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EDITED BY  
Anna Rita Rossi,  
Sapienza University of Rome, Italy

REVIEWED BY  
Qiong Shi,  
BGI Academy of Marine Sciences,  
China  
Zhiqin Xie,  
Guangxi Veterinary Research Institute,  
China

\*CORRESPONDENCE  
Tianxiang Gao  
gaotianxiang0611@163.com

<sup>†</sup>These authors have contributed  
equally to this work and share  
first authorship

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# Profile of the genomic characteristics and comparative studies of five Trichiuridae species by genome survey sequencing

Na Song<sup>1†</sup>, Xiang Zhao<sup>1†</sup>, Chuangeng Cai<sup>1</sup> and Tianxiang Gao<sup>2\*</sup>

<sup>1</sup>The Key Laboratory of Mariculture, Ocean University of China, Ministry of Education, Qingdao, Shandong, China, <sup>2</sup>Fishery College, Zhejiang Ocean University, Zhoushan, China

Trichiuridae fish are economically important species and are widely distributed across the nearshore to the open ocean. In the present study, the genomic survey sequencing method was used to analyze the genomic characteristics of five Trichiuridae fish. The calculated genome size was 913 Mb, 868 Mb, 871 Mb, 747 Mb, and 670 Mb for *Trichiurus japonicus*, *Trichiurus nanhaiensis*, *Trichiurus brevis*, *Lepturacanthus savala*, and *Eupleurogrammus muticus*, respectively. The average GC content of the five Trichiuridae fish ranged from 39.59% to 42.05%, and the repeat sequence content ranged from 33.21% to 45.87%. The heterozygous ratio of *E. muticus* was the highest, and that of *L. savala* was the smallest. The proportion of microsatellite motifs showed a decreasing trend with the increase in repeat numbers: the dinucleotide repeats were dominant, followed by the trinucleotide repeats, tetranucleotide repeats, pentanucleotide repeats, and hexanucleotide repeats. The mitochondrial genomes of five Trichiuridae species were excavated from the genome data, and the ML tree revealed that *T. japonicus*, *T. nanhaiensis*, *T. brevis*, *L. savala*, and *E. muticus* formed into one clade. *E. muticus* showed earlier expansion than the other four species and had a significant population decline at the Last Glacial period by pairwise sequentially Markovian coalescent (PSMC) analysis. This is the first report to sequence and characterize the whole genomes of five Trichiuridae species.

## KEYWORDS

genome survey, Trichiuridae, microsatellite, mitochondrial genome, PSMC

## Introduction

Trichiuridae belongs to Perciformes, Scombroide, which is a group composed of more than 40 species (Hsu et al., 2009; Nelson et al., 2016). Trichiuridae fish are economically important species and are widely distributed across the nearshore to the open ocean (Fischer et al., 1995). It was reported that there are six species distributed in the coastal waters of China, namely, *Trichiurus japonicus*, *Trichiurus nanhaiensis*, *Trichiurus brevis*, *Lepturacanthus savala*, *Eupleurogrammus muticus*, and *Tentoriceps cristatus* (Yi et al., 2022). *T. nanhaiensis* and *T. brevis* are mainly distributed in the South China Sea and the other four species have a wider distribution range in China. There are also six other species distributed in the open sea of China with a depth of more than 100 m (Yi et al., 2022). Trichiuridae fish could be divided into two groups, scabbardfishes and hairtails, which have significant differences in tail shape (Yi et al., 2022). Most scabbardfishes inhabit offshore waters with more than 250 m of water depth (Fischer et al., 1995).

With the development of high-throughput technology, some whole genomes of fishes have been published (Xu et al., 2014; Chen et al., 2019; Kon et al., 2021), which provided abundant information for their further genetic study. The genome survey analysis, *a priori* knowledge of the whole genome, could predict the genome size, the heterozygous ratio, and repeat ratio, which can help us better know the basic information of the whole genome (Huang et al., 2022). In addition, it can also help us identify the genome-wide short sequence repeat (SSR) motifs, separate the mitochondrial genomes, or conduct the demographic history analysis (Xu et al., 2020; Huang et al., 2022). Due to its convenience and low cost, a large number of genome survey was conducted recently (Chen et al., 2019; Schroeter et al., 2020). SSRs are widely distributed in eukaryotic genomes and show polymorphism at both individual and population levels, which can be widely used in constructing linkage maps, and performing population genetic studies and pedigree identification (Xiong et al., 2021). The genomic SSRs have higher polymorphism and better coverage than transcriptome data, and then could be widely used for SSR development (Baeza et al., 2021). Compared with traditional development methods, high-throughput sequencing is more cost-effective, time-saving, and powerful, and then genome

data obtained by high-throughput sequencing have become an important resource for SSR development (Jo et al., 2021).

