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1 *Research article*

2 **Rodents as hosts of pathogens and related zoonotic disease risk**

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20 **Abstract**

21 Rodents are known to be reservoir hosts for at least 60 zoonotic diseases and are
22 known to play an important role in their transmission and spreading in different ways. We
23 sampled different rodent communities within and around human settlements in Northern
24 Senegal, an area subjected to major environmental transformations associated with global
25 changes. Herein, we conducted an epidemiological study on their bacterial communities.

26 One hundred and seventy-one (171) invasive and native rodents were captured, 50
27 from outdoors trapping sites and 121 rodents from indoors habitats, consisting on 5 species.
28 DNA of thirteen pathogens have been successfully screened on the rodent's spleens. We
29 found: 2.3% of positive spleens to *Piroplasmida* and amplified one which gives a potentially
30 new species *Candidatus* "*Theileria senegalensis*"; 9.35% of *Bartonella* spp. and amplified 10,
31 giving three genotypes. 3.5% of filariasis species; 18.12% of *Anaplasmataceae* species and
32 amplified only 5, giving a new potential species *Candidatus* "*Ehrlichia senegalensis*"; 2.33 %
33 of *Hepatozoon* spp.; 3.5% of *Kinetoplastidae* spp; and 15.2% of *Borrelia* spp. and amplified 8
34 belonging all to *Borrelia crocidurae.*

35 Some of the species of pathogens carried by the rodents of our studied area may be
36 unknown because most of those we have identified are new species. In one bacterial taxon,
37 *Anaplasma*, a positive correlation between host body mass and infection was found. Overall,
38 male and invasive rodents appeared less infected than female and native ones, respectively.

39 **Keywords:** Pathogens host; zoonotic disease; rodents; *Bartonella*; *Borrelia crocidurae*;
40 *Anaplasmataceae*; *Piroplasmida*; *Hepatozoon***.**

1. Introduction

Rodents represent the largest order of living mammals (approximately 2,277 known species belonging to 33 families, which is nearly 42% of the global mammalian biodiversity) and have an almost worldwide distribution (to the exception of Antarctica and some islands) [1]. They are well adapted to a wide range of habitats [2] and undoubtedly represent the mammals that have the most often accompanied humans in their global dispersal. As such, they have had the opportunity to settle where they were introduced and then become invasive with several effects on biodiversity and profound impacts on human activities [2] [1]. Especially, the current global change context (e.g., land-use change, urbanization) is particularly suitable for the expansion of several rodent species beyond their natural distribution areas, particularly due to their synanthropic affinities [2]. In this respect, the world's urban population is set to rise by 2.1 billion in 2030, what is likely to induce crucial ecological and sanitary changes [3][4], especially those associated to these rodent species [5].

Indeed, rodents are known to be reservoir hosts for at least 60 zoonotic diseases [4], and to play a major role in their transmission and spreading in different ways [6] [7]. Among the most important diseases in terms of public health are salmonellosis, plague, leptospirosis, leishmaniasis, toxoplasmosis, rat-bit fever, taeniasis-like *Capillaria hepatica*, zoonotic babesiosis, Lassa fever hemorrhagic fever with renal syndrome (HFRS) and the hantavirus cardiopulmonary syndrome (HCPS), both caused by *Hantavirus*, also other Arenaviruses are responsible for South American Hemorrhagic Fevers (SAHF) [8] [9] [10] [11] [12] [7]. More particularly, rodents may harbour different complex bacteria, such as *Mycobacterium tuberculosis* and *Mycobacterium microti*, *Escherichia coli*, agents of tularemia, tick-borne relapsing fever, bartonellosis, listeriosis, Lyme disease, Q fever, ehrlichiosis and others [13] [14] [15].

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65 In Senegal, many studies documented the sanitary effects of invasive rodents (3).
66 Multiple projects studied the distribution of rodents in Senegal [2] [16] [17]. More than 30
67 rodents species have been recorded in this country, belonging to Gliridae, Dipodidae and
68 Muridae (Gerbilinae, Murinae and Dendromurinae) [17] [18]. Simultaneously, follow-ups are
69 usually carried out on certain pathogens potentially transmitted by rodent populations
70 particularly to humans. This allowed to evaluate rodent associated health risk [17]. In
71 addition, new potential bacteria, whose pathogenicity remains unknown, continue to be
72 isolated from rodents [19]. A recent study conducted in Senegal has shown the difficulty of
73 predicting the relationship between biodiversity and the risks of transmission of pathogens
74 especially zoonotic ones, and recommends some prevention strategies based on the global
75 monitoring of pathogens, but especially the precise characterization of the potential zoonotic
76 agents [20].

77 In the frame of various projects on rodents and their bacterial pathogens in Northern
78 Senegal (http://ohmi-tessekere.in2p3.fr/projets; http://projetcerise-ird-frb.fr), we had the
79 opportunity to sample different rodent communities within human settlements from several
80 villages (indoor sites) and natural wild habitats (outdoor sites) in the Ferlo region. This area
81 represents a colonization front for two invasive rodent species: *(i)* The house mouse (*Mus*
82 *musculus*), a major invasive species worldwide [2] that has been introduced in Senegal since
83 the colonial period, and which tends to replace native rodent communities (mainly *Mastomys*
84 *erythroleucus* and *Arvicanthis niloticus*) with various consequences in disease risk and
85 ecological interactions within invaded communities [20][21][22][23]; *(ii)* the Nigerian gerbil
86 (*Gerbillus nigeriae*) that recently colonized North Senegal thanks to climatic and
87 environmental changes experienced by the Sahelian bioclimatic zone during the last three
88 decades, where it now represents the dominant species in outdoor rodent assemblages [24]

89 Here, we conducted an epidemiological investigation of the bacterial communities of
90 different native and invasive rodent populations from North Senegal (Ferlo region). We aimed
91 to *(i)* characterize the presence and phylogenetic position of potentially zoonotic pathogens
92 (including unknown or unsuspected species), *(ii)* identify their distribution within host rodent
93 populations relationships with environmental (indoor *vs* outdoor sites) and host (species,
94 invasive *vs* native), and *(iii)* discuss the potential impact they may have in regard of public
95 health issues.

96 ## 2. Results

97 ### a) Specimens included in the study

98 Among the small mammals caught (complete data not published), 171 spleen samples
99 were considered in the current work, all belonging to rodents of the family Muridae: i) 50
100 rodents from outdoor trapping sites, including 15 *Arvicanthis niloticus*, 20 *Gerbillus nigeriae*
101 and 15 *Taterillus* sp. (most probably corresponding to *T. pygargus*), these species representing
102 by far the three dominant ones of northern Senegal outdoors rodent communities [25] ; ii) 121
103 rodents from indoors trapping sites, including 26 *A. niloticus* (11 from Diagali and 15 from
104 Fourdou), 44 *Mastomys erythroleucus* (12 from Diagali, 10 from Fourdou, 1 from Labgar and
105 21 from Ranerou) and 51 *Mus musculus* (17 from Labgar, 16 from Tessekere and 18 from
106 Yonofere).

107 ### b) Molecular screening

108 All methodological details - such as the type of PCR used, the portion of sequence
109 considered and the spectrum of species targeted - are provided in Table 1. Below, we focused
110 only on bacteria detected and identified in each host species.

111 **Table 1.** Oligonucleotide sequences of primers and probe used for qPCRs and conventional
112 PCRs in this study

Targets	Targeted gene	Name	Primers (5'-3') and probes (used for qPCR screening or sequencing)	Annealing temperature	Specificity	References
Piroplasmida	5.8S	5.8S-F5 5.8S-R 5.8S-S	AYYKTYAGCGRTGGATGTC TCGCAGRAGTCTKCAAGTC FAM-TTYGCTGCGTCCTTCATCGTTGT-MGB	60°C	Broad-range qPCR	[84]
	18S (969-bp)	piro18S-F1 piro18S-F4 piro18S-F3 piro18S-R3	GCGAATGGCTCATTAIAACA CACATCTAAGGAAGGCAGCA GTAGGGTATTGGCCTACCG* AGGACTACGACGGTATCTGA*	58°C	Broad-range conventional PCR	[84]
Anaplasma	23S	TtAna_F TtAna_R TtAna_P	TGACAGCGTACCTTTTGCAT GTAACAGGTTCGGTCCTCCA 6FAM-GGATTAGACCCGAAACCAAG	55C°	Broad-range qPCR	[51]
	23S (520-bp)	Ana23S-212F Ana23S-753R	ATAAGCTGCGGGGAATTGTC TGCAAAAGGTACGCTGTCAC	58C°	Broad-range conventional PCR	[51]

