

Theileria, *Hepatozoon* and *Taenia* infection in great gerbils (*Rhombomys opimus*) in northwestern China

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ABSTRACT

The great gerbil (*Rhombomys opimus*), widely distributed in Asia, is a natural reservoir for *Yersinia pestis*, *Leishmania donovani* and some species of helminths. In this study, 188 great gerbils were sampled in Alataw City and Manas County, northwestern China, and tested for the presence of *Theileria*, *Hepatozoon* and *Taenia* species by molecular methods. *Theileria* sp., named as “*Candidatus Theileria xinjiangensis*”, was detected in heart, liver, spleen, lung, and kidney of 6.9% rodents. Six genotypes of “*Taenia* sp. *Rhombomys opimus*”, which were close to *Taenia laticollis* (87.3–94.0% identities), were detected in cyst liquid of 5.3% rodents. “*Hepatozoon ayorgbor*-like” haemogregarines was detected in spleens of 1.6% rodents. To our best knowledge, *Candidatus Theileria xinjiangensis*, *Hepatozoon ayorgbor*-like and genotypes of “*Taenia* sp. *Rhombomys opimus*” were found for the first time in the great gerbil. These results extend our knowledge on the diversity and pathogenesis of *Theileria*, *Hepatozoon* and *Taenia* species.

1. Introduction

The great gerbil (*Rhombomys opimus*) is widely distributed in Asian countries, such as Afghanistan, China, Iran, Kazakhstan, Kyrgyzstan, Mongolia, Pakistan, Tajikistan, Turkmenistan and Uzbekistan. To date, it is considered as a natural reservoir for *Yersinia pestis*, *Taenia endotheracicus*, *Hymenolepis nana*, *Skrjabinotaenia lobate*, *Trichuris rhombomidis*, *Trichuris muris*, *Syphacia muris* and *Dipetalonema viteae* (Kamranrashani et al., 2013). However, little information is available on the susceptibility of great gerbils to other *Taenia* species and members of the genera *Hepatozoon* and *Theileria*.

Theileriosis is a hemolytic disease caused by protozoan parasites of the genus *Theileria*, belonging to Piroplasmida together with *Babesia* and *Cytauxzoon* (Mehlhorn and Schein, 1985; Kheirandish et al., 2020). Piroplasms may parasitize in the white and red blood cells of red fox, European badger, and wild cat, and can be transmitted by ticks to the domestic animals (Levine, 1988; Barandika et al., 2016). Among the others, members of the genus *Theileria* may infect white-tailed deer (*Odocoileus virginianus*), cheetahs (*Acinonyx jubatus*), wild sika deer (*Cervus nippon yesoensis*), red deer (*Cervus elaphus*), wild Chinese water

deer (*Hydropotes inermis argyropus*), wild boar (*Sus scrofa*), red fox (*Vulpes vulpes*), zebra (*Equus quagga*), and wild donkey (*Equus africanus*) (Tirosh-Levy et al., 2020). Symptoms of affected wildlife include icterus, splenomegaly and lymphadenomegaly (Clift et al., 2020).

Hepatozoonosis, caused by species of the genus *Hepatozoon* (Apicomplexa: Adeleorina), has been described in domestic and wild mammals, reptiles, amphibians, and birds (Maia et al., 2014; Baneth et al., 2003; Smith 1996). Considering rodents, *Hepatozoon* sp. in bank voles (Laakkonen et al., 2001), African jerboas (*Jaculus jaculus*), greater Egyptian jerboas (*Jaculus orientalis*) (Maia et al., 2014), cotton rats (*Sigmodon hispidus*), white-footed mice (*Peromyscus leucopus*) (Johnson et al., 2007) and wild mouse (*Calomys callosus*) (Wolf et al., 2016) were reported. Literature data also suggest that wild rodents (after acquiring the infection following ingestion of vectors) may contribute to the transmission of *Hepatozoon* spp. to predators (Moustafa et al., 2017).

Taeniids (Cestoda: Cyclophyllidea) are tapeworm parasites of terrestrial mammals. Adult taeniids occur in the small intestine of typically carnivorous definitive hosts, and their cystic larvae develop in tissues or body cavities of herbivorous or omnivorous intermediate hosts (Abuladze and Sludskaia 1964). Wild mustelids and canids are definitive

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Table 1
The detection of *Theileria*, *Hepatozoon* and *Taenia* in organs of 188 great gerbils.

