



Morphological and molecular analyses of *Taenia* and *Mesocestoides* species from red foxes (*Vulpes vulpes*) in northwestern China

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ABSTRACT

In this study, 263 tapeworms were collected from eight road-killed red foxes in Xinjiang Uygur Autonomous Region (XUAR, northwestern China). The tapeworms were analyzed based on morphological characters and mitochondrial cytochrome *c* oxidase subunit 1 (*cox1*) gene sequences. Eighty-three *Taenia* and 180 *Mesocestoides* tapeworms were identified according to the presence or absence of rostellum, and the number, the length and the shape of the large rostellar hooks. The morphological and molecular analyses revealed that i) 180 *Mesocestoides* tapeworms, here named as *Mesocestoides* sp. (*Vulpes vulpes*), showed 99.21% (378/381 bp) identity to *Mesocestoides* sp. reported from red fox in Mongolia; and ii) 83 *Taenia* tapeworms belonged to three species. The first *Taenia* species [n = 16, named as *Taenia* sp. (*Vulpes vulpes*)], based on the length of large rostellar hooks (337–342 μm) and its *cox1* sequence, was identified as a potentially novel species, which is phylogenetically close to *Taenia laticollis*. The second species [n = 54, named as *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*)], was morphologically similar to *Taenia endotheracicus* according to the number (n = 52), the length (319–332 μm) and the shape of the large rostellar hooks. This species, infecting three red foxes, shared 100% *cox1* sequence identity with *Taenia* sp. (*Rhombomys opimus*) genotype C found previously in great gerbils (*Rhombomys opimus*) in the same region. The third species (n = 13, named as *Taenia polyacantha*-like), had shorter large rostellar hooks (178–180 μm) and showed 96.27% (361/375 bp) sequence identity to *Taenia polyacantha* reported from red fox in Italy. The “great gerbil-red fox” life cycle of *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*), belonging to the mitochondrial lineage of *T. endotheracicus*, is confirmed. The *T. polyacantha*-like species was firstly found in red fox in China. *Taenia* sp. (*Vulpes vulpes*) is a potentially novel species, which is close to *T. laticollis* based on its phylogenetic properties.

1. Introduction

The red fox (*Vulpes vulpes* Linnaeus, 1758), that is the largest species of true foxes (Carnivora: Canidae: *Vulpes*), is widespread in North-America, Asia, Europe and North Africa (Ablimiti, 2013). Its habitats overlap with activity areas of humans and domestic animals, leading to risks of infectious diseases (e.g. rabies and echinococcosis) relevant to

public and veterinary health (CDC, Zheng et al., 2008).

Tapeworms (cestodes) have a domestic or sylvatic life cycle between definitive hosts and intermediate hosts (Thompson, 2013). Previously, the red fox was reported to harbor many species of cyclophyllidean cestodes, such as *Taenia taeniaeformis*, *Taenia pisiformis*, *Taenia polyacantha*, *Taenia hydatigena*, *Taenia multiceps*, *Taenia serialis*, *Taenia crassiceps*, *Taenia ovis*, *Echinococcus multilocularis*, *Echinococcus*

Abbreviations: *cox1*, cytochrome *c* oxidase subunit 1; XUAR, Xinjiang Uygur Autonomous Region.

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granulosus, *Echinococcus shiquicus*, *Mesocestoides lineatus*, *Mesocestoides litteratus* and *Mesocestoides corti* (Abuladze, 1964, Eira et al., 2006, Barabási et al., 2010, Varcasia et al., 2015, Hofer et al., 2000, Laurimaa et al., 2016, Dybing et al., 2013, Franssen et al., 2014, Karamon et al., 2018, Borgsteede, 1984, Morishima et al., 1999, Petersen et al., 2018, Fiocchi et al., 2016, Brochier et al., 2007, Hanosset et al., 2008, Lahmar et al., 2014, Rataj et al., 2010, Romig et al., 2006, Wright, 2013, Dibble et al., 1983, Loos-frank, 1987, Jiang et al., 2012, Zhang et al., 2021, Li et al., 2013, Bajer et al., 2020).