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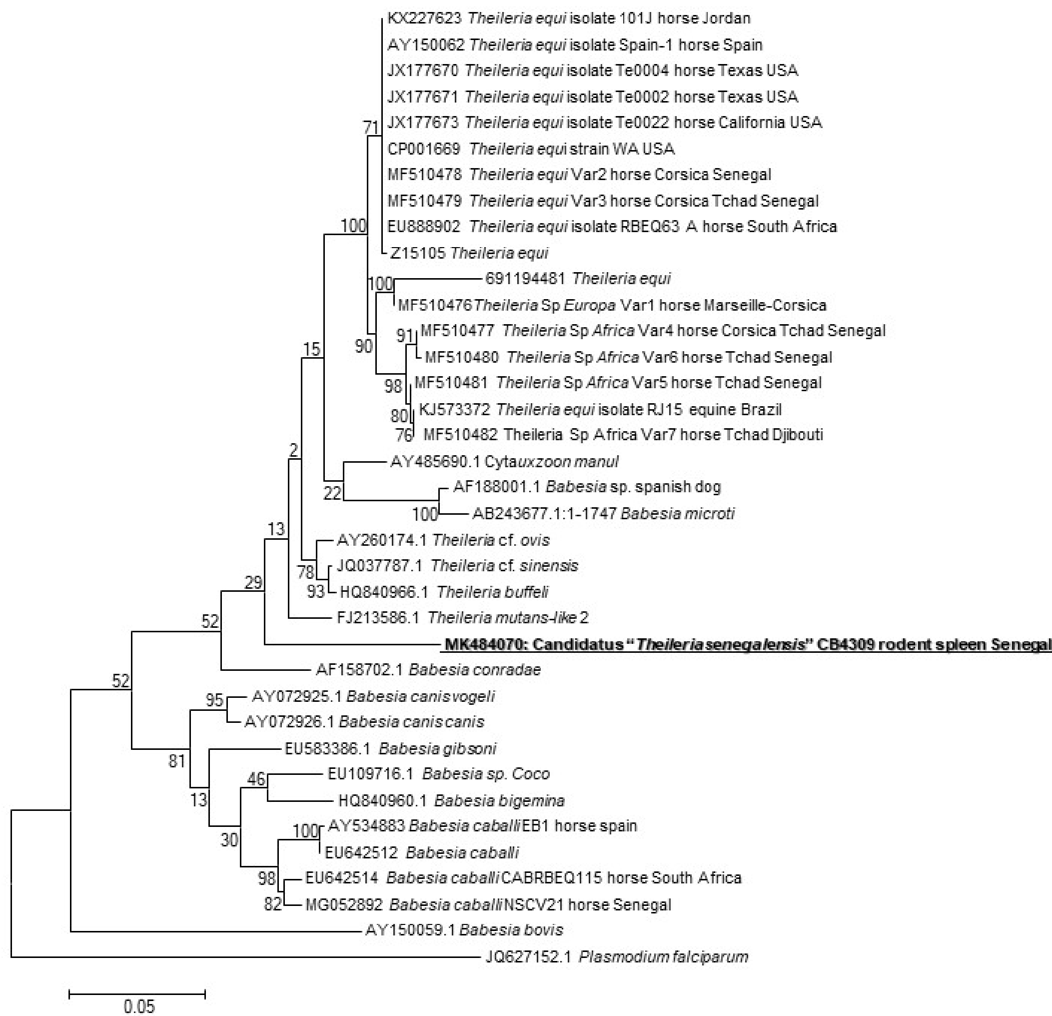
Borrelia	23S	TTB23s F TTB23s R TTB23s P	CGATACCAGGGAAGTGAAC ACAACCCYMTAAATGCAACG 6FAM-TTTGATTTCTTTTCCTCAGGG-TAMRA	60C°	Broad-range qPCR	[85]
	glpQ	Bcroci_glpQ_F Bcroci_glpQ_R Bcroci_glpQ_P	CCTTGGATACCCCAAATCATC GGCAATGCATCAATTCTAAAC 6FAM- ATGGACAAATGACAGGTCTTAC -MGB	60C°	Species-specific qPCR	[85]
	Fla (640-bp)	Fla120F Fla800R	TGATGATGCTGCTGGWATGG TTGGAAAGCACCIARATTTGC	58C°	Broad-range conventional PCR	This study
Bartonella	ITS	Barto_ITS3_F Barto_ITS3_R Barto_ITS3_P	GATGCCGGGGAAGGTTTTC GCCTGGGAGGACTTGAACCT 6FAM-GCGCGCGCTTGATAAGCGTG	60C°	Broad-range qPCR	[86]
	ITS (733-bp)	Urbarto1 Urbarto2	CTTCGTTTCTCTTTCTTCA CTTCTCTTCACAATTTCAAT	50C°	Broad-range conventional PCR	[87]
Streptobacillus monilliformis	*gyrB*	Smoni-gyrB-F Smoni-gyrB-R Smoni-gyrB-P	AGTTTAAAATTCCCTGAACCACAATT ACTTCCAAACACTCCTGAAACTATACTTG 6FAM-TCACAAACTAAGGCAAAACTTGGTTCATCTGAG	60C°	Species-specific qPCR	[88]
Occidentia	*sca*	OMscaA-F OMscaA-R OMscaA-P	AAGGCCAAAAGCATTAGCAA TTCATTTGTATGAATTCCTTGCAT TGAAGTTGAAGATGTCCCTAATAGT	55C°	Species-specific qPCR	This study
Coxiella Burnetti	*IS1111A*	CB_IS1111_0706F CB_IS1111_0706R CB_IS1111_0706P	CAAGAAACGTATCGCTGTGGC CACAGAGCCACCGTATGAATC 6FAM-CCGAGTTCGAAACAATGAGGGCTG	60C°	Species-specific qPCR	[86]
	IS30A	CB_IS30A_3F CB_IS30A_3R CB_IS30A_3P	CGCTGACCTACAGAAATATGTCC GGGGTAAGTAAATAATACCTTCTGG 6FAM-CATGAAGCGATTTATCAATACGTGTATGC	60C°	Species-specific qPCR	[86]
Rickettsia	*gltA (CS)*	RKND03_F RKND03_R RKND03 P	GTGAATGAAAGATTACACTATTTAT GTATCTTAGCAATCATTCTAATAGC 6FAM-CTATTATGCTTGCGGCTGTCGGTTC	60C°	Broad-range qPCR	[86]
Hepatozoon	18S (620-bp)	H14Hepa18SFw H14Hepa18SRv	GAAATAACAATACAAGGCAGTTAAAATGCT GTGCTGAAGGAGTCGTTTATAAAGA	58C°	Broad-range conventional PCR	[89]
Mycoplasma		Mycop_ITS_F Mycop_ITS_R Mycop_ITS_P	GGGAGCTGGTAATACCCAAAGT CCATCCCCACGTTCTCGTAG 6FAM-GCCTAAGGTAGGACTGGTGACTGGGG	60C°	Broad-range qPCR	[90]
Plasmodium	ssrRNA (231-bp)	rPLU1 rPLU2 rPLU3 rPLU4	TCAAAGATTAAGCCATGCAAGTGA ATCTAAGAATTTCACCTCTGACATCTG TTTTTATAAGGATAACTACGGAAAAGCTGT TACCCGTCATAGCCA-TGTTAGGCCAATACC	62C°	Broad-range nested PCR	[91]
Pan-Filarioidea	28S	qFil-28S-F qFil-28S-R qFil-28S-P	TTGTTTGAGATTGCAGCCCA GTTTCCATCTCAGCGGTTTC 6FAM-ACTTTCCCTCACGGTACTTG	60C°	Broad-range qPCR	Laidoudi et al., in press
Pan-Kinetoplastida	28S *LSU*	P LSU 24a F LSU 24a R LSU 24a	6FAM-TAGGAAGACCGATAGCGAACAAGTAG AGTATTGAGCCAAAGAAGG TTGTCACGACTTCAGGTTCTAT	60C°	Broad-range qPCR	Medkour et al., submitted

F2 28S R1 28S	ACCAAGGAGTCAAACAGACG GACGCCACATATCCCTAAG	53C°	Broad-range conventional PCR

113 *: Used only for sequencing

114 The presence of DNA of *Piroplasmida* spp. was screened, and four spleens were
115 positive (4/171, 2.3%) (1 from *Taterillus* sp., 1 from *A. niloticus* and 2 from *M. musculus*).
116 We succeeded to amplify and sequence only one sample (of *A. niloticus*). The phylogenetic
117 analysis showed that this protozoan occupies an intermediate position between the genera
118 *Theileria* and *Babesia* (Figure 2). Its GenBank accession number is MK484070.

119 **Figure 2**: Maximum-likelihood phylogenetic tree of piroplasms, based on partial 880-bp 18S
120 gene including potentially new species identified in this study.



