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Original Article

Genetic Diversity of *Taenia Hydatigena* on the Qinghai-Tibetan Plateau

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Abstract:
Taenia hydatigena (T. hydatigena), a globally distributed parasite, poses a considerable economic burden on livestock industries. The species exhibits an atypical characteristic for tapeworms: a wide range of intermediate hosts. Consequently, a comprehensive analysis of the *T. hydatigena* mitochondrial genome is warranted. A phylogenetic tree was constructed via the maximum likelihood method, and the HKY model was employed for divergence time estimation. The complete mitochondrial genome of *T. hydatigena* was found to be 13490 bp in length, with a high AT content (71%) relative to CG content (29%). Collinearity analysis revealed predominantly forward matching and minimal gaps, suggesting genomic stability. A phylogenetic tree based on 12 protein-coding genes (PCGs) and the cytochrome oxidase subunit I (COI) gene confirmed that *T. hydatigena* belongs to the family Taeniidae. Divergence time analysis using COI data estimated that *T. hydatigena* diverged approximately 19.39 million years ago (Mya), a period coinciding with the transition from the MI-1 glacial period to a warmer climate. We hypothesize that the differentiation of *T. hydatigena* was driven by host differentiation resulting from environmental changes associated with this warming trend. Given the limited existing research on the *T. hydatigena* mitochondrial genome, this study contributes valuable empirical data to further evolutionary investigations of this parasite.
Keywords: mitochondrial genome, *Taenia hydatigena*, divergence time, phylogeny

1. Introduction

Taenia hydatigena (T. hydatigena) is a tapeworm that is ubiquitous in domestic animals worldwide (NGUYEN *et al.* 2016; MIRAN *et al.* 2017). *T. hydatigena* is mainly found in the gastrointestinal tract of canids, where sexual reproduction takes place (SEPPO SAARI *et al.* 2019; GIALLOMBARDO *et al.* 2024; KARAKOC *et al.* 2024). Its larvae (*Cysticercus tenuicollis, C. tenuicollis*) have been

found in the abdominal cavity of many animals examined for meat (NGUYEN *et al.* 2016). Animals such as cattle and sheep become infected by accidentally ingesting food or water contaminated with canine feces containing *T. hydatigena*. When the larvae released from these eggs penetrate the host's intestinal wall, they typically migrate to the omentum, mesentery, peritoneum, and, less commonly, to the pleura and pericardium (SAMUEL AND ZEWDE 2010; ORYAN *et al.* 2012). And then gradually develops into a fluid-filled bladder-like cyst (WANG *et al.* 2021). The massive migration of *C. tenuicollis* can cause acute outbreaks, which can lead to traumatic hepatitis and eventually death (SCALA *et al.* 2014). In developing countries, *T. hydatigena* has a high prevalence in domestic or wild animals. Although *T.hydatigena* is considered to be one of the main causes of economic and production losses in animal husbandry, there is no effective treatment at present (SCALA *et al.* 2015).

T. hydatigena has a large number of intermediate host species (WANG *et al.* 2021). In the case of parasites, it is usually co-evolved with the host. Most tapeworm hosts show high specificity to parasites. However, *T. hydatigena* has a relatively large number of intermediate and definitive hosts, which is relatively rare (WANG *et al.* 2021). Therefore, this study analyzed the mt DNA of *T. hydatigena* to explore the possible reasons for its host diversity.

Mitochondrial DNA (mt DNA) is characterized by no recombination, a maternal inheritance pattern, regional conservatism, a fast mutation rate, and a relatively high rate of evolution. As a result, it has been widely used to study genetic variation in metazoans (BROWN *et al.* 1979; TORGERSON AND HEATH 2003; MUELLER *et al.* 2004; SHEN *et al.* 2010).

