



Review

Bartonella bacteria in nature: Where does population variability end and a species start?

Michael Kosoy^{a,*}, David T.S. Hayman^{b,c,d,e}, Kung-Sik Chan^f

^a Division of Vector-Borne Diseases, Centers for Disease Control and Prevention, Fort Collins, Colorado 80521, USA

^b Cambridge Infectious Diseases Consortium, University of Cambridge, Cambridge CB3 0ES, UK

^c Department of Biology, Colorado State University, Fort Collins, Colorado 80523, USA

^d Institute of Zoology, Zoological Society of London, London NW1 4RY, UK

^e Animal Health and Veterinary Laboratories Agency, Weybridge KT15 3NB, UK

^f Department of Statistics & Actuarial Science, University of Iowa, Iowa City, IA, USA

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ABSTRACT

The application of new molecular approaches has permitted the differentiation of numerous strains belonging to the genus *Bartonella* and identification of new *Bartonella* species. However, the molecular typing of these organisms should be coupled with studies aimed at defining the biological properties of the newly described species. The long-history of co-adaptation between bartonella¹ bacteria and their mammalian hosts and possibly arthropod vectors provides a unique opportunity for applying this information for the sub-genus taxonomy. There can be a varying level of association between the bacteria and their hosts, ranging from animal species to animal genus to animal community. The commonality is that any level of association provides a certain degree of isolation for a given bartonella population that can mimic 'biological isolation'. Such an association defines a specific ecological niche and determines some specific characteristics, including sequence types that can be used as markers for demarcation of bacterial species. Usage of a combination of genetic markers and ecological information can delineate a number of species complexes that might combine several genospecies, named strains, and unique genotypes. The identification of such species complexes can be presented as (1) separate phylogenetic lineages distantly related to other species (e.g. *Bartonella bacilliformis*); (2) clusters of genetically similar strains associated with a specific mammalian group (e.g. *Bartonella elizabethae* species complex); and (3) clusters of genetically similar strains that combine a number of ecotypes (e.g. *Bartonella vinsonii* species complex).

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* Corresponding author. Address: CDC 3150 Rampart Road, Fort Collins, Colorado 80521, USA. Tel.: +1 970 266 3522; fax: +1 970 225 4257.

E-mail address: mck3@cdc.gov (M. Kosoy).

¹ *Bartonella* species are capitalized and italicized in accordance with the guidance for bacterial nomenclature. The common name 'bartonella' is neither capitalized nor italicized and here is commonly used as a non-specific adjective when we talk about a bartonella bacterium or about a bartonella infection. Bartonellae is the plural non-specific and neither capitalized nor italicized.

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1. Introduction

During the last two decades bartonella bacteria have been associated with an increasingly wide range of human and animal diseases. *Bartonella* was also recognized to be globally dispersed, and many *Bartonella* species recognized as emergent pathogens (Anderson and Neuman, 1997; Breitschwerdt and Kordick, 2000; Boulouis et al., 2005) (Fig. 1). Thus, there has been increased interest in bartonella bacteria. The resulting intensification of research has led to the understanding that bartonella bacteria as a group of microorganisms exhibit a unique parasitic strategy (Dehio, 2001; Birtles, 2005; Kaiser et al., 2010) and extremely high prevalence and genetic diversity in certain mammalian orders, especially among a variety of rodent and bat species around the world (Birtles et al., 1994; Kosoy et al., 1997; Ying et al., 2002; Castle et al., 2004; Jardine et al., 2005; Bai et al., 2011a,b). The genetic diversity discovered during this period, however, has made this taxonomic group a challenging assembly of bacteria for testing some general questions about bacterial population biology.

In the early 1990s investigators knew about 4–5 species of *Bartonella*; however now 30–40 species of *Bartonella* are reported in the literature, depending on how species are classified counted. The increasing number of species itself is not the main problem; the more serious problem is a conflict between increasing information about bartonella bacteria diversity and demarcation power for the already declared species. Consequently, this causes growing caution regarding the acceptance of new species when the old criteria obviously do not work. The question about what a bacterial species is has been debated intensively and is not new at all; any attempts to create a universally accepted definition might fail. Nevertheless, now is a good time to define some workable approaches for specific groups of bacteria, such as bartonella bacteria and we provide a theoretical framework using the species complex approach that we hope will help resolve some of the issues relating to species definitions within the *Bartonella* genus.

2. *Bartonella* as a life form

A common feature among almost all *Bartonella* species, which distinguishes them from the most closely related taxa, is their hemotropic lifestyle, characterized by long-lasting intra-erythrocyte infection in specific mammalian hosts, with transmission of

these bacteria by blood-sucking arthropods (Breitschwerdt and Kordick, 2000; Engel and Dehio, 2009). *Bartonella* species are genetically close to species of *Brucella*, *Agrobacterium*, *Ochrobactrum*, and *Rhizobium* within the subdivision of alfa-2-proteobacteria. We should be prepared for genetic distances between some *Bartonella* species and species from other proteobacteria genera, such as *Brucella*, to continue to shrink as more bacteria are discovered. Genomic investigations have demonstrated that all alfa-2-proteobacteria share a specific evolutionary history (Batut et al., 2004; Boussau et al., 2004). However, to paraphrase Richard Birtles, *Bartonella* species are distinct from their taxonomic neighbors as "elegant hemotropic parasites" (Birtles, 2005). This elegance is characterized by low prevalence of clinical manifestations compared to the high prevalence of the infection. This strategy allows bartonella to carefully exploit their hosts in a manner that optimizes their transmission. During infection of their mammalian hosts, these bacteria invade and persistently colonize mature erythrocytes. Besides erythrocytes, the bacteria target endothelial cells involving a unique mechanism for cellular invasion with the activation of a pro-inflammatory phenotype and the formation of cellular invasion (Dehio, 2001). *Brucella* species, the closest bacteria to the *Bartonella* taxon genetically, are not known as hemotropic parasites, but rather have adapted to invade and multiply in macrophages; whereas the soil and plant-associated bacteria of alfa-2-proteobacteria are not currently known to infect mammals. Because of the overwhelming dominance of strictly genetic approaches for awarding new species status within the *Bartonella* genus itself, we wish to stress the point that we believe all *Bartonella* species represent a specific hemotropic life form, and not just a cluster of genetically similar species.

3. Rapidly growing number of *Bartonella* species and genotypes

The genus *Bartonella* was represented by only one species *B. bacilliformis* for more than 80 years. In 1993, the genus was significantly expanded after Brenner et al. (1993) proposed to unify *Bartonella* and *Rochalimaea* genera with descriptions of *Bartonella quintana* combination nova, *Bartonella vinsonii* comb. nov., *Bartonella henselae* comb. nov., and *Bartonella elizabethae* comb. nov. This proposal was based on DNA–DNA hybridization results and comparison of existing 16S rRNA gene sequences. By a number of biological characteristics *B. bacilliformis* is still very dissimilar from all

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