121

122 In *Bartonella* spp. screening, 16/171 (9.35%) of samples were positive (9 from

123 *Taterillus* sp., 4 from *A. niloticus* and 3 from *M. erythroleucus*). We could successfully

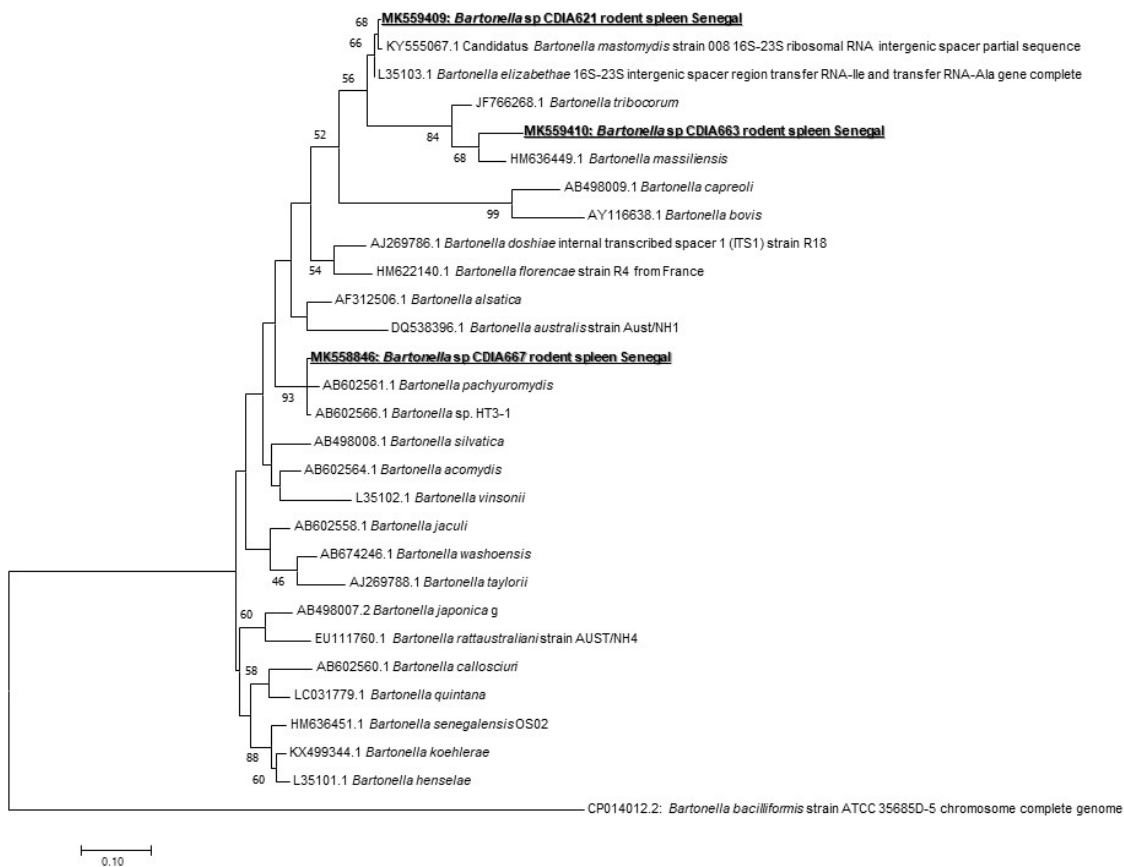
124 amplify 10 positive samples (7 from *Taterillus* sp., 2 from *A. niloticus* and 1 from *M.*

125 *erythroleucus*). The comparison of the sequences obtained showed that there were three

126 different genotypes. When blasted, the first genotype (GenBank accession number:

127 MK558846) corresponded to *B. pachyuromydis* AB602561 the closest validated species with
128 only 92% of homology. The second (GenBank accession number: MK559409) showed 97%
129 with *B. mastomydis* KY555067. The third (GenBank accession number: MK559410) was
130 found to be very different and the closest species is *B. tribocorum* JF766268 having a query
131 cover of 47% and 85% of homology (Figure 3).

132 **Figure 3**: Maximum-likelihood phylogenetic tree of *Bartonella* spp, including new genotypes
133 identified in this study based on partial 733-bp ITS gene.



134

135 We found 31 (18.12%) samples positive for *Anaplasmataceae* species, i.e. 7 *M.*
136 *musculus*, 1 *G. nigeriae*, 1 *Taterillus* sp, 17 *A. niloticus* and 5 *M. erythroleucus*. To identify
137 the species infecting rodents, we used broad species PCR tool targeting 23S gene. Only five
138 positive samples have been successfully amplified and sequenced (1 from *M. erythroleucus*, 4
139 from *A. niloticus*). The comparison of the sequences obtained showed that they were all
140 identical, which may mean that all these sequences belong to the same *Anaplasmataceae*
141 species. When compared with other *Anaplasmataceae* species, the 520 bps-long amplicons of
142 23S rRNA gene obtained from Senegalese rodents did not match to any officially recognized
143 species. Based on its position on the phylogenetic tree (Figure 4), it may be attributed to a
144 potentially new species of *Ehrlichia*. This is clearly reflected by its position on the
145 phylogenetic tree based on 23S gene and by only 95% of identity with the closest species,
146 *Ehrlichia ruminantium* NR077002 (Figure 4). The obtained GenBank accession numbers for
147 its different genotypes are: MK484067, MK484068 and MK484069.

148 **Figure 4**: Maximum-likelihood phylogenetic tree of *Anaplasmataceae* spp, including new
149 genotypes from this study based on partial 520-bp 23S gene

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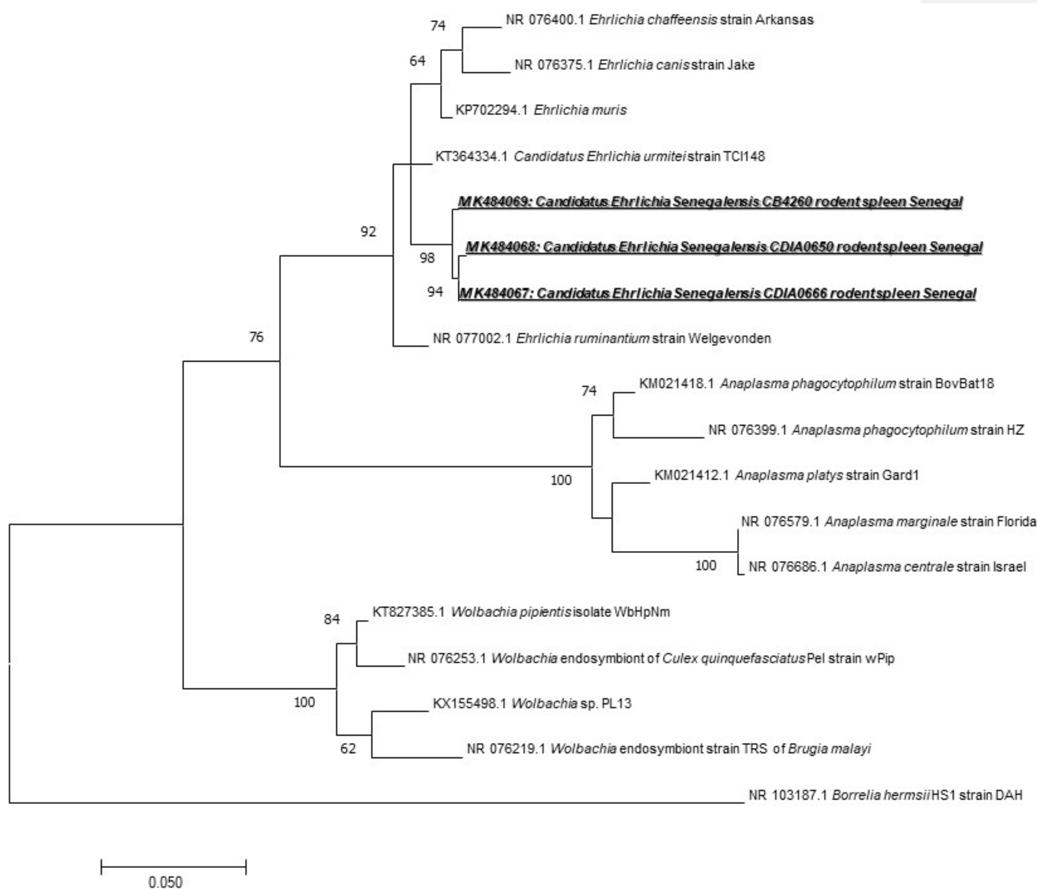

150

151 When screening for the *Hepatozoon* spp. harboured by rodents. We found 4/171
152 (2.33%) positive spleen samples. The sequencing of a 620-bps-long portion revealed 3 species
153 of *Hepatozoon* sp. Two samples corresponded to *Hepatozoon* sp. closely related to those
154 isolated from snakes in the north of Africa [26]: KC696569 found in *M. erythroleucus* and
155 KC696565 that we found in *A. niloticus*. Two other sequences belong to two different
156 genotypes of *Hepatozoon canis*, both of them found in *M. musculus* (Figure 5).

157 **Figure 5**: Maximum-likelihood phylogenetic tree of *Hepatozoon* spp, including new
158 genotypes from this study based on partial 620-bp 18S gene.