Although *T. hydatigena* is one of the most common species of tapeworms in livestock, there is very little molecular genetic information about this parasite (ROSTAMI *et al.* 2015). Therefore, we use the mitochondrial genome to analyze the phylogeny, differentiation time, and nucleic acid diversity of *T. hydatigena*, and provide a new scientific basis for its molecular genetic information.

Material and Methods

Sample Collection and Morphological Observation

In October 2024, a dog was dissected at an altitude of 2,638 meters above sea level in the Huangzhong of Qinghai Province, and eight white parasites were collected in the intestines. All samples were rinsed with 1x phosphate-buffered saline (PBS) and stored in 70% alcohol for further psychological and molecular biology identification.

Place it on a glass dish, rinse it with normal saline, then take photos with a stereo microscope, and further observe it with a scanning electron microscope.

DNA Extraction and Molecular Identification

Using a commercial kit (Cat. DP304-03, TIANamp Genomic DNA Kit, TIANGEN Biotechnology, Beijing, China), extract the sample DNA genome according to the manufacturer's instructions. The extracted DNA was identified by amplification and sequencing according to the conserved primers of the Hypoderma COI gene. The extracted DNA was used as a template for polymerase chain reaction (PCR) to identify the COI gene by amplification and sequencing using conserved primers (OTRANTO *et al.* 2003). The primers used were synthesized by Sangon Biotech (Shanghai, China), and the primer and PCR conditions are shown in Supplementary Table 1. Amplify DNA fragments using a standard 25 μl PCR protocol. Use the TIANgel Midi Purification Kit (Cat. No. DP209-02, Tiangen, China). The final PCR product was sent to Sangon Biotech (Shanghai) Co., Ltd. for library construction and sequencing.

Mitochondrial Genome Sequencing and Assembly

The sequencing raw data is evaluated by Fastp v0.36 (CHEN *et al.* 2018) for quality evaluation, data filtering, effective read statistics, etc., to obtain relatively accurate and effective data. After obtaining high-quality sequencing data, the genome was spliced from scratch according to the principle of high redundancy of high-throughput sequencing data. In the process of mitochondrial genome splicing, the following strategies are adopted: extracting reads aligned to organelle genome sequences for splicing, directly using WGS data for splicing, and then extracting possible genome scaffolds through sequence similarity and splicing features. After the splicing strategy is determined, SPAdes v3.15 (BANKEVICH *et al.* 2012) is used to correct the error sequence, and then the results of each Kmer value are combined to obtain the best result.

After the splicing was completed, the scaffolds were compared with the NCBI nt library (http://ncbi.nlm.nih.gov/) using blastn to extract the sequencing depth and coverage information of each scaffold. Then, GapFiller v1.11 was used to supplement the GAP obtained by contig, and finally, Pilon V1.24 was used for sequence correction to correct the splicing errors and indels of small fragments in the splicing process, and finally, a complete circular gene map was obtained.

Mitochondrial Gene Annotation and Repetitive Element Annotation

Use tblastn and genewise to perform reverse comparison with closely related reference databases to obtain CDS gene boundaries; MiTFi to obtain tRNA sequence annotations; cmsearchrfam to compare and identify non-coding rRNA, and finally summarize into complete annotation results. Then, misa v 2.1(CHEN *et al.* 2016) was used to search for SSR in the whole genome sequence, and rmpture was used to find scattered repetitive sequences and statistically plotted to obtain repetitive element annotations.

Sequence, Alignment, and Phylogenetic Analysis

BLAST searches were performed using the National Center for Biotechnology Information's Genomic Database (http://www.ncbi.nlm.nih.gov) for sequence results. Subsequently, PhyloSuite v1.2.2 (ZHANG *et al.* 2020) was used to determine the phylogenetic relationship of *T. hydatigena*, and the 12 protein-coding genes and the COI phylogenetic tree of *T. hydatigena* were constructed. 76 genomes were used to construct a phylogenetic tree (see Supplementary Table 2-3 for details). The sequence alignment of *T. hydatigena* was performed using MAFFT v7.505 (KATOH AND STANDLEY 2013) software with default settings, while TrimAI v1.2 software was used to remove intergenomic gaps and ambiguous sites (CAPELLA-GUTIÉRREZ *et al.* 2009). Phylogenetic trees were constructed using IQ-TREE v2.2.0 maximum likelihood (ML) (NGUYEN *et al.* 2015). Model selection is done automatically by ModelFinder (KALYAANAMOORTHY *et al.* 2017). The other parameters used are the defaults. Use the online tool TVBOT to view and beautify phylogenetic trees(XIE *et al.* 2023).