Location, coordinates	NO.	Organ	<i>Theileria</i> sp.	<i>Hepatozoon ayorgbor</i> -like	<i>Taenia</i> sp. <i>Rhombomys opimus</i>
Alataw City (45°19'N, 82°56'E)	106	Heart	5 (4.7%)	–	–
		Liver	5 (4.7%)	–	–
		Spleen	5 (4.7%)	3 (2.8%)	–
		Lung	5 (4.7%)	–	4 (3.8%)
		Kidney	5 (4.7%)	–	–
Manas County (43°28'N, 85°34'E)	82	Heart	8 (9.8%)	–	–
		Liver	8 (9.8%)	–	^a 1 (1.1%)
		Spleen	8 (9.8%)	–	–
		Lung	8 (9.8%)	–	6 (7.3%)
		Kidney	8 (9.8%)	–	–
Total	188		13 (6.9%)	3 (1.6%)	10 (5.3%)

^a Found in a cyst-in-thoracic-cavity individual.

hosts of *Taenia* while rodents act as natural intermediate hosts (Deplazes et al., 2019). Within rodents, larval cestodes can cause serious pathological changes in viscera and tissues, and even death (Zhao et al., 2014), as exemplified by *Taenia hydatigena* in bull moose (*Alces alces*), *Taenia taeniaeformis* in house rat (*Rattus rattus*), and *Taenia mustelae* in plateau zokor (*Eospalax baileyi*).

Xinjiang Uygur Autonomous Region (XUAR), northwestern China, is adjacent to eight countries with 5600-km borderline (Wei et al., 2015). Previously, some emerging pathogens, such as Tacheng tick virus 1,

Tacheng tick virus 2, *Hantavirus* and *Babesia occultans*, have been discovered in this region (Guo et al., 2016; Song et al., 2018; Liu et al., 2020). Here, we conducted an investigation on *Taenia*, *Hepatozoon* and *Theileria* in the great gerbils in XUAR (see Table 1).

2. Materials and methods

2.1. Study area, sampling, blood collection and dissection

During 2019–2020, a total of 188 great gerbils were captured at 11 sampling sites in Alataw and Manas located in Gurbantungut Desert, XUAR (Fig. 1), where the predominant vegetation included clostridium (*Haloxylon ammodendron*) and saltcedar (*Tamarix* sp.) (Liu et al., 2012) while the climate was temperate continental climate with cool, dry winters, and hot, dry summers (Shu et al., 2020).

The great gerbils were captured in live traps (30 cm × 15 cm × 15 cm wire mesh), which were placed near the entrances of occupied burrows, baited with walnut, tomato or cucumber. Each survey site included 150 traps that were checked twice a day. Each trap was removed before nightfall and replaced on the survey site the following day (Kamranra-shani et al., 2013). All wild rodents were morphologically identified by an experienced zoologist. The rodents in Manas County were directly transported to our laboratory while the animals in Alataw City were transported to the Vector-borne Laboratory at Alataw Customs. Each animal was weighed, Zoletil 50 (Virbac, Paris, France) was used in anesthesia by intramuscular injection, and blood-taken from heart. The