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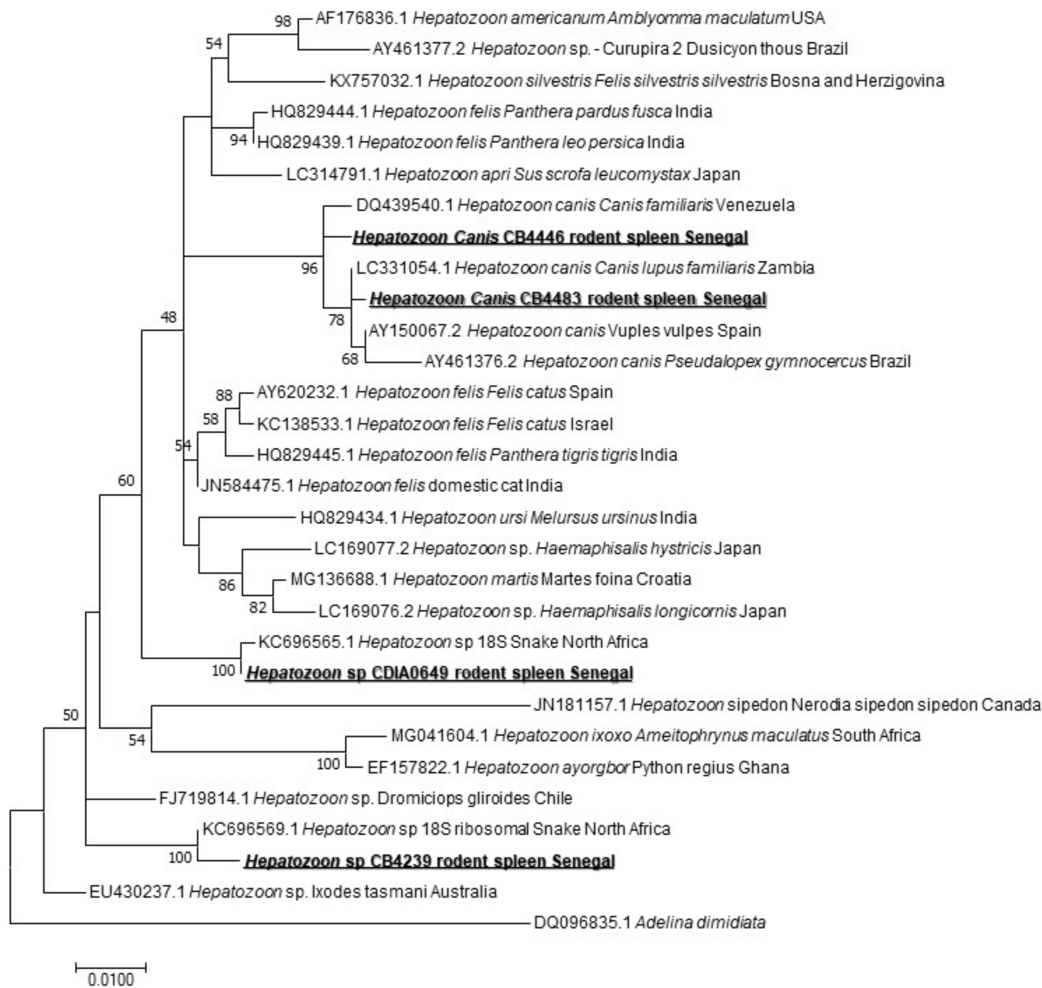


159

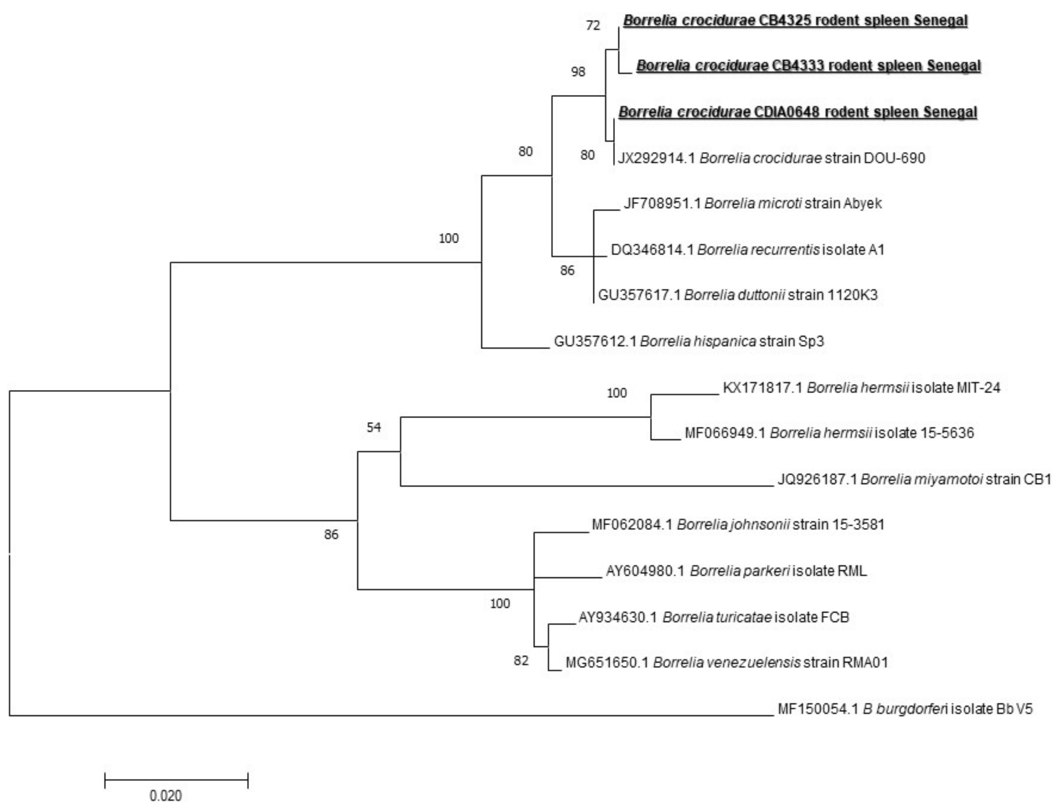
160 We also found 6/171 (3.5%); 1 from *M. musculus*, 1 from *G. nigeriae*, 1 from
161 *Taterillus* sp. and 3 from *M. erythroleucus*) to be positive for *Filarioidea*. In their
162 amplification and sequencing, we failed to get a representative sequence identifying clearly
163 the species infecting the rodents we screened.

164 In order to detect *Leishmania* spp. and *Trypanosoma* spp., the spleen samples were
165 screened for the presence of the *Kinetoplastidae* DNA. We found 6/171 positive (3.5%; 1

166 from *G. nigeriae*, 4 from *Taterillus* sp. and 1 from *M. erythroleucus*). While, in their
167 amplification, we failed to obtain the amplicons to sequence in order to identify the species.

168 We also screened our samples for the presence of *Borrelia* spp. DNA. We found
169 26/171 (15.2%) spleen samples to be positive (5 *M. musculus,* 2 *G. nigeriae,* 5 *Taterillus* sp.,
170 7 from *A. niloticus* and 7 from *M. erythroleucus*). In order to identify the species, we firstly
171 screened the positive samples for the presence of *B. crocidurae* DNA and we found only 8/26
172 (30.76%) to be positive so 8/171 (4.67%) on the total of spleen samples. We designed
173 standard PCR *fla* gene to amplify different representatives of *Borrelia* spp. and all eight
174 samples previously found positive for *B. crocidurae* by qPCR were successfully amplified.
175 The sequenced 640 bps-long amplicons of flagellin gene were identical to *B. crocidurae*
176 (JX292914) for all eight (Figure 6) (1 from *G. nigeriae*, 2 from *M. erythroleucus*, 4 from *A.*
177 *niloticus* and 1 from *Taterillus* sp). It is interesting to note that 5 were found in rodents
178 captured indoors while 3 were found in rodents captured outdoors.

179 **Figure 6**: Maximum-likelihood phylogenetic tree of *Borrelia* spp, including new genotypes
180 based on partial 640-bp flagellin gene (*flaB*)



181

182 We screened our samples for *Orientia* and *O. massiliensis* DNA, the new genus of the
183 *Rickettsiaceae* family. The new specific qPCR tool is very sensitive on our positive controls
184 and does not detect DNA from other bacteria or organisms, but no spleen sample was found
185 positive. Similarly, no positive results were detected for some of the pathogens we tested with
186 the systems we used . It is the case with *Coxiella burnetii*, *Plasmodium* spp., *Rickettsia* spp.,
187 *Mycoplasma* spp. and *Streptobacillus moniliformis.*

188 **c) Host-pathogens relationships**

189 More details regarding the genotypes of pathogens we identified and their related species
190 are provided in Table 2.