Analysis of Divergence Times

We selected different species (*T. saginata*, *T. multiceps*, *T. solium*, *T. ovis*, *T. crassiceps*, *T. twitchelli*, *T. martis*, *T. serialisi*, *T. hydatigena*, *T. asiatica*, *T. laticollis*, *Echinococcus ortleppt*) for divergence-time analysis. The differentiation time of the entire *T. hydatigena* mitochondrial genome was inferred using BEAST v2.7.7, and the optimal HKY model was selected(BOUCKAERT *et al.* 2014). For tree priors, a calibrated Yule model (Nirmala) is used (HELED AND DRUMMOND 2015). Based on the findings of previous studies on the differentiation time of *Teania* spp., the mean and

standard deviation of the existing normal distributions of *T. ovis*, *T. martis*, *T. laticollis*, and *Echinococcus ortleppt* were set at 19.6 Mya, 17.7 Mya, 15.0 Mya, and 25.6 Mya, respectively, for *T. hydatigena*. The probability estimates are extracted every 1000 generations from 10 million generations of each Markov chain Monte Carlo (MCMC-RRB) run, and the initial 25% of the sampled data is discarded. The Family Tree was plotted using Figtree V. 1.4.

Results

Morphological Observation

The results of the stereomicroscope showed that the head of *T. hydatigena* was milky white and fan-shaped, but not very flat, with vertical stripes on the fan-shaped surface (Fig. 1A). The tail is inverted cone-shaped (Fig. 1B). Scanning electron microscopy shows several vertical stripes and folds on the head and tail, see Fig. 1C and Fig. 1D for details.

