



Emerging borreliae – Expanding beyond Lyme borreliosis



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ABSTRACT

Lyme borreliosis (or Lyme disease) has become a virtual household term to the exclusion of other forgotten, emerging or re-emerging borreliae. We review current knowledge regarding these other borreliae, exploring their ecology, epidemiology and pathological potential, for example, for the newly described *B. mayonii*. These bacteria range from tick-borne, relapsing fever-inducing strains detected in some soft ticks, such as *B. mvumii*, to those from bat ticks resembling *B. turicatae*. Some of these emerging pathogens remain unnamed, such as the borrelial strains found in South African penguins and some African cattle ticks. Others, such as *B. microti* and unnamed Iranian strains, have not been recognised through a lack of discriminatory diagnostic methods. Technical improvements in phylogenetic methods have allowed the differentiation of *B. merionesi* from other borrelial species that co-circulate in the same region. Furthermore, we discuss members that challenge the existing dogma that Lyme disease-inducing strains are transmitted by hard ticks, whilst the relapsing fever-inducing spirochaetes are transmitted by soft ticks. Controversially, the genus has now been split with Lyme disease-associated members being transferred to *Borrelia*, whilst the relapsing fever species retain the *Borrelia* genus name. It took some 60 years for the correlation with clinical presentations now known as Lyme borreliosis to be attributed to their spirochaetal cause. Many of the borreliae discussed here are currently considered exotic curiosities, whilst others, such as *B. miyamotoi*, are emerging as significant causes of morbidity. To elucidate their role as potential pathogenic agents, we first need to recognise their presence through suitable diagnostic approaches.

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1. Understanding borrelial taxonomy

When one mentions the genus *Borrelia*, it conjures up the thought of Lyme borreliosis (or Lyme disease); however, the genus contains a heterogeneous range of borreliae with an increasingly recognised diversity. The type species for the genus is *Borrelia*

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anserina, a borrelial spirochaete transmitted by soft ticks of the genus *Argas*, including *A. persicus*. Amedee Borrel noted that this organism, *B. anserina*, showed distinct differences when compared with the other known spirochaete described at the time, *Treponema pallidum*. Although his interpretation of its morphology was flawed in that he described it with peritrichous flagellae, his first description of this species was subsequently honoured with his name [1]. Today, this species is only rarely reported [2–4], but can have a devastating impact upon poultry, its preferred host. Improvements in poultry housing have resulted in the demise of its tick vector and, consequently, the infection; however, this pathogen remains problematic in sub-Saharan Africa and other developing countries [4].

Following the original description of this genus, *Borrelia*, description of relapsing fever-inducing borreliae associated with differing vectors ensued. Historically, the borreliae were classified by the “one vector one species” concept that additionally incorporated geographical location and virulence in animal models [5]. These spirochaetes were collectively considered under the rather arbitrary groupings of Old World and New World borreliae. The subsequent description of the Lyme-associated strains enabled comparison of these deeply divergent clades within the genus. Phylogenetic differences appeared to relate to ecological divides with the relapsing fever species being vectored by soft ticks (with the exception of the human louse-borne *Borrelia recurrentis*), whilst the Lyme disease-associated species were transmitted by hard-bodied ixodid tick species. The recognition of many distinct entities causing Lyme borreliosis and closely related spirochaetes with apparently less pathogenic potential has resulted in this group being known as the *Borrelia burgdorferi* sensu lato complex. This “dogma” held for many years, but is now becoming blurred with the discovery of relapsing fever group spirochaetes that are also transmitted by ixodid ticks (see section below).

Many scientists who are searching for ATCC type strains or depositing GenBank sequences may stumble across a presumptive novel genus aligned within the borreliae, classified as genus *Borreliella* gen. nov [6]. This proposed terminology arises from the analysis of concatenated sequence data for 25 housekeeping proteins derived from the genomic sequences of 38 *Borrelia* strains representing 18 species. The deeply rooted divergence demonstrated between the relapsing fever-inducing and Lyme disease groups of borreliae, corroborating previous findings, resulted in the newly suggested name of *Borreliella* to be applied to members of

the latter group that were described after those of the former group [6]. Many researchers in the field who see this only serving to add confusion to the already complicated taxonomy of this spirochaetal group have largely not welcomed this proposed new genus name. Although currently hotly debated, judgement by appropriate taxonomic committees will be necessary to resolve this debate.