The rich single-nucleotide polymorphisms (SNPs) obtained by next-generation sequencing can be widely used in the phylogenetic reconstruction of objective species (Xu et al., 2019). Moreover, the separated mitochondrial DNA sequence from the genome survey data may be more commonly used in the phylogenetic analysis due to rich sequences, which could be downloaded from databases. The genome survey can also be beneficial for evolutionary biology by analyzing the historical changes in the effective population size (Jia et al., 2020).

The external morphological characters of Trichiuridae fish are similar and some existing taxonomic keys disputes, so it is difficult to identify some species (Tzeng and Chiu, 2012). Until the 1990s, taxonomists believed that there was only one hairtail species in China. Trichiuridae fish are an important resource, but the overall catch was often reported without species distinction. For example, *L. savala* and *E. muticus* were often misidentified as *T. japonicus* in the statistical data. Recently, different molecular markers have been used to study the systematic classification and genetic relationship of Trichiuridae fish, which greatly correct the traditional classification and provide us with a clearer genetic relationship map (Karaiskou et al., 2003; Chakraborty et al., 2006; Hsu et al., 2007; Tzeng et al., 2007; Zheng et al., 2015). However, until now, no genomic information of Trichiuridae fish was available, and the phylogenetic relationship of Trichiuridae fish needs to be reevaluated by more powerful methods. Then, it is necessary to supplement genetic information for their further study. In the present study, the genome survey analysis of five Trichiuridae fishes was firstly conducted, and we aim to evaluate their genome size and characteristics, preparing for further whole genome sequencing. Based on the genome data, microsatellite motifs and mitochondrial genome were also identified, which can profit further population genetic studies.

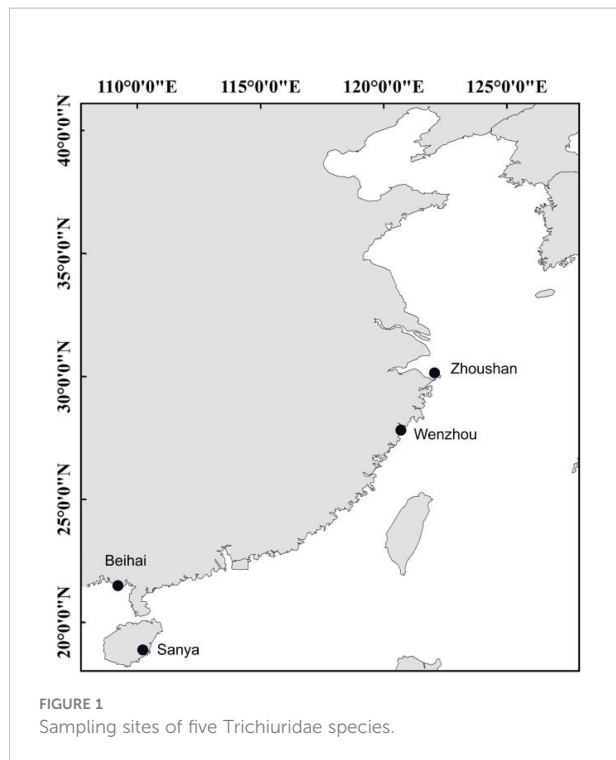
## Materials and methods

### Sample collection and DNA extraction

The specimens used in this study were collected from the coastal waters across the East China Sea and South China Sea

TABLE 1 Sampling information of the five Trichiuridae species in this study.

Genus	Latin name	Sampling time	Sampling site
<i>Trichiurus</i>	<i>Trichiurus japonicus</i>	16 July 2021	Zhoushan, the East China Sea
	<i>Trichiurus nanhaiensis</i>	20 March 2018	Sanya, South China Sea
	<i>Trichiurus brevis</i>	8 April 2019	Beihai, South China Sea
<i>Lepturacanthus</i>	<i>Lepturacanthus savala</i>	7 November 2019	Wenzhou, the East China Sea
<i>Eupleurogrammus</i>	<i>Eupleurogrammus muticus</i>	8 April 2019	Beihai, South China Sea



(Table 1; Figure 1). The individuals were identified based on their morphological characteristics and the muscle tissue was stored in 95% alcohol for DNA extraction. The standard phenol/chloroform method was used for DNA extraction and RNase A was used to purify the DNA template. Fish muscle tissue was first ground in liquid nitrogen, followed by addition of SDS buffer and proteinase K to lyse cells and remove impurities. DNA extraction solution (phenol:chloroform:isoamyl alcohol = 25:24:1) was used for DNA extraction, isopropanol was used to recover the DNA pellet, and finally the DNA was washed with cold 70% ethanol. After the residual ethanol evaporates, add sterile water to dissolve the DNA.

## Library construction and sequencing

The library construction and sequencing were performed in the Gooalgene Technology Company in Wuhan, and the sequence reads reported in this study have been deposited in GenBank with No. PRJNA825079.