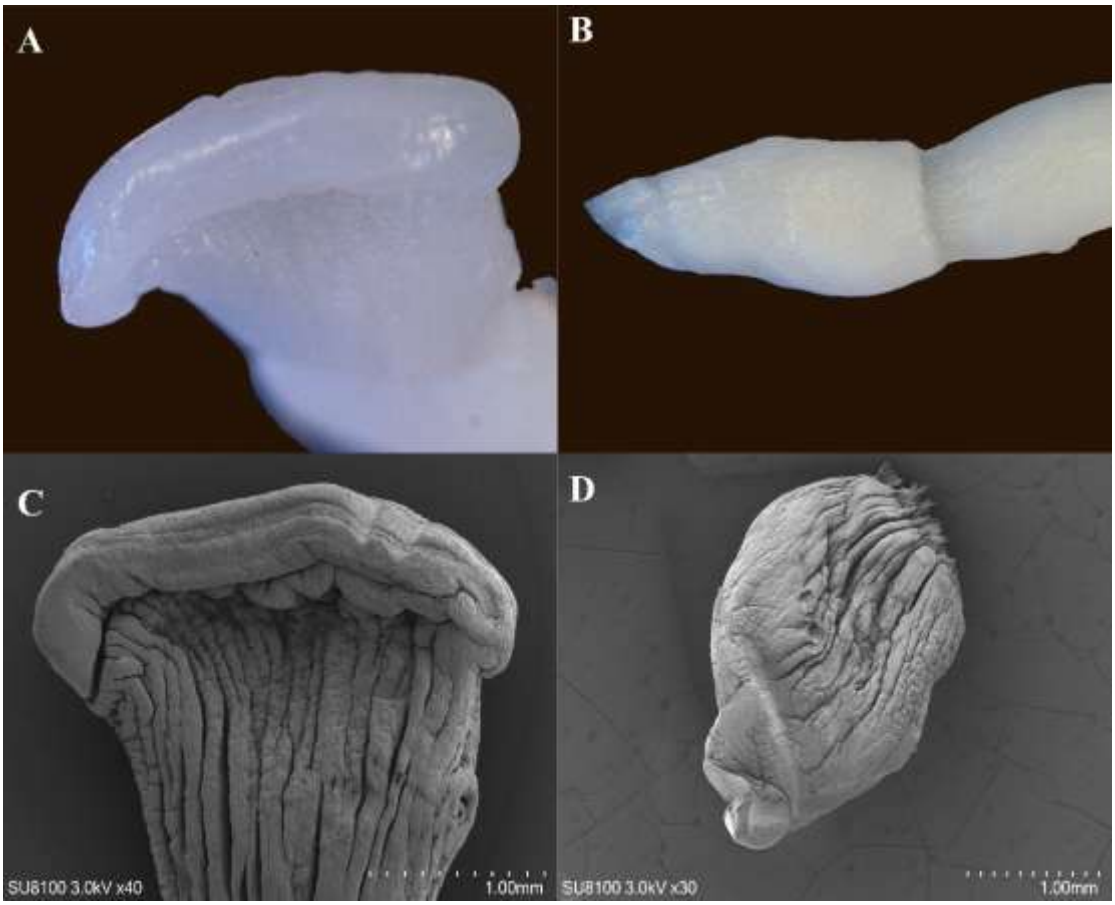

Fig. 1. The morphological observation of *T. hydatigena*.

The structure of the scolex and tail of the *T. hydatigena* as seen under a stereo microscope, respectively (A, B). Scanning electron micrograph of the tail and scolex of the *T. hydatigena* (C, D).

Structure of the Mitochondrial Genome of *T. Hydatigena*

After manual assembly, the total length of *T. hydatigena* mt DNA was 13490 bp (GenBank accession number PV389993), with an A+T content of 71% and a G+C content of 29%. The 37 mt-based genomes of *T. hydatitgena* include 12 PCGs, 22 tRNA genes, 2 rRNA genes (16S rRNA and 12S rRna), 7 NADH dehydrogenases (ND1, ND2, ND4, ND4L, ND5, ND6, ND3), 4 cytochrome c oxidases (See Fig. 2D). In the mitochondrial genome, the gene arrangement is very tight, and the gene spacer is only 87bp, accounting for 0.5% of the total mitochondrial

length, and overlapping genes may occur.

Phylogenetic Relationship

Construct the phylogeny of the *T. hydatigena* using the maximum likelihood method, using 40 species and outgroups based on 12 PCGs. The results showed that *T.hydatigena* belonged to the genus Taeniidae and was closest to the Family diphyllobothriidae (Fig. 2A). In addition, to further verify the relationship between *T. hydatigena* and other genera, we also used the COI gene of *T. hydatigena* for phylogenetic analysis, and the results were consistent with the previous results (Fig. 2B).

