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Molecular surveillance of zoonotic pathogens from wild rodents in the Republic of Korea

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Abstract:	Background Rodents are recognized as major reservoirs of numerous zoonotic pathogens and are involved in the transmission and maintenance of infectious diseases. Most importantly, despite their importance, diseases transmitted by rodents have been neglected. To date, there have been limited epidemiological studies on rodents and their information is still scarce in the Republic of Korea (ROK). Methodology/Principal findings We investigated rodent-borne pathogens by PCR/RT-PCR from 156 rodents, including 151 Apodemus agrarius and 5 Rattus norvegicus collected from 27 regions in eight provinces across the ROK between March 2019 and November 2020. Spleen, kidney, and blood samples were used for detecting Anaplasma phagocytophilum, Bartonella spp., Borrelia burgdorferi sensu lato group, Coxiella burnetii, Leptospira interrogans, and severe fever with thrombocytopenia syndrome virus (SFTSV). Of the 156 rodents, 73 (46.8%) were infected with Bartonella spp., 25 (16.0%) with C. burnetii, 24 (15.4%) with L. interrogans, 21 (13.5%) with A. phagocytophilum, 9 (5.8%) with SFTSV, and 5 (3.2%) with Borrelia afzelli. Co-infections with two and three pathogens were detected in 33 (21.1%) and 11 rodents (7.1%), respectively. A. phagocytophilum was detected in all regions, with a widespread occurrence in the ROK. The infection rates of Bartonella spp. were 83.3% for B. grahamii and 16.7% for B. taylorii. Conclusions/Significance To our best knowledge, this is the first report of C. burnetii and SFTSV infections in rodents in the ROK. Our study also provides the first description of various rodent-borne pathogens through an extensive epidemiological survey in the ROK. Our results suggest that rodents harbor various pathogens, posing a potential threat to public health. Altogether, this study provides useful information on the occurrence and distribution of zoonotic pathogens disseminated among rodents and emphasizes the urgent need for rapid diagnosis, prevention, and control strategies toward these zoonotic diseases.
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Molecular surveillance of zoonotic pathogens from wild rodents in the Republic of Korea

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17 **Abstract**

18 **Background**

19 Rodents are recognized as major reservoirs of numerous zoonotic pathogens and are
20 involved in the transmission and maintenance of infectious diseases. Most importantly, despite
21 their importance, diseases transmitted by rodents have been neglected. To date, there have been
22 limited epidemiological studies on rodents and their information is still scarce in the Republic
23 of Korea (ROK).

24

25 **Methodology/Principal findings**

26 We investigated rodent-borne pathogens by PCR/RT-PCR from 156 rodents, including
27 151 *Apodemus agrarius* and 5 *Rattus norvegicus* collected from 27 regions in eight provinces
28 across the ROK between March 2019 and November 2020. Spleen, kidney, and blood samples
29 were used for detecting *Anaplasma phagocytophilum*, *Bartonella* spp., *Borrelia burgdorferi*
30 sensu lato group, *Coxiella burnetii*, *Leptospira interrogans*, and severe fever with
31 thrombocytopenia syndrome virus (SFTSV). Of the 156 rodents, 73 (46.8%) were infected with
32 *Bartonella* spp., 25 (16.0%) with *C. burnetii*, 24 (15.4%) with *L. interrogans*, 21 (13.5%) with
33 *A. phagocytophilum*, 9 (5.8%) with SFTSV, and 5 (3.2%) with *Borrelia afzelli*. Co-infections
34 with two and three pathogens were detected in 33 (21.1%) and 11 rodents (7.1%), respectively.
35 *A. phagocytophilum* was detected in all regions, with a widespread occurrence in the ROK. The
36 infection rates of *Bartonella* spp. were 83.3% for *B. grahamii* and 16.7% for *B. taylorii*.

37

38 **Conclusions/Significance**

39 To our best knowledge, this is the first report of *C. burnetii* and SFTSV infections in
40 rodents in the ROK. Our study also provides the first description of various rodent-borne

pathogens through an extensive epidemiological survey in the ROK. Our results suggest that rodents harbor various pathogens, posing a potential threat to public health. Altogether, this study provides useful information on the occurrence and distribution of zoonotic pathogens disseminated among rodents and emphasizes the urgent need for rapid diagnosis, prevention, and control strategies toward these zoonotic diseases.

Author summary

Rodents live anywhere in the world and transmit various infectious diseases to humans and other animals. All the six pathogens examined in this study were detected in rodents. Our findings demonstrated that 66.7% (104/156) of rodents were infected with at least one pathogen. We also observed differences in the pathogens detected in rodents by region. Our results support evidence that rodents play an important role in the transmission of SFTSV. Although we did not screen all rodent-borne diseases, these data will help understand the emerging rodent-borne diseases disseminated in the ROK. These results emphasize the risk of occurrence of rodent-borne diseases.

57 # Introduction

58 Rodents are globally abundant and well-known reservoirs and vectors of infectious
59 diseases affecting both livestock and humans [1, 2]. The current global change context (e.g.,
60 land-use change, urbanization, and temperature increase) is particularly suitable for the
61 expansion of several rodent species beyond their natural distribution areas [3, 4]. Rodents are
62 widespread in rural and urban areas and, in particular, cause numerous human infections in
63 areas where humans are in close contact with rodents. Rodents are reservoir hosts for at least
64 60 zoonotic diseases and play a vital role in their transmission, which spread directly through
65 contact or bite or indirectly through arthropods [5-7]. Despite their potential threat to public
66 health, there has been less focus on diseases transmitted by rodents [8, 9]. Moreover, the control
67 of rodents is tremendously difficult, considering their behavioral plasticity, life history traits,
68 and high breeding potential [3].

69 *Anaplasma phagocytophilum* is a tick-transmitted, obligatory intracellular zoonotic
70 bacterium and infects neutrophils of various hosts, including humans, dogs, cats, horses,
71 domestic animals, and wild animals [10-13]. The clinical signs of *A. phagocytophilum* infection
72 range from asymptomatic to serious symptoms of veterinary and public health importance. The
73 occurrence of *A. phagocytophilum* is increasing along with climate change worldwide. A broad
74 variety of animal species are known to harbor *A. phagocytophilum*, and humans are incidental
75 dead-end hosts [14]. Vertebrate hosts are crucial for the maintenance and circulation of this
76 pathogen in enzootic foci. Of them, in particular, small rodents and wild ruminants have been
77 suggested as primary reservoirs [15-19]. In the United States, the white-footed mouse
78 (*Peromyscus leucopus*) is considered a well-established reservoir species [20, 21]. In the

79 Republic of Korea (ROK), *A. phagocytophilum* has also been detected in small mammals such
80 as rodents and shrew (*Crocidura lasiura*) [22, 23].

81 *Bartonella* spp. are facultative intracellular bacteria that cause persistent infections in
82 erythrocytes and endothelial cells of mammalian hosts [24]. The clinical manifestations caused
83 by these species are characterized by fever, endocarditis, myocarditis, neuroretinitis,
84 lymphadenopathy, and a range of vascular pathologies [24-28]. Currently, more than 30
85 *Bartonella* spp. and three subspecies are identified [29], and at least 20 species are associated
86 with rodents, indicating that rodents serve as potential reservoirs for zoonotic *Bartonella* spp.
87 [30-32]. Among the rodent adapted *Bartonella* spp., *B. elizabethae*, *B. grahamii*, *B. rochalimae*,
88 *B. tribocorum*, *B. vinsonii*, and *B. washoensis* have been found to cause human infections [32,
89 33]. In general, *Bartonella* spp. have been considered to be transmitted by arthropods [24, 31].
90 Although *Bartonella* infections are widely distributed in rodents of different geographic
91 regions [34-41], there is extremely little information on the distribution and prevalence of these
92 species in rodents in the ROK [22, 42, 43].

93 Lyme borreliosis (LB) is one of the most common vector-borne diseases in North
94 America and Eurasia and caused by a spirochete belonging to the *Borrelia burgdorferi* sensu
95 lato (s.l.) group [44]. Among this group, *B. burgdorferi* sensu stricto (s.s.), *B. afzelii*, and *B.*
96 *garinii* are the major causative agents of LB in humans and exhibit different geographical
97 distributions [45, 46]. These species are transmitted between vertebrate hosts and tick vectors
98 [47]. *B. burgdorferi* s. s. occurs in North America and Europe and has various reservoir hosts
99 (e.g., rodents and birds), whereas *B. afzelii* and *B. garinii* occur in Eurasia and can only use
100 specific vertebrates such as rodents and birds, respectively [44, 45]. Different *Borrelia* species
101 cause different symptoms in humans. For instance, *B. burgdorferi* s. s. infection is associated
102 with Lyme arthritis, whereas *B. garinii* is mostly linked to neuroborreliosis, and *B. afzelii*

103 infection is related to a chronic skin condition known as acrodermatitis [44, 48-50]. In the ROK,
104 *B. burgdorferi* s.l. was first detected in 1993 and sporadically identified in ticks, dogs, horses,
105 wild rodents, and humans [51-56].