## Sequencing data quality control and K-mer analysis

The software FASTP was used to conduct the quality control of raw sequencing data, and clean data were obtained (Chen et al., 2018). The quality values Q20 (ratio of bases with

sequencing quality value above 20), Q30 (proportion of bases with sequencing quality values above 30), and GC distribution statistics were calculated to evaluate the sequencing quality. A total of 10,000 pairs of clean reads were randomly selected and blasted with the NCBI nucleotide database (NT Library) to confirm that the sequencing reads were not polluted. The software JELLYFISH was used to perform the K-mer analysis, and the genome size was calculated based on the K-mer frequency distributions (Marçais and Kingsford, 2011). The heterozygous ratio and repeat sequence content were obtained by GCE software (Liu et al., 2013).

## Identification of SSR motifs

We used SOAPdenovo2 to assemble the clean reads separately into unique contigs and scaffolds (Luo et al., 2012). The potential microsatellite motifs were searched using the Perl script “misa.pl” of MISA software (Beier et al., 2017). The search parameters were set for the detection of di-, tri-, tetra-, penta-, and hexanucleotide microsatellite motifs with a minimum of six, five, five, five, and five repeats, respectively.

## Mitochondrial genome assembly and single copy gene extraction

The filtered clean reads were also used to assemble the complete mitochondrial genomes by MitoFinder software (Allio et al., 2020). To construct the phylogenetic relationship among Trichiuridae species, the mitochondrial genomes of *Aphanopus carbo* (16406, AP012944), *Assurger anzac* (16510 AP012508), *Benthodesmus tenuis* (16864, AP012522), and *Evoxymetopon poeyi* (16475 AP012509) were downloaded from NCBI. Since the ND6 gene was very ineffective in restoring the expected phylogenetic performance (Miya and Nishida, 2000), we removed it and used IQ-TREE software (Minh et al., 2020) to construct ML phylogenetic trees based on the other 12 protein-coding genes. The OrthoFinder and Busco5 software were used to search for single-copy homologous genes and reconstruct phylogenetic trees (Simão et al., 2015; Emms and Kelly, 2019).

## Population size dynamics

The pairwise sequentially Markovian coalescent method (PSMC) was used to infer the population size history of five Trichiuridae species (Li and Durbin, 2011). The “fq2psmcf” and “splitfa” tools in the PSMC software were used to create the input file for the PSMC modeling. The PSMC analysis command included the options “-N25” for the number of cycles of the algorithm, “-t15” as the upper limit for the most recent common

ancestor (TMRCA), “-r5” for the initial  $\theta/\rho$ , and “-p 4 + 25\*2 + 4 + 6” for atomic intervals. The reconstructed population history was plotted using the “psmc\_plot.pl” script with the substitution rate “-u 2.5e-8” and a generation time of 2 years.

## Results

### Sequence quality estimation of five Trichiuridae genomes

A 300- to 350-bp insert library was constructed for Illumina nova sequencing of the five species, and a total of 53.44 Gb, 45.75 Gb, 52.34 Gb, 49.94 Gb, and 48.60 Gb of clean reads were obtained for *T. japonicus*, *T. nanhaiensis*, *T. brevis*, *L. savala*, and *E. muticus* after the quality control, respectively. All the Q20 values were over 97% and all the Q30 values were over 92%, which ensured the accuracy of sequencing in this study (Table 2). From the results of NT library comparison of sequencing data, the top species blasting against the NT Database were related fish species, which proved no obvious exogenous contamination during the library construction (data not shown).

### Genome size and sequence characteristic

The expected K-mer depth was estimated to be 49, 36, 40, 45, and 49 for the five species, and we can speculate the genome size of these five Trichiuridae species according to the K-mer depth and number (Figure 2, Table 3). The calculated genome size of *E. muticus* was the smallest (680 Mb), and the size of *T. japonicus* was the largest (928 Mb) (Table 3). The repeat sequence content of *T. japonicus* was the smallest (33.21%) and *T. brevis* was the highest (45.87%). The high heterozygous ratio of *E. muticus* was the highest (1.26), and *L. savala* was the smallest (0.72) (Table 3).

The draft genome assembly was performed using the filtered clean data. The assembled information of five Trichiuridae species are shown in Table 4. By comparison, *T. japonicus* had the largest total length and total number, while both the N50 length and N90 length at the contig and scaffold level were the

smallest for *T. japonicus*. The average GC content of the five Trichiuridae fish ranged from 39.59% to 42.05% (Table 2).

### Profile of candidate microsatellite markers

Based on the genome survey data, the total number of identified SSRs of the five Trichiuridae species was 563,132, 383,808, 342,191, 432,258, and 470,603, respectively. The detailed information is shown in Table 5. Among the motif types of microsatellites of the five Trichiuridae species, the dinucleotide repeats were dominant (78.05%–87.24%), followed by the trinucleotide repeats (11.60%–17.07%), tetranucleotide repeats (1.08%–4.36%), pentanucleotide repeats (0.04%–0.4%), and hexanucleotide repeats (0.01%–0.12%) (Figure 3). The proportion of microsatellite motifs showed a decreasing trend with the increase in repeat numbers. The motif AC was the most abundant among the dinucleotide repeat motifs and the motif AAAT was the most among the tetranucleotide repeat motifs for all five Trichiuridae species (Figure 3). The motif CCT of trinucleotide repeats was the most abundant for *T. nanhaiensis* and *T. brevis*, motif GAG was the most abundant for *E. muticus* and *T. japonicus*, and motif AAT was the most abundant for *L. savala*. The numbers of pentanucleotide and hexanucleotide repeat types were relatively small and the difference is not obvious (less than five for pentanucleotide repeats and less than two for hexanucleotide repeats) (Figure 4).

