Emerging rodent-associated *Bartonella*: a threat for human health?

Maria Krügel¹, Nina Król¹, Volkhard A. J. Kempf²,³, Martin Pfeffer¹ and Anna Obiegala*¹

Abstract

Background: Species of the genus *Bartonella* are facultative intracellular alphaproteobacteria with zoonotic potential. *Bartonella* infections in humans range from mild with unspecific symptoms to life threatening, and can be transmitted via arthropod vectors or through direct contact with infected hosts, although the latter mode of transmission is rare. Among the small mammals that harbour *Bartonella* spp., rodents are the most speciose group and harbour the highest diversity of these parasites. Human–rodent interactions are not unlikely as many rodent species live in proximity to humans. However, a surprisingly low number of clinical cases of bartonellosis related to rodent-associated *Bartonella* spp. have thus far been recorded in humans.

Methods: The main purpose of this review is to determine explanatory factors for this unexpected finding, by taking a closer look at published clinical cases of bartonellosis connected with rodent-associated *Bartonella* species, some of which have been newly described in recent years. Thus, another focus of this review are these recently proposed species.

Conclusions: Worldwide, only 24 cases of bartonellosis caused by rodent-associated bartonellae have been reported in humans. Possible reasons for this low number of cases in comparison to the high prevalences of *Bartonella* in small mammal species are (i) a lack of awareness amongst physicians of *Bartonella* infections in humans in general, and especially those caused by rodent-associated bartonellae; and (ii) a frequent lack of the sophisticated equipment required for the confirmation of *Bartonella* infections in laboratories that undertake routine diagnostic testing. As regards recently described *Bartonella* spp., there are presently 14 rodent-associated *Candidatus* taxa. In contrast to species which have been taxonomically classified, there is no official process for the review of proposed *Candidatus* species and their names before they are published. This had led to the use of malformed names that are not based on the International Code of Nomenclature of Prokaryotes. Researchers are thus encouraged to propose *Candidatus* names to the International Committee on Systematics of Prokaryotes for approval before publishing them, and only to propose new species of *Bartonella* when the relevant datasets allow them to be clearly differentiated from known species and subspecies.

Keywords: Rodents, Host association, *Candidatus* species, *Bartonella*, Small mammal, Lagomorphs, Taxon

Background

The genus *Bartonella* (family Bartonellaceae; order Rhizobiales) comprises facultative intracellular alphaproteobacteria. An increasing number of *Bartonella* species are recognized as zoonotic pathogens [1]. In humans, bartonellosis can have a variety of mild and unspecific clinical signs and symptoms, but can also be life threatening [2, 3]. *Bartonella* can be transmitted to humans
indirectly from blood-sucking arthropod vectors through the scratches of an infected reservoir host (e.g. cats) or via contact with infectious faeces of arthropod vectors. Fleas play a major role in the transmission of *Bartonella*, especially the cat flea (*Ctenocephalides felis*), one of the most common flea species in central Europe, which is host opportunistic, and thus a common source of infection of *Bartonella*, and especially *Bartonella henselae* [4]. Direct transmission through contact with reservoir hosts can not be excluded as a possible transmission path, although it is considered highly unlikely.

A wide variety of mammals are suspected of being reservoir hosts of *Bartonella* spp. [2]. Among mammals, small mammals, including bat and rodent species, are the group that harbours by far the highest diversity of *Bartonella* spp. [5]. Moreover, high prevalences of *Bartonella* spp. have been detected in rodents, the most speciose group of mammals [6]. As many rodent species live in proximity to humans in many parts of the world, human-rodent interactions are not unlikely. Nonetheless, very low numbers of clinical cases of bartonellosis in humans have been reported in the context of rodent-less, very low numbers of clinical cases of bartonellosis human-rodent interactions are not unlikely. Nonetheless, very low numbers of clinical cases of bartonellosis in humans have been reported in the context of rodent-associated *Bartonella*. Thus, the purpose of this review is to determine explanatory factors for this unexpected finding. Therefore, we decided to explore (i) potential risk factors for humans; (ii) clinical cases described in recent years connected with rodent-associated bartonellosis; and, additionally (iii) the growing trend in the scientific literature of newly described *Bartonella* taxa, including the reporting of a high number of *Candidatus* species. This review is focussed on rodent, lagomorph and other small mammal species (with the exception of bats) as they may be sympatric and share the same ectoparasites and *Bartonella* species.

**Current knowledge on rodent reservoirs of *Bartonella* spp.**

**Global distribution of *Bartonella* spp. in small mammals**

Rodent-associated bartonelae are distributed worldwide and have been the subject of research on almost every continent. For a systematic review of papers describing the detection of *Bartonella* in small mammal species, the following search engines were used: Google Scholar, PubMed, and Google. The following terms were searched for, solely or in combination: ‘*Bartonella*’; ‘rodent’; ‘small mammal’; and, in addition [name of any country in the world]; or [name of any continent in the world]. Furthermore, a separate search was conducted with the search term [name of any small mammal genus] in combination with one of the following terms: [Bartonella]; [Bartonelae]; [ Bartonellosis]. Only studies published in the English language and in peer-reviewed journals were taken into consideration. In total, 132 studies were included in the analysis, representing research on *Bartonella* in a total of 231 small mammal species and subspecies (excluding bats). Research on *Bartonella* in small mammals has been conducted in 67 of the 195 countries (34.4%) of the world. Most of these studies were conducted in North America [in both Canada and the USA (100%)], followed by Europe [25 out of 44 countries (54.6%)] and Asia [19 out of 48 countries (39.6%)]. The continents/regions for which the lowest numbers of studies were reported are as follows: Africa [15 out of 54 countries (27.8%)], Oceania [two out of 14 countries (14.3%), and Latin America and the Carribean [four out of 33 countries (12.1%)] (Additional file 1: Table S1). Thus, small mammals in a large number of countries have not yet been investigated for the presence of *Bartonella* spp. Most of these countries are located in Latin America, the Middle East, and Central Africa, and the lack of published data from them might be partly due to their economic and/or political situation. However, it is considered important that studies are especially carried out in countries in Central Africa, as they are among those with the lowest health coverage [7]. People from these areas make up a large proportion of those who most frequently need treatment for neglected tropical diseases [7], and infections with rodent-borne *Bartonella* spp. can also be expected to occur more frequently in these areas. It is also worth noting that studies were more frequently conducted in some countries than in others (e.g. there were 17 from the USA but only one from Argentina). The studies undertaken in the USA were conducted thoroughly and, in total, reported 25 small mammal species positive for *Bartonella* (Fig. 1).

The most frequently studied genus was *Rattus*, and in particular the two cosmopolitan species *Rattus norvegicus* and *Rattus rattus*. Members of the genera *Apodemus, Bandicota, Microtus, Mus,* and *Myodes* were very often associated with *Bartonella* spp. The most studied rodent species was *R. norvegicus* (43 studies from four of the seven continents), followed by *R. rattus* (41 studies), *Mus musculus* (25 studies) and *Clethrionomys glareolus* (24 studies). The five *Bartonella* species most frequently detected in small mammal hosts were *Bartonella grahamii* (found in 53 small mammal species, and in 31 countries), *Bartonella elizabethae* (found in 43 small mammal species, and in 34 countries), *Bartonella tribocorum* (found in 30 small mammal species, and in 27 countries), *Bartonella taylorii* (found in 27 small mammal species, and in 21 countries), and *Bartonella queenslandensis* (found in 29 small mammal species, and in 13 countries). Small mammals positive for *Bartonella* were found in 65 (97.0%) of 67 investigated countries (they were not found in Hungary and Pakistan). The five most frequently listed *Bartonella* species in Additional file 1:
Table S1 may, however, be a distortion as, for example, *B. elizabethae* is one of the first rodent-associated species to have been described (in 1993) whereas other rodent-associated species such as *B. kosoyi* were not described until much later (in 2018). Furthermore, it should be noted that various methods were used in the studies, and that not all the published sequences had a homology of 100%.

Clinical cases of bartonellosis in humans in the context of rodent-associated *Bartonella* spp.

Clinical symptoms/clinical cases, diagnostics, and pathogenicity

The most frequently described *Bartonella* species pathogenic for humans include the human-specific species *Bartonella bacilliformis* (transmitted via sand flies), which causes Carrion’s disease in South America; the zoonotic, cat-transmitted species *B. henselae*, which is responsible for cat scratch disease; and the human-specific species *Bartonella quintana* (transmitted via body lice), the causative agent of trench fever [8]. Much less is known about human infections with other *Bartonella* spp. In general, endocarditis, lymphadenopathy and neuroretinitis are common symptoms of severe cases of bartonellosis [9]. A detailed PubMed analysis (performed on 2 October 2021) with the search terms ‘*Bartonella* species’ where the species was one of the 33 *Bartonella* species given in Table 1 [e.g. (*B. alsatica*) and (*infection*)] revealed only 14 publications citing evidence for human infections (see Table 2).

When high diagnostic standards were applied (including direct pathogen detection via culture or PCR), only eight *Bartonella* species or subspecies (*Bartonella vinsonii* subsp. *arupensis* infections, *B. elizabethae* infections, *Bartonella alsatica* infections, *B. tribocorum* or *B. vinsonii* subsp. *vinsonii* infections, *Bartonella doshiae*, *B. grahamii*, *Bartonella rattimassiliensis*) were reported (in total, 24 confirmed patient cases; see Table 2).