106 *Coxiella burnetii* is an obligate intracellular bacterium with a worldwide distribution
107 and is the causative agent of Q fever in humans and a wide range of animals [57]. It is highly
108 infectious and has the ability to form spore-like particles that withstand harsh environmental
109 conditions and can be easily dispersed by airflow [58]. Humans acquire *C. burnetii* infection
110 through inhalation of contaminated aerosols or dust particles [59]. Q fever is a public health
111 concern as it ranks as one of the 13 leading global priority zoonoses. Moreover, it has been
112 considered a potential biological weapon due to its widespread availability, aerosolized use,
113 and environmental stability [60]. The clinical manifestation of *C. burnetii* infection is
114 characterized by fever and flu-like symptoms. The major sources for these infections are
115 infected ruminants in which the agent may cause abortion and infertility. Ticks and rodents are
116 also known as natural reservoirs of *C. burnetii* [61]. Recently, studies have been conducted on
117 the molecular characterization of this pathogen in domestic animals in the ROK [57, 62];
118 however, these studies have limited distribution on spatially and are species-specific.

119 Leptospirosis is a zoonotic infectious disease with a global distribution and is caused
120 by a spirochete of the genus *Leptospira* [63, 64]. It infects more than one million people
121 annually, with 60,000 deaths recorded [65]. *Leptospira* is maintained in several wild and
122 domestic animal hosts through the renal carriage and is excreted in the urine for several months
123 [66, 67]. Infection in humans and animals primarily occurs through direct contact with the urine
124 of infected hosts or indirect exposure to contaminated water, soil, or food [68]. Its clinical
125 manifestations in humans range from mild febrile illness to life-threatening renal failure,
126 pulmonary hemorrhage, and/or cardiac complications [69]. Recent studies suggest that an

127 increase in the incidence of leptospirosis in humans is often associated with climate changes
128 such as heavy rainfall and flooding [70, 71]. Rodents are considered the most important
129 reservoir of pathogenic *Leptospira* spp. because of their close contact with humans and
130 domestic animals, contributing to disease transmission [72]. *L. interrogans*, *L. borgpetersenii*,
131 and *L. kirschneri* are the most abundant species circulating in humans and animals worldwide
132 [73], with *L. interrogans* being the most described in rodents [72].

133 Severe fever with thrombocytopenia syndrome (SFTS) is an emerging tick-borne viral
134 disease and has been primarily reported in China, the ROK, Japan, Vietnam, and Taiwan [74-
135 78]. SFTS is caused by *Huaiyangshan banyangvirus* [formerly the SFTS virus (SFTSV)]
136 belonging to the genus *Banyangvirus* in the family *Phenuiviridae*. SFTSV infections are
137 characterized by high fever, fatigue, myalgia, gastrointestinal symptoms, thrombocytopenia,
138 and multiorgan failures [74, 79]. SFTSV could also spread from person to person through
139 exposure to infected blood [80]. Due to the life-threatening threat to public health, SFTS was
140 chosen as one of the nine emerging diseases given a priority for research and development by
141 the World Health Organization in 2017 [81]. As humans are often in close contact with
142 domestic animals and may encounter rodents when they work outdoors, transmission between
143 animals and humans is another possible major transmission route [82]. The overall mortality
144 rate of this disease has been reported to be 3%–30% in different countries [74, 83, 84].
145 Although SFTSV was identified in various animals, its natural reservoir hosts have not been
146 determined.

147 As such, rodents are involved in the transmission cycles of various diseases. Recently,
148 the incidence of various infectious diseases is rapidly increasing worldwide due to global
149 warming. Rodent populations are also growing exponentially due to climate change and
150 urbanization. To date, most studies on rodent-borne diseases in the ROK have been primarily

151 focused on identifying hantavirus infection. Although rodents are considered important
152 reservoirs of zoonotic infectious pathogens, their epidemiological information has been limited
153 in the ROK. Therefore, the aims of this study were to investigate the occurrence of rodent-
154 borne diseases, characterize the genetic relationship, and determine their role as reservoir hosts
155 for these diseases.
156

157 # Methods

158 ## Ethical statement

159 Rodent collection was approved by the Seoul National University Institutional Animal
160 Care and Use Committee (No. SNU-190524-2-1) and performed according to Seoul National
161 University Guidelines on the care and use of laboratory animals.
162

163 ## Sample collection

164 Rodents were captured using Sherman traps (3 × 3.5 × 9 inches folding traps; H.B.
165 Sherman Traps, Tallahassee, FL, USA) from 27 regions in eight provinces across the country
166 between March 2019 and November 2020. These traps were set where human infections with
167 SFTSV had been reported based on statistical data of the Korea Disease Control and Prevention
168 Agency. They were installed at regions near rivers, valleys, farms, mountains, and lakes
169 between 5 p.m. and 6 p.m. and retrieved the next day between 9 a.m. and 10 a.m. The captured
170 rodents were transported to the laboratory in an icebox with traps, the species was identified,
171 and they were euthanized using CO_2. Thereafter, blood, spleen, and kidney samples were
172 collected from each animal. A whole blood sample was also collected in an SST, and then
173 serum was separated and used for RNA extraction.
174

175 ## DNA/RNA extraction and PCR analysis

176 DNA was extracted from spleen (10 mg) and kidney (25 mg) samples using the
177 DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's
178 instructions and stored at −20°C until analysis. Splenic DNA was subjected to PCR

179 amplification to detect *A. phagocytophilum, Bartonella* spp., *Borrelia* spp., and *C. burnetii*,
180 whereas kidney DNA was subjected to detect *L. interrogans*. These pathogens were screened
181 using each specific primer by the nested PCR method under the following conditions: 93°C–
182 95°C for 5 min, followed by 30-40 cycles of 93°C–95°C for 1 min, the annealing temperature
183 of each pathogen, 72°C for 1 min, and a final extension step at 72℃ for 10 min (Table 1).
184 Distilled water was used as a negative control in all PCRs. Secondary PCR products were
185 visualized on 1.5% agarose gels stained with ethidium bromide.

186 RNA was extracted from 200-μL aliquots of serum using the Gene-spin Viral
187 DNA/RNA Extraction Kit (iNtRON Biotechnology, Seongnam, ROK) according to the
188 manufacturer's instructions. The viral RNA was stored at − 80°C until use. Each RNA sample
189 was tested using nested reverse transcription-polymerase chain reaction (RT-PCR) assays to
190 detect the small (S) segment of SFTSV. Primary PCR was performed using one-step RT-PCR
191 premix (Solgent, Daejeon, ROK) under the following conditions: an initial step of 30 min at
192 50°C and 15 min at 95°C for denaturation, followed by 40 cycles of 20 s at 95°C, 40 s at 52°C,
193 and 30 s at 72°C, with a final extension step of 5 min at 72°C. Nested PCR was conducted
194 using 1 μL of the primary PCR product as a template (BIOFACT, Daejeon, ROK). The reaction
195 for the nested PCR consisted of 25 cycles of 20 s at 94°C, 40 s at 55 °C, and 30 s at 72°C. The
196 primer information used to detect SFTSV was listed in Table 1. Secondary PCR products were
197 visualized on 1.5% agarose gels stained with ethidium bromide.

198

199 **Phylogenetic analysis**

200 The secondary PCR products were purified using an AccuPrep® PCR Purification Kit
201 (Bioneer, Daejeon, ROK) according to the manufacturer's instructions and directly sequenced
202 (Macrogen Inc., Seoul, Korea). All the obtained nucleotide sequences for each pathogen were

203 aligned using the BioEdit software and then compared with reference sequences from the
204 National Center for Biotechnology Information database (http://www.ncbi.nlm.nih.gov) to
205 determine similarity. Phylogenetic analysis of each pathogen was performed using the
206 maximum-likelihood method implemented in MEGA11 using the best substitution model.
207 Bootstrap values were calculated by analyzing 1000 replicates to evaluate the reliability of
208 clusters. The models used in this study were K2 + G for *A. phagocytophilum*, Tamura 3-
209 parameter + G + I for *Bartonella* spp., Tamura-Nei for *Borrelia* spp., and Kimura 2-parameter
210 model for *C. burnetii*, *L. interrogans*, and SFTSV. The nucleotide sequences obtained in this
211 study were assigned the following accession numbers: OR287077–OR287091 for *A.*
212 *phagocytophilum*, OR288176–OR288190 for *B. grahamii*, OR288191–OR288193 for *B.*
213 *taylorii*, OR284310–OR284311 for *B. afzelii*, OR284312–OR284321 for *C. burnetii*,
214 OR284322–OR284324 for *L. interrogans*, and OR257718 – OR257726 for SFTSV.
215

216 # Results

217 ## Collection of samples

218 A total of 175 rodents were captured and morphologically classified as follows:
219 *Apodemus agrarius* (striped field mouse) (*n* = 151), *Rattus norvegicus* (Norway rat) (*n* = 5),
220 and unknown (*n* = 19). Information of the captured rodents was presented in Table 2. Unknown
221 samples were excluded from this study, and the remaining 156 rodents were used for data
222 analysis. *A. agrarius* was mostly found in the ROK, whereas *R. norvegicus* was captured in
223 only two regions.