Previously, *E. granulosus*, *E. multilocularis*, and *E. shiquicus* were found in Tibetan fox (*Vulpes ferrilata*) and red fox in China (Jiang et al., 2012). In addition, multiple *Taenia* species or genotypes were recently confirmed in the great gerbil (*Rhombomys opimus*) and Eurasian lynx (*Lynx lynx*) in Xinjiang Uygur Autonomous Region (XUAR), North-western China (Ji et al., 2021; Liu et al., 2021). The aim of the present study was to identify tapeworms from road-killed red foxes in XUAR.

2. Material and methods

2.1. Sample collection

In this study, eight red foxes were examined. These animals were road-killed in the Gurbantungut Desert, the northern region of XUAR in the period 2015–2019. During necropsy, all tapeworms were removed from the small intestine (Table 1, Fig. S1), subsequently washed in physiological saline prior to morphological identification and DNA extraction.

2.2. Morphological identification

The staining procedure was performed as previously reported (Li et al., 2009). In brief, the scolex of representative tapeworms were stained with acetate carmine and observed with an Olympus DP70 digital camera (Olympus, Tokyo, Japan).

2.3. DNA extraction and molecular analysis

After detailed morphological examination, 40 tapeworm specimens were selected for molecular analysis (as shown in Table 1). DNA was extracted from a small part of the immature strobila using the TIANamp Genomic DNA Kit (TIANGEN, Beijing, China). A conventional PCR was performed to amplify an approximately 450-bp-long part of the mitochondrial cytochrome c oxidase subunit I gene (*cox1*) as reported previously (Hrčková et al., 2011). Sequences from this study were compared to those in GenBank with the BLASTN program (<https://blast.ncbi.nlm.nih.gov>). New sequences were deposited in GenBank (*cox1*: MZ475884, MZ512998–MZ513000). A phylogenetic tree was constructed using the Neighbor-Joining method in MEGA 7.0 software. Amino acid sequences were compared by DNAMAN software.

Table 1
Sampling data of eight red foxes (*Vulpes vulpes*) in XUAR, North-western China.

Serial number	Red fox							
	#1	#2	#3	#4	#5	#6	#7	#8
Age	adult	adult	adult	adult	adult	adult	adult	adult
Habitat type	desert	desert	desert	desert	desert	desert	desert	desert
Genus <i>Taenia</i>	<i>Taenia</i> sp. (<i>Vulpes vulpes</i>)							
	16 (3)*		2 (2)*		5 (2)*		17 (3)*	30 (6)*
	<i>Taenia</i> sp. (<i>Vulpes vulpes</i> & <i>Rhombomys opimus</i>)							
					3 (2)*	4 (2)*		6 (3)*
	<i>Taenia polyacantha</i> -like							
<i>Mesocestoides</i> sp. (<i>Vulpes vulpes</i>)	80 (8)*		100 (8)*					

(n)*: Number of molecular analysis.

3. Results

3.1. Morphological identification

Six foxes (#1, #3, #5, #6, #7 and #8) were found infected with 263 tapeworms. According to the presence or absence of rostellum, 83 were identified as *Taenia* spp., while 180 belonged to the genus *Mesocestoides* spp. According to the number, the length and measurement data (total length, total width, posterior length, anterior length and guard length) of large rostellar hooks, 83 *Taenia* tapeworms were assigned to three species. The first species (n = 16, removed from red fox #1) and the second species (n = 54, from red foxes #3, #5, #7 and #8) were similar to *Taenia endotheracicus*, *Taenia krepkogorski* and *Taenia macrocystis* in the number and length of large rostellar hooks (Tables S1 and S2). The third species (n = 13, from red foxes #5, #6 and #8) belonged to *Taenia polyacantha* according to the number and length of large rostellar hooks.