The analysis of the frequencies of clinical entities showed that 12 patients suffered from acute febrile illness (most likely associated with bacteremia/blood stream infections) (50%), three patients from endocarditis or prosthetic valvular graft infections (12.5%), three patients from lymphadenopathy (12.5%), two from nonspecific
| Order | Host species | Host category | Species name          | Nomenclatural status | Candidatus status | Reviewed name | Former name | References | Year |
|-------|--------------|---------------|-----------------------|----------------------|-------------------|---------------|-------------|------------|------|
| Rodentia | Acomys russatus Rodent | Bartonella acomydis | Validly published under the ICNP | No | Yes | | [51] | 2013 |
| | Apodemus spp. Rodent | Bartonella birtlesii | Validly published under the ICNP | No | Yes | | [175] | 2000 |
| | Callasciurus notatus Rodent | Bartonella callasciuri | Validly published under the ICNP | No | Yes | | [51] | 2013 |
| | Rattus leucopus Rodent | Bartonella coopersplainsensis | Validly published under the ICNP | No | Yes | | [136] | 2009 |
| | Microtus agrestis Rodent | Bartonella dashiae | Validly published under the ICNP | No | Yes | | [176] | 1995 |
| Rodents | Rodent | Bartonella elizabethae | Validly published under the ICNP | No | Yes | Rochalimaea elizabethae | [177] | 1993 |
| | Dipodillus dasyurus Rodent | Bartonella fadhili | Not validly published | Yes (corrected) Bartonella fadhilae | | | [178] | 2017 |
| | Microtus spp. Rodent | Bartonella fuyuanensis | Validly published under the ICNP | No | Yes | | [62] | 2015 |
| | Lophuromys sp. Rodent | Bartonella gabonensis | Not validly published | No | | | [179] | 2020 |
| | Gerbillus spp. Rodent | Bartonella gerbillinarum | Not validly published | Yes | | | [180] | 2018 |
| | Clethrionomys glareolus Rodent | Bartonella grahamii | Validly published under the ICNP | No | Yes | | [176] | 1995 |
| Rodents | Rodent | Bartonella heixiazensis | Validly published under the ICNP | No | Yes | | [62] | 2015 |
| | Jaculus orientalis Rodent | Bartonella jaculi | Validly published under the ICNP | No | Yes | | [51] | 2013 |
| | Apodemus argenteus Rodent | Bartonella japonica | Validly published under the ICNP | No | Yes | | [80] | 2010 |
| | Gerbillus spp. Rodent | Bartonella khokhlovae | Not validly published | Yes (corrected) Bartonella khokhlovae | | | [180] | 2018 |
| | Rattus rattus Rodent | Bartonella kosoyi | Validly published under the ICNP | No | Yes | | [181] | 2020 |
| | Rattus rattus Rodent | Bartonella krasnovi | Validly published under the ICNP | No | Yes | | [181] | 2020 |
| | Marmota monax Rodent | Bartonella marmotae | Not validly published | Yes (corrected) Bartonella marmotae | | | [182] | 2009 |
| | Mastomys erythroleucus Rodent | Bartonella mastomysi | Not validly published | No | Bartonella mastomysid | | [183] | 2018 |
| | Gerbillus spp. Rodent | Bartonella negevensis | Not validly published | Yes (corrected) Bartonella negevensis | | | [180] | 2018 |
| | Pachyuromys duprasi Rodent | Bartonella pachyuromydis | Validly published under the ICNP | No | Yes | | [51] | 2013 |
| Order                  | Host species         | Host category | Species name                          | Nomenclatural status                      | Candidatus status | Reviewed name | Former name | References | Year |
|-----------------------|----------------------|---------------|---------------------------------------|-------------------------------------------|-------------------|---------------|-------------|------------|------|
| Peromyscus spp.       | Rodent               |               | Bartonella peromysci                  | Validly published under the ICNP         | No                | Yes           | [176]       | 1995       |
| Rattus norvegicus     | Rodent               |               | Bartonella phoceensis                 | Not validly published                     | No                |               | [160]       | 2004       |
| Melomys spp.; Rattus  | Rodent               |               | Bartonella queenslandensis            | Validly published under the ICNP         | No                | Yes           | [136]       | 2009       |
| Mastomys erythroleucus| Rodent               |               | Bartonella raultii                    | Not validly published                     | No                |               | [131]       | 2014       |
| Rattus norvegicus     | Rodent               |               | Bartonella ratimassiliensis           | Not validly published                     | No                |               | [160]       | 2004       |
| Sciurus vulgaris      | Rodent               |               | Bartonella rudakovii                 | Not validly published                     | Yes               |               | [184]       | 2012       |
| Gerbilliscus gambianus| Rodent               |               | Bartonella sahelensis                | Not validly published                     | Yes (corrected)   | Bartonella sahelensis | [131]       | 2014       |
| Dipodillus dasyurus   | Rodent               |               | Bartonella sanae                      | Not validly published                     | Yes               |               | [178]       | 2017       |
| Apodemus argenteus    | Rodent               |               | Bartonella silvatica                 | Validly published under the ICNP         | No                | Yes           | [80]        | 2010       |
| Apodemus, Clethrionomys| Rodent              |               | Bartonella taylorii                  | Validly published under the ICNP         | No                | Yes           | [176]       | 1995       |
| Rattus norvegicus     | Rodent               |               | Bartonella thailandensis             | Not validly published                     | Yes               |               | [114]       | 2009       |
| Rattus spp.           | Rodent               |               | Bartonella tribocorum                | Validly published under the ICNP         | No                | Yes           | [185]       | 1998       |
| Voles                 | Rodent               |               | Bartonella vinsonii subsp. vinsonii   | Validly published under the ICNP         | No                | Yes           | [186]       | 1996       |
| Peromyscus yucatanicus| Rodent               |               | Bartonella vinsonii subsp. yucatanensis| Not validly published                     | No                |               | [187]       | 2016       |
| Glaucomys volans      | Rodent               |               | Bartonella volans                    | Not validly published                     | Yes               |               | [182]       | 2009       |
| Cynomys ludovicianus  | Rodent               |               | Bartonella washoensis subsp. cyonmyisi| Not validly published                     | Yes (corrected)   | Bartonella washoensis subsp. cyonmyisi | [188]       | 2008       |
| Lagomorpha            | Oryctolagus cuniculus| Small mammal (rabbit) | Bartonella alsatica                  | Validly published under the ICNP         | No                | Yes           | [185]       | 1999       |
| Diprotodontia         | Antechinus flavipes  | Small mammal (Marsupialia) | Bartonella antechini                 | Not validly published                     | Yes               |               | [189]       | 2011       |
| Macropus giganteus    | Big mammal (Marsupialia) |               | Bartonella australis                  | Not validly published                     | No                |               | [190]       | 2007       |
| Bettongia penicillata | Small mammal (Marsupialia) |               | Bartonella bettongiae                | Not validly published                     | Yes (corrected)   | Bartonella woylei | [189]       | 2011       |
Table 1 (continued)