224

225 ## Prevalence of pathogens detected from captured rodents

226 The presence of six pathogens was investigated by PCR analysis from the two species,
227 *A. agrarius* and *R. norvegicus*. Of the 156 rodents, 104 (66.7%) were infected with at least one
228 pathogen. None of the tested pathogens were detected in 52 rodents (33.3%). In terms of
229 pathogen, *Bartonella* spp. were the mostly detected (73/156, 46.8%), followed by *C. burnetii*
230 (25/156, 16.0%), *L. interrogans* (24/156, 15.4%), *A. phagocytophilum* (21/156, 13.5%),
231 SFTSV (9/156, 5.8%), and then *Borrelia* spp. (5/156, 3.2%) (Table 3). The details of the
232 pathogens determined according to the regions are shown in Table 3. All six pathogens were
233 detected in Gangwon, Chungbuk, and Gyeongbuk provinces. Five pathogens, except for
234 SFTSV, were found in Gyeongnam province, whereas only one pathogen was detected in
235 Chungnam and Jeonnam provinces (Table 3). Co-infections with two and three pathogens from
236 the captured rodents were also detected in 33 and 11 animals, respectively (Table 4), with co-
237 infection with *Bartonella* spp. and *L. interrogans* being most frequently detected (Table 4).
238 SFTSV was co-infected with *Bartonella* spp. The information of pathogens identified

239 according to the region is marked in a map (Fig 1). To the best of our knowledge, this is the
240 first study to report C. *burnetii* and SFTSV infections in rodents in the ROK.
241

242 Phylogenetic trees of rodent-associated pathogens

243 *Anaplasma phagocytophilum*

244 *A. phagocytophilum* was detected only in *A. agrarius* and found in all the examined
245 regions, indicating that this pathogen was spread in the ROK. Of the 21 positive samples, 15
246 were successfully sequenced and confirmed as *A. phagocytophilum* by the phylogenetic tree
247 analysis based on the 16S rRNA gene (Fig 2). Our sequences exhibited 97.6%–99.9% identity
248 to each other and 95.6%–100% identity with those reported from the ROK. The 15 sequences
249 obtained from *A. agrarius* were similar to those previously reported from several different hosts
250 such as cat, cattle, dog, horse, human, tick, and rodents in other countries, sharing 95.9%–100%
251 nucleotide identities with these. Furthermore, several variants co-existed in the same
252 geographical area. According to the phylogenetic tree, *A. phagocytophilum* was divided into
253 clade 1 and clade 2, and all our sequences from *A. agrarius* belonged to clade 1 (Fig 2). The
254 difference in sequences between clade 1 and clade 2 revealed 94.7%–98.5% identities. Clade
255 2 had 10 nucleotide differences compared with those of clade 1. Genetic variants were detected
256 in *A. phagocytophilum* circulating in the ROK.
257

258 *Bartonella* spp.

259 *Bartonella* spp. were the most detected in *A. agrarius* in the ROK, but they were not
260 found in all regions. *Bartonella* spp. were detected in both *A. agrarius* and *R. norvegicus*. Of
261 the 73 ITS PCR-positive samples, 18 sequences were successfully obtained, and all these

262 originated from *A. agrarius*, not *R. norvegicus* (Table 3). According to the phylogenetic tree
263 based on internal transcribed spacer (*ITS*), *Bartonella* spp. circulating in the examined rodents
264 were identified as two species, viz., *B. grahamii*, and *B. taylorii* (Fig 3). The prevalence of *B.*
265 *grahamii* was 83.3% (15/18), and that of *B. taylorii* was 16.7% (3/18). The 15 sequences
266 belonging to *B. grahamii* showed 92.9%–100% identity to each other and formed the same
267 group with leeches (KX270012) and another *A. agrarius* (JN810851) reported in the ROK,
268 exhibiting 95.9%–99.8% identity with those. Furthermore, another sequence (JN810855)
269 reported from *A. agrarius* in the ROK demonstrated 87.1%–90.8% similarity to sequences
270 reported in our study. The three sequences classified into *B. taylorii* exhibited 100% identity to
271 each other and shared 92.5%–100% identity with those belonging to this species.
272
273 ## *Borrelia* spp.
274 *Borrelia* spp. were detected in five *A. agrarius* and the infection rate of *Borrelia* spp.
275 was the lowest (3.2%) compared with that of other pathogens identified. *Borrelia* spp. were
276 found in four regions (Table 3). Among the five PCR-positive samples, only two sequences
277 were obtained and that demonstrated 98.6% identity to each other. The phylogenetic analysis
278 based on outer surface protein A (*ospA*) gene revealed that our sequences were assigned to *B.*
279 *afzelii* (Fig 4). The two sequences exhibited 98.9%−100% homology with *A. agrarius* reported
280 previously in the ROK. Our sequences showed 97.8%−100% identity to those belonging to this
281 group. Furthermore, these sequences displayed 98.2%−99.6% similarity to those reported in
282 humans from Austria, Germany, the Czech Republic, Korea, and Sweden.
283
284 ## *Coxiella burnetii*

285 *C. burnetii* was the second most frequently detected pathogen and identified in both *A.*
286 *agrarius* and *R. norvegicus*. However, it was found in five different regions. Of the 25 positive
287 samples, 10 sequences were obtained and included in the phylogenetic tree based on *IS1111*
288 gene. These sequences showed 97.5%−100% identity to each other. Only one sequence
289 (OR284314) had the closest genetic relationship with those of febrile and pneumonic patients
290 (KP645188 and JF970260), which were known as virulent strains, exhibiting 100% homology
291 with those (Fig 5). The others formed a separate branch, exhibiting 99.0%−99.5% identity to
292 these two human isolates (KP645188 and JF970260). The phylogenetic tree revealed the
293 presence of several genetic clades within *C. burnetii* sequences. These findings indicated the
294 presence of genetic variations in the *C. burnetii* sequences identified in *A. agrarius*.
295

296 ***Leptospira interrogans***

297 *L. interrogans* was the third most detected pathogen and also found in both *A. agrarius*
298 and *R. norvegicus*. Of the 24 positive samples, only three sequences were obtained and had
299 97.7%−99.5% identity to each other. The phylogenetic tree based on the RNA polymerase
300 subunit beta (*rpoB*) gene revealed that these sequences belonged to *L. interrogans* (Fig 6). Two
301 sequences (OR284322 and OR284323) were classified into *L. interrogans* serovar *Lai* and
302 showed 99.2%−100% identity with those reported in China and 99.4%−100% identity with *A.*
303 *agrarius* reported in Korea. The other sequence (OR284324) belonged to *L. interrogans*
304 serovar *Manilae* detected in *Mus musculus* in Japan, exhibiting 98.2% similarity to them (Fig
305 6). At least two serovars of *L. interrogans* were found to be circulating in *A. agrarius* in the
306 ROK.
307

308 **Severe fever with thrombocytopenia syndrome virus**

309 SFTSV was detected in nine *A. agrarius* (5.7%) and found in four different regions
310 (Table 3). Of the nine SFTSV infections, single infection of SFTSV was detected only in two
311 *A. agrarius* and the remaining were primarily co-infected with other pathogens such as
312 *Bartonella* spp. and *L. interrogans* (Table 4). Nine sequences were obtained and included in
313 the phylogenetic tree. These sequences demonstrated 95.95%−100.0% identity to each other.
314 The phylogenetic analysis based on the S segments revealed that five and four sequences were
315 classified into subgenotype B-2 and genotype D, respectively (Fig. 7). The sequences
316 belonging to genotype B-2 exhibited 94.51%−97.4% homology with human and other animal
317 samples reported in the ROK, whereas the four sequences showed 99.71%−100.0% identity
318 with human samples. These results revealed that genotype B-2 is prevalent in the ROK, and
319 genetic variants exist within genotype B-2.
320

Discussion

This study demonstrated the prevalence and genetic characterization of potentially zoonotic pathogens by molecular analysis in rodents captured from throughout the ROK. *A. agrarius* was the most common species in the ROK. Rodents were trapped from areas with frequent movement of people, which may be associated with a high probability of disease transmission because humans and rodents share the same space. All the six pathogens examined in this study were detected in rodents. The results demonstrated that 66.7% (104/156) of rodents were infected with at least one pathogen. According to our findings, *Bartonella* spp. were most frequently detected, and *Borrelia* spp. were least detected in rodents. Although the infection rate was not very high, *A. phagocytophilum* was found in all regions. Considering that the number of rodents captured was different by the region and was small in some provinces, *A. phagocytophilum* may be the most widespread in the ROK. Furthermore, to the best of our knowledge, this is the first study to report *C. burnetii* and SFTSV infections in rodents in the ROK and an extensive study to investigate the infections of various pathogens. ~~Our results demonstrate that rodents play a vital role in the natural infection cycle of *Anaplasma*, *Bartonella*, *Borrelia*, *Coxiella*, *Leptospira*, and SFTSV in the ROK. Therefore, our findings suggest that rodents can directly or indirectly transmit several diseases to humans. Moreover,~~ these data provide valuable information for evaluating the potential risk of rodents in public health.

