subsp. *arupensis* has been reported in rodents such as *N. albigula*, *P. maniculatus*, and *P. leucopus*; however, there was no record of this bacterium in *D. merriami* [12]. In addition, our study adds another rodent species in Chihuahua as carrier of *Bartonella* (*P. boylii*). On the other hand, this is the first time that *B. vinsonii* subsp. *arupensis* is reported in a *P. fraterculus* rodent from Baja California, Mexico.

The second clade (II) consisted of a variant obtained from a *D. merriami* captured in Chihuahua (PQ655038, 737 bp) that had a 98.78% similarity to *B. grahamii* (CP001562), and other species that also parasitize rodents (*B. elizabethae* and *B. tribocorum*). A study conducted in the same state with wild rodents did not report the presence of *B. grahamii* [12]; however, an investigation conducted on rodent fleas reported the presence of this bacterium in *Meringis altipecten*, *Meringis arachis*, and *Meringis parkeri* fleas collected on *D. merriami* [9]. This suggests that *B. grahamii* was already circulating among rodents in the region, despite not having been detected in them until now. *B. grahamii* was recognized of medical importance from its isolation in ocular fluids of a patient, and this *Bartonella* species has been associated with several genera of the

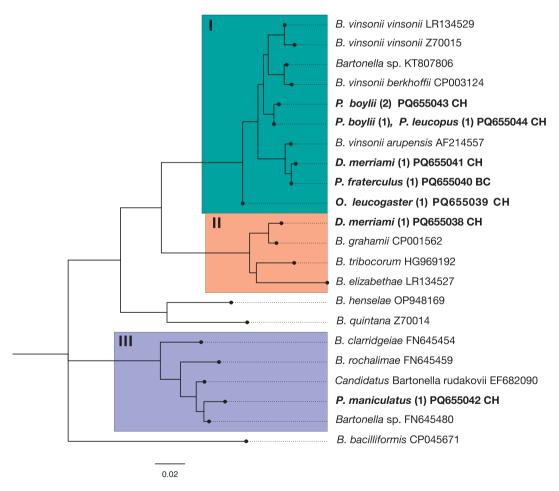


Figure 1. Phylogenetic relationship of Bartonella genotypes based on partial sequences of gltA gene detected in rodents captured in Baja California (BC) and Chihuahua (CH), Mexico. Each genetic variant is indicated in boldface with its accession number, capital letters show the state where the rodents were captured (CH and BC), and numbers in parentheses are the number of sequences obtained from blood. The clades of interest are represented by a rectangle of different colour and by roman numerals (I–III). The phylogenetic tree was constructed by the maximum likelihood method by Tamura 3-parameter and a bootstrap calculation with 1000 replicates.

Epidemiology and Infection 5

order Rodentia (Apodemus, Dryomys, Microtus, Mus, and Myodes) [30, 31].

The third clade (III) consisted of zoonotic Bartonella species mainly associated with carnivores (B. rochalimae and B. clarridgeiae); however, one of our variants obtained from a P. maniculatus collected in Chihuahua (PQ655042, 748 bp) had a similarity of 98.26% with Bartonella sp. (FN645480) and 97.91% with Candidatus Bartonella rudakovii (EF682090). The later was originally detected in voles from Siberia, and recently using genes such as gltA and rpoB, it has been recorded in rodents Myodes glareolus, Microtus oeconomus, and Sciurus vulgaris rodents in Switzerland, Lithuania, and Czech Republic [32-34]. In general, information on Candidatus B. rudakovii worldwide is scarce, and so far, it has not been recognized as zoonotic [35]. This is the first time that a sequence associated with this putative species of Bartonella has been obtained in Mexico, although it has not been recognized as zoonotic, it is found within the clade that integrates species such as B. clarridgeiae and B. rochalimae which compromise human health.

