

1 Emerging borreliae – expanding beyond Lyme 2 borreliosis

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16 ABSTRACT

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

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40 *Key words:* *Emerging Borrelia; tick-borne; Lyme; Relapsing Fever; REP;*
41 *Borreliosis.*

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43 1. Understanding borreliac taxonomy

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45 When one mentions the genus *Borrelia*, it conjures up the thought of Lyme borreliosis
46 (or Lyme disease); however, the genus contains a heterogeneous range of borreliac
47 with an increasingly recognised diversity. The type species for the genus is *Borrelia*
48 *anserina*, a borreliac spirochaete transmitted by soft ticks of the genus *Argas*,
49 including *A. persicus*. Amedee Borrel noted that this organism, *B. anserina*, showed
50 distinct differences when compared with the other known spirochaete described at the
51 time, *Treponema pallidum*. Although his interpretation of its morphology was flawed
52 in that he described it with peritrichous flagellae, his first description of this species
53 was subsequently honoured with his name [1]. Today, this species is only rarely
54 reported [2-4], but can have a devastating impact upon poultry, its preferred host.
55 Improvements in poultry housing have resulted in the demise of its tick vector and,
56 consequently, the infection; however, this pathogen remains problematic in sub-
57 Saharan Africa and other developing countries [4].

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

74 Many scientists who are searching for ATCC type strains or depositing GenBank
75 sequences may stumble across a presumptive novel genus aligned within the
76 borreliac, classified as genus *Borreliella* gen. nov. [6]. This proposed terminology
77 arises from the analysis of concatenated sequence data for 25 housekeeping proteins
78 derived from the genomic sequences of 38 *Borrelia* strains representing 18 species.
79 The deeply rooted divergence demonstrated between the relapsing fever-inducing and
80 Lyme disease groups of borreliac, corroborating previous findings, resulted in the
81 newly suggested name of *Borreliella* to be applied to members of the latter group that
82 were described after those of the former group [6]. Many researchers in the field who
83 see this only serving to add confusion to the already complicated taxonomy of this
84 spirochaetal group have largely not welcomed this proposed new genus name.
85 Although currently hotly debated, judgement by appropriate taxonomic committees
86 will be necessary to resolve this debate.

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

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90 The Lyme associated members have expanded over recent years, largely through the
91 application of highly discriminatory molecular typing that can discern distinct groups
92 within this spirochaetal complex (see Table 1 for a list of current species). Although

93 the pathogenic potential of many of these variants remains to be established,
94 recognition is an essential first step towards unravelling their ecological role(s) and
95 pathogenic capability. Within this category are borreliae, including *B. americana*, *B.*
96 *bavariensis*, *B. bissetiae*, *B. californiensis*, *B. finlandensis*, *B. kurtenbachii*, *B.*
97 *mayonii*, *B. sinica*, *B. tanukii*, *B. turdi* and *B. yangtzensis*, which share their vector
98 with known pathogenic species. This raises the possibility of mixed infections and
99 thus complicates assessment of pathogenic potential of these newly recognised
100 species. Furthermore, some show geographical divide into “Old World” or “New
101 World” species; however, others, such as *B. bissetiae* and *B. carolinensis*, have
102 global distribution [7].

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

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

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130 **3. Emerging relapsing fever borreliae**

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132 As evidenced for the Lyme borreliae, the impact of discriminatory molecular
133 approaches has resulted in change. In some cases there has been rediscovery of
134 forgotten species, such as *B. merionesi* [13, 14], whilst new species have been
135 described, including *B. miyamotoi*, and proposed *Candidatus* species *B. johnsonii*, *B.*
136 *lonestari*, *B. mvumii* and *B. texasensis* (see Table 2 for a list of names). Geographic
137 areas, such as Iran, have reported clinical cases of relapsing fever associated with
138 spirochaetes that align most closely with species present in East Africa [15]. Whether
139 this is a unique description or rediscovery of *B. baltazardi* or *B. latyschewii* remains
140 unresolved given the absence of publicly available sequence data (in GenBank) for
141 these spirochaetes. Similarly, another relapsing fever-inducing spirochaete has been
142 reported in both human blood and ticks of the *Ornithodoros moubata* complex in