Anaplasma phagocytophilum has been known as the third most common tick-borne pathogen in the USA and Europe [85] and was detected in 20 different rodent species [86]. *A. phagocytophilum* infection varies considerably in rodent species [86], which may be explained by differences in small mammals that maintain the tick species. In this study, the prevalence of

A. phagocytophilum from *A. agrarius* was 13.5%, which was rather low compared with that reported in a previous study conducted in the ROK (19.1%) [87]. To date, there has been no report of *A. phagocytophilum* infection from *Rattus* spp. in the ROK, although a high infection rate (31.5%) of *A. phagocytophilum* was reported in *Rattus* spp. from China [88]. ~~This suggests that *Rattus norvegicus* is not involved as a reservoir in the transmission cycle of this bacterium in the ROK.~~ *A. phagocytophilum* has been detected in a variety of animals, including ticks in the ROK, but its pathogenicity still remains unclear. ~~When our sequences were compared with those of *A. phagocytophilum* human agent, we observed differences in four of the six nucleotides [89]. According to the phylogenetic analysis, *A. phagocytophilum* circulating in the ROK had several genetic variants. As of now, we cannot conclude whether these variants are pathogenic or non-pathogenic because *A. phagocytophilum* was detected using the 16S rRNA gene. Nevertheless, these variants can infect other hosts as well as humans irrespective of their pathogenicity, and they have been considered zoonotic.~~ *Haemaphysalis longicornis* found primarily in the ROK may tend to use *A. agrarius* as the major host to maintain *A. phagocytophilum*, indicating that *A. agrarius* is an enzootic reservoir. Hence, further studies are required to determine its pathogenicity of *A. phagocytophilum* variants circulating in the ROK.

The overall prevalence of *Bartonella* spp. in *A. agrarius* was 46.8% and the highest compared with that of all other pathogens examined in this study. However, compared with a previous report (62.0%) based on *ITS*, the detection rate in the present study was rather low [43]; this difference may be because of the location where the rodents were captured. Moreover, its prevalence in rodents varied across countries, e.g., 5.5% in Turkey [37], 23.7% in Lithuania [90], 36.3% in Chile [32], 40.4% in Slovenia [34], and 65.8% in Eastern Germany [41]. ~~The difference in prevalence by country may be due to rodent species. Nonetheless, *Bartonella* spp.~~

~~infections are highly prevalent in rodents. Moreover,~~ *Bartonella* spp. that are prevalent in each country are different [27, 32, 34, 38, 90-93]. Although *Bartonella* was detected in both *A. agrarius* and *R. norvegicus*, it was not possible to confirm which species was detected in *R. norvegicus* because the amplified samples from only *A. agrarius* were sequenced. *R. norvegicus* and *R. rattus* have been known as major reservoirs for *Bartonella* spp. in several countries [27, 94-96], but there has been no report of *Bartonella* detection from other rodent species as well as *R. norvegicus* in the ROK [22]. Further studies are necessary to investigate *Bartonella* spp. infection in *R. norvegicus*. The present results demonstrated that *B. grahamii* was most predominant and *B. taylorii* was found in three rodents, a finding consistent with a previous study [43]. *B. grahamii* is a zoonotic pathogen and associated with neuroretinitis and retinal artery occlusion in humans [25]. *B. taylorii* can cause infection in animals [90], but its pathogenicity remains yet unclear. In Europe, *B. taylorii* is dominant in rodents [24, 37]. Although *B. taylorii* has been detected in some *A. agrarius* in the ROK, its transmission route remains unknown. ~~*B. grahamii* identified in this study showed 87.1%–99.8% similarity to those detected previously in the ROK, indicating that genetic diversity exists. At this point, we cannot determine whether the difference is due to host adaptation. Several studies have reported that although the ITS region has high sensitivity in detection, it provides a higher sequential diversity than to other genes [34, 43], which supports our results. Considering the high infection rate in *A. agrarius* and its close contact with humans and other animals, the importance of *Bartonella* as a potential public health concern should not be ignored.~~

The detection rate of *Borrelia* spp. from *A. agrarius* was 3.2% and also the lowest compared with that of other pathogens examined in this study. Our result was different from that of previous studies conducted on heart from *A. agrarius* (29.6%) [56] and in ticks (33.6%) collected from wild rodents [97] in the ROK. This can be explained by the difference in the

392 sample used. For instance, Kim et al. reported that *B. burgdorferi* s.s. and *B. garinii* infected
393 the spleen and *B. afzelii* exhibited a high detection rate in the heart [56]; however, *B.*
394 *burgdorferi* s.s. and *B. garinii* were not detected in the spleen. ~~It is speculated that the number~~
395 ~~of positive samples was small and could not be detected.~~ Among the *Borrelia burgdorferi* s.l.
396 group, only *B. afzelii* was identified in *A. agrarius*, which supports previous findings that *B.*
397 *afzelii* is the predominant species in the ROK [54, 97]. Furthermore, our results were
398 significantly lower than those reported in rodents from other countries, e.g., 24% in Austria
399 [98], 16% in the Czech Republic [99], and 6.3% in Spain [100]. These differences in prevalence
400 may be due to the tick vectors; the common tick vectors of *Borrelia* spp. in the ROK are *Ixodes*
401 *persulcatus*, *I. nipponensis*, and *I. granulatus* [101]. *B. afzelii* is transmitted by *Ixodes ricinus*
402 and hosted by small mammals, and it is the most common causative agent of human LB [45,
403 102]. ~~*B. afzelii* is known to cause acrodermatitis; it readily disseminates from the skin (ear) to~~
404 ~~joint and heart tissue in its primary natural hosts. The bacterial loads in each tissue differed~~
405 ~~between host species [44], which may depend on the host species it infects. Collectively, *B.*~~
406 ~~*afzelii* possesses the ability to replicate in and attach to a variety of tissues.~~ In the ROK, *B.*
407 *afzelii* has been primarily reported in ticks [54, 97, 103] and rarely in humans [104]. However,
408 there is still a lack of information on *B. afzelii*. ~~Considering that the infection rate of *B. afzelii*~~
409 ~~in the ROK is 62.5% in ticks [97] and 25.9% in rodents [56], the possibility that it also occurred~~
410 ~~in humans cannot be ruled out. In particular, there is very low awareness of the importance of~~
411 ~~most vector-borne diseases (VBDs) in the ROK, which may have resulted in an underdiagnosis~~
412 ~~of LB due to similar clinical manifestations of VBDs. Because a high prevalence of *B. afzelii*~~
413 ~~infection was detected in ticks and rodents, and most importantly, the possibility of LB~~
414 ~~transmission to humans due to climate change will increase, there exists a need for a systematic~~
415 ~~strategy for diagnosis, distribution, and control.~~

This is the first report of *C. burnetii* in *A. agrarius* in the ROK. In this study, *C. burnetii* exhibited the second highest infection rate (16%)~~, which was higher than that we anticipated.~~ Nevertheless, our results were lower than those reported in China (18%) [105], Senegal (22.4%) [106], and Zambia (45%) [107], but higher than those reported in Brazil (4.6%) [93], Egypt (6.7%) [58], and Italy (1.4%) [61]. These differences may be explained by the rodent species and samples used for detection. ~~Rodent species, which are predominant, differ in each country.~~ In those studies, *C. burnetii* detection was performed using various samples such as blood, spleen, livers, and feces. Consequently, liver and spleen are considered suitable for the identification of *C. burnetii*. According to a previous study, the infection rate of *C. burnetii* in domestic livestock ranged from 6% to 22.7%, depending on the species [57]. ~~Despite its significance, *C. burnetii* is an underestimated pathogen in the ROK, and there has been no sufficient research on this pathogen.~~ Although *C. burnetii* is a tick-borne pathogen, there are only a few reports of *C. burnetii* in ticks in the ROK [108, 109]. Recent studies have reported about the co-infection of *C. burnetii* and SFTSV in ticks and humans [110, 111]; however, there was no co-infection with two pathogens in rodents. ~~Once *C. burnetii* is detected in rodents, the possibility that *C. burnetii* infection in livestock is transmitted by rodents cannot be ruled out because rodents can frequently enter the barn and infected rodents can contribute to the spread and transmission of this pathogen. Despite the small number of *R. norvegicus* captured, *C. burnetii* infection was mostly detected in *R. norvegicus*, which can be because *R. norvegicus* may also serve as a reservoir in the ROK.~~ A phylogenetic analysis based on *IS1111* gene revealed the presence of two different genotypes within the sequences identified in *A. agrarius*. One sequence formed the same clade with virulent strains reported in Brazil, whereas the others exhibited high similarity to strains reported in different countries. ~~Furthermore, the possibility that the remaining sequences are pathogenic cannot be ignored.~~ The disadvantage of *IS1111*

gene is that it does not provide exact information, such as pathogenicity and species specificity (Fig 5); hence, currently, we cannot draw any conclusions on what separate groupings within *C. burnetii* sequences might represent. Further research is necessary to determine the pathogenicity of *C. burnetii* circulating in the ROK. The results obtained in the present study suggest that *A. agrarius* plays a~~n important~~ role in the transmission of *C. burnetii* in humans and animals.