It is important to note that certain rodent species can adapt to environments near human settlements, where they exploit available resources for their survival. This proximity can increase the likelihood of rodent-human interactions, potentially facilitating the transmission of bacteria or other infectious agents. In our study, some of the cricetid and heteromyid species (N. albigula, N. mexicana, P. boylii, C. baileyi, D. merriami, and P. fraterculus) presented high prevalence and/or zoonotic species of Bartonella; these rodents are usually found far from human settlements, as they are distributed in landscapes composed of forests, shrublands, deserts, and grasslands, so the risk of transmission of Bartonella bacteria to humans could be low [23]. However, some rodent species found in our study, such as N. albigula and N. mexicana, may occasionally be found in abandoned buildings [36, 37]. Furthermore, it should be considered that some human activities such as agricultural and livestock production, animal trade, deforestation, travel, and tourism, among others, imply the entry of humans into areas inhabited by wild animals, which increases the probability of contact and, in turn, the risk of transmission of Bartonella or other infectious agents [38].

Our study, in conjunction with existing research, indicates that *Bartonella* is a persistent agent in wild rodents in north-western Mexico. The identification of certain sequences that correspond to zoonotic species underscores the necessity for preventive measures to avert the dissemination and occurrence of cases in humans. *Bartonella* species identification was carried out with the *gltA* gene, which is a reliable and widely used gene; however, for further studies, we recommend the use of multiple genes to discern between *Bartonella* species [17, 39]. Additionally, it is recommended that further research be conducted on this bacterium in Baja California to gain a deeper understanding of its prevalence and diversity within the state.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0950268825000238.

Data availability statement. The genetic variants are all available at the NCBI repository as described in materials and methods under accession numbers (PQ655038-PQ655044).

Acknowledgments. We thank to Ana L. Vigueras Galván, Paulina A. Pontifes, Paulina Álvarez Mendizábal, Paola Martínez-Duque, and Julio J. Barrón-Rodríguez during fieldwork and logistic support and Hugo Mendoza, Sofía Chewtat, Sandra Rodríguez for their help in the fieldwork. Special thanks to Milena Argüello for the support in the molecular work at the Laboratorio de Medicina de la Conservación at the Universidad de Costa Rica. Thanks to Fernanda

I. Soto-López for the support in the laboratory work (Taller de Sistemática y Biogeografía, Departamento de Biología Evolutiva, Facultad de Ciencias, UNAM).

Author contribution. A. M. F. G., A. M. L. P., and G. S. contributed to conceptualization and methodology. A. M. F. G. and A. M. L. P. contributed to the formal analysis and writing the manuscript's original draft. Investigation was conducted by A. M. F. G., A. H. M., A. C., and F. R. C. Resources were achieved by the following persons G. S., A. M. L. P., A. C., and F. R. C. All the authors contributed with the review writing and editing of the manuscript, and G. S. contributed with the funding acquisition.

Funding statement. This work was supported through the Programa de Apoyo a Proyectos de investigación e Innovación Tecnológica (PAPIIT) No. IN225219 and Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT) No. 2016-01-1851. Fernández-González AM was supported by a scholarship by Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT, CVU 492438).

Competing interest. The authors declare no conflict of interest.

Ethical standard. All procedures were performed in accordance with the American Society of Mammologists (2011) and were approved by the Animal Care Committee of the Veterinary School (Universidad Nacional Autónoma de México) and by the Secretaría de Medio Ambiente y Recursos Naturales (Permit: FAUT-025).