### Characterization of mitochondrial DNA genomes

The mitochondrial genomes of five Trichiuridae species were excavated from the genome survey data. The total length of mitogenome for *T. japonicus*, *T. nanhaiensis*, *T. brevis*, *L. savala*, and *E. muticus* was 16,513 bp, 16,722 bp, 16,921 bp, 16,506 bp, and 15,906 bp, respectively. The closed circular molecule of the five species was incomplete because of the lack of the second half of the control region and tRNA-pro. The structure diagram of five mitochondrial genomes is shown in Figure 5. To infer the

TABLE 2 The statistical information of sequencing quality control of five Trichiuridae species.

Species	Read number	Base count (Gb)	Read length (bp)	Q20 (%)	Q30 (%)	GC_Content (%)
<i>T. japonicus</i>	356,281,940	53.44	150	92.93	93.31	40.49
<i>T. nanhaiensis</i>	307,386,374	45.75	150	97.59	93.46	42.05
<i>T. brevis</i>	354,230,582	52.34	150	97.26	92.76	41.57
<i>L. savala</i>	335,525,760	49.94	150	97.39	92.72	39.59
<i>E. muticus</i>	325,848,140	48.60	150	97.46	93.01	41.68

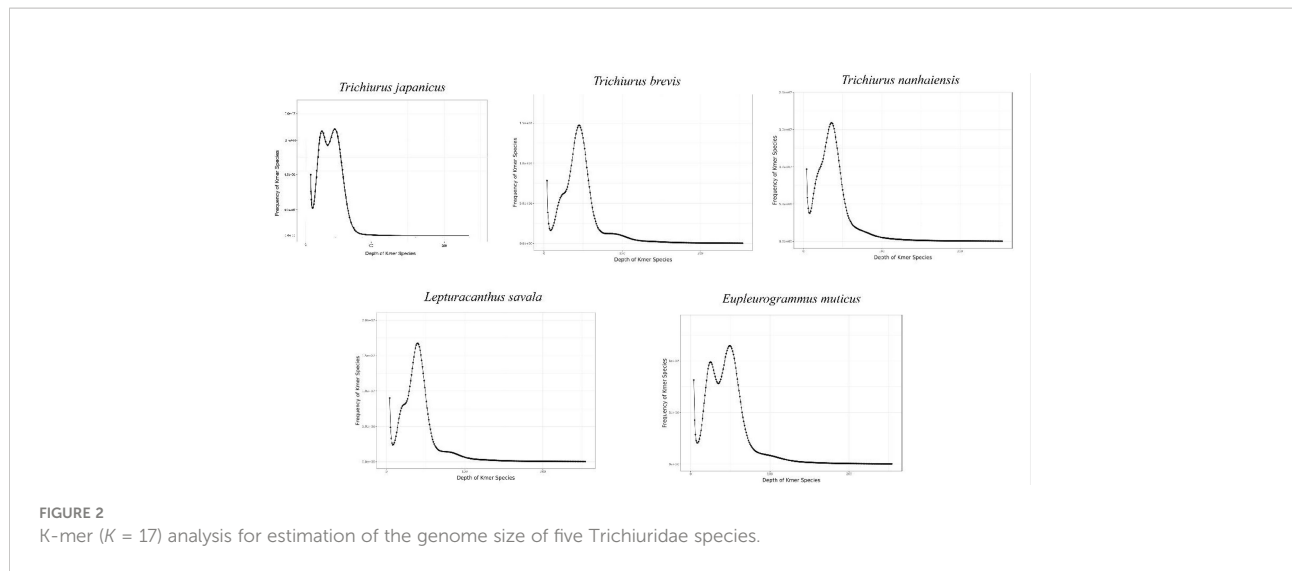


FIGURE 2 K-mer ( $K = 17$ ) analysis for estimation of the genome size of five Trichiuridae species.

TABLE 3 The statistical information of K-mer analysis of five Trichiuridae species.

Species	K-mer number	K-mer depth	Genome size (Mb)	Revised genome size (Mb)	Heterozygous ratio (%)	Repeat ratio (%)
<i>T. japonicus</i>	44,764,803,566	49	928	913	0.98	33.21
<i>T. nanhaiensis</i>	32,823,385,484	36	881	868	0.85	44.80
<i>T. brevis</i>	36,447,834,040	40	884	871	0.77	45.87
<i>L. savala</i>	35,344,340,130	45	758	747	0.72	39.73
<i>E. muticus</i>	35,180,122,113	49	680	670	1.26	35.33

TABLE 4 The genome assembly result of five Trichiuridae species.