Leptospira interrogans is a ~~representative~~ rodent-borne pathogen and accordingly, it was the third most frequently detected (15.4%) in this study. Our results demonstrated a relatively high prevalence compared with that of previous studies [87, ~~112]; this difference is due to the regions examined.~~ This is the first time that *Leptospira* has been investigated in rodents through sampling of extensive regions in the ROK. Compared with those reported in other countries, the infection rates ranged from 1.3% to 35.2%, which differed in countries [113-117]. *R. norvegicus* is also an important reservoir of this pathogen [72]; however, *L. interrogans* was detected in only one *R. norvegicus* and mostly detected in *A. agrarius*, which can be due to the limited sample number. ~~Considering that *R. norvegicus* is easily found around barns and farmhouses, it also plays a critical role in the transmission of leptospirosis in domestic animals and humans.~~ To date, *L. interrogans* has been divided into 23 serogroups based on serological methods, with subdivision into more than 300 serovars [72]. The serovars circulating in each country are different, but the most frequently reported serovar worldwide is *Icterohaemorrhagiae* [72]. In the ROK, only a few studies have been conducted on serovar *lai* [87, 118]. Of the three sequences from rodents, two were classified as serovar *lai* and one as serovar *manila*, consistent with a previous study [87]. Consequently, *lai* and *manilae* are considered epidemic serovars in the ROK. However, the biggest limitation of the present study is that a serological analysis such as microscopic agglutination test was not performed, and the

PCR target gene used was also different from that used in other studies. Nonetheless, our results suggest that *rpoB* gene used in this study can be applicable for detection and serovar identification of *L. interrogans*. Furthermore, for an accurate identification of *L. interrogans* serovars, a serological test along with PCR method is absolutely necessary. ~~Leptospirosis has a higher prevalence in tropical or warm-climate countries [72]. Due to global warming, Korea has recently shifted to a subtropical warm and wet climate, and the most representative characteristic is the frequent localized heavy rain, such as flooding. Although there is a lack of sufficient research on leptospirosis in the ROK, the higher incidence observed in the present study than that reported previously may be related to climate change. This provides the opportunity of contamination of rivers or soil and, consequently, the potential risk of leptospirosis. These data highlight the need for prevention and control of leptospirosis.~~

Since its first identification in China, SFTSV has been primarily detected in Asia [74-78]. Due to its high mortality rate, there is significant interest in SFTSV [74, 83, 84]. In the present study, the infection rate of SFTSV in *A. agrarius* was 5.7%, and this is the first report to describe SFTSV infection from *A. agrarius* in the ROK. Our results were significantly lower than those reported in China (32.3%) [119]. When the infection rates are compared with those in other animals reported in the ROK, the prevalence in rodents was similar to that in wild boars (5.2%) [120] and ticks (6.0%) [121], but higher than that in cats (4.0%) [122], dogs (2.9%) [123], pigs (1.7%) [124], black goats (2.4%) [125], and wild animals (3.3%) [126]. However, the prevalence of SFTSV was highest in feral cats (17.5%) in the ROK [127]. Recently, there is an increase in the populations of feral cats, and they are sharing habitats with wildlife, domestic animals, and humans. Several studies have demonstrated that SFTSV is transmitted to humans through direct contact with cats [128, 129], suggesting that feral cats are infected from rodents. It is believed that SFTSV circulates in a zoonotic cycle between ticks and

vertebrates [130]. Rodents are considered the representative reservoirs in maintaining tick-borne pathogens and may play a vital role in the transmission of SFTSV. ~~Interestingly, in this study, *A. agrarius* was primarily co-infected with *Bartonella* spp. rather than infected with SFTSV alone. As of now, we cannot provide any explanation for the pathogenesis of co-infections. SFTSV can also be transmitted through mouth mucosa or conjunctiva to cause infection [128].~~ The sequences obtained from *A. agrarius* belonged to subgenotype B-2 and D genotype; the results revealed a similar distribution in both genotypes. Sequences belonging to subgenotype B-2 were the most prevalent and associated with the highest mortality rate (43.8%) in the ROK [131], whereas genotype D was primarily found in China. Four sequences belonging to genotype D were identical to those of a human patient reported in the ROK, suggesting that this genotype is pathogenic. Different genotypes of SFTSV are known to trigger different clinical manifestations in a ferret model [130]; however, although clinical manifestations have not been confirmed in rodents, they may be pathogenic to humans. To date, SFTSV has been detected in various animals, but no conclusions could be drawn on how the virus is transmitted to these animals. The results of the present study provide a clue for understanding the transmission route of SFTSV, thereby suggesting the need to establish a continuous monitoring and surveillance system to minimize a serious risk of SFTSV infection.

Conclusions

Urbanization and climate change affect not only on humans but also wildlife. The biggest concern caused by these changes is that the probability of disease transmission through ecosystem destruction has been significantly increasing compared with that in the past. This study investigated the prevalence of zoonotic pathogens in rodent populations through a

511 systematic epidemiological investigation. Although we did not screen all rodent-borne
512 pathogens, the results indicated that, at least, rodents act as critical reservoirs for *A.*
513 *phagocytophilum*, *Bartonella* spp., *B. afzelli*, *C. burnetii*, *L. interrogans*, and SFTSV in the
514 ROK. Our findings also demonstrated that rodents harbor several pathogens, implying the
515 possibility of simultaneous transmission to humans. Most importantly, except for SFTSV, the
516 pathogens investigated in this study are misdiagnosed or underdiagnosed in the ROK, so their
517 importance is being neglected. Therefore, our findings indicate that rodents pose a potential
518 risk to public health. Overall, our study provides useful information on rodent-borne pathogens
519 and underscore the urgent need for rapid diagnosis, prevention, and control strategies toward
520 zoonotic diseases.

521

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525

526 **Author Contributions**

527 KSC and JSC designed the experiments, SH and MCK performed the experiments and
528 sample collection. HCC, YJP, MJJ, and SWH carried out data analysis. KSC wrote the
529 manuscript, which was reviewed by HCC, YJP, MJJ, and JSC.

530

531 **Data Availability Statement**

532 All data generated during this study are included in the article. The nucleotide
533 sequences obtained in the present study have been deposited in the GenBank database under
534 the accession numbers.

535

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538

539 **Competing interests**

540 The authors declare that no competing interests exist.

541

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995

996 **Figure legends**

997 **Fig 1.** Maps showing the regions where rodent-borne pathogens were detected in the Republic
998 of Korea. Marks are differently indicated according to each pathogen.

999 **Fig 2.** Phylogenetic tree inferred by maximum-likelihood analysis using the K2 + G model of
1000 16S rRNA gene sequence of *Anaplasma phagocytophilum*. The numbers at the nodes are
1001 bootstrap values expressed as percentage of 1000 replicates. Scale bar indicates nucleotide
1002 substitution per site. Samples sequenced from *Apodemus agrarius* are shown in filled circles.

1003 **Fig 3.** Phylogenetic analysis based on *ITS* region of *Bartonella* spp. (maximum-likelihood
1004 analysis using the Tamura 3-parameter + G + I model with of 1000 replicates). Scale bar
1005 indicates nucleotide substitution per site. Sequences determined from *Apodemus agrarius* are
1006 indicated in filled circles.

1007 **Fig 4.** Maximum-likelihood phylogenetic tree using the Tamura-Nei model based on *ospA* gene
1008 of *Borrelia* spp. Bootstrap values were calculated with 1000 replicates of the alignment. Scale
1009 bar indicates nucleotide substitution per site. Sequences obtained from *Apodemus agrarius* are
1010 symbolized in filled circles.

1011 **Fig 5.** Maximum-likelihood phylogenetic tree from *IS1111* gene of *Coxiella burnetii*. The
1012 evolutionary analysis was inferred using the Kimura 2-parameter model. Bootstrap values
1013 (1000 replicates) are indicated in each node. Scale bar implies nucleotide substitution per site.
1014 Sequences determined from *Apodemus agrarius* are highlighted in filled circles.

1015 **Fig 6.** Phylogenetic analysis based on *rpoB* gene of *Leptospira interrogans*. The tree was
1016 inferred in MEGA X using maximum-likelihood and Kimura 2-parameter with 1000 replicates.
1017 Scale bar implies nucleotide substitution per site. Sequences obtained from *Apodemus agrarius*
1018 are shown in filled circles.