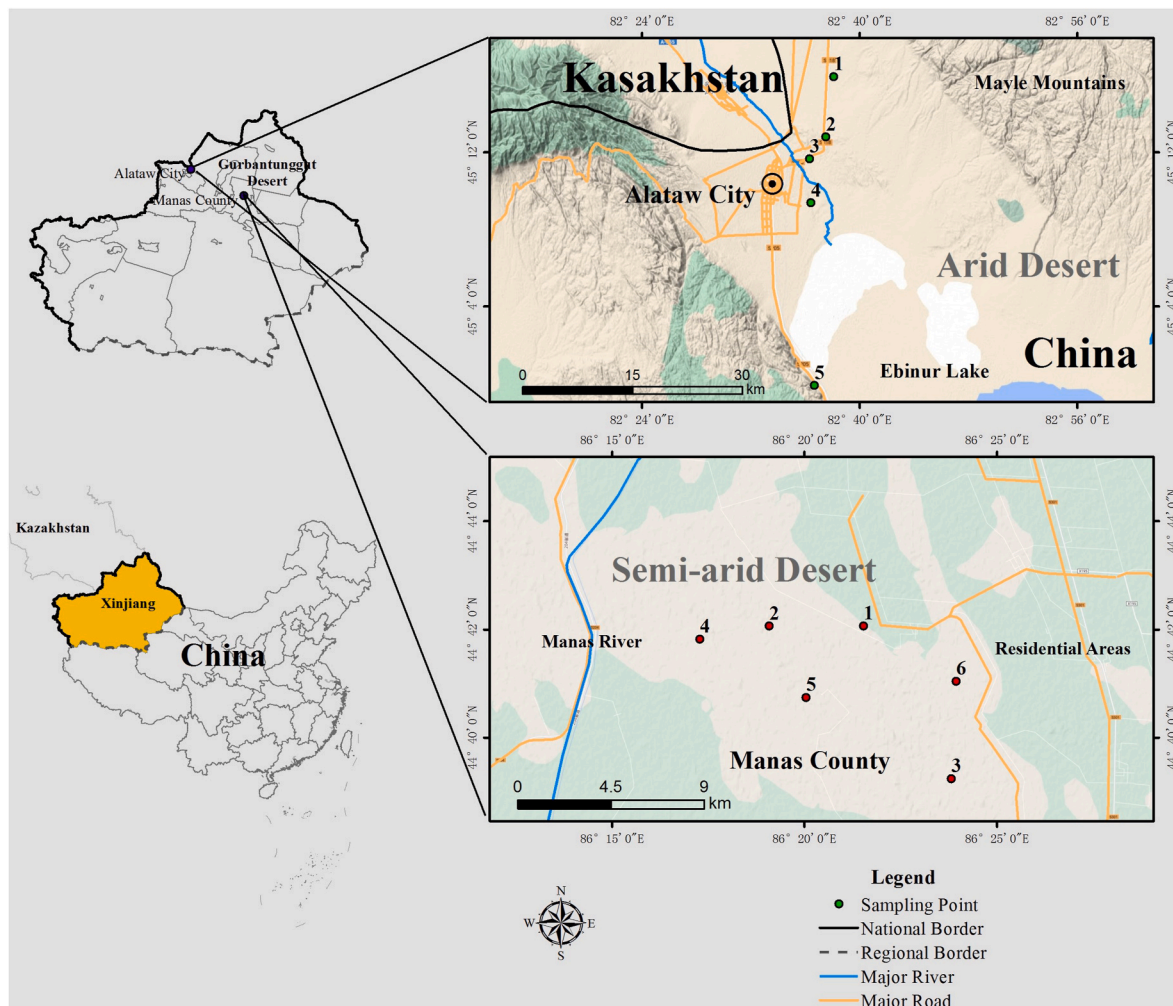


Fig. 1. Map showing the sampling sites in Alataw City (China-Kazakhstan border), Manas County (center of Gurbantungut Desert).

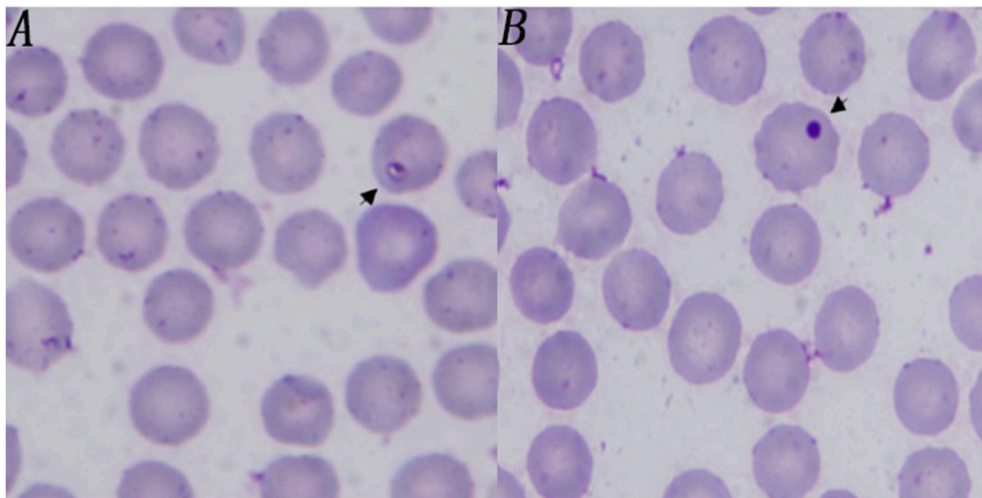


Fig. 2. A-C Piroplasmic forms of *Candidatus Theileria xinjiangensis* in a microscopic field by Giemsa staining method [A single annular forms; B single circular form]. C The macroscopic appearance of splenomegaly in piroplasm-positive the great gerbil.

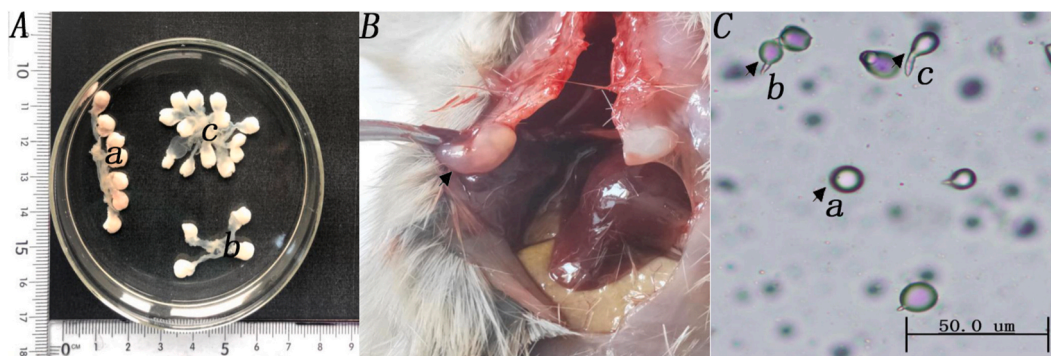


Fig. 3. A-C A Three kinds of cyst in thoracic cavity of great gerbils. The a-type cyst, belonging to *Taenia* sp. *Rhombomys opimus* A, contained 7 protoscolices. The b-type cyst, belonging to *Taenia* sp. *Rhombomys opimus* B, contained 13 protoscolices. The c-type cyst, belonging to *Taenia* sp. *Rhombomys opimus* C, contained 4 protoscolices. B A cyst attaching to the liver of a great gerbil in Manas County, XUAR. C Cysticercoids in cyst from the great gerbil in microscopic field by malachite green stain-method. . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