References

- Dehio C (2001) Bartonella interactions with endothelial cells and erythrocytes. Trends in Microbiology 9, 279–285. https://doi.org/10.1016/S0966-842X(01)02047-9.
- [2] Gutiérrez R, et al. (2015) Bartonella infection in rodents and their flea ectoparasites: an overview. Vector-Borne and Zoonotic Diseases 15, 27–39. https://doi.org/10.1089/vbz.2014.1606.
- [3] Breitschwerdt EB (2017) Bartonellosis, One Health and all creatures great and small. Advances in Veterinary Dermatology 8, 111–121. https://doi. org/10.1111/vde.12413.
- [4] Okaro U, et al. (2017) Bartonella species, an emerging cause of bloodculture-negative endocarditis. Clinical Microbiology Reviews 30, 709–746. https://doi.org/10.1128/cmr.00013-17.
- [5] Billeter SA, et al. (2008) Vector transmission of *Bartonella* species with emphasis on the potential for tick transmission. *Medical and Veterinary Entomology* 22, 1–15. https://doi.org/10.1111/j.1365-2915.2008.00713.x.
- [6] Chomel BB, et al. (2003) Clinical impact of persistent Bartonella bacteremia in humans and animals. Annals of the New York Academy of Sciences 990, 267–278. https://doi.org/10.1111/j.1749-6632.2003.tb07376.x.
- [7] Buffet JP, Kosoy M, Vayssier-Taussat M (2013) Natural history of Bartonella-infecting rodents in light of new knowledge on genomics, diversity and evolution. Future Microbiology 8, 1117–1128. https://doi. org/10.2217/fmb.13.77.
- [8] Burgin CJ, et al. (2018) How many species of mammals are there?. *Journal of Mammalogy* 99, 1–14. https://doi.org/10.1093/jmammal/gyx147.
- [9] Fernández-González AM, et al. (2016) Molecular survey of *Bartonella* species and *Yersinia pestis* in rodent fleas (Siphonaptera) from Chihuahua, Mexico. *Journal of Medical Entomology* 53, 199–205. https://doi.org/10.1093/jme/tjy181.
- [10] Inoue K, et al. (2011) Multi-locus sequence analysis reveals host specific association between *Bartonella washoensis* and squirrels. *Veterinary Microbiology* 148, 60–65. https://doi.org/10.1016/j.vetmic.2010.08.007.
- [11] Bai Y, et al. (2011) Persistent infection or successive reinfection of deer mice with *Bartonella vinsonii* subsp. arupensis. Applied and Environmental Microbiology 77, 1728–1731. https://doi.org/10.1128/AEM.02203-10.
- [12] Rubio AV, et al. (2014) Prevalence and genetic diversity of *Bartonella* strains in rodents from northwestern Mexico. *Vector-Borne and Zoonotic Diseases* 14, 838–845. https://doi.org/10.1089/vbz.2014.1673.
- [13] **Stevenson HL**, et al. (2003) Detection of novel *Bartonella* strains and *Yersinia pestis* in prairie dogs and their fleas (Siphonaptera: Ceratophyllidae

- and Pulicidae) using multiplex polymerase chain reaction. *Journal of Medical Entomology* **40**, 329–337. https://doi.org/10.1603/0022-2585-40.3.329.
- [14] Kosoy M, et al. (2004) Prospective studies of *Bartonella* of rodents. Part II. Diverse infections in a single rodent community. *Vector-Borne & Zoonotic Diseases* 4, 296–305. https://doi.org/10.1089/vbz.2004.4.29.
- [15] Morick D, et al. (2011) Investigation of Bartonella acquisition and transmission in Xenopsylla ramesis fleas (Siphonaptera: Pulicidae). Molecular Ecology 20, 2864–2870. https://doi.org/10.1111/j.1365-294X.2011.05033.x.
- [16] Brinkerhoff RJ, et al. (2010) Detection of multiple Bartonella species in digestive and reproductive tissues of fleas collected from sympatric mammals. The ISME Journal 4, 955–958. https://doi.org/10.1038/ismej.2010.22.
- [17] Kosoy M, et al. (2018) Genotyping of *Bartonella* bacteria and their animal hosts: current status and perspectives. *Parasitology* 145, 543–562. http:// doi.org/10.1017/S0031182017001263.
- [18] Bai Y, et al. (2007) Acquisition of nonspecific Bartonella strains by the northern grasshopper mouse (Onychomys leucogaster). FEMS Microbiology Ecology 61, 438–448. https://doi.org/10.1111/j.1574-6941.2007.00364.x.
- [19] Morway C, et al. (2008) A longitudinal study of *Bartonella* infection in populations of woodrats and their fleas. *Journal of Vector Ecology* 33, 353–364. https://doi.org/10.3376/1081-1710-33.2.353.
- [20] Rolain JM, et al. (2004) Recommendations for treatment of human infections caused by *Bartonella* species. *Antimicrobial Agents and Chemotherapy* 48, 1921–1933. https://doi.org/10.1128/aac.48.6.1921-1933.2004.
- [21] Ceballos G (2014) Mammals of Mexico. Baltimore: Johns Hopkins University, pp. 140–449.
- [22] Zapata-Valdés C, et al. (2018) Mammalian hosts, vectors, and bacterial pathogens in communities with and without black-tailed prairie dogs (Cynomys ludovicianus) in northwestern Mexico. Journal of Wildlife Diseases 54, 26–33. https://doi.org/10.7589/2016-09-214.
- [23] **Reid F** (2006) A Field Guide to Mammals of North America. New York: Houghton Mifflin.
- [24] Billeter SA, et al. (2011) Molecular detection and identification of Bartonella species in Xenopsylla cheopis fleas (Siphonaptera: Pulicidae) collected from Rattus norvegicus rats in Los Angeles, California. Applied and Environmental Microbiology 77, 7850–7852. https://doi.org/10.1128/AEM.06012-11.
- [25] Tamura K, Stecher G, Kumar S (2021) MEGA 11: Molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 38, 3022– 3027. https://doi.org/10.1093/molbev/msab120.
- [26] Bai Y, et al. (2009) Effects of rodent community diversity and composition on prevalence of an endemic bacterial pathogen-*Bartonella*. *Biodiversity* 10, 3–11. https://doi.org/10.1080/14888386.2009.9712856.