1019 **Fig 7.** Phylogenetic tree of the severe fever with thrombocytopenia syndrome virus based on

1020 the analysis of partial sequences of small segments. Maximum-likelihood analysis was used to
1021 construct by the Kimura 2-parameter model (1000 bootstrap replicates). Scale bar implies
1022 nucleotide substitution per site. The sequences identified from *Apodemus agrarius* are
1023 indicated in filled circles.
1024

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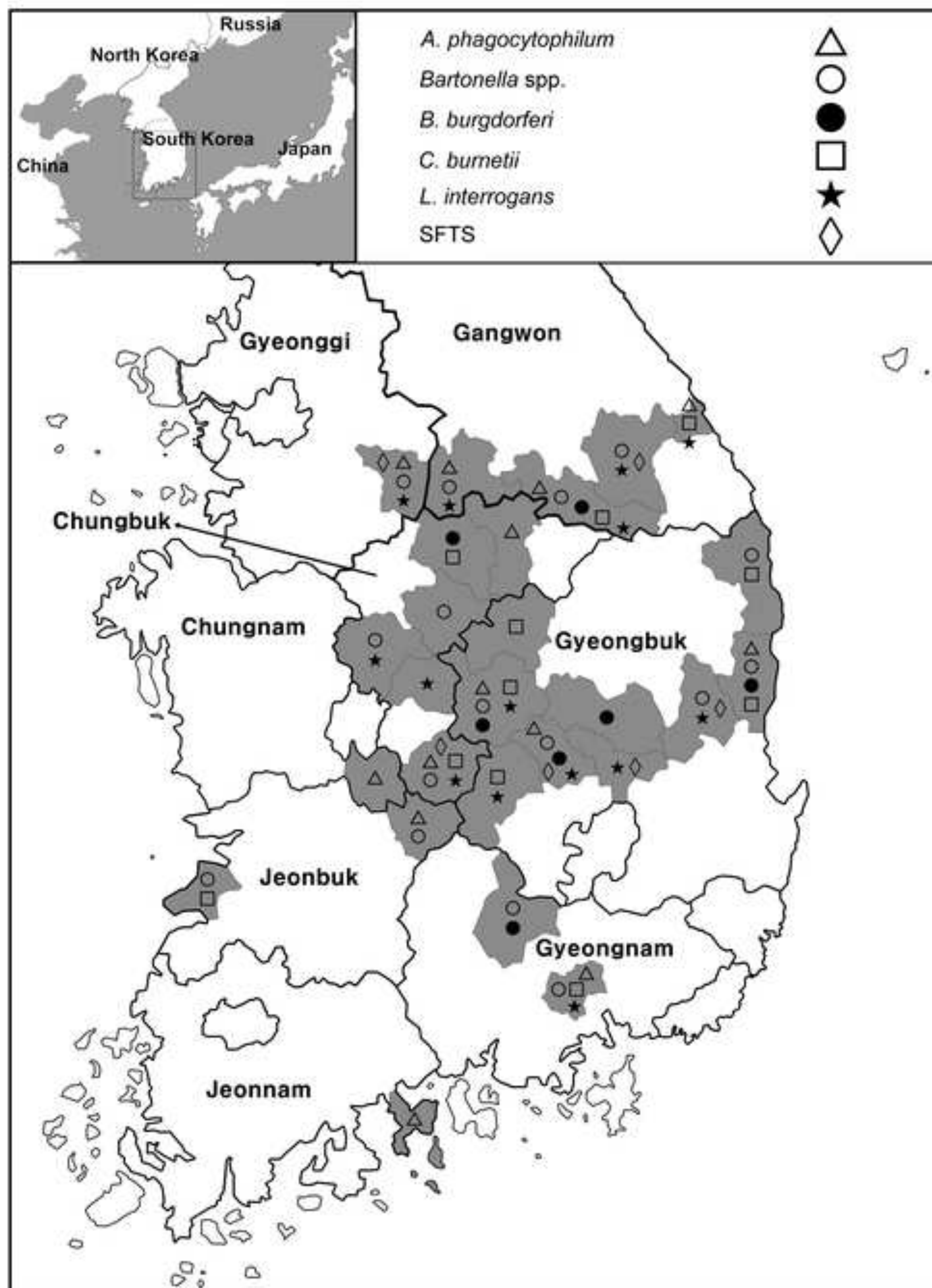

Figure 2

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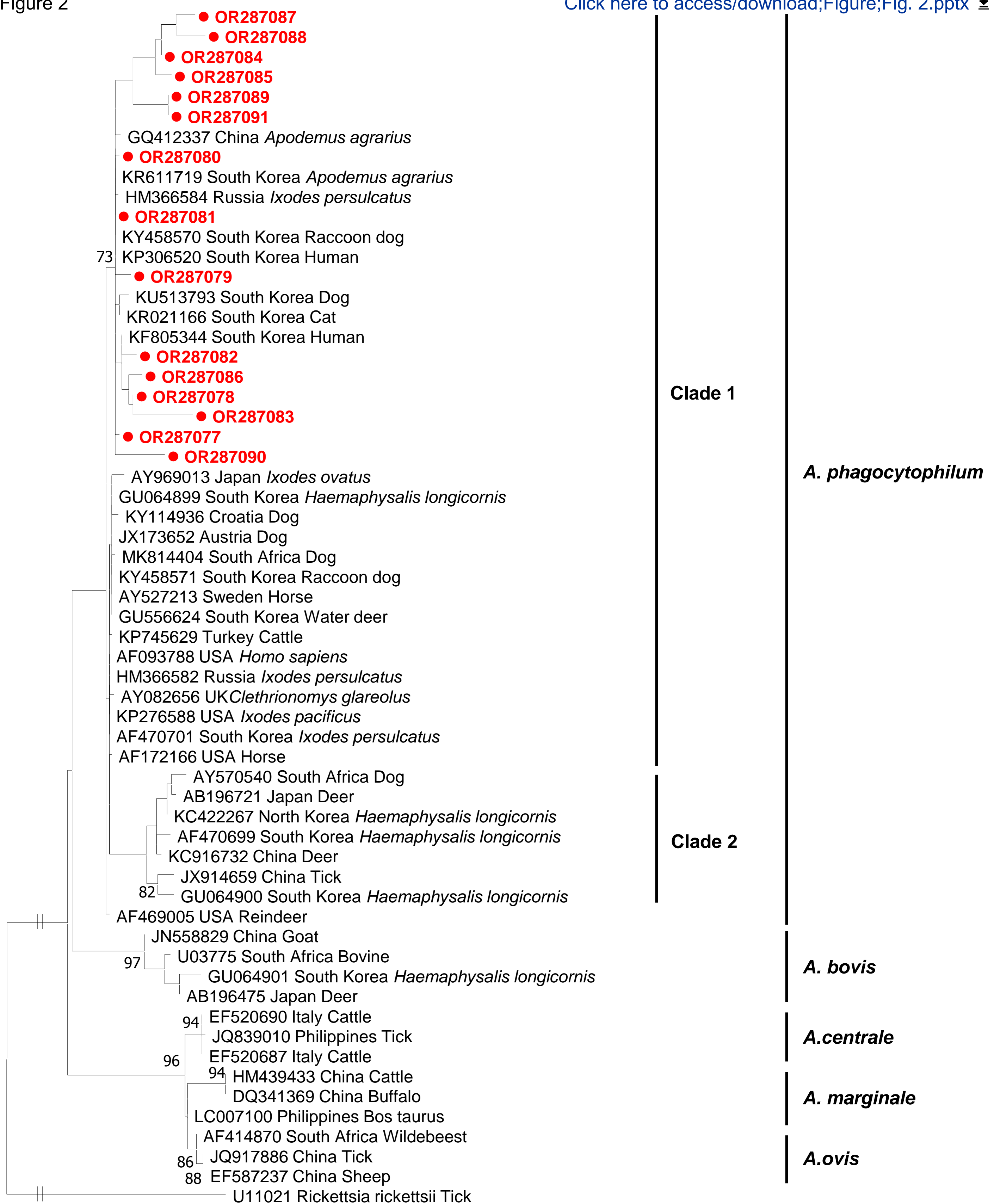

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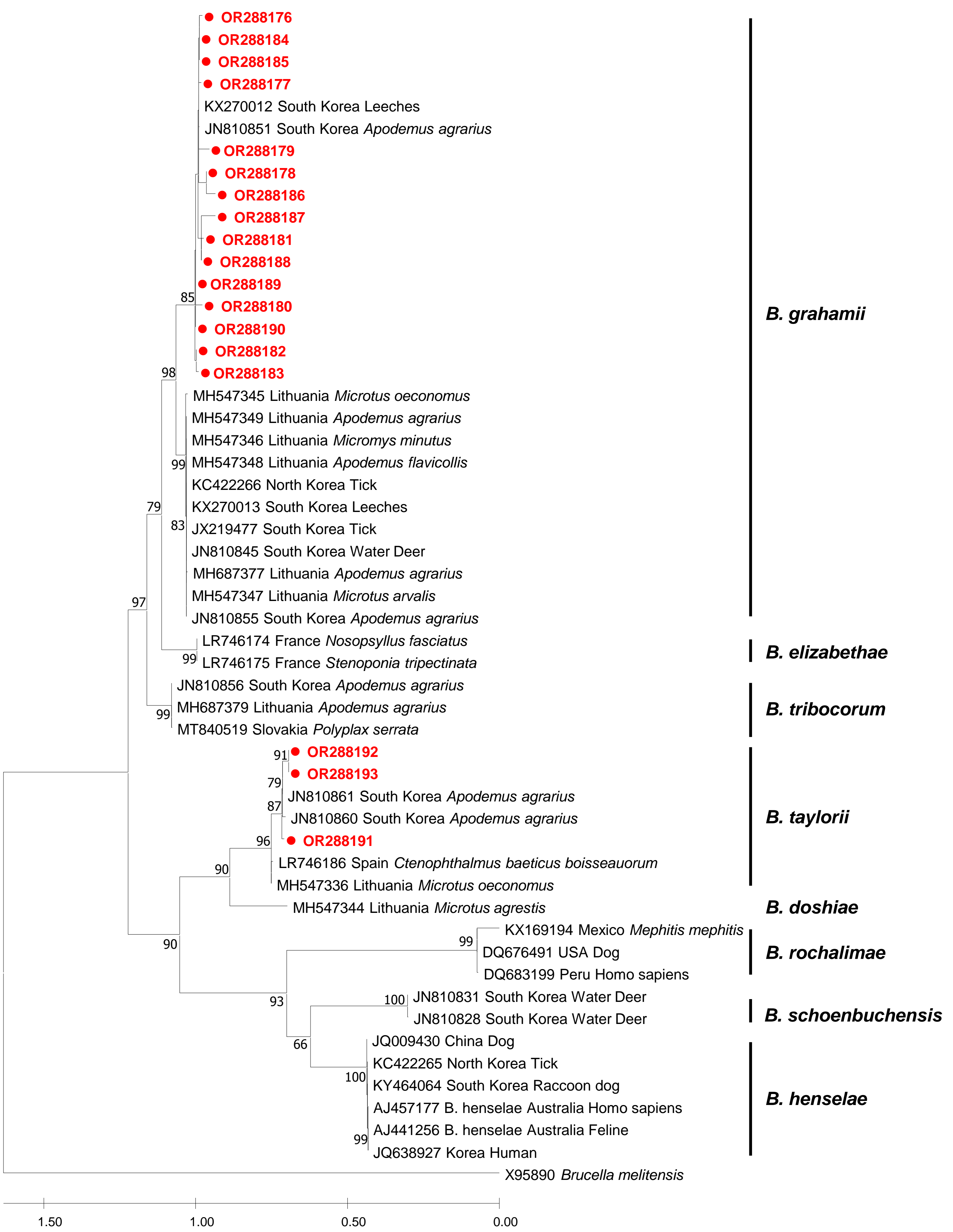