143 Tanzania [16, 17]. Surprisingly, this strain, *Candidatus B. mvumi*, showed greater
144 homology to *B. hermsii* rather than the relapsing fever-inducing species known to be
145 endemic in East Africa [18]. These findings are echoed by the description of a case of
146 relapsing fever presumably acquired by a traveller returning from the Kalahari Desert,
147 *Candidatus B. kalaharica*, which similarly resembled “New World” species [19].

148 Sporadic reports have been published, describing other relapsing fever-like
149 organisms, but their pathogenic significance remains unclear. Frequently, bats
150 colonise buildings, thus bringing both bats and their ticks into close proximity to
151 humans. A study of the soft bat tick, *Argas vespertilionis* (also known as *Carios*
152 *vespertilionis*), in France revealed the presence of a relapsing fever-inducing *Borrelia*
153 species (CPB1) akin to that linked to a fatal infection in a bat in the UK [20, 21].
154 Sporadic reports of a relapsing fever *Borrelia* closely related to *B. turicatae* have been
155 published, but a comprehensive phylogenetic comparison with existing species has
156 not been conducted [22-24]. The name *Candidatus Borrelia johnsonii* has been
157 proposed for this *Carios kelleyi* spirochaete [24].

158 The presence of relapsing fever-inducing infections in livestock and wildlife have
159 been reemphasised in recent publications [4, 25-27]. Indeed, infections by *B. theileri*
160 can be considered as being rediscovered. This infection has veterinary significance
161 and appears to exist in regions where diagnostic ability is limited; hence, its impact on
162 productivity is largely unexplored. Notably, this species, despite belonging to the
163 relapsing fever borreliae, is transmitted by hard ticks, such as *Rhipicephalus*
164 (*Boophilus*). Phylogenetically, *B. theileri* clusters closely with another hard tick-
165 transmitted, relapsing fever-inducing species described in the USA, *B. lonestari*,
166 which is transmitted by *Amblyomma americanum* and other species of predominantly
167 hard ticks [28]. *Amblyomma americanum* is particularly aggressive and has recently
168 been shown to carry other potential pathogens making clinical attribution to *B.*
169 *lonestari* complicated [29]. Though not yet cultivated in axenic medium, *B. lonestari*
170 has been associated with human skin lesions following tick bite. Furthermore, it is
171 believed to interfere with serological test results for Lyme borreliosis. Recently, a *B.*
172 *lonestari*-like organism has been reported in *Haemaphysalis* ticks and Sika deer
173 (*Cervus nippon yesoensis*) in Japan [30], suggesting that this species has a much more
174 global distribution than previously appreciated. This observation is further
175 corroborated by the finding of a closely related sub-group of relapsing fever-inducing
176 *Borrelia* species residing in *Haemaphysalis punctata* and *Rhipicephalus sanguineus*
177 ticks collected from Portugal [31]. To challenge existing dogma even further, this
178 species has additionally been detected in *Argas* spp., thus occurring in both hard and
179 soft tick species, with its presence being detected in the seabird tick *Carios capensis*
180 [32].

181 In wildlife, there have been reports of a relapsing fever-inducing species of
182 *Borrelia* infecting penguins at a rehabilitation centre in South Africa. [33]. This
183 spirochaete resembled a novel relapsing fever-inducing species identified within
184 *Carios sawaii* ticks feeding on seabirds [34]. Furthermore, there are reports of a
185 relapsing fever-inducing spirochaete with greatest homology with *B. turicatae*
186 reported from *Dermacentor variabilis* feeding upon coyote in Texas, USA. This has
187 tentatively been designated *Candidatus B. texasensis* [35], and was followed by
188 reports of *B. turicatae* in dogs in Texas [36]. The recognition that dogs are susceptible
189 to relapsing fever-inducing spirochaetes has been followed by other members of this
190 group, such as *B. hermsii* and *B. persica*, which cause canine infections [37, 38].