2. New players and emerging concepts in the Lyme borreliosis arena

The Lyme associated members have expanded over recent years, largely through the application of highly discriminatory molecular typing that can discern distinct groups within this spirochaetal complex (see Table 1 for a list of current species). Although the pathogenic potential of many of these variants remains to be established, recognition is an essential first step towards unravelling their ecological role(s) and pathogenic capability. Within this category are borreliae, including *B. americana*, *B. bavariensis*, *B. bissettiae*, *B. californiensis*, *B. finlandensis*, *B. kurtenbachii*, *B. mayonii*, *B. sinica*, *B. tanukii*, *B. turdi* and *B. yangtzensis*, which share their vector with known pathogenic species. This raises the possibility of mixed infections and thus complicates assessment of pathogenic potential of these newly recognised species. Furthermore, some show geographical divide into “Old World” or “New World” species; however, others, such as *B. bissettiae* and *B. carolinensis*, have global distribution [7].

The ecological cycle for Lyme borreliosis has been extensively studied over the years, with the role of rodents as essential vertebrate reservoirs being established as being of paramount importance. Indeed, exceptions to known ecological associations have provided clues as to undifferentiated species misclassified amongst close genotypic relatives such as the inclusion of *B. bavariensis* as a rodent-adapted variant of the avian-adapted *B. garinii* species [8]. Even amongst *B. bavariensis* alone, strain diversity is becoming increasingly recognised [9]. It is undoubtedly true that rodents have a vital part to play in the ecology of Lyme borreliosis, but this has given an unconscious bias away from the role of other vertebrate species and their significance in maintaining ecological cycles for Lyme borreliae. Similarly, it is believed that tick species with diverse hosts will maintain greater diversity amongst the borreliae that they carry; however, this proposal is challenged by findings of greater diversity amongst *B. garinii* detected in the sea-bird feeding tick *Ixodes uriae* when compared with the diversity of *B. garinii* detected within *I. ricinus* ticks [10].

The recent description of *B. mayonii* has drawn attention as a potentially more virulent member of the *B. burgdorferi* sensu lato complex, also transmitted by *I. scapularis* [11]. Current evidence suggests that this organism produces higher numbers of spirochaetes in the blood than its *B. burgdorferi* sensu stricto counterpart. Whether this impacts upon other clinical consequences remains to be elucidated. Intriguingly, when virulence is compared between or among members of the same species, but derived from either European or American locations, differences have been reported in clinical presentation as well as in their ability to provoke cytokine and chemokine cascades associated with induction of both innate and Th1 immune reactivity [12]. It is probable that subspecies “pathotypes” might account for differences in immunostimulatory potential between isolates from both sides of the Atlantic.

3. Emerging relapsing fever borreliae

As evidenced for the Lyme borreliae, the impact of discriminatory molecular approaches has resulted in change. In some cases there has been rediscovery of forgotten species, such as *B. merionesi* [13,14], whilst new species have been described, including

Table 1
Names of *B. burgdorferi* sensu lato complex.

Name	Year	Reference
<i>B. afzelii</i>	1994 Confirmed	[57]
<i>B. americana</i>	2010 Confirmed	[58]
Candidatus <i>B. andersonii</i>	1995 Proposed	[59]
<i>B. bavariensis</i>	2013 Confirmed	[60]
<i>B. bissettiae</i>	2016 Confirmed	[61]
<i>B. burgdorferi</i> sensu stricto	1984 Confirmed	[62]
<i>B. californiensis</i>	2016 Confirmed	[61]
<i>B. carolinensis</i>	2011 Confirmed	[63]
<i>B. chilensis</i>	2014 Proposed	[64]
Candidatus <i>B. finlandensis</i>	2011 Proposed	[65]
<i>B. garinii</i>	1992 Confirmed	[66]
<i>B. japonica</i>	1994/3 Confirmed	[67]
<i>B. kurtenbachii</i>	2014 Confirmed	[68]
<i>B. lusitaniae</i>	1997 Confirmed	[69]
Candidatus <i>B. mayonii</i>	2016 Proposed	[11]
<i>B. sinica</i>	2001 Confirmed	[70]
<i>B. spielmanii</i>	2006 Confirmed	[71]
<i>B. tanukii</i>	1997/6 Confirmed	[72]
<i>B. turdi</i>	1997/6 Confirmed	[72]
<i>B. valaisiana</i>	1997 Confirmed	[73]
<i>B. yangtzensis</i>	2015 Confirmed	[74]

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