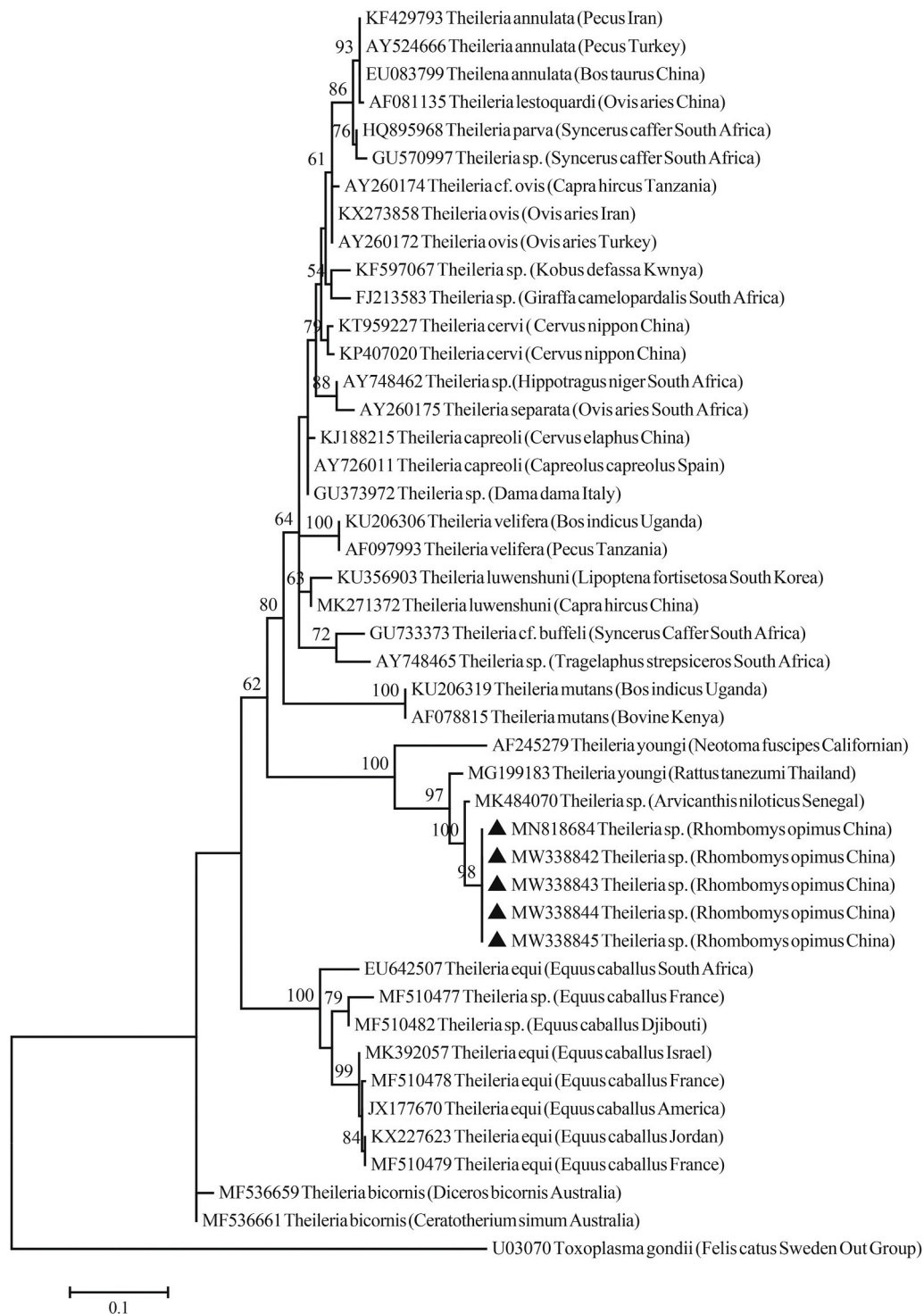


Fig. 4. Phylogenetic analysis of *Candidatus Theileria xinjiangensis* based on 18S rRNA gene with MEGA7.0. The tree was constructed with the Maximum Likelihood method (ML; bootstrap replicates: 1000). Branch lengths correlate to the number of substitutions inferred according to the scale shown. Sequences of *Candidatus Theileria xinjiangensis* obtained in this study are indicated by triangles (▲).

heart, liver, spleen, lung and kidney of 188 wildlife carcasses were weighed, examined and stored at -80°C .