| Order            | Host species            | Host category | Species name          | Nomenclatural status                      | Candidatus status | Reviewed name             | Former name            | References   | Year |
|------------------|-------------------------|---------------|-----------------------|-------------------------------------------|-------------------|---------------------------|------------------------|--------------|------|
| Eulipotyphla     | Crocidura rutilus       | Small mammal  | Bartonella florencae  | Validly published under the ICNP          | No                | Yes (corrected) Bartonella florencae | [131] 2014         |              |      |
|                  | Crocidura suaveolens    | Small mammal  | Bartonella rifkiaydamii | Not validly published                     | No                | [191] 2021                 |                        |              |      |
|                  | Talpa europaea          | Small mammal  | Bartonella talpae     | Validly published under the ICNP          | No                | Yes                       | [176] 1995          |              |      |
| Chiroptera       | Myotis daubentonii      | Small mammal  | Bartonella hem sundetensis | Not validly published                     | Yes               | Yes (corrected) Bartonella hem sundetensis | [192] 2015         |              |      |
|                  | Bats                    | Small mammal  | Bartonella lascolai   | Not validly published                     | No                | [193] 2016                 |                        |              |      |
|                  | Bats                    | Small mammal  | Bartonella naantaliensis | Not validly published                     | No                | [194] 2014                 |                        |              |      |
|                  | Bats                    | Small mammal  | Bartonella rolani     | Not validly published                     | No                | [193] 2016                 |                        |              |      |
|                  | Fruit bats              | Small mammal  | Bartonella rosetti    | Not validly published                     | Yes               | [188, 195] 2020            |                        |              |      |
| Peramelemorphia  | Perameles bougainville  | Small mammal  | Bartonella perametis  | Not validly published                     | Yes               | [189] 2011                 |                        |              |      |
| Xenarthra        | NA                      | Small mammal  | Bartonella wachoensis subsp. brasilien | Not validly published                     | Yes               | [196] 2020                 |                        |              |      |
| Primates         | Homo sapiens sapiens    | Human         | Bartonella bacilliformis | Validly published under the ICNP          | No                | [197] 1913                 |                        |              |      |
|                  | Homo sapiens sapiens    | Human         | Bartonella mayotimonensis | Not validly published                     | Yes               | [143] 2010                 |                        |              |      |
|                  | Homo sapiens sapiens    | Human         | Bartonella quintana   | Validly published under the ICNP          | No                | [177] 1993                 |                        |              |      |
|                  | Homo sapiens sapiens    | Human         | Bartonella tamiae     | Not validly published                     | No                | [198] 2008                 |                        |              |      |
|                  | Homo sapiens sapiens    | Human         | Bartonella vinsoni subsp. arupensis | Validly published under the ICNP          | No                | [199] 1999                 |                        |              |      |
|                  | Canis familiaris/ Human | Human         | Bartonella vinsoni    | Validly published under the ICNP          | No                | [177] 1993                 |                        |              |      |
|                  | Homo sapiens sapiens    | Human         | Bartonella washoensis subsp. vinsoni | Not validly published                     | Yes               | Bartonella washoensis            | [200] 1998         |              |      |
| Carnivora        | Felis silvestris catus  | Big mammal    | Bartonella claridgeae | Validly published under the ICNP          | No                | [201] 1996                 |                        |              |      |
|                  | Felis silvestris catus  | Big mammal    | Bartonella henselae   | Validly published under the ICNP          | No                | [177] 1993                 |                        |              |      |
|                  | Felis silvestris catus  | Big mammal    | Bartonella koechlerae | Validly published under the ICNP          | No                | [202] 2000                 |                        |              |      |
|                  | Puma concolor, Lynx rufus | Big mammal | Bartonella koechlerae subsp. bothien | Not validly published                     | No                | [203] 2016                 |                        |              |      |
| Order      | Host species                      | Host category | Species name                  | Nomenclatural status                        | Candidatus status            | Reviewed name | Former name | References | Year |
|------------|----------------------------------|---------------|-------------------------------|---------------------------------------------|-----------------------------|---------------|-------------|------------|------|
|            | Puma concolor, Lynx rufus        | Big mammal    | Bartonella koehlerae subsp. boulouisii | Not validly published                      | No                          |               |             | [203]      | 2016 |
|            | Felis silvestris catus           | Big mammal    | Bartonella koehlerae subsp. koehlerae | Not validly published                      | No                          |               |             | [202]      | 2000 |
|            | Procyon lotor, Canis familiaris  | Big mammal    | Bartonella rochalimae         | Validly published under the ICNP           | Yes                         |               |             | [204]      | 2012 |
|            | Canis familiaris                 | Big mammal    | Bartonella meleuxii           | Not validly published under the ICNP        | Yes                         |               |             | [184]      | 2012 |
|            | Canis familiaris                 | Big mammal    | Bartonella vinsonii subsp. berkhoffi | Validly published under the ICNP           | Yes                         |               |             | [186]      | 1996 |
|            | Urva aurapunctata                | Big mammal    | Bartonella kit tensis         | Not validly published under the ICNP        | No                          |               |             | [205]      | 2021 |
| Artiodactyla | Bos taurus                      | Big mammal    | Bartonella bovis              | Validly published under the ICNP           | No                          | Yes           | Bartonella weissii | [206]      | 2002 |
|            | Capreolus capreolus              | Big mammal    | Bartonella capreoli           | Validly published under the ICNP           | No                          | Yes           |             | [206]      | 2003 |
|            | Bos taurus                       | Big mammal    | Bartonella chornelii          | Validly published under the ICNP           | No                          | Yes           |             | [207]      | 2004 |
|            | Bos taurus                       | Big mammal    | Bartonella davoustii          | Not validly published under the ICNP        | Yes                         | Bartonella davoustii | [208]      | 2017 |
|            | Camelus dromedarius              | Big mammal    | Bartonella dromedani          | Not validly published under the ICNP        | No                          |               |             | [209]      | 2014 |
|            | Ovis aries                       | Big mammal    | Bartonella melophagi          | Not validly published under the ICNP        | Yes                         |               |             | [210, 211] | 2016 |
|            | Ovis aries                       | Big mammal    | Bartonella ovis               | Not validly published under the ICNP        | Yes                         |               |             | [212]      | 2018 |
|            | Odocoileus virginianus           | Big mammal    | Bartonella odocoilei         | Not validly published under the ICNP        | No                          |               |             | [213]      | 2021 |
|            | Bos taurus, Capreolus capreolus  | Big mammal    | Bartonella schoenbuchensis    | Validly published under the ICNP           | Yes                         | Bartonella schoenbuchii | [214]      | 2001 |
|            | Enhydrurus microcristatus         | Big mammal    | Bartonella cariots            | Not validly published under the ICNP        | Yes                         | Bartonella rondoniensis | [215]      | 2017 |
| Ixodida   | Ornithodoros sonrai              | Arthropoda    | Bartonella senegalensis       | Validly published under the ICNP           | No                          | Yes           |             | [131]      | 2014 |
|            | Ornithodoros sonrai              | Arthropoda    | Bartonella massiliensis       | Not validly published under the ICNP        | No                          |               |             | [216]      | 2019 |
|            | Siphonaptera                     | Arthropoda    | Bartonella durdenii           | Not validly published under the ICNP        | Yes                         |               |             | [182]      | 2009 |
|            | Hymenoptera                      | Arthropoda    | Bartonella apis               | Validly published under the ICNP           | No                          | Yes           |             | [217]      | 2016 |
|            | ND                               | ND            | Bartonella ancashensis        | Validly published under the ICNP           | No                          | Yes           | Bartonella ancashi | [218]      | 2015 |

Subsp. Subspecies, ND not determined
symptoms (8.3%), and one each from bacillary angiomatosis, hepatic lesions or neuroretinitis (4.2%). Two of these patients were uncompromised (human immunodeficiency virus infection, leukemia); no clear association with an underlying comorbidity was reported for the remaining patients. The reported antibiotic therapy regime varied but often included the administration of a macrolide combined with doxycycline for some weeks, which often resulted in clinical improvement.

From a clinical point of view, ‘acute febrile illness’ and ‘endocarditis’ can be classified as ‘bacteremia/blood stream infections’, which 15 of 24 reported patients (62.5%) suffered from. Although these cases were anecdotal, it can be suggested that human infections by rodent-associated Bartonella spp. are rare. To our knowledge, there are several possible reasons for this low number of case reports: (i) physicians are very likely unaware of Bartonella infections (especially when rodent-associated), and thus do not include them in their differential diagnosis; (ii) laboratories may not be able to detect these pathogens due to their fastidious nature, and because their diagnostic portfolio does not include PCR tests for the detection of Bartonella spp. or they do not carry out long, sterile microaerophilic incubations for the cultivation of samples from patients. Moreover, (iii) bartonellosis might only cause mild and unspecific symptoms; and (iv) rodent-associated Bartonella infections of humans may simply be rare medical entities. A possible molecular explanation for the latter is the host restriction of Bartonella species mediated by their respective Trw type IV secretion systems (T4SSs) [10]. The Trw T4SS (originally described as a plasmid conjugation system) is crucial for adhesion to erythrocytes and subsequent erythrocyte invasion, and Bartonella with mutations in the trwE gene (signature-tagged mutagenesis) are unable to establish long-lasting bacteremia in certain rodent infection models. It has been demonstrated that the Trw systems of certain Bartonella spp. are responsible for species-specific host-restricted adhesion to erythrocytes. For instance, the Trw T4SS of B. tribocorum mediates a significant bacterial infection in Wistar rats, but infection human erythrocytes is 23 times less efficient. It seems likely that infections of humans by rodent-adapted Bartonella spp. rarely occur because the rodent-pathogen Trw system and humanerythrocyte host receptors simply do not match.

**Groups at risk of Bartonella infection in the context of rodent-associated Bartonella spp.**

Many Bartonella species are pathogenic for humans. However, B. henselae, B. bacilliformis and B. quintana cause most cases of Bartonella disease in humans [8, 11]. Veterinarians, veterinary nurses and people that work with and care for animals seem to be at increased risk of infection as they are particularly exposed to reservoir hosts and vectors of Bartonella spp. [12–14]. Oteo et al. [15] found that 11.2–56% of tested veterinary professionals in Spain showed seroreactivity for B. henselae, B. quintana, and/or B. vinsonii berkhoffii. Bartonella spp. were even isolated from 7.9% of the positive individuals, although all of them were asymptomatic [15]. Bartonella henselae is also reported to have possibly contributed to the death of two veterinarians [16]. Cat and dog owners also appear to be at increased risk of infection. Transmission of B. henselae is associated with scratches received from both cats and dogs [17]. Owners of a cat ≤ 12 months old have an increased risk of infection with B. henselae compared to those with a cat > 12 months old [18]. Forest workers and orienteers seem to be the other groups at risk [19, 20]. Furthermore, a higher risk of infection has also been described for homeless people, alcoholics, and drug addicts who administer substances intravenously [21, 22]. Though an intravenous transmission route seems unlikely, one study did show that drug addicts who administered substances intravenously were more at risk of contracting Bartonella spp. [20]. Infection with ectoparasites such as lice and fleas due to poor hygiene may also lead to bartonellosis, especially in homeless people [23].

The risk factors for rodent-associated Bartonella infections in humans are similar to those mentioned above for Bartonella transmitted via other animals (Table 2). Most of the patients listed in Table 2 were either young, old, pregnant or immunosuppressed. We assume that inclusion in one of these groups is a risk factor for developing clinical symptoms after infection with rodent-associated bartonellae because these groups are associated with an impaired or not yet fully developed immune system. Thus, rodent-associated bartonellosis seems to be opportunistic and might be more likely to develop when a person has a pre-existing medical condition. Furthermore, the studies showed that being homeless [24], abusing drugs [20], or being in contact with animals, e.g. through hunting or animal breeding, may increase the risk of rodent-associated Bartonella infection.