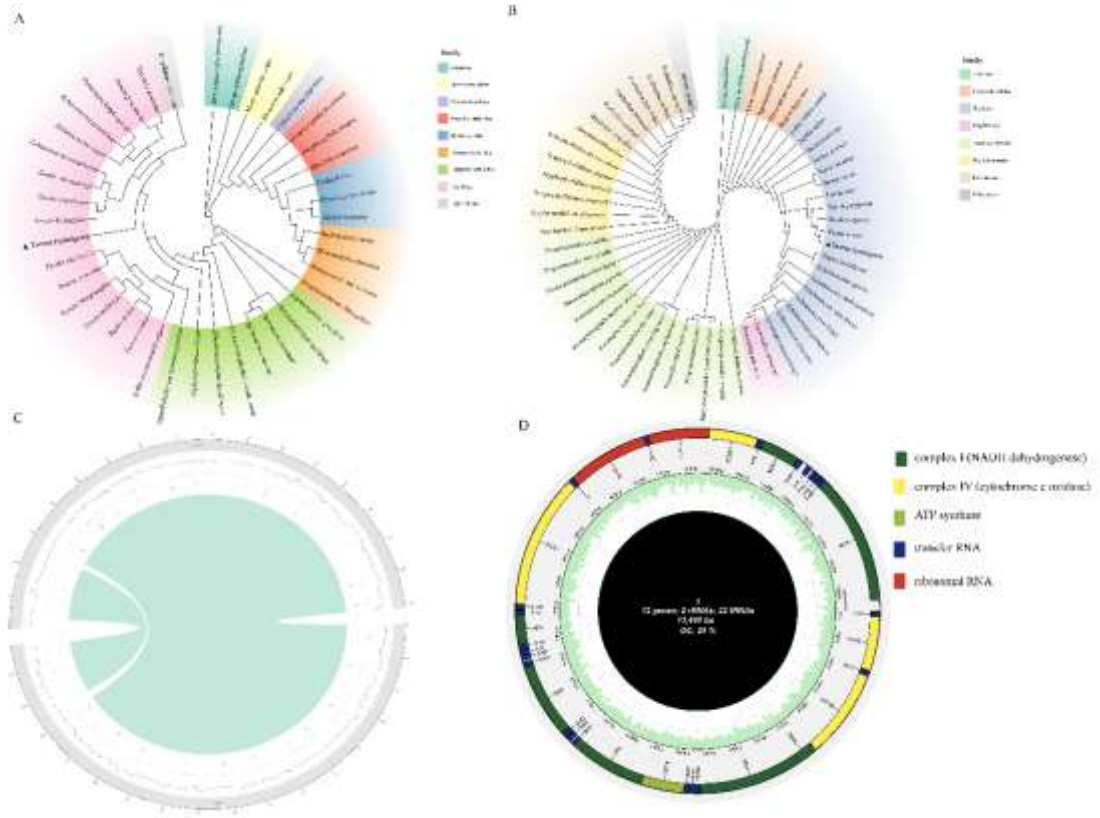

Fig. 2. Phylogenetic relationship and genome circle.

Based on 12 mitochondrial gene sequences (A), combined with COI sequences (B), the phylogenetic relationship between *T. hydatigena* and other species was verified using the maximum likelihood method. Colinearity circle (C). The circle plot represents the GC and gene name from the outside to the inside, and the lines represent its collinearity region (cyan indicates a forward match, and the red table represents the inverse matching). Genome annotation circle diagram (D).

Collinearity Analysis

The collinearity of *T. hydatigena* has only forward matching and no reverse matching. In the collinearity region of *T. hydatigena*, the genes are very tightly linked, except for ND5 and COX3, ND5 and ND6 genes have a space, but the interval is very small, and there are no gaps in the others (Fig. 2C). The size of the collinearity fragment has a great relationship with the differentiation time between species: the shorter the differentiation time between species, the less variation accumulated, and more characteristics inherited from ancestors will be retained (YANG *et al.* 2023). Thus, *T. hydatigena* inherited more genetic traits from its ancestors.

Nucleotide Diversity Analysis

As we all know, species' heredity in nature is

polymorphic, and understanding the basis of variation is still a core issue in evolutionary biology (ZHANG AND YANG 2015). We used DNASP to calculate the nucleotide polymorphism index between multiple genomes in the mitochondrial whole genome. The results showed that the coefficient of variation (pi) of methionine (trn cua) and NADH dehydrogenase (ND4) nucleotides was higher (Fig. 3).