2.2. Microscopic examination and quantitative inoculation

The weight ratio of each organ/corpse was recorded. Thin blood films were stained with Giemsa (Soulsby, 1982) and cysticercoids with malachite green stain-method. Briefly, the fixed smears were stained

with 5% Giemsa diluted in phosphate buffer (pH 7.2). Microscopic examination was performed at $1000\times$ magnification (oil immersion) in 6 samples (Aziz and Al-Barwary, 2019).

To study the transmission of the cyst liquid from naturally infected great gerbils to laboratory mouse, four C57BL/6 and four Balb/c mice were intra-peritoneally injected with 0.2 mL fresh cyst liquid (~1000 cysticercoids), respectively. On the 90th day and 350th day after injection, two C57BL/6 and two Balb/c mice were dissected. The

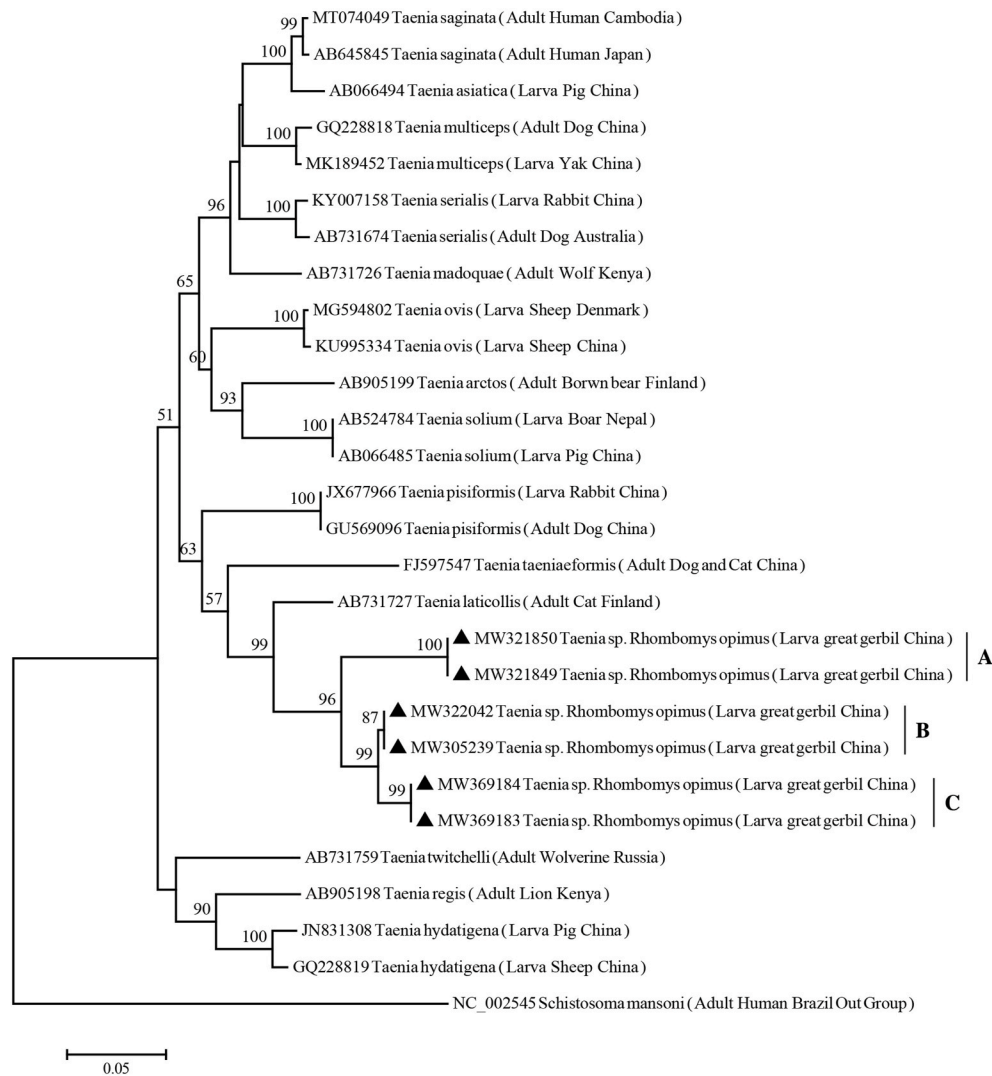


Fig. 5. Phylogenetic analysis of “*Taenia sp. Rhombomys opimus*” based on *cox1* gene with MEGA7.0. The tree was constructed with the Neighbor-Joining method (NJ; bootstrap replicates: 1000). Branch lengths correlate to the number of substitutions inferred according to the scale shown. Sequences of “*Taenia sp. Rhombomys opimus*” obtained in this study are indicated by triangles (▲).

morphological observation and molecular identification of cyst were carried out. All procedures performed in this study involving animals were in accordance with the ethical standards of Animal Ethics Committee of Shihezi University (Approval No. A2018-143-01).