**Reservoir role and clinical cases of pet animals infected with rodent-associated Bartonella spp.**

Cats are known hosts of B. henselae (and Bartonella claridgeiae and Bartonella kohlerae) and dogs of Bartonella rochalimae. Thus far, there have only been occasional reports of clinical symptoms in cats and dogs related to Bartonella spp. infection, and even fewer related to rodent-associated bartonellae. Whether bartonellae are primary or opportunistic pathogens for cats and dogs is not entirely clear. Clinical manifestations of bartonellosis
| Bartonella spp. | Clinical disease | Patient details | Microbiological diagnosis | Antimicrobial therapy | Clinical outcome | References |
|----------------|-----------------|-----------------|---------------------------|-----------------------|-----------------|------------|
| *Bartonella alsatica* | Prosthetic vascular graft infection | Male, 66 years old, hunter | PCRs (biopsies), sequence analysis | Doxycycline 2 × 100 mg/day (6 months) | Improvement of renal function (no comprehensible link to antibiotic treatment) | [219] |
| Endocarditis | Female, 77 years old, rabbit breeder | Serology (not standardized), culture and PCR (blood) negative | Gentamicin (15 days), amoxicillin (6 weeks) | Clinical improvement, no details given | [220] |
| Lymphadenopathy | Female, 79 years old, rabbit butcher | PCRs (lymph node), sequence analysis, serology (not standardized), histology (unspecific) | Doxycycline 200 mg/day (3 weeks) | Surgical removal of lymph nodes, no further details given | [115] |
| Endocarditis | Male, 74 years old, bioprosthetic aortic valve, parotideal cancer | Shell vial culture, PCR (valves and blood), sequence analysis, histology (unspecific) | Amoxicillin 12 g/day, gentamicin 320 mg/day changed to doxycycline 200 mg/day (6 weeks), ceftriaxone 2 g/day | Valve replacement, patient became apyretic | [221] |
| *Bartonella dashiae* | Unspecific (fatigue, blurred vision, arthralgia) | Female, 45 years old | Prolonged cultivation, PCR detection from blood | NA | NA | [222] |
| *Bartonella elizabethae* | Bacillary angiomatosis | Male, 35 years old, human immunodeficiency virus-positive | PCR (biopsy), sequence analysis, histology (unspecific) | NA | No patient follow-up (patient incompliance) | [223] |
| Acute febrile illness | Patients from rural Thailand (n = 2/14) | PCR from shell vial cultures, sequence analysis | NA | NA | [224] |
| Lymphadenopathy | Female, 18 years old, culture negative | PCRs (lymph node) | Azithromycin 3 × 250 mg/day, duration NA | Restitutio ad integrum | [225] |
| *Bartonella grahamii* | Lymphadenopathy | Female, 57 years old, cat scratch (exposed to infected rodents), leukaemia and bone marrow transplantation | Several PCRs (lymph node) and sequence analysis, histology (unspecific) | Azithromycin 250 mg/day (5 weeks) | Clinical restitutio ad integrum, no abnormal findings by ultrasound examination | [25] |
| B. grahamii | Neuroretinitis | Male, 55 years old, dog owner | PCRs (anterior chamber fluid), sequence analysis, serology (not standardized) | Doxycycline 200 mg/day, rifampin 600 mg/day | Intraocular inflammation extinguished, cataract development | [226] |
| *Bartonella rattimassiliensis* | Acute febrile illness | Patients from rural Thailand (n = 1) | PCR from shell vial cultures, sequence analysis | NA | NA | [224] |
| *Bartonella tribocorum* | Acute febrile illness, unspecific (fatigue, muscle pain, headache) | Patients from rural Thailand (n = 1) | Shell vial culture, PCR (blood) and sequence analysis | NA | NA | [224] |
| *Bartonella vinnicii* subsp. vinnicii | Acute febrile illness | Male, 64 years old, dog owner | Prolonged cultivation, PCR detection from blood | NA | NA | [222] |
| *Bartonella vinnicii* subsp. vinnicii | Blood stream infection (fever, unspecific neuropsychiatric symptoms) | Patients from rural Thailand (n = 1) | PCR from shell vial cultures, sequence analysis | NA | NA | [224] |
are rarely seen in domestic cats, and to the best of our knowledge, there have been no case reports of rodent-associated bartonellosis in them. However, there is one report of a cat which was thought to have transmitted rodent-associated \textit{B. grahamii} to a human via a scratch [25]. Unlike cats, dogs may develop severe clinical symptoms of bartonellosis that are similar to those displayed by humans [26]. Thus far, rodent-associated \textit{B. elizabethae}, \textit{B. grahamii}, \textit{B. taylori} and a \textit{Bartonella volans}-like strain have been detected in dogs [27–29]. However, only \textit{B. elizabethae} infections could be linked directly to a canine clinical case. An 8-year-old dog suffering from unspecific symptoms including lethargy, appetite and weight loss was diagnosed with \textit{B. elizabethae} infection in the blood stream. The dog died immediately before the diagnosis was confirmed, and no other pathogen was detected in the blood [28]. Furthermore, there is one record of a dog with a previously unspecific clinical record which was found to be positive for a strain of \textit{B. volans} after its death [29]. \textit{Bartonella grahamii}, \textit{B. elizabethae}, \textit{B. taylori} were found to have a moderate prevalence (9.4%) in stray dogs without a clinical record in Thailand, highlighting the potential reservoir competence of dogs for rodent-associated bartonellae [27].

### Current insights into \textit{Bartonella} taxonomy with a focus on recently discovered small mammal-associated \textit{Bartonella} spp.

Bartonellae can be divided into eubartonellae and other ancient clades according to their genetic features [5]. Eubartonellae can further be subdivided into four lineages, one of which is the most diverse with regard to potential host species as well as species and subspecies of \textit{Bartonella}. There are presently 84 known species and subspecies of \textit{Bartonella}, of which 38 were initially found in specimens belonging to the order Rodentia, followed by 10 species each in specimens of the orders Carnivora and Artiodactyla, and seven in humans. The number of newly described species has been increasing in the past decade [5]. Forty-five new \textit{Bartonella} species have been proposed and/or published since 2011 (Table 1). Most of these newly described \textit{Bartonella} species (\(n = 30\)) were reported in wild small mammal or specifically rodent species such as \textit{Acomys russatus} (golden spiny mouse), \textit{Mastomys erythroleucus} (Guinea multimammate mouse), and \textit{Pachyuromys duprasi} (fat-tailed gerbil) (Table 1). Out of the 51 proposed or published rodent- or other small mammal-associated species, 19 have \textit{Candidatus} status.

There is an increasing number of newly discovered, not yet fully characterized, \textit{Bartonella} species with \textit{Candidatus} status. Labelling a potentially new species \textit{Candidatus} is a new concept that began in the 1990s [30] and allows researchers to propose prokaryotic taxa that are well characterized but as yet uncultured. In contrast to official

| \textit{Bartonella} spp. | Clinical disease | Patient details | Microbiological diagnosis | Antimicrobial therapy | Clinical outcome | References |
|-------------------------|-----------------|-----------------|---------------------------|-----------------------|-----------------|------------|
| \textit{B. vinsonii} subsp. \textit{arupensis} | Acute febrile illness | Patients from rural Thailand (\(n = 2\)) | PCR from shell vial cultures, sequence analysis | NA | NA | [224] |
| | Acute febrile illness, unspecific (fever, myalgia, fatigue), elevated liver enzymes | Patients from rural Thailand (\(n = 4\)) | Pre-enriched media PCR, sequence analysis | NA | NA | [228] |
| | Hepatic granulomatous lesions | Female, 11 years old, cat exposure | PCR (liver biopsy, cat blood) | Azithromycin 500 mg (4 weeks) followed by doxycycline 2 x 100 mg (four weeks) | Clinical improvement (decrease in size of hepatic lesions) | [229] |
| | Endocarditis | Male, 79 years old, bioprosthetic aortic valve | Serology (non-standardized), PCR, (serum) sequence analysis | Doxycycline 200 mg/ day, ofloxacin 200 mg/ day, duration NA | Clinical improvement (no details given) | [230] |

\(n\) Number of patients examined; NA not available

\(a\) Experimental approach; applied serology not evaluated according to laboratory diagnostic standards

\(b\) Detection of structures under Warthin–Starry staining or similar staining (no specific staining for \textit{Bartonella} spp.)

\(c\) Species identification questionable, more likely \textit{Bartonella} tribocorum [25]
species names, there is no official process for reviewing proposed Candidatus species and their names before they are published (A. Oren, personal communication). Authors are welcome to submit the proposed names to the Judicial Commission on Prokaryote Nomenclature of the International Committee on Systematics of Prokaryotes (ICSP), but they are not obliged to do so. The committee reviews Candidatus species through an extensive literature review, as many Candidatus names have not been qualitatively validated or do not follow the rules of the International Code of Nomenclature of Prokaryotes [31], which explains why many Candidatus names in use for newly described Bartonella species are malformed. However, suggested corrections for these malformed names are regularly published [32]. Nevertheless, due to the large number of new Candidatus taxa being proposed, particularly those with rodents and other small mammals as their origin and likely reservoir hosts, the lists of corrected names are not exhaustive and constantly evolving [31, 32].

Thus, the above should be borne in mind with respect to newly described Candidatus species and their published names. A mandatory submission process for the validation of species names prior to the publication of newly proposed Candidatus species would help to avoid the time-consuming renaming process carried out by the ICSP, and would further help to avoid the circulation in the literature of malformed Candidatus names. For example, the ICSP proposes that ‘Bartonella bandicootii’ should be re-named ‘Bartonella paramelis’ (Table 1). ‘Bandicoot’ is the English name of the animal from which this species of Bartonella was isolated, but the proposed specific epithet ‘bandicootii’ (rather than ‘bandicooti’) is both malformed and in violation of recommendation 6 (3) of the ICNP. The genus name of the host animal, which is Parameles, should be used as the basis for the specific epithet of the Bartonella species rather than the English common name, bandicoot, which is why the current name of this species should be Bartonella paramelis [33].

