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Research article

Genetic diversity of *Rhombomys opimus* and *Meriones meridianus* with potential divergence of plague resistance in the Junggar Basin plague focus based on RT1-Db1*exon1

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ABSTRACT

In the Junggar Basin plague focus, *Rhombomys opimus* and *Meriones meridianus* live together, and their parasitic fleas have a similar community structure. However, *R. opimus* has significantly higher positive rates of *Yersinia pestis* and anti-F1 antibody compared with *M. meridianus*. In this study, *Y. pestis*- and antiF1 antibody-negative *R. opimus* and *M. penicilliger* were collected in Qitai county, Fukang city and Mulei county of the eastern part of the Junggar Basin. The genomic DNA was extracted from their spleen tissues, and RT1-Db1*exon1 was amplified through PCR procedure and then sequenced. Sequence analysis was performed and molecular diversity parameters were calculated and compared. The results showed that there were significant differences in nucleotide composition, amino acid composition, number and distribution of single nucleotide polymorphism (SNP) sites and number of haplotypes between *R. opimus* and *M. penicilliger*. The nucleotide diversity (π) for *R. opimus* was 0.00420 ± 0.00139, the haplotype diversity (h) was 0.833 ± 0.086, and the average number of nucleotide differences (K) was 2.02564. The π for *M. penicilliger* was 0.06569 ± 0.02524, and the h was 1.000 ± 0.045, and the K was 10.4444. The fixation index (F_{ST}) value between *R. opimus* and *M. penicilliger* was 0.9207. Furthermore, the F_{ST} value within *R. opimus* (0.0275) was significantly lower than that within *M. penicilliger* (0.2106), indicating a greater genetic variation of *M. penicilliger* compared with *R. opimus*. In conclusion, the genetic diversity analysis based on RT1-Db1*exon1 showed that *M. penicilliger* had higher gene polymorphism and greater genetic differentiation compared with *R. opimus* in the Junggar Basin plague focus, which might be associated with the low infection rate of *Y. pestis*.

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1. Introduction

The major histocompatibility complex (MHC) genes are highly polymorphic, and the polymorphism is associated with a plenty of diseases through affecting antigen presentation in vertebrates [1,2]. The rat MHC, also known as the RT1 complex, is located on the short arm of chromosome 20 in rats. Studies have found that the rat RT1 complex includes classical MHC Class II genes such as RT1-Db1, RT1-Bb, RT1-DMb and so on [3–5].

The MHC genes are the most studied genetic basis for pathogen resistance, and the difference in MHC diversity may explain asymmetrical infection patterns in closely linked species [6]. Plague, induced by *Yersinia pestis* infection, is a natural infectious disease with rapid onset, rapid transmission and high mortality. The challenge experiment of *Y. pestis* shows that the polymorphism of MHC class II gene β may affect the plague resistance of *Lasiopodomys brandtii* and *Neodon fuscus* in natural populations [7].

The Junggar Basin plague focus is a new type of plague foci discovered in 2005 with great gerbils (*Rhombomys opimus*) as the main host, and *Y. pestis* is also isolated from midday gerbils (*Meriones meridianus*) [8]. In the Junggar Basin, *R. opimus* and species of *M. meridianus* complex live together, and their parasitic fleas have a similar community structure [9]. However, *R. opimus* has significantly higher positive rates of *Y. pestis* and anti-F1 antibody compared with species of *M. meridianus* complex. There may be divergence of plague resistance between them, but the genetic mechanisms are still not investigated. In this study, the genetic diversity of *R. opimus* and *M. penicilliger* is analyzed based on RT1-Db1*exon1 to explore the genetic mechanisms for their potential divergence of plague resistance.

2. Material and methods

2.1. Animals and laboratory detection

Between 2020 and 2023, *R. opimus* and *M. penicilliger* were captured in the eastern part of the Junggar Basin, respectively with arched mousetraps and medium mousetraps. Finally, this study selected 39 adult *R. opimus* including 15 in Qitai county (8 males and 7 females), 12 in Fukang city (6 males and 6 females) and 12 in Mulei county (6 males and 6 females), as well as 30 adult *M. penicilliger* including 12 in Qitai county (6 males and 6 females), 9 in Fukang city (5 males and 4 females) and 9 in Mulei county (5 males and 4 females). As shown in Fig. 1, the three counties are located in the eastern part of the Junggar Basin with a straight-line distance less than 200 km.