Figure 4

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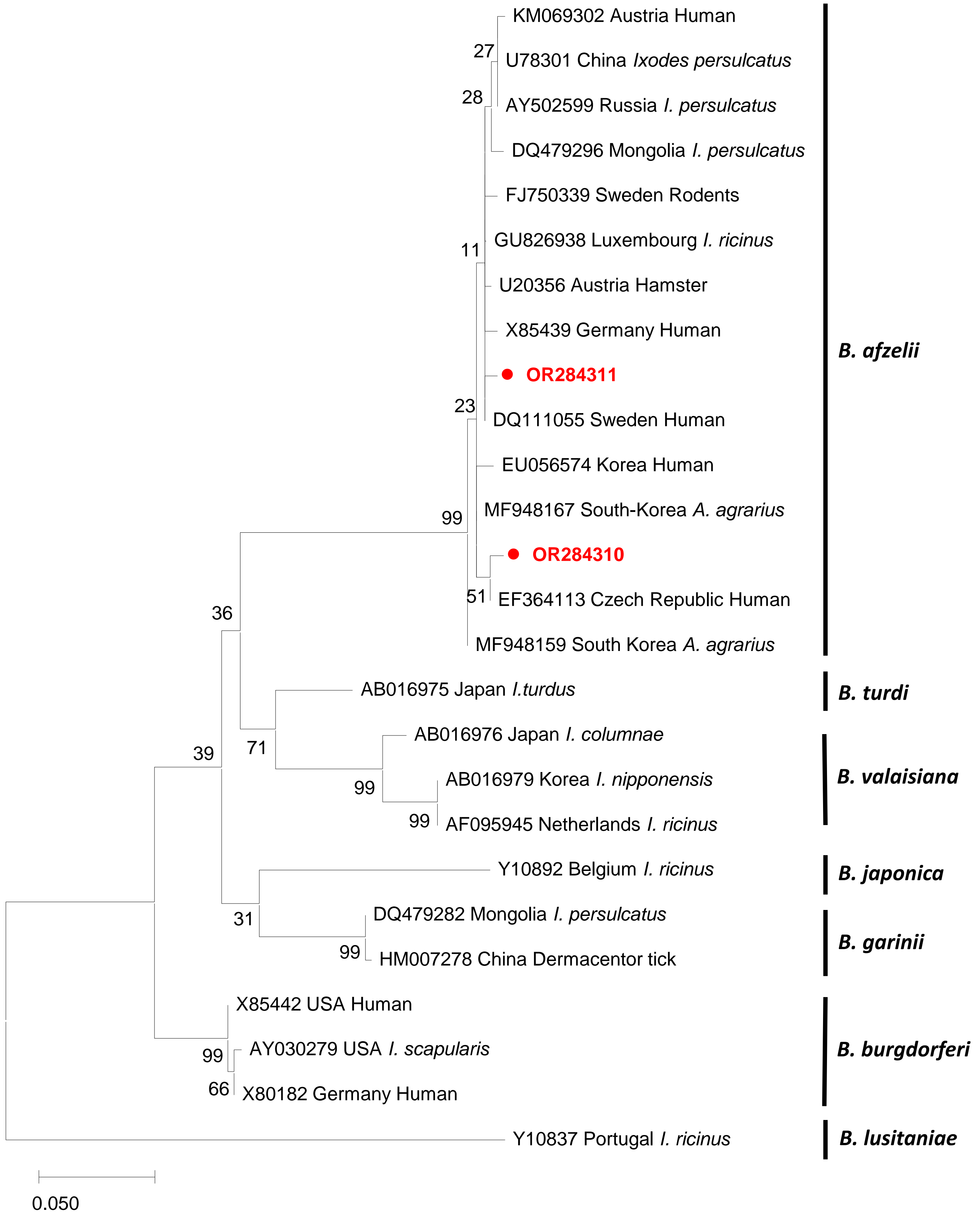

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Figure 6

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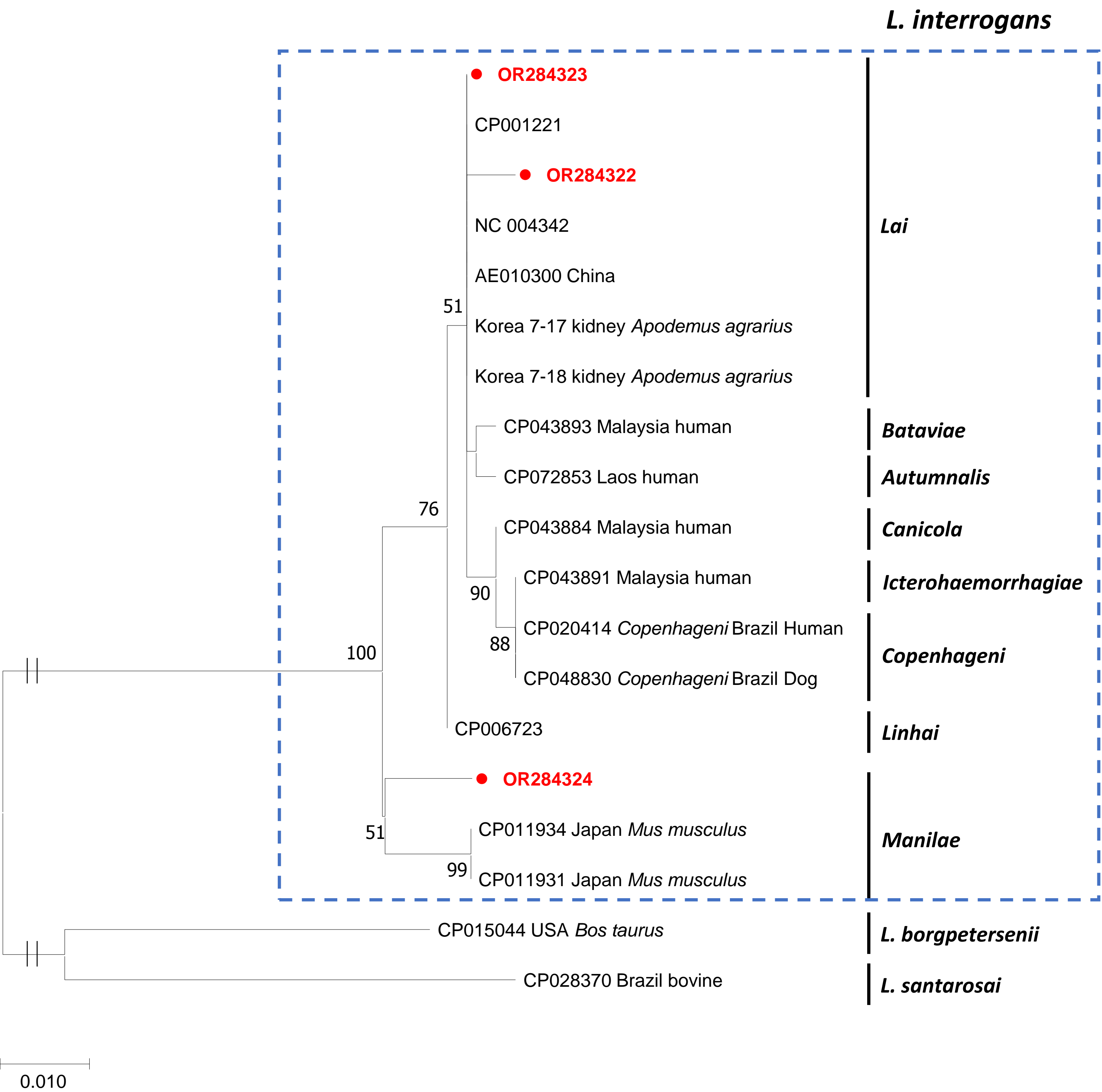