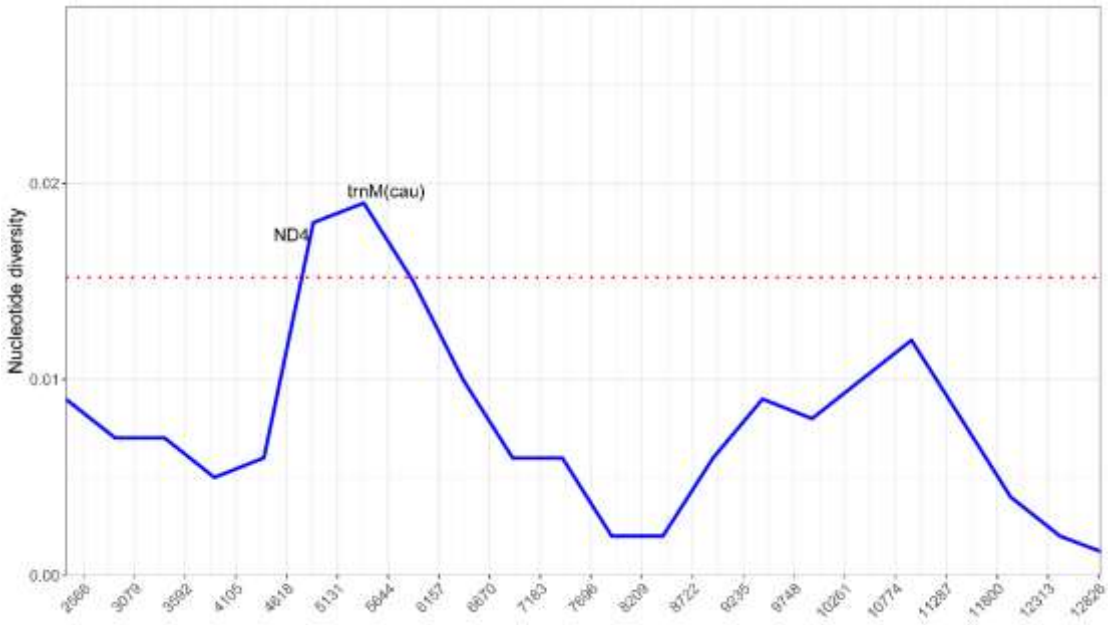

Fig. 3 Nucleic Acid Polymorphism Analysis Chart

Nucleotide polymorphisms (PIs) calculated based on multiple genomes are shown in the figure, and the peak regions represent regions with large variations in different genome domains, which in turn identify the conserved nature of the gene or IR.

Divergence Time Analysis

The divergence time of *T. hydatigena* was estimated by the Beast2 relaxation molecular clock method. Divergence time analysis of the *T. hydatigena* showed that the common ancestor of *Taenia* spp. Existed in about 19.39 Mya (17.82–22.66 Mya, 95% highest probability density). The divergence times of *T. laticollis*, *T. ovis*, *T. multiceps*, and *T. hydatigena* were 15.14 Mya, 17.73 Mya, and 19.39Mya, respectively (Fig. 4).