191 **Table 2:** Different genotypes of pathogens identified in this study and their related rodent

192 species

Pathogen	qPCR positive samples	Amplified genotypes	About the amplified genotypes	Total	Native						Invasive			
					Arvicanthis niloticus		*Mastomys erythroleucus*		*Taterillus* sp.		*Mus musculus*		*Gerbillus nigeriae*	
					Indoor (N= 26)	Outdoor (N= 15)	Indoor (N= 44)	Outdoor (N= 0)	Indoor (N= 0)	Outdoor (N= 15)	Indoor (N= 51)	Outdoor (N= 0)	Indoor (N= 0)	Outdoor (N= 20)
Piroplasma	4/171 (2.3%)	*Piroplasmida* sp. "*Arvicantis* CB4309"	Potential new species	1	1/26 (3.8%)	0	0	0	0	0	0	0	0	0
Bartonella	16/171 (9.35%)	Genotype 1	Potential new genotype: 92% of homology with *B. pachyuromydis* AB602561	4	0	0	1 (2.3%)	0	0	3/15 (20%)	0	0	0	0
		Genotype 2	Potential new genotype: 97% of homology with B. mastomydis KY555067	1	0	0	0	0	0	1/15 (6.7%)	0	0	0	0
		Genotype 3	Potential new genotype: 85% of homology with *B. tribocorum* (JF766268)	5	1/26 (3.8%)	1/15 (6.7%)	0	0	0	3/15 (20%)	0	0	0	0
Borrelia	26/171 (15.2%)	*Borrelia crocidurae*	Identical to *B. crocidurae* JX292914	8	3/26 (11.5%)	1/15 (6.7%)	2 (4.5%)	0	0	1/15 (6.7%)	0	0	0	1/20 (5%)
Anaplasma	31 (18.12%)	Candidatus "*Ehrlichia senegalensis*"	Potential new species	5	1/26 (3.8%)	3/15 (20%)	1 (2.3%)	0	0	0	0	0	0	0
Hepatozoon	4/171 (2.33%) by conventional PCR tool	*Hepatozoon* sp.	Closely related to *Hepatozoon* sp. KC696569	1	0	0	1 (2.3%)	0	0	0	0	0	0	0
		Hepatozoon sp.	Closely related to *Hepatozoon* sp. KC696565	1	0	1/15 (6.7%)	0	0	0	0	0	0	0	0
		Hepatozoon canis	Closely related to *H. canis*	2	0	0	0	0	0	0	2/51 (3.9%)	0	0	0

193

194 For overall prevalence, the best model selected revealed a significant effect of the

195 gender (LRT = 4.5226, $p = 0.0335$) and the species status (LRT = 18.2631, $p < 0.0001$). Male

196 and invasive rodents appeared to be less infected than female and native ones, respectively.

197 For specific prevalence, model selection was carried out only for *Borrelia* and *Anaplasma* as

198 the prevalence of the other bacterial taxa did not exceed 10% in the entire dataset. We

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199 exclusively found a positive correlation between host body mass and infection by *Anaplasma*
200 (LRT = 13.519, $p = 0.0002$). For individual richness, the most parsimonious model contained
201 host gender and species status as explanatory variables. Nonetheless, only the species status
202 had a significant effect (LRT = 10.6649, $p = 0.0011$) with native rodent individuals
203 harbouring a greater diversity of bacterial taxa than invasive ones.

204 **3. Discussion**

205 A rise in human diseases associated with small-mammals reservoirs was documented
206 and studies were conducted to better assess the link between vertebrate host ecology and
207 human diseases [7]. Diseases of public health interest which can be transmitted by rodents are
208 extensively studied [20] [27] [15] [28] [29] [30] [31].

209 Here, an epidemiological investigation of potentially zoonotic bacteria and parasites
210 from native and invasive rodent communities in Senegal was carried out principally using
211 PCR tools designed to amplify a broad range of species. From the 13 pathogens we tested, 7
212 were detected using the broad range of qPCR tools, while 5 (*Piroplasmida* spp., *Hepatozoon*
213 spp., *Bartonella* spp., *Borrelia* spp. and *Anaplasmatacea* spp.) were amplified and sequenced
214 in order to be identified and to investigate their phylogeny. We also found that indoor rodents
215 appeared generally less infected than outdoor ones and that invasive rodents are less infected
216 than native ones.

217 We used widespread species and sensitive qPCR system targeting the 16S-23S rRNA
218 internal transcribed spacer region ITS gene to be able to detect the largest range of *Bartonella*
219 species. Sixteen individuals (9.35%) (9 from *Taterillus* sp., 4 from *A. niloticus* and 3 from *M.*
220 *erythroleucus*) were positive. This global prevalence is particularly similar to those previously
221 reported 9%) [32]. Diagne *et al.* [19] have previously reported *Bartonella* spp. in *R. rattus*, *M.*
222 *erythroleucus*, *M. natalensis* and *M. musculus* from Senegal without identifying the species.

223 In Spain, a study showed a prevalence of 18.8% in rodents, while 13.6% of their ectoparasites
224 were also infected, highlighting that humans are at risk of infection for *Bartonella* [33]. Only
225 10 samples were successfully amplified by standard PCR (7 from *Taterillus* sp., 2 from *A.*
226 *niloticus* and 1 from *M. erythroleucus*). The amplicons give three potentially new genotypes.
227 Several studies showed different genotypes of the same species [32] or even new species [19].
228 The first new genotype with 92% of homology with *B. pachyuromydis* AB602561 (the closest
229 validated species) was detected in 4 rodents, 3 *Taterillus* sp. and 1 *M. erythroleucus*). The
230 second, only observed in *Taterillus* sp, exhibited 97% of homology with *B. mastomydis*
231 KY555067. The third genotype is quite distant from all known *Bartonella* species, showing
232 only 85% of homology with *B. tribocorum* (JF766268). It was found in 5 rodents (2 *A.*
233 *niloticus* and 3 *Taterillus* sp.). New species isolated recently from rodents in southern part of
234 Senegal named *Candidatus* "*B. raoultii*" and "*B. mastomydis*" were recovered from *M.*
235 *erythroleucus* while *Candidatus* "*B. saheliensis*" was recovered from *G. gambianus* [19]. The
236 number of *Bartonella* species is increasing and have doubled over the last 15 years [34]. More
237 than 30 species are currently described and, interestingly, more than half are harbored by
238 rodents. With such number of new species with unknown pathogenicity, rodents may
239 constitute potential effective reservoirs for *Bartonella* that threatens public health. Among
240 those known to be potentially zoonotic, we can cite: *B. tribocorum*, *B. grahamii*, *B.*
241 *elizabethae*, *B. vinsonii* subsp. *arupensis*, *B. washoensis* and *B. alsatica* [32]. Also in rodents
242 ectoparasites, high prevalence of zoonotic bartonellosis agents are found (43.75% of *B.*
243 *elizabethae* in *Stenoponia tripectinata tripectinata*) [33]. The close contacts among humans
244 and rodents seem to create excellent conditions for transmission of *Bartonella* spp. [34]. Here,
245 the contacts between *A. niloticus*, *M. erythroleucus* and humans can be very frequent as these
246 rodents are very anthropophilic and often commensal, although they are gradually being
247 replaced by the house mouse *M. musculus* in Senegal [3].

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248 *Borrelia* are spirochete bacteria infecting humans or animals and are transmitted to
249 both of them by bite of arthropods like ticks, mites and lice. They are usually divided in two
250 taxonomic groups: lyme disease group and relapsing fever group, both containing many
251 human pathogens. An increasing number of emerging or novel borrelial species are reported
252 [35]. Tick-borne relapsing fever (TBRF) is an acute febrile illness caused by several *Borrelia*
253 species [36]. They are usually transmitted by bites of *Ornithodoros* soft ticks [37] [38].
254 Endemic in Senegal, *B. crocidurae* is responsible for West African tick-borne relapsing fever
255 (TBRF) and *Ornithodoros sonrai*, living in rodents burrows is its vector [39]. Humans
256 contract the disease when they are bitten by a tick living in rodent's habitats. It may cause up
257 to 5% of mortality if left untreated [7]. TBRF is a very important disease in Northern Senegal.
258 The morbidity rates may be very high in rural areas and, overlapping malaria may be the most
259 frequent cause of acute febrile disease consulted in rural dispensaries [40], so it is very
260 important to understand its epidemiology. We detected 26/171 (15.2%) positive samples by
261 broad species qPCR system. Only 8 of these 26 samples were confirmed as *B. crocidurae*.
262 *Borrelia crocidurae* was reported in Senegal [20], Mauritania, Algeria, Mali [39], Morocco,
263 Libya, Egypt, Iran and Turkey [7]. A longitudinal study conducted on the West African tick-
264 borne relapsing fever reported that the average incidence of TBRF over 14 years was 11 per
265 100 person-years. The average *B. crocidurae* infection rate of its vector *O. sonrai* was 31%
266 [41]. In our study, all 8 sequences were identical to *B. crocidurae* JX292914 (1 from *G.*
267 *nigeriae*, 2 from *M. erythroleucus*, 4 from *A. niloticus* and 1 from *Taterillus* sp.). Studies
268 conducted in West African countries, especially Senegal, have shown that using direct thick
269 blood film examinations that *Meriones* spp., *Tatera gambiana*, *Taterillus gracilis* (complex),
270 *Cricetomys gambianus*, *M. erythroleucus*, *Rattus rattus*, *A. niloticus*, *Mus musculus*,
271 *Taterillus* sp. and *M. huberti* and some insectivores such as *Crocidura* sp. function as hosts
272 for *B. crocidurae* [42] [7] [43] [44] [45] [46]. New genotypes of this TBRF agent continue to

273 be isolated and identified [36] [47]. In our study, the presence of this neglected bacterium in
274 *M. musculus*, *M. erythroleucus*, *A. niloticus* and *Taterillus* sp. was confirmed using molecular
275 tools. We report it for the first time in *G. nigeriae*, which is an invasive species in Senegal,
276 which may have acquired the infection by exchange from native rodent species. It should be
277 pointed out that there is a possibility that it was brought by the species probably from
278 Mauritania.