Blood, liver and spleen samples were collected from *R. opimus*, and heart, liver and spleen samples were collected form *M. penicilliger*. Indirect hemagglutination assay (IHA) was used to detect the anti-F1 antibody in the serum of *R. opimus* and in the heart infusion of *M. penicilliger*, and Luria-Bertani (LB) plates were used to isolate *Y. pestis* from the liver and spleen of *R. opimus* and *M. penicilliger* at 28 °C. According to laboratory detection results, all animals were *Y. pestis*-negative and antiF1 antibody-negative. The spleens used for extracting DNA were stored in RNA long-term preservation solution at −80 °C ultra-low temperature refrigerator.

2.2. DNA extraction

The spleen tissue of 50 mg was ground with liquid nitrogen, and the genomic DNA was then extracted according to the instructions of Animal Tissues/Cells Genomic DNA Extraction Kit (Solarbio, Beijing Solarbio Science & Technology Co., Ltd.). DNA concentration

Fig. 1. Sampling locations of *R. opimus* and *M. meridianus* in the Junggar Basin, Xinjiang, China.

and purity were detected by Nano-100 Microspectrophotometer (Allsheng, Hangzhou Allsheng Instruments Co., Ltd.), and DNA integrity was evaluated through 0.5 % (w/v) agarose gel electrophoresis. The qualified DNA was stored at −20 °C for later use.

2.3. Sequencing primers

The sequencing primers were designed with Primer3 and synthesized (Xinjiang Ouyi Biotechnology Co., Ltd.) according to the sequence of exon 1 of rat RT1-Db1 gene (Gene ID: 294270). The primer sequences were forward (5′-AGATCTGGGAGCACGAACAT-3′) and reverse (5′-CCAGGCTGAGTGTCCCTTTA-3′). All 69 samples were sequenced successfully, and their length included the exon and partial intron at both ends.

2.4. PCR procedure

PCR amplification of 50 μL was employed, including 25 μL of 2 × Super Taq PCR Mix, 2 μL of forward primer (10 μM), 2 μL of reverse primer (10 μM), 21 μL of ddH_2O, and 2 μL of template DNA. The following protocol was used to perform amplifications: predenaturation at 94 °C for 3 min; and then 35 cycles of denaturation at 94 °C for 30 s, annealing at 56.7 °C for 30 s and extension at 72 °C for 33 s; and lastly a final extension at 72 °C for 5 min.

2.5. Data analysis

SeqMan and EditSeq program in DNAStar software package were used to obtain the RT1-Db1*exon1 gene sequence by splining the sequencing results. ClustalX 1.83 software was used to conduct multiple alignment of the RT1-Db1*exon1 homologous sequences to detect variation sites. Nucleotide and amino acid composition were calculated using MEGA 7.0 software, and intraspecific and interspecific genetic distance were calculated based on Kimura two-parameter model. DnaSP 6.0 software was used to calculate the haplotype diversity (h), nucleotide diversity (π), average number of nucleotide differences (K) and fixation index (F_{ST}). Arlequin 3.0 software was used to perform Analysis of Molecular Variance (AMOVA). SPSS 22.0 software was used to analyze the differences of nucleotide and amino acid composition between *R. opimus* and *M. penicilliger* through Mann-Whitney U test or Student's t-test. Statistical significance was set at two sided $P < 0.05$.