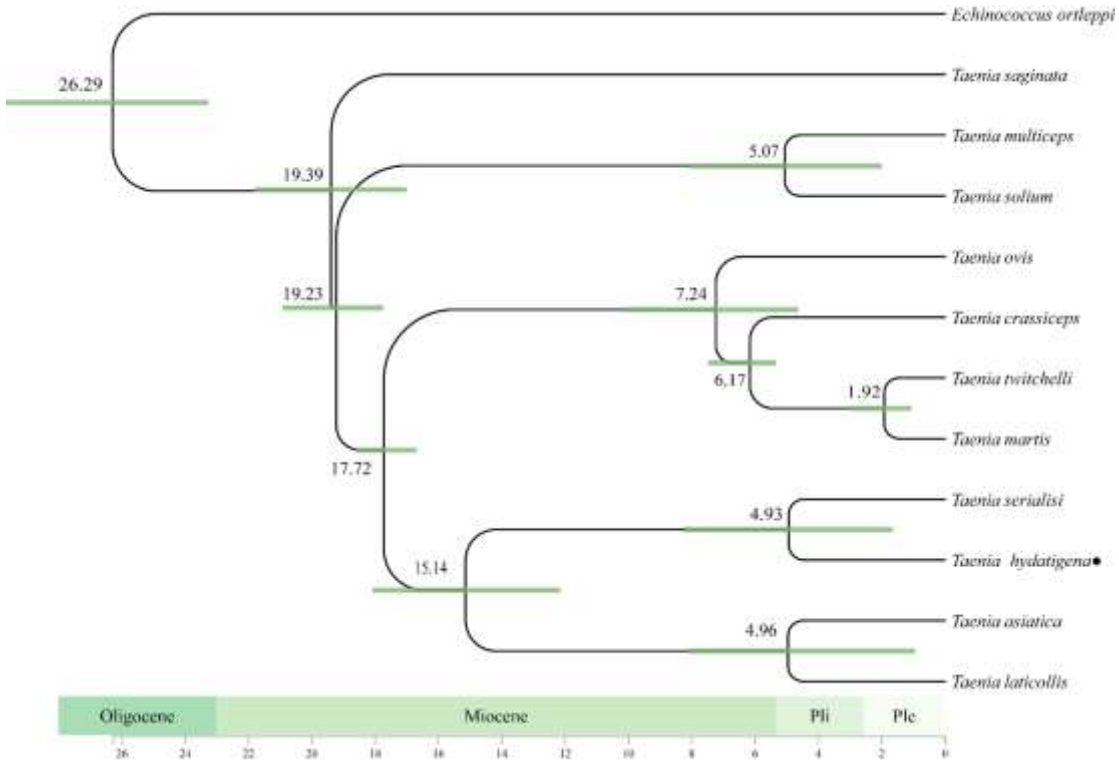

Fig. .4 Divergence times

Inferred divergence times based on COI of *T. hydatigena* mitochondria and other *Taenia* spp. Numbers at the nodes represent the divergence times between the two lineages. The green bar represents the time interval of the 95% highest probability density. Time scales show the range of the Oligocene, Miocene, Pliocene, and Pleistocene periods.

Discussion

The morphology of *T.hydatigena* has not yet been reported, and our morphological observations have revealed the head and tail morphology of adult *T. hydatigena*. It is worth noting the difficulties in collecting the sample; we cannot rule out the possibility of damage during the collection. Therefore, we believe that there is a need to further understand *T. hydatigena* through molecular biology. In this case, the combination of morphological and molecular biology methods is more convincing.

In recent years, researchers have made extensive use of use of stable genetic molecular markers to identify parasites (PADGETT *et al.* 2005; TRAN THI *et al.* 2022). The mt DNA contains a large amount of genetic information, short in length, and simple in structure DNA molecules (GRAY 2012). Therefore, we performed mitochondrial genome sequencing by the collected parasites. In this study, the phylogeny of *T. hydatigena* was reconstructed from the mitochondrial whole genome sequence. Through sequencing, assembly, and annotation, we found that the complete mitochondrial genome of *T. hydatigena* is consistent with the structure of most tapeworms (Fig. 2D). This is consistent with previous research reports (JIA *et al.* 2010; LIU *et al.* 2010). The reliability of the topology is improved by using ML analysis to perform a comprehensive analysis of the nodes. The phylogenetic tree generated based on 12 PCGs and COIs showed that *T. hydatigena* was closely related to species of the genus, which was consistent with previous studies (KNAPP *et al.* 2011).

Mt DNA collinearity analysis of *T. hydatigena* showed that the genes of *T. hydatigena* were very

tightly knit (Fig. 2C). Collinearity describes the positional relationship of genes on the same chromosome: the type of genes differentiated from the same ancestral type and the preservation of the relative order. The size of the collinearity fragment has a lot to do with the time of differentiation between species: between species with a shorter differentiation time, there is less variation accumulated, and more traits inherited from ancestors are retained(COGHLAN *et al.* 2005). Consequently, the mitochondrial genome of *T. hydatigena* retains a greater amount of genetic material from its ancestors.