279 Within the order of *Rickettsiales*, we find the *Anaplasmataceae* family which is
280 composed of Gram-negative *Alphaproteobacteria*, including genera *Anaplasma*, *Ehrlichia*,
281 *Neorickettsia*, *Neoehrlichia*, *Aegyptianella* and *Wolbachia.* They are known to cause
282 infections in humans as well as in domestic and wild animals [48] and previous studies have
283 reported a high prevalence of *Anaplasmataceae* in rodents [7] in Senegal [20]. Rodents are
284 often the hosts for ticks and reservoirs of pathogens. Wood rats, white-footed mice and
285 squirrels, for instance, are hosts of *Ixodes* spp., and reservoirs of *Anaplasma* spp. ticks are
286 easily infected on rodents and then, when bitten humans, transmit the agent that causes human
287 granulocyte anaplasmosis (HGA) in several regions of the world [7]. Previous studies
288 reported the detection of *Anaplasma phagocytophilum* and *A. ovis* in sheep in Senegal [49].
289 We used broad species qPCR tool to detect *Anaplasmataceae* [50]. We found 31/171
290 (18.12%) positive spleens. In only five individuals, *Anaplasmataceae* bacteria have been
291 successfully amplified and sequenced (1 from *M. erythroleucus*, 4 from *A. niloticus*). The
292 analysis of the amplicons obtained suggests that it may represent a potentially new species of
293 *Ehrlichia.* It is clearly visible by the position of this sequence on the phylogenetic tree based
294 on 23S gene and which have 95% of homology with *Ehrlichia ruminantium* NR077002
295 (Figure 4). According to the current taxonomy rules [51] we propose the *Candidatus* status
296 and the following provisional name *Candidatus* "*Ehrlichia senegalensis*", whose
297 pathogenicity remains unknown. Recently, there has been an increase in the genetic diversity

298 of *Anaplasmataceae* and newly described species worldwide [48] [52] [53] [54] [55]. Other
299 species isolated from rodents such as *A. phagocytophilum* and *A. muris* may affect humans. It
300 would be necessary to isolate it and to pursue studies on its epidemiology and microbiology.

301 *Hepatozoon* genus, apicomplexan blood parasites described in snakes and also in all
302 tetrapod groups [56] is known to use a wide range of vertebrates as intermediate hosts, like
303 amphibians, reptiles, birds, as well as domestic and wild mammals. They commonly get the
304 parasite by the ingestion of infected invertebrate hosts (diverse blood-sucking arthropods)
305 [57]. They are transmitted also by arthropods like ticks [58] or arthropod are ingested by the
306 definitive host (Snakes versus Mosquitoes) [59]. Non-vector transmission may also happen,
307 like vertical transmission demonstrated in dogs [60] The screening of *Hepatozoon* spp.
308 revealed 4/171 (2.33%) positive (1 *M. erythroleucus,* 1 *A. niloticus,* 2 *M. musculus*). A
309 screening for *Hepatozoon* spp. in rodents reported in USA, 47% of positivity rate [58] and up
310 to 67% in Finland, 17% in Spain and up to 41.6% in Poland [61], which is much higher than
311 our results. The sequencing of the amplicons revealed 3 genotypes of *Hepatozoon* sp. Two of
312 them were found in *M. erythroleucus*, and in *A. niloticus*. Both are very close to two
313 *Hepatozoon* sp. identified in snakes in North Africa (KC696569 and KC696565). In snakes,
314 the genus *Hepatozoon* is the (most identified) hemogregarine prey-predator transmitted agent,
315 and various studies reported a possible connection between the lineages found in predators
316 and those found in the respective preys [56]. A study carried out in the Mediterranean region,
317 showed 2 *Hepatozoon* types that have been previously reported in lacertids and gekkonids,
318 identified from 2 genera of snakes known to have a diet including such lizards [56]: two ball
319 pythons experimentally infected by *Hepatozoon* using laboratory mice livers that have been
320 previously inoculated with *Hepatozoon ayorgbor* [59]. We can suggest that the rodents we
321 studied harbour *Hepatozoon* species and act like intermediate hosts for snakes
322 hepatozoonosis. The third genotype identified is represented by two slightly different

323 sequences, both of them found in *M. musculus*. This genotype is very close to *H. canis*.
324 Various studies support the idea that *Hepatozoon americanum,* the causative agent of canine
325 hepatozoonosis, can be transmitted by predation, and *Hepatozoon* spp. have been widely
326 reported from rodents in Europe, Africa, North and South America [57].

327 *Kinetoplastidae* are widely reported from rodents, especially *Leishmania* [62] and
328 *Trypanosoma* [63]. Their ability to infect humans has been evaluated and proven for some
329 species [63]. We also detected them in group-specific qPCR, but were unable to amplify any
330 specific gene. This may be explained by the lack of broad-range PCR tools for the
331 amplification of potentially unknown *Kinetoplastidae*.

332 We found 4 qPCR-positive samples (4/171: 2.33%) to piroplasmids. Only one (1/171: 0.58%)
333 was successfully amplified from *A. niloticus* spleen sample. To the best of our knowledge, our
334 study is the first to provide evidence of piroplasmids circulating in *A. niloticus*. We can find
335 some studies screening the presence of piroplasmids (belonging to the genera *Babesia*,
336 *Theileria*, *Cytauxzoon* and *Rangelia*) in different rodent species [64] [65] [11]. These tick-
337 borne apicomplexan protozoans cause typical zoonotic diseases by parasitizing blood cells of
338 numerous wild and domestic vertebrates worldwide, resulting in major economic and
339 veterinary impacts[64]. Hundreds of human babesiosis cases are attributed to rodent *Babesia*
340 transmitted by *Ixodes scapularis* [66]. Analysis of the sequence of a portion of 18S rRNA
341 gene obtained from *A. niloticus* revealed that it may represent a new species having 90% of
342 identity with several *Theileria* species. The phylogenetic tree based on 880 bps-long portion
343 of the 18S gene show that our sequence is comprised between those of *Babesia* and *Theileria*
344 species. Unable to attribute obtained sequence to one of the closest genera (*Theileria* or
345 *Babesia*), we retain the provisional name *Piroplasmida* sp. "*Arvicantis* CB4309". While
346 investigating the diversity of piroplasmids in wild rodents, a study conducted in Brazil on
347 *Thrichomys fosteri* (N=77), *Oecomys mamorae* (N=25) and *Clyomys laticeps* (N=8) revealed

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348 that 6/77 (7.8%) *T. fosteri* were infected. The sequencing of the 18S rRNA gene showed 99%
349 of identity with *B. vogeli* KT323934 for five of them, while the last one showed 99% of
350 identity with *T. equi* KU672386 using BLAST analysis [64]. Another study investigating *B.*
351 *microti* in rodents in Croatia reported a prevalence of 6% (2/36 individuals) in *Myodes*
352 *glareolus*, and 16.2% (6/37) in *Apodemus flavicollis,* highlighting the need for more serious
353 consideration of *Babesia* infection in humans [67]. New species or new genotypes of
354 piroplasmids are sometimes found in rodents samples [66] [68], and their pathogenicity
355 remains unknown. It may make a risk for public health, so it is necessary that they be given
356 more attention.

357 The PCR tools we have used for our screening are specific to the genus or family of
358 microorganisms, which may allow us to detect new potential pathogens. Subsequently, almost
359 of the pathogens we found in our study are new genotypes or new species. However, some
360 positives detected in qPCR were not amplified. This may be due to the fact that the
361 conventional tools are not degenerated enough to amplify them to that is added the high
362 sensitivity of the qPCR tools compared to the conventional ones.