191

192 Unresolved dilemmas were raised by the discovery of *B. miyamotoi*, a relapsing
193 fever-inducing spirochaete that is vectored by hard tick species (*I. scapularis*, *I.*
194 *persulcatus* and *I. ricinus*). *Borrelia miyamotoi* is another member affiliated with the
195 relapsing “fever group of species” and, like *B. lonestari* above, is also transmitted by
196 hard ticks. This spirochaete was first described in Japan, where it was isolated from *I.*
197 *persulcatus* ticks collected in Hokkaido, but this report was soon followed by
198 descriptions from the USA and Russia, and later throughout Europe [39]. Initially
199 treated as an anomaly, this species has recently drawn global attention with
200 recognition of its ability to cause human infection. Clinical features and diagnostics
201 can overlap with Lyme borreliosis and are likely to have obscured its recognition as a
202 species that is pathogenic in humans. Although clustering amongst the relapsing fever
203 group, and, indeed, possessing variable small and large proteins [40], the clinical
204 presentation is not characteristic of classical relapsing fever [41, 42]. Now that its
205 infectious potential has been established and increasing reports are being accrued
206 from Eurasia, Europe and the USA [42-44], it is apparent that three genotypes exist
207 within this species showing geographical separation within US, Europe and the
208 Russia-Far East [45].

209 Subsequently, further *Borrelia* that appear to represent the relapsing fever-inducing
210 group, but have been found in hard tick species are being disclosed. Japanese studies
211 have revealed a relapsing “fever-like” spirochaete (AGRF) present in *Amblyomma*
212 *geoemydae* ticks [46]. A relapsing “fever-like” spirochaete has been reported from
213 blood films collected from penguins at a rehabilitation unit in South Africa [33].
214 Interestingly, Lyme disease-associated borreliae have also been described to infect
215 penguins, presumably through exposure to *I. uriae* [47].

216

217 **4. The non-conformist third borrelial cluster**

218

219 Another “orphan” *Borrelia* was described in *Hyalomma aegyptium* ticks removed
220 from tortoises in Turkey [48, 49]. Now named *B. turicata* (also known as REP or
221 tAG; see table 3), these spirochaetes have a natural ecology involving reptiles and
222 their ticks [50, 51]. Phylogenetic analysis of these *Borrelia* taxa has revealed that they
223 are deeply divergent from both the Lyme disease-associated clade and those causing
224 relapsing fever, justifying their inclusion as a separate cluster within the over-arching
225 genus of *Borrelia* [50, 51]. Intriguingly, these presumed reptile-associated species
226 have subsequently been detected in *Amblyomma maculatum* collected in the Gulf
227 Coast [52]. Similarly, related *Borrelia* have been detected in *Amblyomma varanense*
228 collected from pythons in Thailand [53]. These findings suggest a global dispersion of
229 these borreliae.

230 Closely related to these stains, but potentially distinct are newly described *Borrelia*
231 species identified in *Ixodes holocyclus* (Australian tick paralysis species) removed
232 from the echidna (Tachyglossidae) [54, 55]. The presence of Australian borreliae has
233 long been predicted, and this tick species is known to feed upon multiple vertebrate
234 species, thus may account for serological exposure to borreliae in humans in
235 Australia. Other reports have described a novel *Borrelia* species present in ticks
236 collected from cattle in Ethiopia that fails to cluster with either Lyme disease-
237 associated or relapsing fever-inducing borreliae [56]. These observations underscore
238 our incomplete understanding of this genus and its diverse members.

239

240 **5. Future perspectives**

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242 It is apparent in this brief review that we have a multitude of knowledge gaps and
243 unanswered questions. For those Lyme borreliae established as pathogens, we have
244 yet to explore the reasons for differential virulence and tissue tropisms. Exploration of
245 the cross-talk between spirochaete and host responses is an essential pre-requisite to
246 decipher pathological mechanisms. Indeed, application of high-resolution genetic
247 typing tools, in conjunction with assessment of the host inflammasome, might yield
248 greater insights towards this goal, but much research remains to be done.