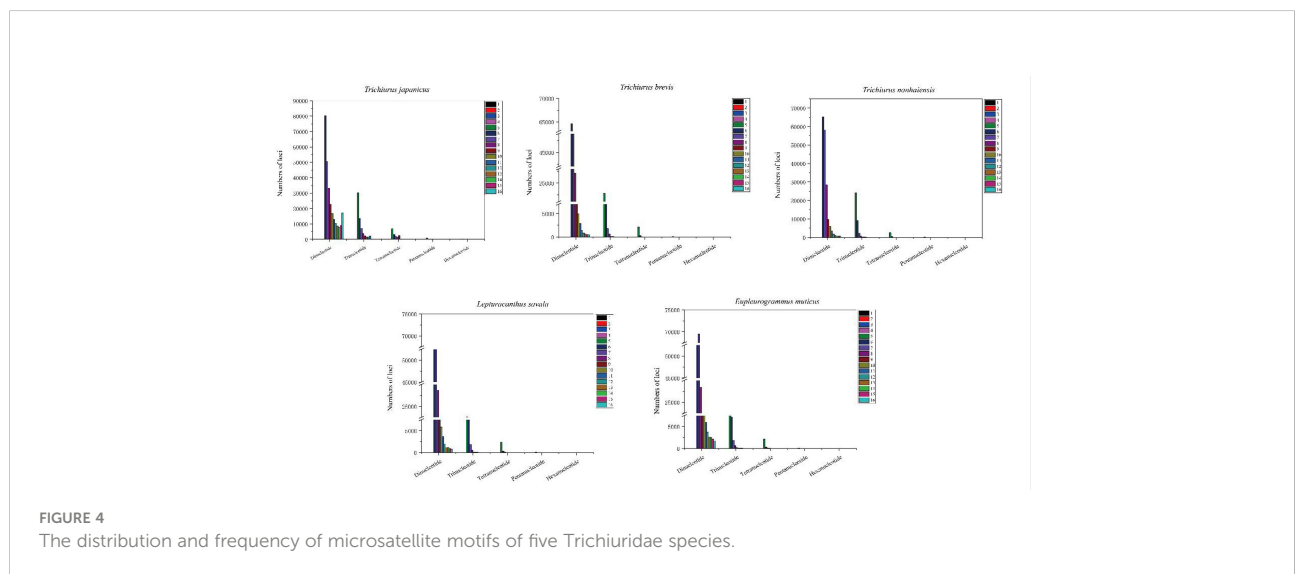
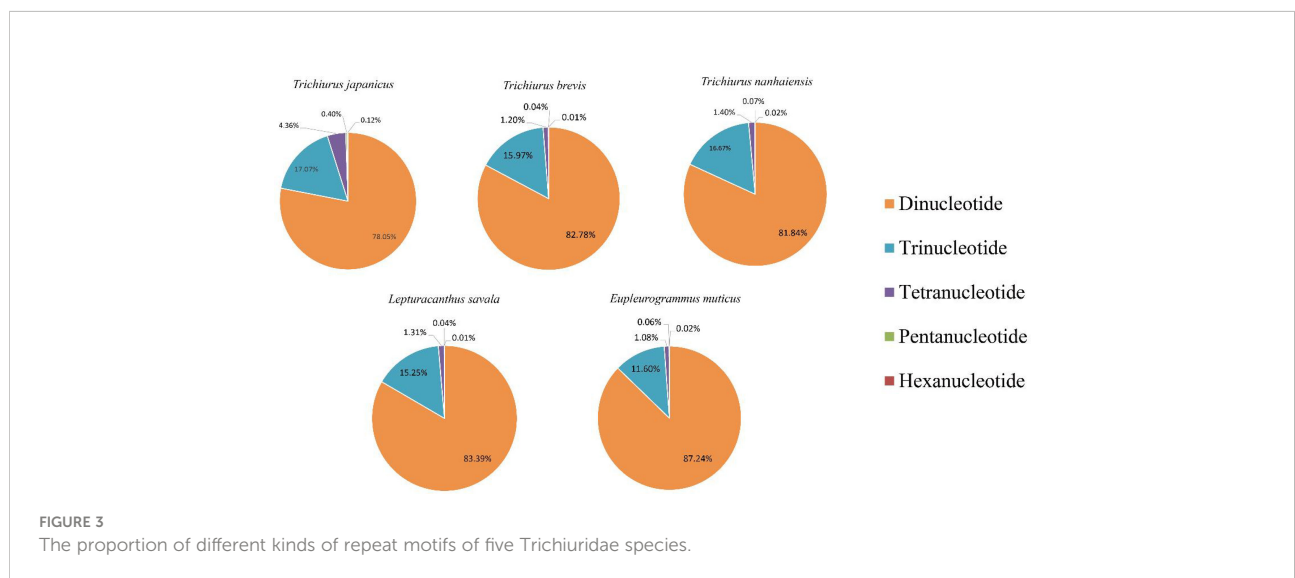
Species	Assembly level	Total length (bp)	Total number	Max length (bp)	N50 length (bp)	N90 length (bp)
<i>T. japonicus</i>	Contigs	821,429,052	3,175,137	24,843	348	119
	Scaffolds	806,040,585	2,173,413	33,595	813	130
<i>T. nanhaiensis</i>	Contigs	574,454,185	1,702,578	8,788	498	141
	Scaffolds	616,492,838	778,987	28,423	1,915	323
<i>T. brevis</i>	Contigs	550,187,406	1,523,098	8,207	519	156
	Scaffolds	589,744,661	619,948	23,724	2,019	435
<i>L. savala</i>	Contigs	561,400,235	1,564,908	9,305	527	152
	Scaffolds	608,518,016	556,218	31,014	2,898	519
<i>E. muticus</i>	Contigs	512,804,229	1,764,321	8,586	381	132
	Scaffolds	555,195,856	800,016	30,384	2,024	233