363 As previously shown in commensal rodents from Senegal [20], our data revealed that
364 gender and body mass, as well as the native/invasive status of the rodents may significantly
365 drive the bacterial infection in rodents. These preliminary results must be interpreted with
366 caution regarding the distribution of our data (*e.g.* only a single species was captured in both
367 indoor and outdoor habitats) and call for more refined and specific analyses. Nevertheless, our
368 findings provided interesting and surprising preliminary patterns. First, we found that
369 individuals with higher body mass were more susceptible to infection by *Anaplasma*. The
370 reasons potentially explaining why larger rodents may be more prone to higher infection
371 levels than lighter ones were already discussed elsewhere [20], although other specific
372 mechanisms can be involved. Second, we found that females were overall more infected than

373 males, which was not consistent with neither the common trend of higher parasitism rates in
374 males [69][70], nor previous findings on bacterial communities of commensal rodents in
375 Senegal [20]. Indeed, this result rather corroborated the hypothesis according to which sex
376 bias in pathogen infection natural small mammal populations may depend on a variety of
377 interacting parasite-related, host-related and environmental factors that can vary in both space
378 and time within natural (small mammal) populations, even within the same host–parasite
379 association [71,72]. Indeed, sexual differences in physiology, behaviour and evolutionary
380 roles –have been shown to impact both the susceptibility and the exposition to different
381 pathogens [69]. For instance, Gryzbek *et al.* [73] evidenced that mature and reproductively
382 active female bank voles are subject to higher exposure to helminths . Also, the interplay
383 between resistance and tolerance - the two main immune strategies implemented by a host
384 when it is challenged by a parasite [74,75], was shown to substantially differ between male
385 and female rodents [76]. Gender-biased infections remain therefore a challenging area in
386 ecological research. Third, our results were in line with the expectation of lower parasitism
387 highly documented in invading populations during their geographical spread (*enemy release*
388 hypothesis; [77–79]) ; details and potential mechanisms are presented and discussed
389 elsewhere (*e.g.* [21,80–82]). Our findings were consistent with previous ones obtained for the
390 house mouse in Senegal (e.g. [21]) and might provide a first empirical evidence for either low
391 infection rates and/or potential parasite reduction experienced by the Nigerian gerbil during
392 its geographical spread in West Africa. However, concluding on this point requires a robust
393 biogeographical comparison between well-defined source and currently invading populations
394 of this rodent species. Nonetheless, our work brought novel evidence for lower infection
395 levels in invasive *vs* native rodents, which may translate into competitive advantage for both
396 resources and space due to higher fitness and body condition [77]. Finally, this would

397 contribute to explain why both exotic rodents currently experience a successful ongoing
398 spread in Senegal.

399 Presented here, the results of a screening of different species of rodents from Senegal
400 for multiple zoonotic agents. We confirmed that rodents constitute the powerful source of
401 zoonotic pathogens that are still poorly studied, especially in Africa. The presence of rodents
402 in human dwellings can present a significant risk of contracting infectious diseases. In the
403 present case, domestic and peri-domestic rodents in Senegal were confirmed to be the host of
404 an important human pathogen, *B. crocidurae*, constituting a reservoir for this endemic
405 infection. Roles of other bacteria and protozoa identified in the present study in human and
406 animal pathology is yet to be identified.

407 4. Materials AND METHODS

408 d) Ethics statement

409 Fieldwork was carried out under the framework agreements established between the
410 French National Research Institute for Development (IRD) and the Republic of Senegal, as
411 well as with the Senegalese Water and Forest Management Head Office of the Ministry of
412 Environment and Sustainable Development. None of the rodent species investigated in the
413 present study has protected status (see UICN and CITES lists). Handling procedures were
414 performed under the CBGP agreement for experiments on wild animals (no. D-34-169-1), and
415 follow the official guidelines of the American Society of Mammalogists [83]. Trapping
416 campaigns were systematically performed with prior explicit agreement from relevant local
417 authorities, and from the owners of the buildings/houses where domestic trapping was
418 performed.

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419 **e) Study area and samples collection**

420 The following localities and their immediate surroundings were sampled: *(i)* four
421 localities along the national road n°3 crossing the Ferlo eastwards, visited in February-March
422 2017: Diagali (15.27°N, 14.67°W), Yonofere (15.27°N, 14.46°W), Fourdou (15.22°N,
423 14.16°W) and Ranerou (15.30°N, 13.96°W) , *(ii)* two localities within the Great Green Wall
424 area in north-western Ferlo, visited in May 2017: Labgar (15.83°N, 14.81°W) and Tessekere
425 (15.86°N, 15.06°W) (Figure 1). We used both locally made single capture wire-mesh live
426 traps (8.5 × 8.5 × 26.5 cm) and Sherman folding box traps (8 × 9 × 23 cm), baited once a day
427 with peanut butter pasted on fresh onion slices. Indoor traps were set inside buildings
428 (dwelling houses, storehouses or shops) for trapping sessions of one to three consecutive days.
429 A variable number of rooms were sampled in each site and trapping session, with typically
430 two traps (one wire-mesh and one Sherman) set per room. Outdoor traps were installed for 1-
431 3 days in lines with an inter-trap interval of 10m, or were grouped in *a priori* favourable
432 microhabitats (as suggested by the conspicuous presence of active burrows). Traps were
433 checked every morning for night captures, and every afternoon (while re-baiting) for daily
434 captures.

435 **Figure 1.** Map of localities where samples were collected in Ferlo (North Senegal)

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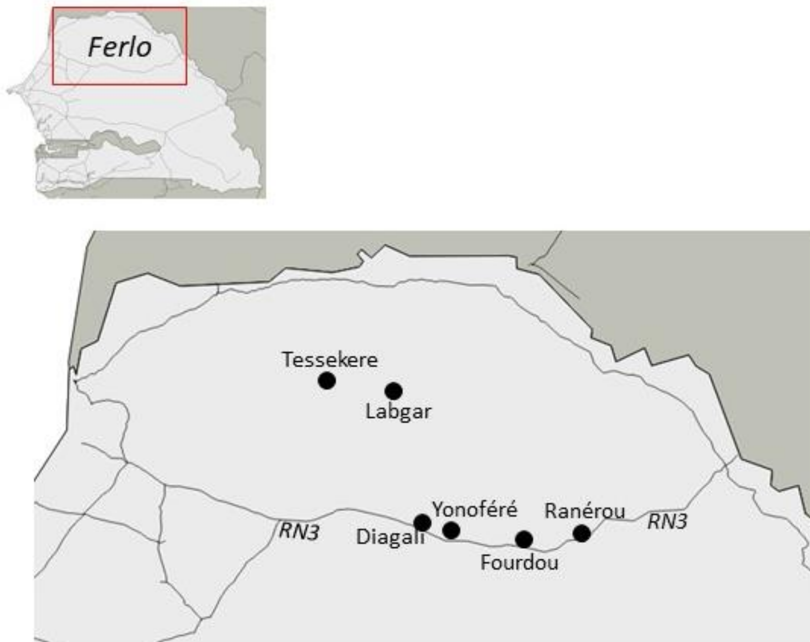

436

437 The small mammals specimens that were caught were identified according to
438 morphological, and, when necessary, molecular (using cytochrome *b* gene sequence) criteria,
439 as previously reported [17]. Upon autopsy, classical body measurements were taken,
440 reproductive status was noted and organ samples (including spleen used in the present study)
441 were preserved in ethanol 95% for further analyses. Small mammals were captured and
442 handled in accordance with relevant requirements of Senegalese legislation and live animal
443 capture and handling guidelines described at
444 http://ilmbwww.gov.bc.ca/risc/pubs/tebiodiv/capt/assets/capt.pdf.

445 **f) DNA extraction**

446 For each spleen, a small piece was crushed and incubated overnight with lysis buffer
447 and proteinase K, before DNA extraction performed using EZ1 DNA kits (Qiagen,

448 Courtaboeuf, France), according to the manufacturer's protocol. The DNA extracts were then
449 stored at -20°C until PCR analysis.

450 **g) Pathogens DNA detection, PCR amplification and phylogenetic analysis**

451 Thirteen groups of pathogens, most of them zoonotic, have been screened: *Piroplasma*
452 spp., *Coxiella burnetii*, *Bartonella* spp., *Plasmodium* spp., *Hepatozoon* spp., *Borrelia* spp.,
453 *Anaplasmataceae*, *Rickettsia* spp., *Mycoplasma* spp., *Orientia* spp. and *Occidentia*
454 *massiliensis*, *Streptobacillus moniliformis*, *Filarioidea* spp., *Kinetoplastida* spp.).

455 The initial screening of samples was performed using qPCR systems with wide
456 specificity (genus- or family-specific) (Table 1). For real-time qPCR, reaction mix contained
457 5 µl of the DNA template, 10 µl of EurogentecTakyon™ Mix (Eurogentec, Liège, Belgium),
458 0.5 µl (20 µM) of each reverse and forward primers, 0.5 µl (5 µM) of the FAM-labeled probe)
459 and 3.5 µl of distilled water DNAse and RNAse free, for a final volume of 20 µl. The real-
460 time qPCR amplification was carried out in a CFX96 Real-Time system (Bio-Rad
461 Laboratories, Foster City, CA, USA) using the following thermal profile: Incubation at 50°C
462 for two minutes for UDG action (eliminating PCR amplicons contaminant), then activation
463 step at 95°C for three minutes followed by 40 cycles of denaturation at 95°C for 15 seconds
464 and annealing-extension at 60°C for 30 seconds.

465 **Table 1.** Oligonucleotide sequences of primers and probe used for qPCRs and conventional
466 PCRs in this study.