Furthermore, an increasing number of Bartonella species without Candidatus status have not been validly published according to the ICNP. In total, there are 44 Bartonella species names currently in use that have not been validly published. Of these species, 40 have been described since 2007, and 17 are from rodents or other small mammals (Table 1). As the number of newly described Bartonella species is increasing, in particular with respect to those isolated from rodents and other small mammals, it would be helpful if their names were proposed for approval under the ICNP before they were published, and that these should only be published when the relevant dataset allows these Bartonella species to be clearly differentiated from known species and subspecies of the genus. At present, it is not always easy to define a species or subspecies, but with whole genome sequencing becoming more affordable, it is highly likely that this issue will be resolved in the future through the sufficient description of new Candidatus species through the use of this genetic technique [34].

Further reasons for low numbers of cases of bartonellosis in humans despite high prevalences of Bartonella spp. in rodents and other small mammals

At first glance, it appears to be a phenomenon that Bartonella spp. from small mammals seem to be the least pathogenic for humans and their companion animals, and especially so in the case of rodents, as these comprise the group of small mammals with the highest prevalences and diversities of recorded Bartonella species, are commonly found in urban areas, and are known to harbour and spread disease [35]. Recent work demonstrated that one third of Norway rats in the Belgian region of Flanders harboured B. tribocorum, yet no human cases of infection with this parasite have been reported there [36]. Although it does not seem plausible that there is no transmission of Bartonella spp. from rodents to humans, in particular when taking into consideration the prevalences of Bartonella spp. in rodents and the frequent proximity of the latter to humans, there are several factors that might account for this.

Rodent-associated Bartonella spp. are probably arthropod-borne pathogens, but transmission through rodent scratches or bites (as is often reported for B. henselae infections) cannot be completely ruled out [1, 37]. Several studies have reported possible vertical transmission in naturally infected rodents [37–39]. However, a study on infected Clethrionomys glareolus could not experimentally prove transplacental or transovarial transmission of B. taylorii and B. grahamii to the offspring. There is one report of possible vertical transmission of B. birtlesii in BALB/c mice [40]. Most rodent-associated flea species are host specific and do not infest humans, which further limits potential zoonotic transmission of Bartonella spp. However, a few flea species are known to be more host opportunistic [41]. Yersinia pestis, the causative agent of the plague, is known to be transmitted from rats to humans mainly through Xenopsylla cheopis, the oriental rat flea [42], which can cause severe outbreaks of the disease. Xenopsylla cheopis is also known to harbour DNA of zoonotic Bartonella spp. such as B. elizabethae, and it was experimentally shown that X. cheopis can excrete this species over time [43, 44]. Nonetheless, there are, to the best of our knowledge, no reported cases of bartonellosis in humans previously infested with this flea species.
Another possible means of infection is direct contact with a reservoir host. Cats may transmit *B. henselae* to humans through their scratches [45]. There is even one report of a cat transmitting *B. grahamii*, which is a rodent-associated pathogen, to its owner [25]. The explanation for this was that the cat came into contact with an infected rodent when it caught it with its paws, which then became infectious. As rodents are not predators of humans and tend to avoid them, direct contact between the two is highly unlikely, with the exception of small mammals kept as pets [46]. However, indirect transmission via a cat is a possible, though unlikely, transmission path [25].

Notwithstanding the cases described above, rodent-associated bartonellae are the principal cause of bartonellosis in humans. However, how and to what extent rodents and their ectoparasites are involved in the zoonotic transmission cycle of *Bartonella* is not fully understood. Studying the transmission of *Bartonella* spp. from rodents to humans would help in assessing the potential risk of the former for the latter.

Conclusions

The zoonotic transmission cycle of rodent-associated bartonellae is not fully understood. It is especially unknown whether *Bartonella* infections in humans arise from direct contact with small mammals or rather indirectly via infestation with a rodent-associated ectoparasite vector. The total number of confirmed human cases of bartonellosis worldwide caused by rodent-associated bartonellae is much lower than expected when taking into account the abundance of *Bartonella* spp. in rodents, and possible reasons for this have been discussed in this review. Many small mammal species are considered reservoir hosts for the increasing number of newly described *Bartonella* spp., although some of the latter have yet to be experimentally confirmed. Even though most *Bartonella* spp. show high adaptation to their hosts, this is not the case for all rodent-associated species. That is why further experimental research is needed to increase our understanding of host–pathogen interactions between rodents and *Bartonella* species.

Acknowledgements

The authors wish to thank Prof. Aharan Oren for providing information on the submission process for Candidatus taxa and updated information on the nomenclatural status of certain Bartonella species.

Authors’ contributions

MP and AO organized and drafted the manuscript. AO, MK, VAJK, NK and MP wrote the final version of the manuscript. All the authors read and approved the final manuscript.

Funding

VK is funded by the LOEWE Centre DRUID (Novel Drug Targets against Poverty-Related and Neglected Tropical Infectious Diseases [project C2]) and the Robert Koch-Institute, Berlin, Germany (Bartonella Consiliary Laboratory, 1369-354).

Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

1 Institute of Animal Hygiene and Veterinary Public Health, University of Leipzig, An den Tierkliniken 1, 04103 Leipzig, Germany. 2 Institute for Medical Microbiology and Infection Control, University Hospital, Goethe University, Frankfurt am Main, Germany. 3 National Consiliary Laboratory for Bartonella, Frankfurt am Main, Germany.

Received: 1 November 2021 Accepted: 11 January 2022

Published online: 31 March 2022

References

1. Gutiérrez R, Krasnov B, Morick D, Gottlieb Y, Khokhlova IS, Harrus S. Bartonella infection in rodents and their flea ectoparasites: an overview. Vector Borne Zoonotic Dis. 2015;15:27–39. https://doi.org/10.1089/vbz.2014.1606.

2. Breitschwerdt EB, Maggi RG, Chomel BB, Lappin MR. Bartonellosis: an emerging infectious disease of zoonotic importance to animals and human beings. J Vet Emerg Crit Care. 2010;20:8–30. https://doi.org/10.1111/j.1476-4431.2009.00496.x.

3. García-Quintanilla M, Dichter AA, Guerra H, Kempf VAJ. Carrion’s disease: more than a neglected disease. Parasit Vectors. 2019;12:141. https://doi.org/10.1186/s13071-019-3390-2.

4. Portillo A, Santibañez V, García-Álvarez L, Palomar AM, Oteo JA. Rick-ettssies in Europe. Microbes Infect. 2015;17:834–8. https://doi.org/10.1016/j.micinf.2015.09.009.

5. Wagner A, Dehio C. Role of distinct type-IV-secretion systems and secreted effector sets in host adaptation by pathogenic Bartonella species. Cell Microbiol. 2019;21: e13004. https://doi.org/10.1111/cmi.13004.

6. Michaux J, Reyes A, Catzeflis F. Evolutionary history of the most speci-ose mammals: molecular phylogeny of muroid rodents. Mol Biol Evol. 2001;18:2017–31. https://doi.org/10.1093/oxfordjournals.molbev.a003743.

7. Report WHO: World health statistics 2021: monitoring health for the SDGs, sustainable development goals. Geneva: WHO; 2021.

8. Kaiser PO, Riess T, ORourke F, Linke D, Kempf VAJ. Bartonella spp.: throwing light on uncommon human infections. Int J Med Microbiol. 2011;301:7–15. https://doi.org/10.1016/j.ijmm.2010.06.004.

Abbreviations

ICNP: International Code of Nomenclature of Prokaryotes; ICSP: International Committee on Systematics of Prokaryotes; Trw T4SS: Trw type IV secretion system.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13071-022-05162-5.

Additional file 1: Table S1. Worldwide prevalence levels of Bartonella spp. in small mammal species including the detection method.
12. Oliveira AM, Maggi RG, Woods CW, Breitschwerdt EB. Suspected needle stick transmission of Bartonella vinsonii subspecies berkoffi to a veterinarian. J Vet Intern Med. 2010;24:1229–32. https://doi.org/10.1111/j.1933-6677.2010.05633.x.

13. Maggi RG, Mascarelli PE, Pultorak EL, Hegarty BC, Bradley JM, Mozayeni BR, Breitschwerdt EB. Bartonella spp. bacteremia in high-risk immuno-compotent patients. Diagn Microbiol Infect Dis. 2011;71:430–7. https://doi.org/10.1016/j.diagmicrobio.2011.09.001.

14. Lantos PM, Maggi RG, Ferguson B, Varkey J, Park LP, Breitschwerdt EB, et al. The Trw type IV secretion system of Bartonella mediates host-specific adhesion to erythrocytes. PLoS Pathog. 2010;6:e1000946. https://doi.org/10.1371/journal.ppat.1000946.

15. Lamarra C, Curi A, Bóia MN, Lemos ERS. Human bartonellosis: seroepidemiological and clinical features with an emphasis on data from Brazil—a review. Mem Inst Oswaldo Cruz. 2008;103:221–35. https://doi.org/10.1590/S0074-02762008000300001.

16. Zangwill KM, Hamilton DH, Perkins BA, Regnery RL, Plikaytis BD, Hadler JB, et al. Bartonella quintana (Candidatus) bacteremia in inner-city patients with chronic alcoholism. N Engl J Med. 1995;332:424–8.

17. Purcell RH, Spaeh DH, Kippen DA, Sugg NK, Regnery RL, Sayers MH, et al. Prevalence of Bartonella spp. from embryos and neonates of naturally infected Microtus townsendii females. J Biogeogr. 2007;34:1679–90. https://doi.org/10.1111/j.1365-2699.2007.01736.x.