2.3. DNA extraction and molecular identification

Each sample (~0.2 g) of the heart, liver, spleen, lung and kidney was used to extract genomic DNA using the TIANGEN Genomic DNA Kit (TIANGEN, Beijing, China), following the manufacturer’s instructions. The DNA quantity and purity were assessed on a NanoDrop 2000 spectrophotometer analyzer (Thermo Fisher Scientific, USA). The concentration of DNA was at least 50 ng/μL for further detecting pathogens. A total of 940 organ samples were subjected to specific polymerase chain reaction (PCR) for Piroplasmida, *Hepatozoon* and *Taenia*. Two different (438-bp-long and 487-bp-long) fragments of the 18S ribosomal RNA (18S *rRNA*) gene of Piroplasmida were targeted with the primers BJ1/BN2 (Farkas et al., 2015) and PIRO-A/B (Sun et al., 2007), respectively. A longer, 1100 bp fragment of the 18S *rRNA* was used to detect *Hepatozoon* species. The genomic DNA was also extracted from cyst liquid, and two genetic markers (including a 450-bp-long fragment of the cytochrome *c* oxidase subunit I (*cox1*) gene (Liu et al., 2011) were used to

identify members of the genus *Taenia*. The primers and PCR cycling conditions in this study are shown in Appendix Table 1. Each PCR assay included a negative control and a positive control (Yan et al., 2018; Song et al., 2018; Tian et al., 2011). The amplification products were cloned and sequenced.

Sequences were manually edited, aligned with software BioEdit, and compared to the reference GenBank sequences (<http://www.ncbi.nlm.nih.gov/BLAST/>). Phylogenetic trees were constructed using the Maximum Likelihood or Neighbor Joining method with the MEGA 7.0 software (Kumar et al., 2016).

3. Results

Among the 188 the great gerbil samples analyzed, the hearts, livers, spleens, lungs and kidneys of 13 animals (6.9%, 13/188) were positive for both fragments of Piroplasmida 18S *rRNA*. Blood smear of PCR-positive animals showed an intraerythrocytic ring form piroplasm that measured about $2.98 \times 2.24 \mu\text{m}$ (Fig. 2 A and B). Splenomegaly was observed in the piroplasm-positive animals (Fig. 2 C). The index of spleen/corpus ratio was significantly different ($F_{st} = 20.015$, $P < 0.05$) between piroplasm-positive and piroplasm-negative animals. BLASTn analysis showed that i) DNA sequences obtained in this study were 100%