3.2. Molecular identification

Based on the *cox1* gene, BLASTN analysis indicated that i) sixteen *Mesocestoides* tapeworms from red foxes #1 (n = 8) and #3 (n = 8) were most closely related to *Mesocestoides* sp. (accession number: AB792718) from red fox in Mongolia, showing 99.21% (378/381 bp) sequence identity to it. Provisionally, this species was named as *Mesocestoides* sp. (*Vulpes vulpes*) (MZ475884); ii) the first *Taenia* species was most closely related to *Taenia* sp. (*Rhombomys opimus*) (accession numbers: MW321849 and MW321850) detected in great gerbils in our previous work (Ji et al., 2021), but sharing only 88.03% (309/351 bp) sequence identity with it. Provisionally, this species was named as *Taenia* sp. (*Vulpes vulpes*) (MZ512998), and it belonged to Clade B of the *cox1* phylogenetic tree (Fig. 1); iii) the second *Taenia* species was 100% identical in its *cox1* sequence to *Taenia* sp. (*Rhombomys opimus*) genotype C (accession numbers: MW321849 and MW321850) detected in great gerbils, originating from the same region as the relevant three road-killed red foxes (#5, #7 and #8) in this study. Provisionally, this species was named as *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*) (MZ512999), and belonged to Clade A of the *cox1* phylogenetic tree (Fig. 1); and iv) the third *Taenia* species was most closely related to *T. polyacantha* (accession number: MT806362) from red fox in Italy, sharing 96.27% (361/375 bp) *cox1* sequence identity. Provisionally, this species was named as “*T. polyacantha*-like” (MZ513000), and it belonged to Clade C of the *cox1* phylogenetic tree (Fig. 1).

Analysis of COX1 amino acid sequences showed that i) *Mesocestoides* sp. (*Vulpes vulpes*) has 100% (127/127 aa) identity to *Mesocestoides* sp. (accession number: AB792718) from red fox in Mongolia; ii) *Taenia* sp. (*Vulpes vulpes*) shares 93.16% (109/117 aa) identity with *Taenia* sp. (*Rhombomys opimus*) (MW321849) (Fig. S2A); and iii) “*T. polyacantha*-like” (from Clade C in Fig. 1) has 100.00% (125/125 aa) identity to *T. polyacantha* (MT806362) (Fig. S2B).