18. Shenbrot G, Krasnov B, Lu L. Geographical range size and host specificity: a systematic review and narrative synthesis of literature regarding the ecology of rat-associated zoonoses in urban centers. Vector Borne Zoonotic Dis. 2017;17:42–50. https://doi.org/10.1089/ vbz.2016.1956.

19. Bajer A. Bartonella infections in three species of Microtus: prevalence and genetic diversity, vertical transmission and the effect of concurrent Babesia microti infection on its success. Parasit Vectors. 2018;11:491. https://doi.org/10.1186/s13071-018-3047-6.

20. Tołkacz K, Alsarraf M, Kowalec M, Dwużnik D, Grzybek M, Behnke JM, et al. Bartonella infection on its success. Parasit Vectors. 2018;11:491. https://doi.org/10.1186/s13071-018-3047-6.

21. Bown KJ, Bennett ML, Begon M. Flea-borne Bartonella henselae and Bartonella elizabethae in flea-vectors: a systematic review and narrative synthesis of literature regarding the ecology of rat-associated zoonoses in urban centers. Vector Borne Zoonotic Dis. 2013;13:349–59. https://doi.org/10.1089/vbz.2012.1195.

22. Krügel M, Pfeffer M, Król N, Imholt C, Baert K, Ulrich RG, Obiegala A. Bartonella and pathogenic effect on reproductive functions. Infect Immun. 2015;83:652–62. https://doi.org/10.1128/IAI.001715.

23. Oren A, Garity GM, Parker CT, Chuvochina M, Trujillo ME. List of names of prokaryotic Candidatus taxa. Int J Syst Evol Microbiol. 2020;70:4017–36. https://doi.org/10.1093/ijsem/skaa133.

24. Oren A, Garity GM. Candidatus list no. 2. Lists of names of prokaryotic Candidatus taxa. Int J Syst Evol Microbiol. 2021. https://doi.org/10.1099/ijsem.0.004671.

25. Oren A. A plea for linguistic accuracy—also for Candidatus taxa. Int J Syst Evol Microbiol. 2017;67:1085–94. https://doi.org/10.1099/ijsem.0.001715.

26. McGill S, Hjelm E, Rajs J, Lindquist O, Friman G. Bartonella quintana (Candidatus) bacteremia in inner-city residents of New York City. Emerg Infect Dis. 2004;10:684–7. https://doi.org/10.3201/eid1004.040345.

27. Bown KJ, Bennett ML, Begon M. Flea-borne Bartonella species. Xenopsylla cheopis and X. canadensis (Siphonaptera: Pulicidae) collected from rats in Los Angeles, California. Appl Environ Microbiol. 2011;77:3850–2. https://doi.org/10.1128/AEM.06012-11.

28. Bown KJ, Bennett ML, Begon M. Flea-borne Bartonella henselae and Bartonella quintana (Candidatus) bacteremia in inner-city patients with chronic alcoholism. N Engl J Med. 1995;332:424–8.

29. Bown KJ, Bennett ML, Begon M. Flea-borne Bartonella henselae and Bartonella quintana (Candidatus) bacteremia in inner-city patients with chronic alcoholism. N Engl J Med. 1995;332:424–8.

30. Oren A, Garity GM, Parker CT, Chuvochina M, Trujillo ME. List of names of prokaryotic Candidatus taxa. Int J Syst Evol Microbiol. 2020;70:4017–36. https://doi.org/10.1093/ijsem/skaa133.

31. Oren A, Garity GM. Candidatus list no. 2. Lists of names of prokaryotic Candidatus taxa. Int J Syst Evol Microbiol. 2021. https://doi.org/10.1099/ijsem.0.004671.

32. Oren A, Garity GM. Candidatus list no. 2. Lists of names of prokaryotic Candidatus taxa. Int J Syst Evol Microbiol. 2021. https://doi.org/10.1099/ijsem.0.004671.

33. Oren A, Garity GM. Candidatus list no. 2. Lists of names of prokaryotic Candidatus taxa. Int J Syst Evol Microbiol. 2021. https://doi.org/10.1099/ijsem.0.004671.

34. Bown KJ, Bennett ML, Begon M. Flea-borne Bartonella henselae and Bartonella quinta (Candidatus) bacteremia in inner-city patients with chronic alcoholism. N Engl J Med. 1995;332:424–8.
82. Schmidt S, Essbauer S, Mayer-Scholl A, Poppert S, Schmidt-Chanasit J, Klempa B et al. Multiple infections of rodents with zoonotic pathogens in Austria. Vector Borne Zoonotic Dis. 2014;14:467–75. https://doi.org/10.1089/vbz.2013.1504.

83. Engbaek K, Lawson PA. Identification of Bartonella species in rodents, shrews and cats in Denmark: detection of two B. henselae variants, one in cats and the other in the long-tailed field mouse. APMIS. 2004;112:336–41. https://doi.org/10.1111/j.1600-0463.2004.apm1120603.x.

84. Tea A, Alexiou-Daniel S, Papoutsi A, Papa A, Antoniadis A. Bartonella species isolated from rodents. Greece. Emerg Infect Dis. 2004;10:963–4. https://doi.org/10.3201/eid1005.030040.

85. Lipatova I, Paulauskas A, Puraitė I, Radziejewska J, Balciuskaus L, Gedminas V. Bartonella infection in small mammals and their ectoparasites in Lithuania. Microbes Infect. 2015;17:884–8. https://doi.org/10.1016/j.micinf.2015.08.013.

86. Paziewska A, Harris PD, Zvolinska L, Bajer A, Sinski E. Differences in the ecology of Bartonella infections of Apodemus flavicollis and Myodes glareolus in a boreal forest. Parasitology. 2012;139:881–93. https://doi.org/10.1017/S0031182012000170.

87. Welc-Faleciak R, Paziewska A, Bajer A, Behnike JM, Sinski E. Bartonella spp. infection in rodents from different habitats in the Mazury Lake District, northeast Poland. Vector Borne Zoonotic Dis. 2008;8:467–74. https://doi.org/10.1089/vbz.2008.0291.

88. Welc-Faleciak R, Bajer A, Behnike JM, Sinski E. The ecology of Bartonella spp. infection in two rodent communities in the Mazury Lake District region of Poland. Parasitology. 2010;137:1069–77. https://doi.org/10.1017/S003118201000992058.

89. Spitalska E, Minchova L, Kocianova E, Skultety L, Harnikova L, Hamilkova Z et al. Diversity and prevalence of Bartonella species in small mammals from Slovakia, Central Europe. Parasitol Res. 2017;116:3087–95. https://doi.org/10.1007/s00436-017-5620-x.

90. Gil H, García-Esteban C, Barandika JP, Peig J, Toledo A, Escudero R et al. Variability of Bartonella genotypes among small mammals in Spain. Appl Environ Microbiol. 2010;76:8062–70. https://doi.org/10.1128/AEM.01186-10.

91. Holmberg M, Mills JN, McGill S, Benjamin G, Ellis BA. Bartonella infection in sylvatic small mammals of central Sweden. Epidemiol Infect. 2003;130:149–57. https://doi.org/10.1017/S0950268802008075.

92. Celebi B, Karagöz Alper, Özkazanc N, Babur C, Kilic S, et al. Bartonella species in wild small mammals from the Lao PDR. Pathogens. 2021;10:1331. https://doi.org/10.3390/pathogens10101331.

93. Castillo KT, Kosoy M, Lerdthusnee K, Phelan L, Bai Y, Gage KL et al. Prevalence and genetic diversity of Bartonella species in rodents from southern China. Am J Trop Med Hyg. 2004;70:429–33. https://doi.org/10.4269/ajtmh.2004.70.429.

94. Baj Y, Kosoy MY, Merheuter Y, Welegerima K, Breno M, Tomás Z, Kidane D et al. Bartonella prevalence and genetic diversity in small mammals from Ethiopia. Vector Borne Zoonotic Dis. 2013;13:164–75. https://doi.org/10.1089/vbz.2012.1004.

95. Gundi VAKB, Kosoy MY, Makundi RH, Laudisoit A. Identification of diverse Bartonella genotypes among small mammals from democratic Republic of Congo and Tanzania. Am J Trop Med Hyg. 2012;87:319–26. https://doi.org/10.4269/ajtmh.2012.11-0555.

96. Gundi VAKB, Billetter SA, Rood MP, Kosoy MY. Bartonella spp. in rats and zoosinises, Los Angeles, California, USA. Emerg Infect Dis. 2012;18:631–3. https://doi.org/10.3201/eid1804.110816.

97. Gelling M, Macdonald DW, Telfer S, Jones T, Bown K, Birtles R, Mathews F. Parasites and pathogens in wild populations of water voles (Arvicola amphibius) in the UK. Eur J Wildl Res. 2012;58:615–9. https://doi.org/10.1007/s10344-011-0584-0.

98. Bitam I, Rolain J-M, Kemf T, Baziz B, Paorao P, Raoult D. Bartonella spp. detected in rodents and hedgehogs from Algeria. Clin Microbiol Infect. 2009;15:102–3. https://doi.org/10.1111/j.1469-0691.2008.02180.x.

99. Holmberg M, Mills JN, McGill S, Benjamin G, Ellis BA. Bartonella species in Apodemus flavicollis and Myodes glareolus in a boreal forest. Parasitology. 2012;139:881–93. https://doi.org/10.1017/S0031182012000170.