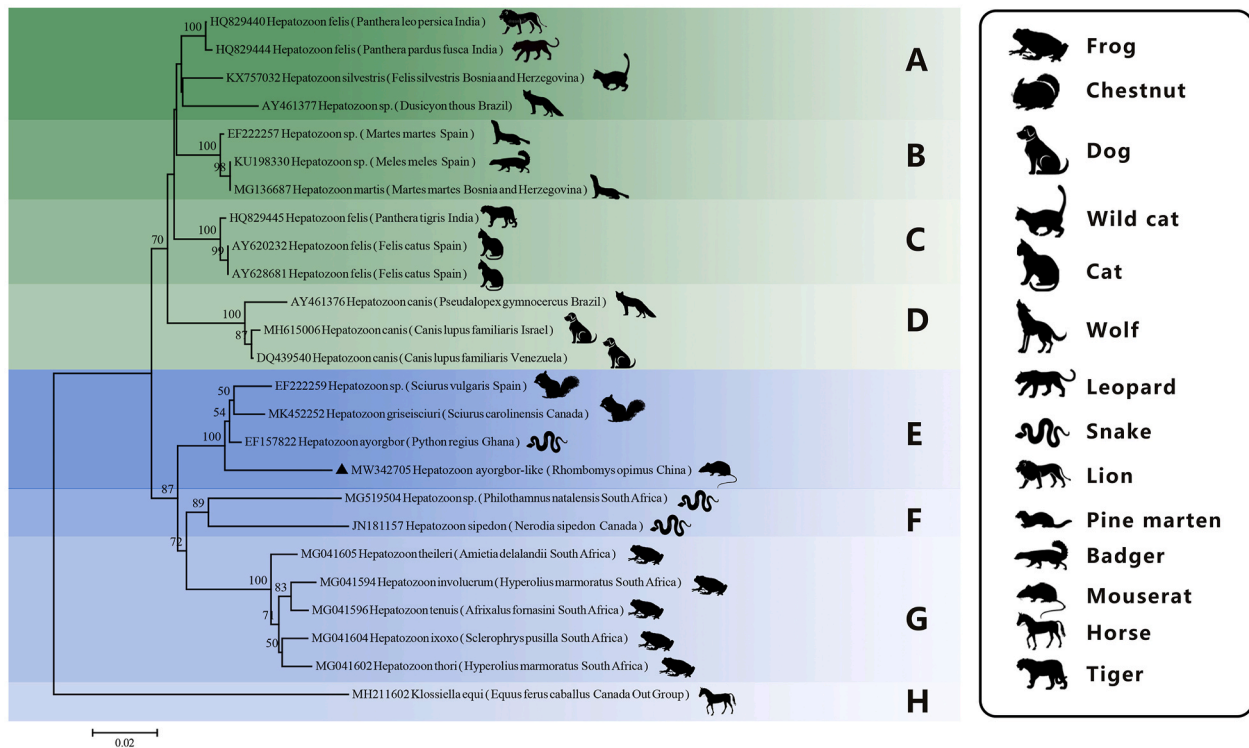


Fig. 6. Phylogenetic analysis of *Hepatozoon ayorgbor*-like based on 18S rRNA gene with MEGA7.0. The tree was constructed with the Neighbor-Joining method (NJ; bootstrap replicates: 1000). Branch lengths correlate to the number of substitutions inferred according to the scale shown. Sequence of *Hepatozoon ayorgbor*-like obtained in this study is indicated by triangles (▲).

identical to each other; and ii) *Theileria* sp., provisionally named here as “Candidatus *Theileria xinjiangensis*”, was closest related to Candidatus *Theileria senegalensis* from Nile rat (*Arvicanthis niloticus*) in Senegal (MK484070), with 97.4% sequence identity (Fig. 4).

Hepatozoon sp. were molecularly detected in three spleens (1.6%, 3/188). There was no obvious difference in the results of clinical pathological observation and spleen index analysis between PCR-positive and PCR-negative animals. BLAST and phylogenetic analysis showed that i) *Hepatozoon* species in this study, here designated as *Hepatozoon ayorgbor*-like, shared 98.2% (1020/1039) identity to *Hepatozoon ayorgbor* (EF157822) detected in ball pythons (*Python regius shaw*) in Ghana, and ii) *Hepatozoon ayorgbor*-like from great gerbils was an ancestral species compared to *Hepatozoon* sp. (FJ719818 [Chile]), *Hepatozoon ayorgbor* (EF157822 [Ghana]), *Hepatozoon griseisciuri* (MK452252 [Canada]) and *Hepatozoon* sp. (EF222259 [Spain]) (Fig. 6).

During the necropsy of great gerbils, large white and web-shaped cyst was found in the thoracic cavity of ten rodents (5.3%, 10/188), which showed three types of cyst morphology according to the numbers of protoscolices (Fig. 3A), causing the lung parenchyma to shrink, and leading to darkness and stiffness in texture. In addition, an oval shape cyst with the diameter of 0.8–1.1 cm, attaching to the liver, was also found in an individual with cyst in its thoracic cavity (Fig. 3B). Many cysticercoids with 5–8 μm in diameter were found in cysts both from thoracic cavity and liver by malachite green stain-method (Fig. 3C). There was no apparent morphologic difference between the cysticercoids of *Taenia* sp. *Rhombomys opimus* A, B and C. BLASTn analysis indicated that i) the sequences for cysticercoid *cox1* genes from thoracic cavity were identical to that from the liver of the same individual; ii) some novel *Taenia* genotypes, here named as “*Taenia* sp. *Rhombomys opimus*” including *Taenia* sp. *Rhombomys opimus* A, B and C, showed remarkable genetic diversity (90.9%–97.6%) based on *cox1*, as six significantly different sequences were found; and iii) “*Taenia* sp. *Rhombomys opimus*” was closest related to *Taenia laticollis* detected in Finland (AB731727) with 87.3–94.0% identities (Fig. 5). No cyst was

found in any organ or tissue of either C57BL/6 or Balb/c mice injected with cyst liquid from thoracic cavity after 90 days and 350 days.

The sequences from our study were deposited into GenBank (*Hepatozoon* 18S rRNA: MW342705; *Theileria* 18S rRNA: MW338842-MW338845 and MN818684; *Taenia cox1*: MW369183-MW369184, MW321849-MW321850, MW322042 and MW305239).

4. Discussion

Host specificity of *Theileria*, such as *Theileria capreoli* in cervids, *Theileria* sp. (sable) and *Theileria* sp. (sable-like) in African Bovidae, as well as *Theileria taurotragi* in members of Bovidae, was reported (Pienaar et al., 2018). In this study, Candidatus *Theileria xinjiangensis* caused splenomegaly in great gerbils with 6.9% (13/188) prevalence rate. Phylogenetic analysis showed that Candidatus *Theileria xinjiangensis* in the great gerbil, Candidatus *Theileria senegalensis* from Nile rat, *Theileria youngi* in dust-footed woodrat and Asian house rat belong to the same clade. These findings suggest that *Theileria* species in rodents have high rate of sequence similarity according to their hosts.

