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Review

Bartonella species and their ectoparasites: Selective host adaptation or strain selection between the vector and the mammalian host?

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ABSTRACT

A wide range of blood-sucking arthropods have either been confirmed or are suspected as important vectors in *Bartonella* transmission to mammals, including humans. Overall, it appears that the diversity of *Bartonella* species DNA identified in ectoparasites is much broader than the species detected in their mammalian hosts, suggesting a mechanism of adaptation of *Bartonella* species to their host-vector ecosystem. However, these mechanisms leading to the fitness between the vectors and their hosts still need to be investigated.

Contents

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1. Introduction

Several blood-feeding arthropods, such as sandflies (*Lutzomyia verrucarum*), human lice (*Pediculus humanus humanus*, also known as *Pediculus humanus corporis*), cat fleas (*Ctenocephalides felis*) and some rodent fleas (*Ctenophthalmus nobilis*) have been confirmed to be competent vectors for transmission of *Bartonella* species [1–5]. However, an increasing number of *Bartonella* species have been isolated or detected within the last 15 years from a wide range of hematophagous arthropods, including human fleas (*Pulex irritans*), various hard tick species, such as *Ixodes* spp., *Dermacentor* spp., *Rhipicephalus sanguineus*, *Haemaphysalis* spp., deer keds (*Lipoptena cervi*, *Lipoptena mazamae*) or various species of biting flies [6–13]. *Bartonella* detection in arthropods was mainly based on PCR amplification and sequencing of the *glt*A, *fts*Z, 16S rRNA genes and the intergenic transcribed spacer (ITS) region, as well as restriction fragment length polymorphism (RFLP) analysis of PCR-amplified genes. However, the role of these potential vectors in the transmission of *Bartonella* species among mammalian hosts remained to be confirmed.

The objective of this review is to perform an exhaustive inventory of confirmed and potential vectors for *Bartonella* spp. collected from around the world (Tables 1–3). A special insight is also given to the recent detection of *Bartonella* species in various mammals and their ectoparasites in Taiwan. A wide range of *Bartonella* species were identified to infect domestic and wild mammals and their ectoparasites in that country. Interestingly, the *Bartonella* species identified in the ectoparasites was more diverse than in their mammalian hosts [14–16]. Such a larger *Bartonella* species diversity in the ectoparasites could suggest a selective adaptation of *Bartonella* species to the mammalian host and vector ecosystem.

2. *Bartonella* species detected in confirmed or potential vectors for various mammalian species

2.1. Sandflies

A night-active sandfly, *L.* (previously called *Phlebotomus*) *verrucarum*, was proposed as a potential vector for transmitting *B. bacilliformis* to humans, based on the correlation between the presence of these blood sucking insects in endemic areas and the epidemiology of human bartonellosis [17]. In the following years, Battistini [1,2] demonstrated that sandflies could transfer *B. bacilliformis* to monkeys by blood feeding and Hertig [18] proved that *L. verrucarum* was the main vector for transmission of *B. bacilliformis* to humans. Wild caught sandflies were experimentally fed on rhesus monkeys leading to the isolation of *B. bacilliformis* from the blood of the infected monkeys [18]. Hertig [18] also demonstrated the presence of *B. bacilliformis* in the midgut and feces of the sandflies and isolated the bacteria from the tip of the proboscis of *L. verrucarum*. Besides *L. verrucarum*, *L. noguchii* was able to induce *B. bacilliformis* bacteremia in sandfly-inoculated monkeys and therefore also considered as a possible vector of *B. bacilliformis* [19]. However, *L. noguchii* mainly feeds on rodents and therefore unlikely to be an efficient vector of *B. bacilliformis* to humans [20]. The existence of possible other sandfly species as vectors was suspected because of the inconsistency between the geographic distribution of *L. verrucarum* and the occurrence of human bartonellosis in Peru, Ecuador and Colombia [20–22]. It was suggested that in Colombia, the vector involved could be *L. colombiana* [20,22]. During the investigation of an acute bartonellosis outbreak in the Urubamba region of Peru in 1998, 104 of 312 *L. peruensis* sandflies were tested for the presence of *Bartonella* DNA and two (1.9%) of them were confirmed by sequencing to be infected respectively with *B. bacilliformis* and one novel *Bartonella* with 96% similarity to *B. grahamii* [23].

2.2. Biting flies

Among Hippoboscidae flies, *Lipoptena*, *Hippobosca* and *Melophagus* are obligate parasites of mammals [24], and were shown a few years ago to harbor *Bartonella* species, suggesting a possible role in the transmission of the infection to ruminants [8]. The deer ked, *L. cervi*, the predominant *Lipoptena* species in Europe, parasitizes cervids, whereas the louse fly (*Hippobosca equina*) parasitizes cows and horses, and the sheep ked (*Melophagus ovinus*) is a permanent ectoparasite of sheep. In North America, the deer ked *L. mazamae* infests white-tailed deer (*Odocoileus virginianus*) and *L. cervi* is thought to have been introduced into New England from Europe during the 1800s [25,26]. In France, *Bartonella* DNA was detected by amplification of the *Bartonella* citrate synthase gene (*glt*A) in 85.5% of 83 Hippoboscidae flies, including 94% of 48 adult *L. cervi* flies, 71% of 17 adult *H. equina* flies, 100% of 20 adult *M. ovinus* flies, and 100% of 10 *M. ovinus* pupae. The amplified sequences were identical or closely related to *Bartonella schoenbuchensis* and *B. chomelii* [8]. Dehio et al. [6] isolated *B. schoenbuchensis* from *L. cervi* collected on roe deer and red deer in Germany, and showed presence of large bacterial aggregates in the midgut of these arthropods suggesting that the pathogen may be efficiently transmitted by the bite of these flies. In the USA, a horn fly pool (*Haematobia* spp.) and a stable fly (*Stomoxys* spp.) collected in a cattle barn in California were PCR positive for *B. bovis* and *Bartonella henselae*, respectively [27]. *B. henselae* and a novel *Bartonella* closely related to *B. schoenbuchensis* were detected from deer keds (*L. mazamae*), collected from white-tailed deer in Georgia and South Carolina [11]. Similarly, *B. schoenbuchensis* was detected in 5 of 6 *L. cervi* collected from white-tailed deer