100. Meheretu Y, Leirs H, Welegerima K, Breno M, Tomás Z, Kidane D et al. Bartonella prevalence and genetic diversity in small mammals from Ethiopia. Vector Borne Zoonotic Dis. 2013;13:164–75. https://doi.org/10.1089/vbz.2012.1004.
northwestern Mexico. Vector Borne Zoonotic Dis. 2014;14:838–45. https://doi.org/10.1089/vbz.2014.1673.

119. Bai Y, Kosoy MY, Cully JF, Bala T, Ray C, Collinge SK. Acquisition of non-sporic Bartonella strains by the northern grasshopper mouse (Onychomys leucogaster). FEMS Microbiol Ecol. 2007;61:438–48. https://doi.org/10.1111/j.1574-6941.2007.00364.x.

120. Kamani J, Morick D, Mumcuoglu KY, Harrus S. Prevalence and diversity of Bartonella species in commensal rodents and ectoparasites from Nigeria. West Africa PLOS Negl Trop Dis. 2013;7:e2246. https://doi.org/10.1371/journal.pntd.0002246.

121. Billetter SA, Bochert JN, Atiku LA, Mpanga JT, Gage KL, Kosoy MY. Bartonella species in invasive rats and indigenous rodents from Uganda. Vector Borne Zoonotic Dis. 2014;14:182–8. https://doi.org/10.1089/vbz.2013.1375.

122. Mangombi JB, N’dilimabaka N, Lekana-Douki J-B, Banga O, Maghendji-Diouf K, Diarra AZ, Kone AK, Doumbo Niare S, Laroche M, Diatta G, Atteynine GL. Halliday JEB, Knobel DL, Agwanda B, Bai Y, Breiman RF, Cleaveland S, et al. Temporal and spatial patterns of Bartonella infection in black-tailed prairie dogs (Cynomys ludovicianus) in the southeastern United States. Am J Trop Med Hyg. 1997;57:578–88. https://doi.org/10.4266/ajtmh.1997.57.578.

123. Gundi VAKB, Taylor C, Raoult D, La Scola B. Bartonella queenslandensis sp. nov., Bartonella queenslandensis sp. nov. and Bartonella cooperiplanensis sp. nov., identified in Australian rats. Int J Syst Evol Microbiol. 2009;59:2956–61. https://doi.org/10.1099/ijs.0.028865-0.

124. Obiegala A, Jeske K, Augustin M, Kröl N, Fischer S, Mertens-Scholz K, et al. Highly prevalent bartonellae and other vector-borne pathogens in small mammal species from the Czech Republic and Germany. Parasit Vectors. 2019;12:332. https://doi.org/10.1186/s13071-019-3576-7.

125. Kosoy MY, Regnery RL, Tzanabos T, Marston EL, Jones DC, Green D, et al. Distribution, diversity, and host specificity of Bartonella in Rodents from the southeastern United States. Am J Trop Med Hyg. 1997;57:578–88. https://doi.org/10.4266/ajtmh.1997.57.578.

126. Ye X, Li G-w, Yao M-h, Luo W, Su L-q. Study on the prevalence and genotypes of Bartonella species in rodent hosts from Fujian coastal regions. Zhonghua Liu Xing Bing Xue Za Zhi. 2009;30:989–92.

127. Halliday JEB, Agwanda B, Bai Y, Breiman RF, Cleaveland S, et al. Bartonella mayotimonensis sp. nov., identified in the Huayllacallán Valley, Ancash, Peru, a region endemic for human bartonellosis. Am J Trop Med Hyg. 1999;60:799–805. https://doi.org/10.4266/ajtmh.1999.50.799.

128. Birtles RJ, Canales J, Ventosilla P, Alvarez E, Guerra H, Llanos-Cuentas A. et al. Survey of Bartonella species infecting intradomestic animals in the Huayllacallán Valley, Ancash, Peru, a region endemic for human bartonellosis. Am J Trop Med Hyg. 2019;100:506–9. https://doi.org/10.4269/ajtmh.2019.18-0616.

129. Rao HX, Yu J, Guo P, Ma YC, Liu QY, Jiao M, et al. Longitudinal study of Bartonella infection in rodents from south-western Spain. Vector Borne Zoonotic Dis. 2008;8:695–700. https://doi.org/10.1089/vbz.2007.0257.

130. Jardine C, Appleyard G, Kosoy MY, McColl D, chirino-Trojo M, Wobeser G, Leighton FA. Rodent-associated Bartonella in Saskatchewan, Canada. Vector Borne Zoonotic Dis. 2005;5:402–9. https://doi.org/10.1089/vbz.2005.5.402.

131. Buffet J-P, Marsot M, Vaumourin E, Gasqui P, Masséglia S, Marcheteau N. et al. Co-infection of Borrelia afzelii and Bartonella spp. in bank voles from a suburban forest. Comp Immunol Microbiol Infect Dis. 2012;35:583–9. https://doi.org/10.1016/j.cimid.2012.07.002.

132. Matsu moto K, Cook JA, Goethert HK, Telford SR. Bartonella sp. infection of voles trapped from an interior Alaskan site where ticks are absent. J Wild Dis. 2010;46:173–8. https://doi.org/10.7580/jwdis.2009-5358-46.1.173.

133. Hidalgo-Fuentes A, Barreiro J, Alfredo Carrión C, Foronda P, Javier Buitrago-Sánchez, Ana Rodríguez, et al. Bartonella infection in rodents and Shrews in Taiwan. Zoonoses Public Health. 2010;57:439–46. https://doi.org/10.1111/j.1863-2378.2009.01234.x.

134. Colin EY, Tiscrèlis C, Baddour LM, Lepidi H, Rolain JM, Patel R, Raoult D. Candidatus Bartonella mayotimonensis and endocarditis. Emerg Infect Dis. 2010;16:500–3. https://doi.org/10.3201/eid1603.081673.

135. Márquez FJ. Molecular detection of Bartonella in wood ticks collected from yaks and plateau pikas (Ochotona curzoniae) in Shiqu County, China. BMC Vet Res. 2020;16:235. https://doi.org/10.1186/s12917-020-02452-x.

136. Rao HK, Yu J, Guo P, Ma YC, Liu QY, Jiao M, et al. Bartonella species detected in the plateau pikas (Ochotona curzoniae) from Qinghai Plateau in China. Biomed Environ Sci. 2015;28:674–8. https://doi.org/10.3967/bes.2015.094.

137. Kik MLI, Jaarsma RL, Izer J, Sprong H, Grone A, Rijks JM. Bartonella aliscaxica in wild and domestic rabbits (Oryctolagus cuniculus) in the Netherlands. Microbiol Res. 2021;125:524–7. https://doi.org/10.1016/j.micres.2021.04.022.

138. Medialamkov O, Aubadie M, Bassene H, Diatta G, Granjon L, Fenollar F. Three new Bartonella species from rodents in Senegal. Int J Infect Dis. 2014;21:335. https://doi.org/10.1016/j.ijid.2013.03.1112.

139. Kleyhans DJ, Sarli J, Hatylko LM, Alagali AN, Bennett NC, Mohammed OB, Bastos AD. Molecular assessment of Bartonella in Gerbillus nanus from Saudi Arabia reveals high levels of prevalence, diversity and co-infection. Infect Genet Evol. 2018;65:244–50. https://doi.org/10.1016/j.meegid.2018.07.036.

140. Rocchigiani G, Ebani VV, Nardoni S, Bertelloni F, Bascherini A, Leoni A, et al. Molecular survey on the occurrence of arthropod-borne pathogens in wild brown hares (Lepus europaeus) from central Italy. Infect Genet Evol. 2018;59:142–7. https://doi.org/10.1016/j.meegid.2018.02.003.

141. Diagne C, Galan M, Tamisier L, D’Ambrosio J, Dalecky A, Bâ K, et al. Ecological and sanitary impacts of Bartonella species in wild rabbits (Oryctolagus cuniculus) in France. Comp Immunol Microbiol Infect Dis. 2008;31:465–50. https://doi.org/10.1016/j.cimid.2008.01.008.

142. Afzali H, Keshtkar MH, Pooyanpour M, Rabiei M, Alizadeh R, Shokri V, et al. Bartonella infection in rodents and Shrews in Taiwan. Zoonoses Public Health. 2010;57:439–46. https://doi.org/10.1111/j.1863-2378.2009.01234.x.

143. Birtles RJ, Canales J, Ventosilla P, Alvarez E, Guerra H, Llanos-Cuentas A. et al. Survey of Bartonella species infecting intradomestic animals in the Huayllacallán Valley, Ancash, Peru, a region endemic for human bartonellosis. Am J Trop Med Hyg. 1999;60:799–805. https://doi.org/10.4266/ajtmh.1999.50.799.

144. Hidalgo-Fuentes A, Barreiro J, Alfredo Carrión C, Foronda P, Javier Buitrago-Sánchez, Ana Rodríguez, et al. Bartonella infection in rodents and Shrews in Taiwan. Zoonoses Public Health. 2010;57:439–46. https://doi.org/10.1111/j.1863-2378.2009.01234.x.
155. Fichet-Calvet E, Jomla J, Ben Ismail R, Ashford RW. Patterns of infection of haemoparasites in the fat sand rat, *Psammomys obesus*, in Tunisia, and effect on the host. Ann Trop Med Parasitol. 2000;94:55–68. https://doi.org/10.1080/00207190010813513

156. Tay ST, Mohar AS, Zain SNM, Low KC. Isolation and molecular identification of bartonellae from wild rats (*Rattus* species) in Malaysia. Am J Trop Med Hyg. 2014;90:1039–42. https://doi.org/10.4269/ajtmh.13-0273

157. Billeter SA, Colton L, Sangmaneetee S, Sukawatt F, Evans BP, Kosoy MY. Molecular detection and identification of *Bartonella* species in rat fleas from northeastern Thailand. Am J Trop Med Hyg. 2013;89:462–5. https://doi.org/10.4269/ajtmh.12-0485

158. Obiega A, Heuser E, Ryll IR, Imholt C, Fürst J, Prautsch L-M, et al. Norway and black rats in Europe: potential reservoirs for zoonotic arthropod-borne pathogens. Pest Manag Sci. 2019;75:1556–63.