To date, nine *Hepatozoon* species, including *H. akodoni*, *H. ayorgbor*, *H. americanum*, *H. milleri*, *H. erhardovae*, *H. muri*, *H. normanin*, *H. dolichomorphon*, and *H. balfouri*, were detected in rodents (Killck-Kendrick 1984; De Castro Demoner et al., 2019; Maia et al., 2014; Rigó et al., 2016; Sloboda et al., 2008). In addition, some unidentified *Hepatozoon* species have been also reported in some rodent species including field mouse (*Apodemus flavicollis*), plains woodrat (*Neotoma micropus*), African giant rat (*Cricetomys gambianus Waterhouse*), house mouse (*Mus musculus*), black rat (*Rattus rattus*), flying squirrel (*Idiurus macrotis*) and bushveld gerbil (*Gerbilliscus leucogaster*) (James Harris et al., 2017; Charles et al., 2012; Kamani et al., 2018; Killck-Kendrick, 2010; Moustafa et al., 2017). In the present study, *Hepatozoon ayorgbor*-like sequence was detected in three spleen samples of great gerbils in northwestern China, which shared 98.2% (1020/1039) identity to *Hepatozoon ayorgbor* in blood and liver of a ball python (*Python regius*)

(Sloboda et al., 2007). Interestingly, ball python was also infected after it was fed with tissues of mice experimentally infected with *H. ayorgbor* (Sloboda et al., 2008). This finding suggests that the great gerbil and the mouse have an important role in the life cycle of *H. ayorgbor*-related genotypes. In addition, phylogenetic analysis indicated that the *Hepatozoon ayorgbor*-like sequence form great gerbils was clustered with *Hepatozoon* sp. from red squirrel (*Sciurus vulgaris*) (EF222259), *Hepatozoon griseisciuri* from grey squirrel (*Sciurus carolinensis*) (MK452252), *Hepatozoon ayorgbor* from ball pythons (*Python regius*) (EF157822) and *Hepatozoon* sp. from Olive Grass Mouse (*Abrothrix olivaceus*) (FJ719818). This result suggests that host specificity is low with respect to intermediate and definitive hosts, consistently with the report by Sloboda et al. (2007).

Both inter- and intraspecific genetic diversities of *Taenia* species are known to exist in the same rodent species. For example, *Taenia martis*, *Taenia mustelae*, *Taenia polyacantha* were reported in bank voles (*Myodes glareolus*) (Lavikainen et al., 2008). At the same time, intraspecific genetic diversity of *Taenia* species, such as *Taenia pisiformis* (98.4%) and *Taenia hydatigena* (99.5%–99.7%), was also reported (Sarvi et al., 2020; Yang et al., 2013). Here “*Taenia* sp. *Rhombomys opimus*” A, B and C were found in great gerbils, which only shared 90.9%–97.6% identities based on *cox1* analysis, and also showed three distinctive morphological characters based on the numbers of protoscolices. This finding suggests that “*Taenia* sp. *Rhombomys opimus*” has both inter- and intraspecific genetic diversity. The field investigation revealed that the cyst of “*Taenia* sp. *Rhombomys opimus*” is mostly present in the thoracic cavity. This finding suggests that “*Taenia* sp. *Rhombomys opimus*” has anatomical predilection site when infecting great gerbils, which is different from *Taenia endothoracicus* in the great gerbil (*Rhombomys opimus*) and Lybian jird (*Meriones libycus*) (Kamranrashani et al., 2013; Mowlavi et al., 2004). Previously, *Taenia taeniaeformis* from house rat (*Rattus norvegicus*) was highly infective to SD, HA or AS rats but not infective to CBA or ICR mice, and *Taenia crassiceps* showed differences in susceptibility for the rat (Anderson and Griffin 1979; Azuma et al., 1995). Here a wild-type *Taenia* species, belonging to *Taenia* sp. *Rhombomys opimus* A, could naturally infect great gerbils, but didn't infect C57BL/6 or Balb/c mice after being intraperitoneally inoculated with ~1000 cysticercoids. This survey findings demonstrate the transmission between genera of rats and mice has a biological barrier for “*Taenia* sp. *Rhombomys opimus*” cysticercoids.

Great gerbils located in the unique geographical environment between China and Kazakhstan serve as reservoirs for *Hepatozoon ayorgbor*-like genotype, “*Taenia* sp. *Rhombomys opimus*”, and Candidatus *Theileria xinjiangensis*. In the future, definitive hosts of the *Hepatozoon ayorgbor*-like genotype and “*Taenia* sp. *Rhombomys opimus*” should be identified among carnivores (eg. red foxes and wolves), and snakes including pythons. Previously, *Hyalomma asiaticum* and *Dermacentor niveus* were reported from great gerbils (Ye et al., 2006). Here Candidatus *Theileria xinjiangensis* was found in organs of great gerbils. Therefore, it will be important to extend the scope of these studies to larger sample size of great gerbils and their infesting ticks, in order to uncover their role in the life cycle of theileriae.

5. Conclusion

This study provided new data regarding Candidatus *Theileria xinjiangensis*, *Hepatozoon ayorgbor*-like genotype and “*Taenia* sp. *Rhombomys opimus*” which appear to be mostly associated with great gerbils. These results highlight the importance to continue research on vector-borne and zoonotic pathogens in wildlife in the region of Central Asia.

Declaration of competing interest

All authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijppaw.2021.04.002>.

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