- [27] Ziedins AC, et al. (2016) Molecular epidemiology of Bartonella species isolated from ground squirrels and other rodents in northern California. Epidemiology & Infection 144, 1837–1844. https://doi.org/10.1017/S09502 68816000108.
- [28] Goodrich I, McKee C, Kosoy M (2020) Longitudinal study of bacterial infectious agents in a community of small mammals in New Mexico. Vector-Borne and Zoonotic Diseases 20, 496–508. https://doi.org/10.1089/ vbz.2019.2550.
- [29] Kosoy M, Goodrich I (2019) Comparative ecology of Bartonella and Brucella infections in wild carnivores. Frontiers in Veterinary Science 5, 322. https://doi.org/10.3389/fvets.2018.00322.
- [30] Kerkhoff FT, et al. (1999) Demonstration of Bartonella grahamii DNA in ocular fluids of a patient with neuroretinitis. Journal of Clinical Microbiology 37, 4034–4038. https://doi.org/10.1128/jcm.37.12.4034-4038 1999
- [31] Inoue K, et al. (2009) Evolutional and geographical relationships of Bartonella grahamii isolates from wild rodents by multi-locus sequencing analysis. Microbial Ecology 57, 534–541. https://doi.org/10.1007/s00248-009-9488-x
- [32] Mardosaitė-Busaitienė D, et al. (2019) Prevalence and diversity of Bartonella species in small rodents from coastal and continental areas. Scientific Reports 9, 12349. https://doi.org/10.1038/s41598-019-48715-y.
- [33] Divari S, et al. (2021) Biomolecular investigation of *Bartonella* spp. in wild rodents of two Swiss regions. *Pathogens* 10, 1331. https://doi.org/10.3390/ pathogens10101331.
- [34] Majerová K, et al. (2021) Hedgehogs and squirrels as hosts of zoonotic Bartonella species. Pathogens 10, 686. https://doi.org/10.3390/pathogens10060686.
- [35] Cheslock MA, Embers ME (2019) Human bartonellosis: an underappreciated public health problem?. *Tropical medicine and infectious disease* 4, 69. https://doi.org/10.3390/tropicalmed4020069.
- [36] Macêdo RH, Mares MA (1988) Neotoma albigula. Mammalian species, 1–7. https://doi.org/10.2307/3504165.
- [37] Cornely JE, Baker RJ (1986) Neotoma mexicana. Mammalian Species, 1–7. https://doi.org/10.2307/3504054.
- [38] Esposito MM, et al. (2023) The impact of human activities on zoonotic infection transmissions. *Animals* 13, 1646. https://doi.org/10.3390/ani 13101646
- [39] La Scola B, et al. (2003) Gene-sequence-based criteria for species definition in bacteriology: the *Bartonella* paradigm. *Trends in Microbiology* 11, 318–321. https://doi.org/10.1016/S0966-842X(03)00143-4.