Fossil data are one of the main bases for studying the origin and evolution of different species (DENG *et al.* 2020). The differentiation time of *T. hydatigena* in this study was 19.39 Mya in the early Miocene. This period is considered to be part of the transition from the Mi-1 to the Mid-Miocene Warm Period (SULLIVAN *et al.* 2023). Based on existing studies, ice sheet expansion events that occurred in the Miocene will lead to global ocean climate change(HOLBOURN *et al.* 2005; GASSON *et al.* 2016), resulting in species diversity (MARX AND UHEN 2010). In the process of climate and temperature changes, the QTP is rapidly uplifted, the altitude rises rapidly, the summer monsoon strengthens, and the climate warms (ZHISHENG *et al.* 2001; RENNER 2016; KAPP AND DECELLES 2019; AO *et al.* 2021). Therefore, it is reasonable to speculate that global climate change and the rapid uplift of the Tibetan Plateau drove the evolution of *T. hydatigena*.

The definitive hosts of *T. hydatigena* are canids, which originated in North America (NAKAO *et al.* 2007). Therefore, we suspect that *T. hydatigena* migrated from North America to Europe and finally to Asia along with canines. (FILIP *et al.* 2019). During migration, the feces excreted by canines contain *T. hydatigena*, which contaminates food and water sources, and cattle, after ingestion, evolve in the body of cattle (NGUYEN *et al.* 2016; RAISSI *et al.* 2021).

Originating from a small species in North America, the equidae evolved around 20 Mya, diverging into at least 19 species (LIBRADO AND ORLANDO 2021). Thus, horses, as intermediate hosts of *T. hydatigena*, evolved to adapt to equine differentiation. Equidae, in turn, diverged into many species, and *T. hydatigena* was able to survive in the differentiated species (MIHLBACHLER *et al.* 2011). Therefore, we speculate that *T. hydatigena* parasitic canids migrated from North America to Asia and that *T. hydatigena* evolved with changes in the external environment and the evolution of intermediate hosts.

Conclusion

In conclusion, we reveal the complete mitochondrial genome of *T. hydatigena* and explore the system of *T. hydatigena* from the perspective of morphology and molecular biology. We identified this family as a tapeworm family by morphological observations. Phylogenetic analyses were performed using 12 PCGs and COIs, and these results provide strong evidence for the relationship of *T. hydatigena* with other tapeworms. In addition, divergence times suggest that the differentiation of *T. hydatigena* is related to global warming and host evolution. Therefore, we speculate that the differentiation of *T. hydatigena* may be closely related to global climate change and biological factors. By making reasonable assumptions about host evolution, the evolution of *T. hydatigena* may depend on the host-parasitism relationship. We looked at the structural characteristics, evolutionary stress selection, phylogenetic analysis, and divergence timing of *T.hydatigena*, were made reasonable speculations to provide a reasonable explanation. The results obtained have important implications for a better understanding of the evolutionary role of *T. hydatigena*. We are confident that with our continuous efforts in the future, we will be able to understand that significant progress will be made in the details of

T. hydatigena.

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Credit Authorship Contribution Statement

YF, RM, and FZ conceived the study and drafted the manuscript. FZ, ZL, and YH carried out the experiments and analyzed the data. ZZ, YM, DJRQ, and RM contributed to the collection of the samples. XY, CGG, YF, and FZ contributed material, discussions of the results, and to the final version of the manuscript. All authors read and approved the final manuscript.

Declaration of Competing Interests

The authors declared that they have no conflicts of interest in this work.

Code Availability Not applicable

Data availability

Data will be made available on request.

Declarations Ethical Approval

All animal experiments were performed in accordance with the guidelines of the Institutional Animal Care and Use Committee of the Qinghai University (PJ202501-102).

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