phylogenetic relationship among five Trichiuridae species, the mitochondrial genomes of four scabbardfishes were downloaded and the 12 protein-coding genes (except ND6) were used to construct the ML tree. We chose “TIM2+F+I+G4” as the best-fit model according to Bayesian Information Criterion (BIC), and then used IQ-TREE software to construct ML tree based on

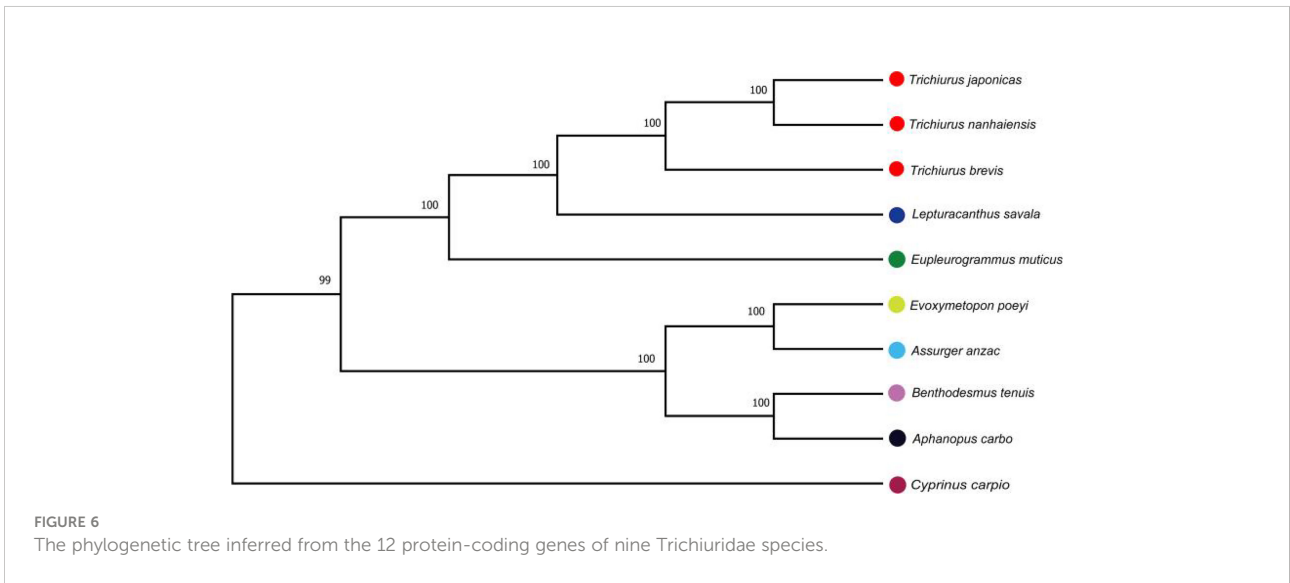
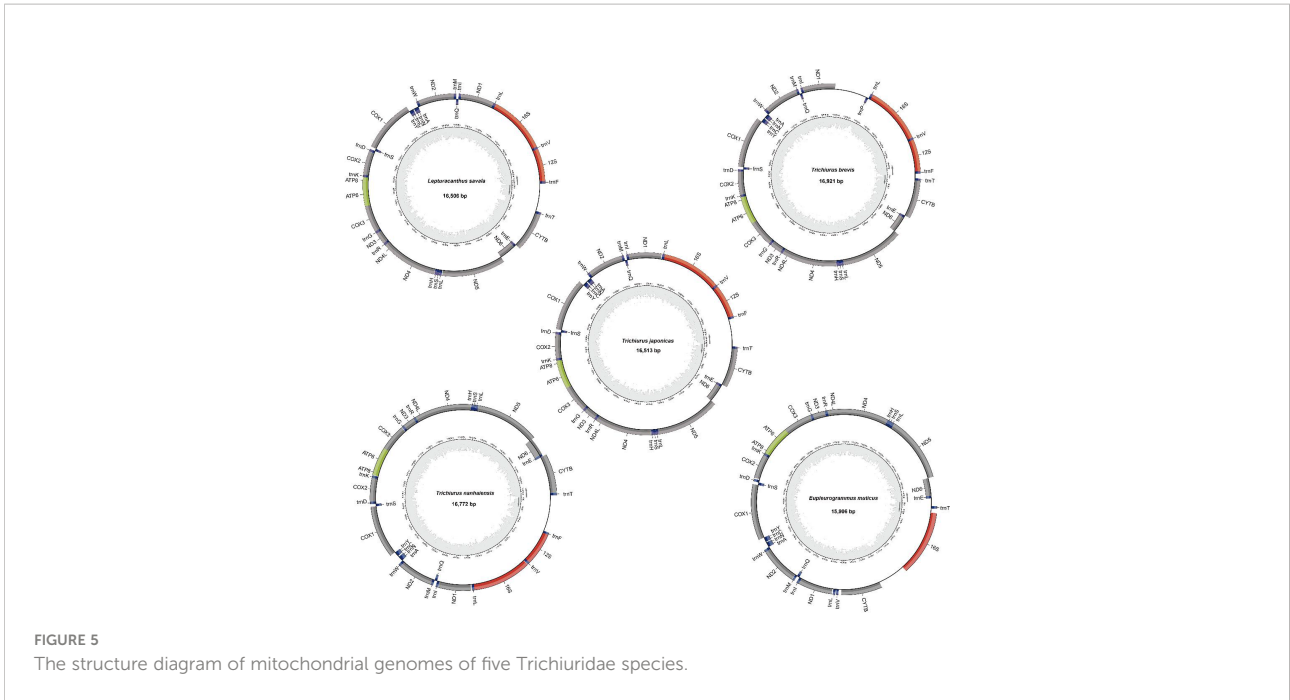
1,000 bootstraps. The results revealed that five *Trichiurus* species in the present study formed into one clade, and the other four species formed into another clade (Figure 6). Additionally, the phylogenetic tree inferred from the single-copy homologous genes showed that three *Trichiurus* species clustered firstly, and the other two species formed into another clade (Figure 7).