4. Discussion

The previously known geographical range of *T. endotheracicus*, with

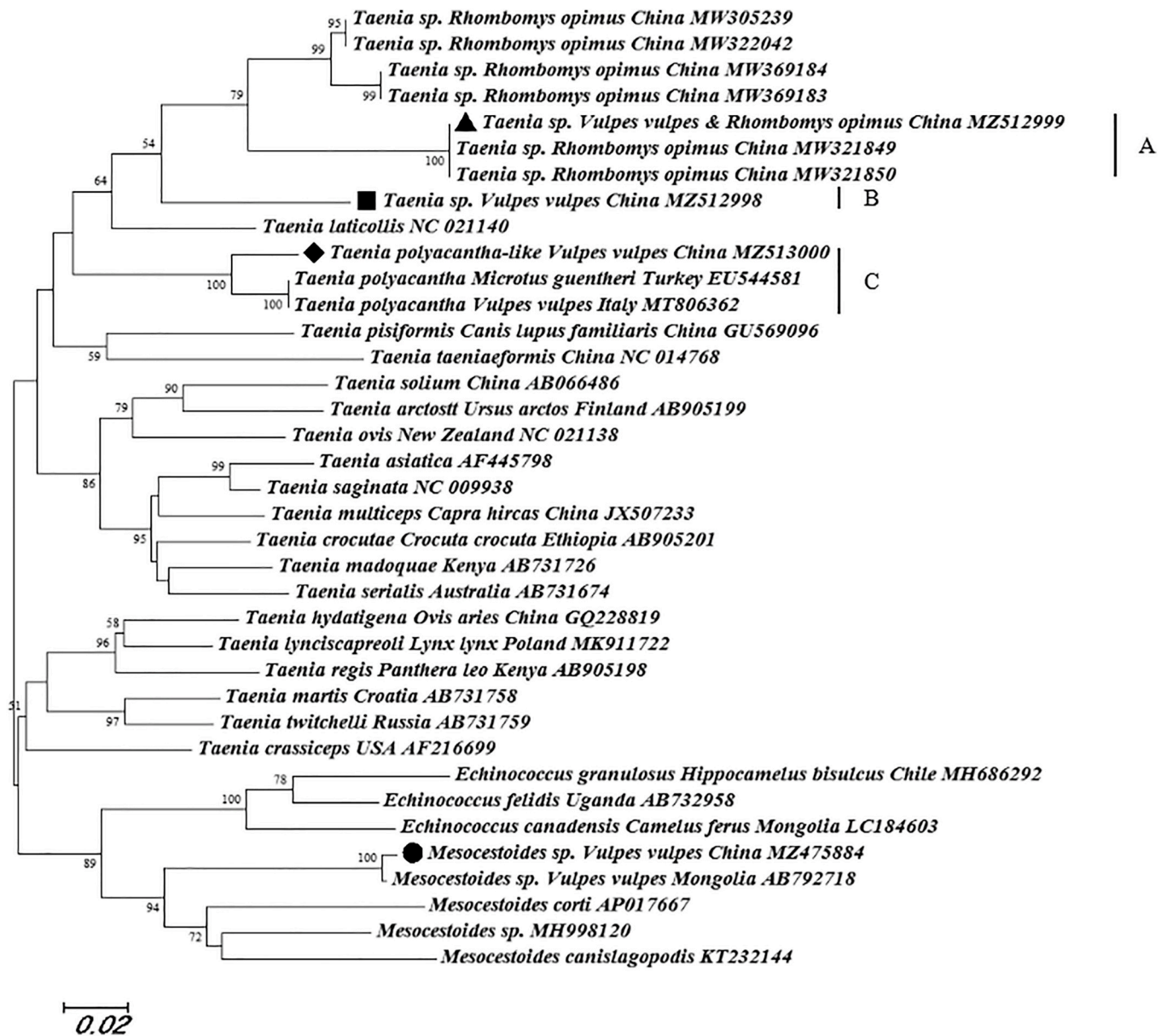


Fig. 1. Phylogenetic relationships of *Taenia* and *Mesocostoides* species from red foxes based on *cox1* sequences.

red fox as its definitive host, included Iran and North Africa. Polyccephalic larvae occur in the thoracic cavity of rodents from the genera *Meriones*, *Gerbillus* and *Rhombomys*. In our previous work, *Taenia* sp. (*Rhombomys opimus*) genotypes A, B and C were demonstrated from the thoracic cavity of great gerbils in Gurbantungut Desert with 5.3% (10/188) prevalence (Ji et al., 2021). A lot of protoscoleces were observed in large white and web-shaped cysts, which caused shrinking and stiffness in the lung parenchyma (Ji et al., 2021). Interestingly, here adults of *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*) were found in four red foxes, and the corresponding *cox1* sequence had 100% identity to that of *Taenia* sp. (*Rhombomys opimus*) genotype C in great gerbils. Furthermore, the sampling sites of the three red foxes (#5, #7 and #8) and of the two great gerbils (#27 and #31) infected with *Taenia* sp. (*Rhombomys opimus*) genotype C are situated in the same area (44°67'–44°70' N, 86°34'–86°39' E) (Ji et al., 2021). Previously, Lin et al. (2010) reported that great gerbils are important in the diet composition of red foxes in Gurbantungut Desert, and accounted for 16.48% of prey items based on 273 fecal samples of red foxes. These findings suggest that the life cycle of *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*) involves the great

gerbil and the red fox (Fig. S3). In addition, the shape of large rostellar hooks was compared among *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*), *T. endothoracicus*, *T. krepkogorski* and *T. macrocystis* (as shown in S pptx). The results indicated that the shape of large rostellar hooks is similar between *T. endothoracicus* and *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*). Interestingly, the shape of cysts showed significant difference between *T. endothoracicus* reported from Iran and *Taenia* sp. (*Rhombomys opimus*) in previously in North-western China (Fig. S4) (Ji et al., 2021; Mowlavi et al., 2004; Dautel et al., 2013), suggesting that *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*) belongs to a genetic lineage separate from *T. endothoracicus*. However, unfortunately, the *cox1* sequence of the latter species is not available in GenBank to confirm this.