3. Results

3.1. Nucleotide composition

Partial results of agarose gel electrophoresis for genomic DNA and PCR amplification of the RT1-Db1*exon1 were shown in Fig. 2A and B, respectively. The lengths of the sequenced fragments were 487–501 bp, and the NW 018657794.1 sequence in GenBank was used as the reference sequence for alignment (Fig. 3). The nucleotide compositions of *R. opimus* and *M. penicilliger* were shown in Table 1. The contents of G, C and G + C of the RT1-Db1*exon1 sequence were significantly lower in *R. opimus* than in *M. penicilliger*,

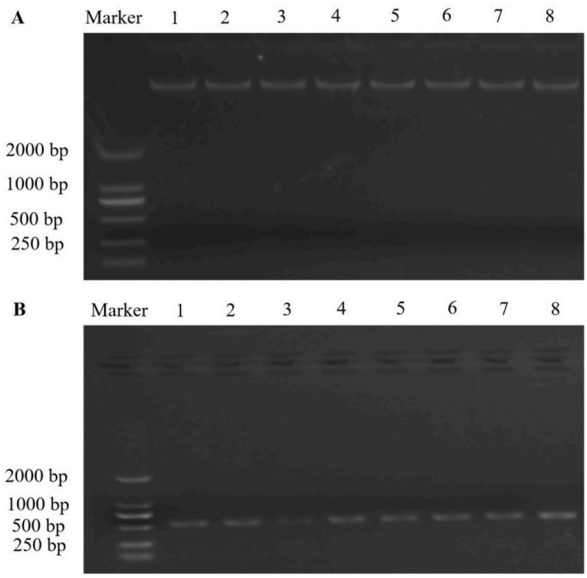

Fig. 2. A: Partial results of agarose gel electrophoresis for the genomic DNA of *R. opimus* and *M. meridianus*; B: Partial results of agarose gel electrophoresis for PCR amplification of the RT1-Db1*exon1.

while the contents of A, T and A + T were significantly higher in *R. opimus* than in *M. penicilliger*. The coding sequence of the RT1-Db1*exon1 gene included 99 bases, encoding 33 amino acids. In 1st codon positions (Pos1), the content of T was significantly higher in *R. opimus* than in *M. penicilliger*, and C was significantly lower in *R. opimus* than in *M. penicilliger*, and A and G were not statistically different (Table 2). In 2nd codon positions (Pos2), the contents of G and C were significantly lower in *R. opimus* than in *M. penicilliger*, and A and T were significantly higher in *R. opimus* than in *M. penicilliger* (Table 2). In 3rd codon positions (Pos3), the content of A was significantly higher in *R. opimus* than in *M. penicilliger*, and C was significantly lower in *R. opimus* than in *M. penicilliger*, and G and T were not statistically different (Table 2).

3.2. Gene polymorphsims

Multiple alignment was performed on the RT1-Db1*exon1 sequences of *R. opimus* and *M. penicilliger*. A total of 39 single nucleotide polymorphism (SNP) sites were detected, including 10 parsimony informative sites and 29 singleton variable sites. The 10 parsimony informative sites were located at the 93, 101, 114, 150, 166, 167, 202, 203, 218 and 225 base, and the 29 singleton variable sites were located at the 72, 73, 74, 80, 125, 130, 133, 134, 138, 143, 153, 163, 173, 184, 186, 192, 199, 207, 208, 210, 222, 223, 224, 229, 230, 232, 233, 235 and 238 base. Among them, there were 13 transition sites, 11 transmutation sites, 17 transition/transmutation coexistence sites and 10 indel sites.

In *R. opimus*, 10 SNP sites were detected, including 2 parsimony informative sites and 8 singleton variable sites. Among them, there were 3 transition sites, 2 transmutation sites, 5 transition/transmutation coexistence sites and 4 indel sites. In *M. penicilliger*, 39 SNP sites were detected, including 9 parsimony informative sites and 30 singleton variable sites. Among them, there were 10 transition sites, 9 transmutation sites, 20 transition/transmutation coexistence sites and 6 indel sites.

A total of 13 haplotypes were identified in *R. opimus* and *M. penicilliger*, without shared haplotypes. Three haplotypes were identified in *R. opimus* and 10 haplotypes were identified in *M. penicilliger*.

3.3. Molecular diversity parameters

The π for *R. opimus* and *M. penicilliger* was 0.04277 ± 0.01417, and the h was 0.783 ± 0.093, and the K was 6.71542. The π for *R. opimus* was 0.00420 ± 0.00139, and the h was 0.833 ± 0.086, and the K was 2.02564. The π for *M. penicilliger* was 0.06569 ± 0.02524, and the h was 1.000 ± 0.045, and the K was 10.4444.