159. Costa F, Porter FH, Rodrigues G, Farias H, de Faria MT, Wunder EA, et al. Identification of *Bartonella* species in rats from the Greater Jakarta area. Vector Borne Zoonotic Dis. 2014;14:33–40. https://doi.org/10.1089/vbz.2013.1378

160. Gundi VAKB, Davoust B, Khamis A, Boni M, Raoult D, Scala B. Isolation of *Bartonella ratti* from *Rattus norvegicus* from the urban slum environment in Malaysia. Vector Borne Zoonotic Dis. 2014;14:33–40. https://doi.org/10.1089/vbz.2013.1378

161. Laakkonen J. Microparasites of three species of shrews from Finnish Lapland. Annal Zoolog Fennici. 2000:37–41.
et al. Parasites & Vectors (2022) 15:113

(Cymomyx ludovicianus). Vector Borne Zoonotic Dis. 2008;8:1–5. https://doi.org/10.1089/vbz.2007.0136.

189. Kaewmongkol G, Kaewmongkol S, McIntee LM, Burmeij H, Bennett MD, Adams PI, et al. Genetic characterization of Lea-derived Bartonella species from native animals in Australia suggests host-parasite co-evolution. Infect Genet Evol. 2011;11:1988–72. https://doi.org/10.1016/j.ijmeegid.2011.07.021.

190. Fournier PE, Taylor C, Rolain J-M, Barralass L, Smith G, Raoult D. Bartonella australis sp. nov. from kangaoros, Australia. Emerg Infect Dis. 2007;13:1961–2. https://doi.org/10.3201/eid1312.060559.

191. Celebi B, Anani H, Zgheib R, Carhan A, Raoult D, Fournier P-E. Genomic characterization of the novel Bartonella refkaydami sp. isolated from the blood of a Crocodyra saevoendes (Pallas, 1811). Vector Borne Zoonotic Dis. 2021. https://doi.org/10.1089/vbz.2020.2626.

192. Lilley TM, Veikkolainen V, Pulliainen AT. Molecular detection of Candidatus Bartonella mansuetadiensis in bats. Vector Borne Zoonotic Dis. 2015;15:706–9. https://doi.org/10.1089/vbz.2015.1785.

193. Davoust B, Marie J-L, Dahmani M, Berenger J-M, Bompar J-M, Blanche D, et al. Evidence of Bartonella spp. in blood and ticks (Oinithorodos hasei) of bats, in French Guinea. Vector Borne Zoonotic Dis. 2016;16:516–9. https://doi.org/10.1089/vbz.2016.1603.

194. Veikkolainen V, Vesterinen EJ, Lilley TM, Pulliainen AT. Bats as reservoir hosts of human bacterial pathogen, Bartonella mooytononisens. Emerg Infect Dis. 2014;20:960–7. https://doi.org/10.3201/eid2006.130956.

195. Qiu Y, Kajihara M, Nakao R, Mulenga E, Harima H, Hangôngome BM, et al. Isolation of Bartonella rouxii from bats and other bat-associated Bartonella spp. isolated from bats and their flies in Zambia. Pathogens. 2020;9:496. https://doi.org/10.3390/ pathogens9060469.

196. Calchi AC, Gobardi Vulturio J, Alves MH, Yogui DR, Desbiez AJL, Bres-sianini Amaral R, et al. Multi-locus sequencing reveals a novel Bartonella species in mammals from the superorder Xenarthra. Transbound Emerg Dis. 2021;69:20003 9013.

197. Kosoy M, Morvay C, Sheff KV, Bai V, Colborn J, Chalcraft L, et al. Bartonella tamiae sp. nov., a newly recognized pathogen isolated from three human patients from Thailand. J Clin Microbiol. 2008;46:772–5. https://doi.org/10.1128/JCM.02120-07.

198. Welch DF, Carroll KC, Hofmeister EK, Persing DH, Robison DA, Steiger- sonrai, et al. An unexpected case of Bartonella endocarditis in a French patient in close contact with bats. J Clin Microbiol. 2001;39:278–9. https://doi.org/10.1128/JCM.39.1.278-279.2001.

199. Lawanson PA, Collins MD. Description of Bartonella clarridgeiae sp. nov. isolated from the cat of a patient with Bartonella henselae septicaemia. Med Microbiol Lett. 1996:64–73.

200. Dror S, Chi B, Horn E, Steigerwalt AG, Whitney AM, Brenner DJ. Bartonella koehlerae sp. nov., isolated from aortic valve of a patient with endocarditis. J Clin Microbiol. 1999;37:1117–22. https://doi.org/10.1128/JCM.37.4.1117-1122.1999.

201. Chomel BB, Molia S, Kasten RW, Borgo GM, Stuckey MJ, Maruyama J, et al. Isolation of Bartonella rondoensis in cattle from Senegal. Comp Immunol Microbiol Infect Dis. 2017;50:63–9. https://doi.org/10.1016/j.cimid.2016.11.010.

202. Dahmani M, Sambou M, Scandola P, Raoult D, Fenollar F, Mediannikov M, et al. Isolation of Bartonella clarridgeiae sp. nov., isolated from domesticated camels (Camelus dromedarius) in Israel. Vector Borne Zoonotic Dis. 2014;14:775–82. https://doi.org/10.1089/vbz.2014.1663.

203. Maggi RG, Kosoy M, Mintzer M, Breitschwerdt EB. Isolation of Candidatus Bartonella melophagi from human blood. Emerg Infect Dis. 2009;15:66–71. https://doi.org/10.3201/eid1501.081080.

204. Deyrup P, Jaffe DA, Chomel BB, Orts MS, Tsou PM, Davis AZ, et al. Detection of Bartonella species, including Candidatus Bartonella ovis sp. nov., in ruminants from Mexico and lack of evidence of Bartonella DNA in saliva of common vampire bats (Desmodus rotundus) preying on them. Vet Microbiol. 2018;222:69–74. https://doi.org/10.1016/j.vetmic.2018.06.018.

205. Charvet E, Keshnerová L, Moritz R, Engel P. Bartonella koehlerae sp. nov. isolated from cats. J Clin Microbiol. 2005;43:897–903. https://doi.org/10.1128/JCM.43.3.897-903.2005.

206. Bermond D, Boulouis H-J, Heller R, van Laere G, Monteil H, Chomel B, et al. Bartonella bovis Bermond et al. sp. nov. and Bartonella capreoli sp. nov., isolated from European ruminants. Int J Syst Evol Microbiol. 2002;52:383–90. https://doi.org/10.1099/ijs.0.027713-52-3-383.

207. Maillard R, Riegel P, Barat F, Bouillin C, Thibault D, Gandon C, et al. Bartonella chomelii sp. nov., isolated from French domestic cattle (Bos taurus). Int J Syst Evol Microbiol. 2004;54:215–20. https://doi.org/10.1099/ijs.0.02770-0.

208. Dahmani M, Sambou M, Scandola P, Raoult D, Fenollar F, Mediannikov M, et al. Isolation of Bartonella bovis and Candidatus Bartonella dianthicus in cattle from Senegal. Comp Immunol Microbiol Infect Dis. 2017;50:63–9. https://doi.org/10.1016/j.cimid.2016.11.010.

209. Rasis M, Rudoler D, Schwartz J, Gladis M. Bartonella dromedarii sp. nov. isolated from domesticated camels (Camelus dromedarius) in Israel. Vet Borne Zoonotic Dis. 2014;14:775–82. https://doi.org/10.1089/vbz.2014.1663.
223. Corral J, Manríquez Robles A, Toussaint Caire S, Hernández-Castro R, Moreno-Coutiño G. First report of bacillary angiomatosis by *Bartonella elizabethae* in an HIV-positive patient. Am J Dermatopathol. 2019;41:750–3. https://doi.org/10.1097/DAD.0000000000001439.

224. Kosoy M, Bai Y, Sheff K, Morway C, Baggett H, Maloney SA, et al. Identification of *Bartonella* infections in febrile human patients from Thailand and their potential animal reservoirs. Am J Trop Med Hyg. 2010;82:1140–5. https://doi.org/10.4269/ajtmh.2010.09-0778.

225. Kandelaki G, Malania L, Bai Y, Chakvetadze N, Katsitadze G, Imnadze P, et al. Human lymphadenopathy caused by ratborne *Bartonella*, Tbilisi, Georgia. Emerg Infect Dis. 2016;22:544–6. https://doi.org/10.3201/eid2203.151823.

226. Kerkhoff FT, Bergmans AMC, van DerZee A, Rothova AJCM. Demonstration of *Bartonella grahamii* DNA in ocular fluids of a patient with neuroretinitis. J Clin Microbiol. 1999;37:4034–8. https://doi.org/10.1128/JCM.37.12.4034-4038.1999.

227. Breitschwerdt EB, Maggi RG. *Bartonella quintana* and *Bartonella vinsonii* subsp. *vinsonii* bloodstream co-infection in a girl from North Carolina USA. Med Microbiol Immunol. 2019;208:101–7. https://doi.org/10.1007/s00430-018-0563-0.

Publisher’s Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.