According to the length of the large rostellar hooks and definitive host (*Vulpes*), *Taenia* sp. (*Vulpes vulpes*) is similar to *T. endothoracicus*, *T. krepkogorski* and *T. macrocystis*. However, when the shape of the large rostellar hooks was compared among them, *Taenia* sp. (*Vulpes vulpes*) showed obvious differences from these three tapeworm species (as shown in S pptx). Due to the lack of *cox1* data of *T. endothoracicus*, *T.*

krepkogorski and *T. macrocystis*, the taxonomy of *Taenia* sp. (*Vulpes vulpes*) should be further investigated in the future.

T. polyacantha, infecting red foxes, was previously reported from Finland, Norway, Denmark, Wales, Germany, France, Switzerland, Austria, Poland, Bulgaria, Italy, Yugoslavia and Japan (Loos-Frank and Zeyhle, 1982; Ihama et al., 2000; Trachsel et al., 2007; Lavikainen et al., 2008). In this study, 13 adult tapeworms of "*T. polyacantha*-like" were found for the first time in three red foxes (#5, #6 and #8) in China. At the same time, differences between these isolates are obvious in the shape of the large rostellum hooks and sequences of the *cox1* gene (96.27%, 361/375 bp).

Previously, *M. lineatus*, *M. corti*, *M. litteratus* and *Mesocestoides* spp. were found in red foxes in Portugal, Romania, Denmark, Slovak Republic, Tunisia, Italy, Poland and Mongolia (Bajer et al., 2020; Barabási et al., 2010; Saeed et al., 2006; Fiocchi et al., 2016; Varcasia et al., 2018). Hitherto only *M. lineatus* and *M. litteratus* were reported from this genus in China (Zhou 2015; Zhang et al., 2021; Li et al., 2013). In our study, however, *Mesocestoides* sp. (*Vulpes vulpes*) (accession number: MZ475884) was found in two red foxes. This species candidate is phylogenetically most closely related to *Mesocestoides* sp. (accession number: AB792718) collected from red fox (*Vulpes vulpes*) in Mongolia, with which it shared 99.21% (378/381 bp) *cox1* sequence homology. These two clustered as a sister group to *M. corti* and *Mesocestoides canislagopodis* (Fig. 1). Since the latter species has a broad range of canid and felid definitive hosts (Skirnisson et al., 2016), it should be examined in the future if further predator species may harbor adult *Mesocestoides* sp. (*Vulpes vulpes*) in northwestern China. In addition, the taxonomic relationships and the geographical distribution of *Mesocestoides* sp. (*Vulpes vulpes*) should also be explored.

It is a principle phenomenon that coinfection with multiple tapeworm species may occur in the same red fox individual. In a previous report from the Netherlands, up to eight cestode species were found together in the same red fox (Franssen et al., 2014). Here *Taenia* sp. (*Vulpes vulpes*) coinfecting with *Mesocestoides* sp. (*Vulpes vulpes*), "*T. polyacantha*-like" coinfecting with *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*) the same red fox in China. The broad range of food items of red foxes in the Gurbantunggut Desert might account for this coinfection phenomenon.

5. Conclusion

The life cycle of *Taenia* sp. (*Vulpes vulpes* & *Rhombomys opimus*), belonging to the mitochondrial lineage of *T. endothoracicus*, involves the great gerbil and the red fox. "*Taenia polyacantha*-like" was found for the first time in red fox in China. *Taenia* sp. (*Vulpes vulpes*), a potentially novel species, is phylogenetically closely related to *T. laticollis* based on the *cox1* gene.

Ethical approval and consent to participate

This study was approved by the Animal Ethics Committee of Shihezi University (Approval No. A2015-063-01 and A2018-143-01).

Declaration of competing interest

No conflicts of interest exists in the submission of this manuscript, and the manuscript was approved for publication by all authors.

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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.2021.11.003>.

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