3.4. Genetic structure

AMOVA and pairwise F_{ST} values were employed to analyze the genetic structure of *R. opimus* and *M. penicilliger*. The results showed that 92.07 % of the genetic variation corresponded to interspecific variation while 7.93 % corresponded to intraspecific variation, and the F_{ST} value between *R. opimus* and *M. penicilliger* was 0.9207. Furthermore, the F_{ST} value within *R. opimus* (0.0275) was significantly lower than that within *M. penicilliger* (0.2106), indicating a greater genetic variation of *M. penicilliger* compared with *R. opimus*.

3.5. Amino acid composition

The coding sequence of the RT1-Db1*exon1 gene included 99 bases, encoding 13 kinds of 33 amino acids in *R. opimus* and 12 kinds

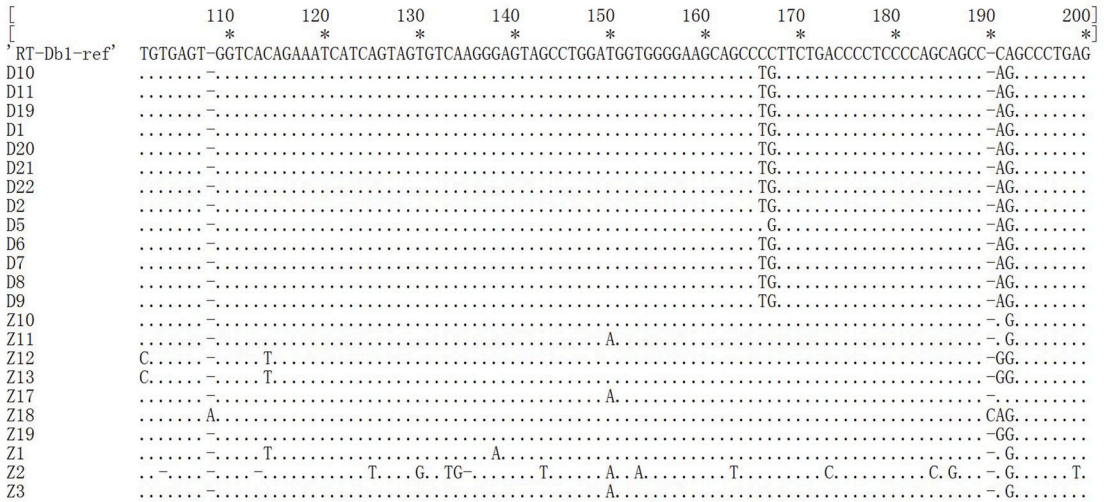

Fig. 3. Partial results of multiple alignment of the RT1-Db1*exon1 homologous sequences.

Table 1
Nucleotide composition of the RT1-Db1*exon1 in *R. opimus* and *M. meridianus*.

	G	A	T	C	G%	A%	T%	C%	G + C%	A + T%
R. opimus	147.3	119.3	103.5	124.7	29.8	24.1	20.9	25.2	55.0	45.0
M. meridianus	154.4	114.9	92.8	134.7	31.1	23.1	18.7	27.1	58.2	41.8
t/Z	−7.522	4.166	15.573	−14.730	−6.304	6.385	18.145	−15.269	−19.190	19.169
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 2
Nucleotide composition of the codons of RT1-Db1*exon1 in *R. opimus* and *M. meridianus*.

	Pos1				Pos2				Pos3			
	G(G%)	A(A%)	T(T%)	C(C%)	G(G%)	A(A%)	T(T%)	C(C%)	G(G%)	A(A%)	T(T%)	C(C%)
R. opimus	13.00	3.00	7.00	10.00	9.00	15.00	2.00	7.00	9.00	6.00	4.00	14.00
M. meridianus	12.89	3.00	5.11	12.00	10.44	13.55	1.00	8.00	8.89	5.11	4.00	15.00
t/Z	0.238	0.000	20.662	−4.583	−8.222	9.993	−4.583	−4.583	1.215	9.723	0.000	−4.583
P	0.111	1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.238	<0.001	1	<0.001

Pos1: 1st codon positions, Pos2: 2nd codon positions, Pos3: 3rd codon positions.

of 33 amino acids in *M. penicilliger* (Table 3). According to Table 3, the constituent ratios of Ala, Pro and Arg were significantly lower in *R. opimus* than those in *M. penicilliger*, and Leu, Met, Gln and Thr were significantly higher in *R. opimus* than those in *M. penicilliger*.