467 The identification of qPCR positive samples is based on the amplification and then
468 sequencing using wide range genus or family specific systems. We designed new tools for this
469 study and we confirmed their sensitivity and specificity before using them (Table S1). PCR
470 reactions contained 5 µl of the DNA template, 25 µl of Amplitaq-Gold STAR™ Mix
471 (Eurogentec), 10 µM (1 µl) of each primer and 18 µl of distilled water DNAse and RNAse

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472 free. The amplifications were performed in a Peltier PTC-200 model thermal cycler (MJ
473 Research Inc., Watertown, MA, USA).
474 The conditions for conventional PCR were as follows: one incubation step at 95°C for
475 15 minutes, 40 cycles of one minute at 95°C, 30 seconds annealing at a different hybridization
476 temperature for each PCR assay and one minute at 72°C followed by a final extension for five
477 minutes at 72°C (Table 1). Negative and positive controls were included in each molecular
478 assay. The success of amplification was confirmed by electrophoresis on a 1.5% agarose gel.
479 The purification of PCR products was performed using NucleoFast 96 PCR plates (Macherey-
480 Nagel, Hoerdt, France) according to the manufacturer's instructions.
481 The amplicons were sequenced using the Big Dye Terminator Cycle Sequencing Kit
482 (Perkin Elmer Applied Biosystems, Foster City, CA, USA) with an ABI automated sequencer
483 (Applied Biosystems). The obtained sequences were assembled and edited using ChromasPro
484 software (ChromasPro 1.7, Technelysium Pty Ltd., Tewantin, Australia). Then, the sequences
485 were compared with those available in the GenBank database by NCBI BLAST
486 (http://blast.ncbi.nlm.nih.gov/Blast.cgi). Phylogenetic analyses and tree construction were
487 performed using MEGA software version 7.0.21 [84] with 100 bootstrap replications.

488 **h) Statistical analysis**

489 Generalised linear mixed models (GLMMs) were used to evaluate whether host factors
490 (species, gender, body mass), the status (native vs invasive) and/or the type of habitat (indoor
491 vs outdoor) influence the infection level of the rodents. We considered individual bacterial
492 richness (number of bacterial taxa recorded in a single individual host) and both specific
493 (infection by a bacterial taxon for which prevalence reached at least 10% in the global dataset)
494 and overall (infection by any bacterial taxon, combining all taxa) prevalence as response
495 variables. We assumed a binomial distribution for prevalence data and a Poisson distribution
496 for richness data, respectively. The sampling site was considered as a random factor. A model

497 selection approach was performed, using the Akaike information criterion with correction for
498 samples of finite size (AICc). The starting models included all the factors as possible
499 predictors. The most parsimonious model among those selected within two AIC units of the
500 best model was chosen. The significance of explanatory variables and their interactions was
501 determined by deletion testing and log-likelihood ratio tests (LRT). The assumptions of each
502 final model were ensuring by checking the model dispersion and normality, independence and
503 variance homogeneity of the residuals. All analyses were performed using the packages
504 MuMIn v1.15.1[27] and lme4 v1.1-8 [28] implemented in R software v3.2.1 [29].

505 **Supplementary Materials:** The following are available online (Figure S1).

506 **Author Contributions:**

507 • Handi DAHMANA: Methodology; investigation; software; writing—original draft
508 preparation
509 • Laurent GRANJON: Conceptualization; investigation; methodology; validation;
510 writing—review and editing;
511 • Christophe DIAGNE: Conceptualization; methodology; software; validation;
512 writing—review and editing;
513 • Bernard DAVOUST: Conceptualization; methodology; writing—review and editing.
514 • Florence FENOLLAR: Methodology; validation; writing—review and editing;
515 supervision.
516 • Oleg MEDIANNIKOV: Conceptualization; methodology; validation; writing—review
517 and editing; supervision.

518 All authors have read and agreed to the published version of the manuscript.

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523 **Conflicts of Interest:**

524 The authors declare no conflict of interest.

525 The funders had no role in study design, data collection, and analysis, decision to publish, or
526 preparation of the manuscript.

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Mis en forme : Français (France)

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804 **Figure 1.** Map of localities where samples were collected in Ferlo (North Senegal)**.**

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805 **Figure 2**: Maximum-likelihood phylogenetic tree of piroplasms, based on partial 880-bp 18S
806 gene including potentially new species identified in this study

807 **Figure 3**: Maximum-likelihood phylogenetic tree of *Bartonella* spp, including new genotypes
808 identified in this study based on partial 733-bp ITS gene

809 **Figure 4**: Maximum-likelihood phylogenetic tree of *Anaplasmataceae* spp, including new
810 genotypes from this study based on partial 520-bp 23S gene

811 **Figure 5**: Maximum-likelihood phylogenetic tree of *Hepatozoon* spp, including new
812 genotypes from this study based on partial 620-bp 18S gene

813 **Figure 6**: Maximum-likelihood phylogenetic tree of *Borrelia* spp, including new genotypes
814 based on partial 640-bp flagellin gene (*flaB*)

815

816

817 **List of tables**

818 **Table 1.** Oligonucleotide sequences of primers and probe used for qPCRs and conventional
819 PCRs in this study

820 **Table 2:** Different genotypes of pathogens identified in this study and their related rodent
821 species

822

823 **Supplementary documents:**

824

825 **Table S1**: The list of negative and positive DNA controls, used to confirm the sensitivity and
826 specificity of the PCR systems designed for this study

Microorganism	Name	Origin
Bacteria	*Staphylococcus haemolyticus*	Laboratory colony
Bacteria	*Staphylococcus aureus*	Laboratory colony

Bacteria	*Rickettsia felis*	Laboratory colony
Bacteria	*Wolbachia* PL13	Laboratory colony
Bacteria	*Stenotrophomonas maltophilia*	Laboratory colony
Bacteria	*Acinetobacter* sp.	Laboratory colony
Bacteria	*Enterobacter aerogenes*	Laboratory colony
Bacteria	*Yersinia pestis*	Laboratory colony
Bacteria	*Rickettsia montanensis*	Laboratory colony
Lice	Head lice *(Pediculus humanus capitis)*	Homo sapiens (Amazonia)
Lice	*Pediculus humanus*	Laboratory breeding
Bacteria	*Ehrlichia*	Laboratory colony
Bacteria	*Coxiella burnetii*	Laboratory colony
Bacteria	*Borrelia recurrentis*	Laboratory colony
Bacteria	*Staphylococcus hominis*	Laboratory colony
Bacteria	*Asaia bogorensis*	Laboratory colony
Bacteria	*Haemophilus influenzae*	Laboratory colony
Bacteria	*Wolbachia*	Laboratory colony
Bacteria	*Anaplasma phagocytophilum*	Laboratory colony
Bacteria	*Enterobacter aerogenes*	Laboratory colony
Bacteria	*Acinetobacter baumannii*	Laboratory colony
Bacteria	*Streptococcus pneumoniae*	Laboratory colony
Bacteria	*Salmonella enterica*	Laboratory colony
Bacteria	*Citrobacter koseri*	Laboratory colony
Bacteria	*Gardnerella vaginalis*	Laboratory colony
Bacteria	*Streptococcus pyogenes*	Laboratory colony
Parasite	*Plasmodium falciparum*	Laboratory colony
Bacteria	*Rickettsia typhi*	Laboratory colony
Bacteria	*Enterococcus faecium*	Laboratory colony
Bacteria	*Streptococcus agalactiae*	Laboratory colony
Bacteria	*Rickettsia conorii*	Laboratory colony
Bacteria	*Asaia bogorensis*	Laboratory colony
Bacteria	*Bacillus thuringiensis*	Laboratory colony
Tick	*Amblyomma variegatum*	Senegal
Dog	DH62 cell line	Cell line
Tick	BME (*Rhipicephalus microplus*)	Cell line
Horse	CV.G 22 (*Equus caballus*)	French Guiana
Donkey	ANE 4 (*Equus asinus*)	Egypt
Human	HL60 cell line (*Homo sapiens*)	Cell line
Mouse	L929 cell line	Cell line
Flea	*Ctenocephalides felis*	Laboratory colony
Bedbugs	*Cimex lectularius*	Laboratory colony
Tick	*Hyalomma marginatum*	Senegal
Bacteria	*Bartonella henselae*	Laboratory colony
Bacteria	*Bartonella* sp.	Laboratory colony
Bacteria	*Rickettsia canadensis*	Laboratory colony
Bacteria	*Bartonella quintana*	Laboratory colony
Bacteria	*Rickettsia australis*	Laboratory colony
Bacteria	*Borrelia crocedurae*	Laboratory colony

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Parasite	*Hepatozoon canis*	Laboratory colony
Parasite	*Dirofilaria immitis*	Laboratory colony
Parasite	*Trypanosoma evansi*	Laboratory colony
Parasite	*Leishmania*	Laboratory colony
Parasite	*Leishmania major*	Laboratory colony
Parasite	*Trypanosoma congolense*	Laboratory colony
Parasite	*Trypanosoma gambiense*	Laboratory colony
Bacteria	*Streptobacillus moniliformis*	Laboratory colony
Bacteria	*Borrelia theileri*	Laboratory colony
Bacteria	*Borrrelia* sp.	Laboratory colony
Bacteria	*Vibrio cholerae*	Laboratory colony
Bacteria	*Treponema pallidum*	Laboratory colony

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