249 With the advent of more whole genome studies, it is probable that we will gain a
250 deeper understanding of borrelial diversity. The impact of molecular techniques has
251 enabled us to explore the diversity of borrelial species using targeted approaches.
252 However, technological improvements enabling multiplex analysis or even whole
253 genome studies are resulting in us stumbling across more unexpected findings that
254 challenge existing dogma. From such studies, it is anticipated that improved
255 diagnostics will emerge. The need for improved molecular diagnostic approaches is
256 becoming increasingly apparent, not only to embrace co-infections with other
257 microbes, but also to address potential co-infection with other borrelial species.

258

259 **6. Concluding remarks**

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261 Advances in molecular diagnostics have enabled us to start to explore the complexity
262 within the borrelial genus. We are still firmly in the discovery phase, but molecular
263 data sets are providing us with some insights into the intriguingly divergent host-
264 microbial interfaces utilised by these enigmatic microbes. Exploration of host-
265 microbial interactions of the both natural and accidental host species infections is
266 likely to elucidate the pathological mechanisms employed and differences in immune
267 response provoked by divergent strains and species. What is becoming increasingly
268 apparent is that we need to reconsider our out-dated and rather simplistic model for
269 these organisms, whereby the members of the Lyme disease group are transmitted by
270 hard ticks, whilst the relapsing fever-inducing group are transmitted by soft ticks
271 (with the exception of lice, in some cases).

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603

604 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]
<i>Candidatus B. andersonii</i>	1995 proposed	[59]
<i>B. bavariensis</i>	2013 confirmed	[60]
<i>B. bissettae</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]
<i>Candidatus 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]
<i>Candidatus 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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608 Table 2: List of Relapsing Fever group borreliae.

Name	Year	Reference
<i>B. anserina</i>	1891 Confirmed	[75]
<i>B. baltazardii</i>	1983 Confirmed	[76]
<i>B. brasiliensis</i>	1952 Confirmed	[77]
<i>B. caucasica</i>	1945 Confirmed	[78]
<i>B. coriaceae</i>	1987 Confirmed	[79]
<i>B. crocidurae</i>	1917 Confirmed	[80]
<i>B. dugesii</i>	1949 Confirmed	[81]
<i>B. duttonii</i>	1906 Confirmed	[82]
<i>B. graingeri</i>	1953 Confirmed	[83]
<i>B. harveyi</i>	1947 Confirmed	[84]
<i>B. hermsii</i>	1942 Confirmed	[85]
<i>B. hispanica</i>	1926 Confirmed	[86]
<i>Candidatus B. johnsonii</i>	2009 Proposed	[87]
<i>Candidatus B. kalaharica</i>	2016 Proposed	[19]
<i>B. latyschewii</i>	1941 Confirmed	[88]
<i>Candidatus B. lonstari</i>	1996 Proposed	[89]
<i>B. mazzottii</i>	1956 Confirmed	[90]
<i>B. merionesi</i>	1947/8 Confirmed	[91]
<i>B. microti</i>	1947 Confirmed	[92]
<i>B. miyamotoi</i>	1995 Confirmed	[93]
<i>Candidatus B. mvumii</i>	2004 Proposed	[18]
<i>B. parkeri</i>	1942 Confirmed	[85]
<i>B. persica</i>	1913 Confirmed	[94]
<i>B. recurrentis</i>	1874 Confirmed	[95]
<i>Candidatus B. texasensis</i>	2005 Proposed	[35]
<i>B. theileri</i>	1903 Confirmed	[96]
<i>B. tillae</i>	1961 Confirmed	[97]
<i>B. turicatae</i>	1933 Confirmed	[98]
<i>B. venezulensis</i>	1921 Confirmed	[99]

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611 Table 3: List of non-conformist borreliae

Name	Year	Reference
<i>B. turica</i>	2004 Confirmed	[49]
<i>Candidatus B. queenslandica</i>	1962 Proposed	[100]

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