4. Discussion

Plague epizootic has been in active period in the Junggar Basin plague focus since its discovery, and 59 outbreaks among *R. opimus* have been monitored in 14 counties/cities around this focus [10,11]. In recent years, the number of people moving in and out of this focus continues to increase with the development of desert tourism, agriculture construction and oil exploitation, leading to an elevated risk of transmission of plague epizootic to humans. Therefore, it is important to strengthen the study of plague host animals in this focus. *R. opimus* and species of *M. meridianus* complex are the main species of rodent community in the Junggar Basin [8]. Moreover, *R. opimus* has been confirmed as the main host in the Junggar Basin plague focus, and *Y. pestis* is also isolated from species of *M. meridianus* complex [8]. Up to now, *Y. pestis* has not been isolated from other *Meriones* species. Therefore, this study selected these two rodents as the object.

As for divergence of plague resistance, it has been confirmed in black-tailed prairie dogs, *L. brandtii* and *N. fuscus*. Prairie dogs in South Dakota were far more susceptible to plague than prairie dogs in Colorado and Texas [12], and the plague resistance of *L. brandtii* is stronger than that of *N. fuscus* [7]. Both *R. opimus* and *M. meridianus* belong to the subfamily Gerbillinae. Phylogenetic analyses show that the genus *Meriones* is not monophyletic, and *R. opimus* is closely associated with *Meriones tamariscinus* and *Brachiones przewalskii* [13]. Divergence of plague resistance between *R. opimus* and *M. meridianus* has been well known and experimentally demonstrated in the neighboring Central Asian Desert natural plague foci in the former Soviet Union (FSU) region. However, the Junggar Basin plague focus is a new type of plague foci discovered in 2005. This focus may be different from the Central Asian Desert plague foci in terms of genetic characteristics of *Y. pestis*, host animal genetic characteristics and so on, and our previous study has confirmed that the major genotype of *Y. pestis* in the Junggar Basin plague focus is similar to but did not recently originate from the *Y. pestis* strains of the Central Asian Desert plague foci [14]. Most important of all, the divergence of plague resistance between *R. opimus* and species of *M. meridianus* complex in the Junggar Basin plague focus has not been experimentally demonstrated. In the Junggar Basin plague focus, both *R. opimus* and species of *M. meridianus* complex are distributed in clusters, and there is a positive correlation between their distribution. At the present time, it has been confirmed that both *R. opimus* and species of *M. meridianus* complex can be infected by *Y. pestis* in this focus. However, both the *Y. pestis*-positive rate and anti-F1 antibody-positive rate in *R. opimus* are significantly higher than those in species of *M. meridianus* complex (*Y. pestis*-positive rate: 1.21 % (15/1243) *vs* 0.16 % (2/1230) and anti-F1 antibody-positive rate: 12.1 % (164/1356) *vs* 0.7 % (9/1255) [8,15], suggesting that the two gerbils may have different plague resistance.

The MHC genes encode glycoproteins that bind peptides and present them to T-cells for initiation of T-cell responses, playing an important role in adaptive immunity of vertebrates [16]. The classical MHC I genes induce immune reactions against viruses, while MHC II genes initiate defenses against ectoparasites and bacteria. Characterized with abundant polymorphism, especially in the sites of binding peptides, the MHC genes have been extensively applied in the study of pathogen-mediated selection [17–19]. The challenge experiment of *Y. pestis* demonstrates that the plague resistance of *L. brandtii* is stronger than that of *N. fuscus*, and meanwhile the polymorphism of MHC class II gene β in *L. brandtii* is higher than that in *N. fuscus* [7]. Thus, the polymorphism of MHC class II gene β may affect the plague resistance of *L. brandtii* and *N. fuscus* in natural populations. Additionally, researchers uncover a species-specific duplication of the MHC II gene in *R. opimus*, which can provide high peptide binding affinity for *Y. pestis* epitopes, putatively inducing increased capability to defense against *Y. pestis* infection [20].