TABLE 5 Microsatellite motifs of five Trichiuridae species.

	<i>T. japonicus</i>	<i>T. nanhaiensis</i>	<i>T. brevis</i>	<i>L. savala</i>	<i>E. muticus</i>
Total number of sequences examined	2,173,413	778,987	619,948	556,218	800,016
Total size of examined sequences (bp)	824,855,521	631,933,681	603,826,712	624,244,638	570,081,961
Total number of identified SSRs	563,132	383,808	342,191	432,258	470,603
Number of SSR containing sequences	370,907	204,805	192,647	200,286	233,530
Number of sequences containing more than 1 SSR	106,043	82,846	74,374	92,743	95,802
Number of SSRs present in compound formation	71,344	35,098	28,056	40,380	48,145







### Demographic history of five Trichiuridae fish

The PSMC analysis was conducted to estimate the demographic history of five Trichiuridae species, and the changes in effective population size between 10 ka and 1 ma are shown in Figure 8. The population expansion event for *T. japonicus*, *T. nanhaiensis*, *T. brevis*, and *L. savala* exhibited a similar trend, which was about 100 ka YBP, while *E. muticus* showed earlier expansion and has a significant population decline

during the Last Glacial period. Among five Trichiuridae fish, *T. japonicus* and *T. nanhaiensis* showed obvious larger effective population sizes than the other three species.

### Discussion

The improvement of high-throughput sequencing technology and the development of sequence assembling algorithms have made it possible to obtain plenty of whole

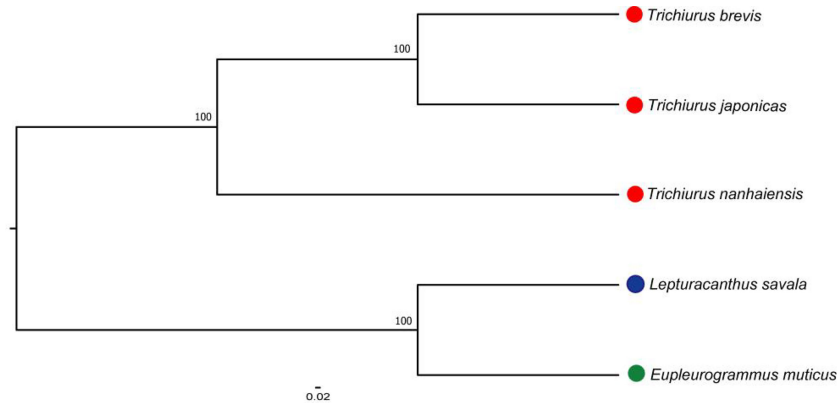


FIGURE 7 The phylogenetic tree inferred from the single-copy homologous genes of five Trichiuridae species.