Figure 7

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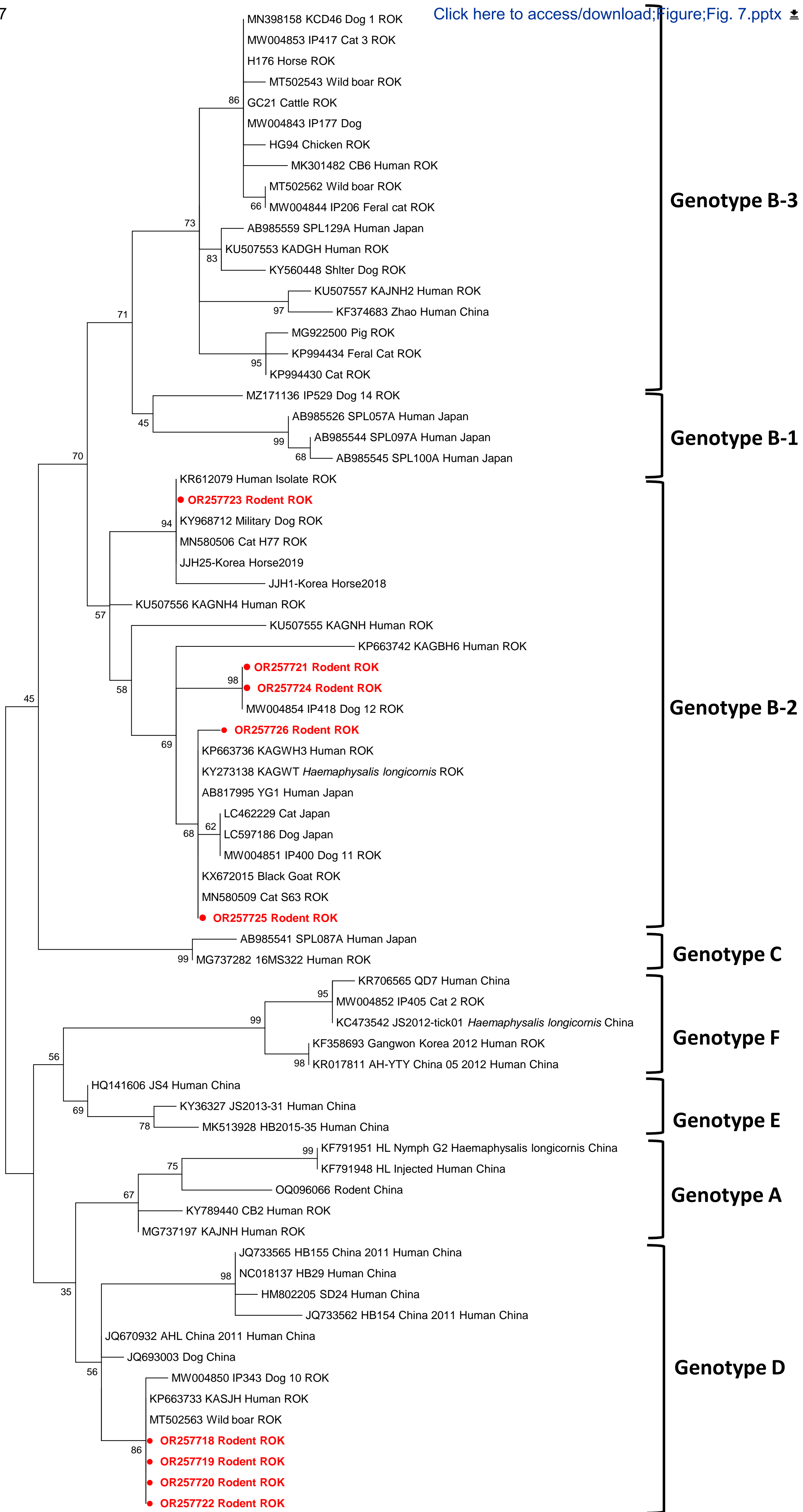

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Table 1. Primer information used for PCR analysis.

Pathogens	Target genes	Sequences (5′–3′)	Sizes (bp)	Annealing temp./Time	References
Anaplasma phagocytophilum	16S rRNA	TCCTGGCTCAGAACGAACGCTGGCGGC	1433	50°C/30 s	Han et al., 2019
		AGTCACTGACCCAACCTTAAATGGCTG			
		GTCGAACGGATTATTTTTATAGCTTGC	926	56°C/30 s	
		CCCTTCCGTTAAGAAGGATCTAATCTCC			
Bartonella spp.	*ITS*	TTCAGATGATGATCCCAAGC	639	55°C/30 s	Ko S 2016
		AACATGTCTGAATATATCTTC			
		CCGGAGGGCTTGTAGCTCAG	499	55°C/30 s	
		CACAATTTCAATAGAAC			
Borrelia spp.	*ospA*	GGGAATAGGTCTAATATTAGCC	665	42°C/60 s	Priem S 1998
		CACTAATTGTTAAAGTGGAAGT			
		GCAAAATGTTAGCAGCCTTGAT	392	56°C/60 s	
		CTGTGTATTCAAGTCTGGC			
Coxiella burnetii	*IS1111*	TATGTATCCACCGTAGCCAGTC	687	54°C/30 s	Parisi A 2006
		CCCAACAACAACCTCCTTATTC			
		GAGCGAACCATTGGTATCG	203	54°C/30 s	
		CTTTAACAGCGCTTGAACGT			
Leptospira interrogans	*rpoB*	GTTCCAACATGCAACGYCAR	1649	52°C/60 s	Bang MS 2019
		GTTGAAGGATTCRGGRATAC			
		TYATGCCKTGGGAAGGWTAC	1023	56°C/30 s	
		GCATRTCRTCKGACTTGATG			
SFTSV	S	CATCATTGTCTTTGCCCTGA	461	52°C/40 s	Yoshikawa T et al 2014
		AGAAGACAGAGTTCACAGCA			
		AAYAAGATCGTCAAGGCATCA	346	55°C/40 s	Oh SS 2015
		TAGTCTTGGTGAAGGCAT CTT			

*SFTS: severe fever with thrombocytopenia syndrome virus

Table 2. Number of rodents captured by regions.

Province/Species	*Apodemus agrarius*	*Rattus norvegicus*	Unknown	Total
Gyeonggi	12	–	2	14
Gangwon	18	–	5	23
Chungbuk	19	–	3	22
Chungnam /Daejeon	4	–	–	4
Jeonbuk	13	–	–	13
Jeonnam	4	–	–	4
Gyeongbuk	76	4	9	89
Gyeongnam	5	1	–	6
Total	151	5	19	175

"–": none of rodents captured

Table 3. Number of positive samples in which pathogens were identified from captured rodents.

Variables	*A. phagocytophilum*	*Bartonella* spp.	*Borrelia* spp.	*C. burnetii*	*L. interrogans*	SFTSV
Species						
Apodemus agrarius (*n* = 151)	21	72	5	22	23	9
Rattus norvegicus (*n* = 5)	–	1	–	3	1	–
Total (*n* = 156)	21	73	5	25	24	9
Province						
Gyeonggi (*n* = 12)	1	5	–	–	2	2
Gangwon (*n* = 18	4	12	1	5	6	1
Chungbuk (*n* = 19)	3	10	1	2	6	2
Chungnam/Daejeon (*n* = 4)	1	–	–	–	–	–
Jeonbuk (*n* = 13)	3	8	–	3	–	–
Jeonnam (*n* = 4)	1	–	–	–	–	–
Gyeongbuk (*n* = 80)	7	32	2	14	6	4
Gyeongnam (*n* = 6)	1	6	1	1	4	–
Total (*n* = 156)	21 (13.5%)	73 (46.8%)	5 (3.2%)	25 (16.0%)	24 (15.4%)	9 (5.8%)

Table 4. Co-infections of two or three pathogens detected from captured rodents.

Pathogens	No. of positive samples
A. phagocytophilum + *Bartonella* spp.	7
A. phagocytophilum + *Borrelia* spp.	1
A. phagocytophilum + *C. burnetii*	1
Bartonella spp. + *Borrelia* spp.	2
Bartonella spp. + *C. burnetii*	7
Bartonella spp. + *L. interrogans*	10
Bartonella spp. + SFTSV	3
C. burnetii + *L. interrogans*	2
A. phagocytophilum + *Bartonella* spp.+ *C. burnetii*	1
A. phagocytophilum + *Bartonella* spp.+ *L. interrogans*	3
A. phagocytophilum + *Bartonella* spp.+ SFTSV	2
A. phagocytophilum + *C. burnetii* + *L. interrogans*	1
Bartonella spp. + *Borrelia* spp. + *C. burnetii*	1
Bartonella spp. + *C. burnetii* + *L. interrogans*	1
Bartonella spp. + *L. interrogans* + SFTSV	2