In our study, there were significant differences in nucleotide composition, amino acid composition, SNP sites, haplotypes and molecular diversity parameters (π, h and K) between *R. opimus* and *M. penicilliger*, and moreover the F_{ST} value within *R. opimus* was significantly lower than that within *M. penicilliger*, indicating a greater genetic variation of *M. penicilliger* compared with *R. opimus*. The

Table 3
Amino acid composition of the RT1-Db1*exon1 in *R. opimus* and *M. meridianus*.

	Ala	Cys	Asp	Gly	Leu	Met	Pro	Gln	Arg	Ser	Thr	Val	Trp
R. opimus	9.09	3.03	3.03	3.03	21.21	9.09	12.12	3.03	9.09	3.03	6.06	15.15	3.03
M. meridianus	13.8	3.03	3.03	3.03	18.18	6.4	15.15	0.00	12.12	3.03	2.69	16.5	3.03
t/Z	−4.430	0.000	0.000	0.000	−4.583	−4.163	−4.583	−4.583	−4.583	0.000	−4.520	−2.596	0.000
P	<0.001	1.000	1.000	1.000	<0.001	<0.001	<0.001	<0.001	<0.001	1.000	<0.001	0.082	1.000

F_{ST} value within *M. penicilliger* was 0.2106 in our study, which was basically consistent with the result of a previous study. Liu et al. reported that the F_{ST} value within *M. meridianus* was 0.2585, but the samples were collected in the Turpan Basin and the northern part of the Tarim Basin, respectively, while all the samples in our study were collected in the eastern part of the Junggar Basin [21]. Therefore, the F_{ST} value in our study was relatively low.

In summary, the genetic diversity analysis based on RT1-Db1*exon1 showed that *M. penicilliger* had higher gene polymorphism and greater genetic differentiation compared with *R. opimus* in the Junggar Basin plague focus, which might be associated with the low infection rate of *Y. pestis*. The main limitations of our study included the small sample size and absence of *Y. pestis* challenge experiment on *R. opimus* and *M. penicilliger*. However, our results provide a clue for exploring plague resistance divergence between *R. opimus* and *M. penicilliger*, and we will perform the *Y. pestis* challenge experiment based on a large sample size in the next step to verify the results and elucidate the potential mechanisms.

5. Conclusion

The genetic diversity analysis based on RT1-Db1*exon1 showed that *M. penicilliger* had higher gene polymorphism and greater genetic differentiation compared with *R. opimus* in the Junggar Basin plague focus, which might be associated with the low infection rate of *Y. pestis*.

Ethics statement

This study received the approval of the institutional research commissions of Xinjiang Center for Disease Control and Prevention (No.XJCDC2020-16). All experiments were carried out in accordance with ARRIVE guidelines, and all methods were carried out in accordance with relevant guidelines and regulations.

Data availability statement

Data will be made available on request.

CRediT authorship contribution statement

Qiguo Wang: Writing – original draft, Project administration, Investigation, Funding acquisition. **Wenting Mou:** Writing – original draft, Project administration, Investigation, Funding acquisition. **Tao Luo:** Writing – original draft, Project administration, Investigation, Funding acquisition. **Guliayi Baokaixi:** Investigation, Formal analysis, Data curation. **Yongjun Luo:** Investigation, Formal analysis, Data curation. **Maidina Xiaokaiti:** Investigation, Data curation. **Xiaowukaiti Saimaiti:** Investigation, Data curation. **Xinhui Wang:** Methodology, Formal analysis. **Junhui Hao:** Methodology, Investigation. **Youjun Gui:** Methodology, Formal analysis. **Xiaojun Wang:** Methodology, Formal analysis. **Haiyan Wu:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Xijiang Wang:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

All the authors do not have any conflict of interest.

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