genome sequences at low cost and high efficiency (Gaither et al., 2018; Kon et al., 2021). The exponentially increasing number of genome sequences has greatly promoted the rapid development of life science (Xu et al., 2017). However, the genome size and complexity of different species vary significantly, and then the genome survey analysis played a key role in whole genome sequencing (Xu et al., 2019; Jo et al., 2021). In the present study, all the Q20 values were over 97% and all the Q30 values were over 92%, which ensure the sequencing quality. As the important sequence index, the GC content could affect the randomness of genome sequencing (Xu et al., 2014). The average GC content for Trichiuridae species ranged from 39.59% to 42.05% in this study, which was mid-GC content and in the normal range (Zhou et al., 2013; Chen et al., 2020). According to the K-mer analysis index, the calculated genome size of the five Trichiuridae species was

913 Mb (*T. japonicus*), 868 Mb (*T. nanhaiensis*), 871 Mb (*T. brevis*), 747 Mb (*L. savala*), and 670 Mb (*E. muticus*), respectively. Most reported fish genomes were less than 1 Gb (Chen et al., 2019), and five Trichiuridae fish in this study fit this pattern. However, it is worth noting that the heterozygous ratio for *T. japonicus* and *E. muticus* was high, and they had two K-mer peaks, which may affect actual genome assembly. In conclusion, the genomes of five Trichiuridae fish species are relatively simple and suitable for further whole genome sequencing.

In the present study, the dinucleotide repeat was the most abundant SSR motif for the five species, which is similar to other reported data (Zeng et al., 2013; Chen et al., 2020). *E. muticus* has the largest total number of identified SSRs among five Trichiuridae species. The proportion of the motif types for *T.*

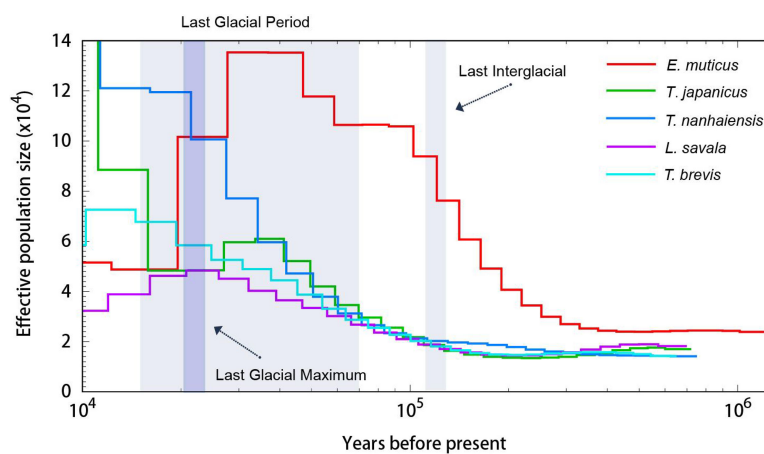


FIGURE 8 The effective population size estimates of five Trichiuridae fish in this study.



*japonicus*, *T. nanhaiensis*, *T. brevis*, and *L. savala* was similar, while *E. muticus* showed a significant difference with them. Moreover, the proportion of trinucleotide repeats for *E. muticus* was the highest and that of tetranucleotide repeats was the lowest, which indicated its distinctiveness. We speculated that this may be related to its higher genomic heterozygosity (Yang et al., 2019). The phylogenetic tree inferred from two methods also validated the above presumption. According to our results, the number of identified SSRs was not related to the genome size. The proportion in the motif types showed a decreasing trend with the increase in repeat numbers, and the differences of the motif types may be related to the selection and evolution mechanisms of different species (Doris et al., 2000). SSRs in different genomic regions may have various characteristics to perform different functions (Sonah et al., 2011). Although longer motifs are much less and more difficult for isolation, they are also important for having more accuracy in allele assignment than shorter repeats (Qiu et al., 2020). Until now there are few reported microsatellite markers for Trichiuridae fish (but see Bi et al., 2009; Guo et al., 2012; Zhang et al., 2019), and therefore, the results of this study could provide strong support for their subsequent study on the population genetics and breeding.

The mitogenomes of *T. japonicus* (No. NC\_011719.1, 16796), *T. nanhaiensis* (No. NC\_018791.1, 17060), *T. brevis* (No. MW694877, 15688), *E. muticus* (No. MN067886.1, 18251), and *L. savala* (MT269921, 17146) have been reported in the previous study (Liu and Cui, 2009; Liu et al., 2013; Fan et al., 2019; Cai et al., 2020). The genome length of four Trichiuridae species in this study was shorter than the reported sequences except for *T. brevis*. The tRNA-Pro was absent in the *Trichiurus* mitochondrial genome, which was consistent with the results of Yi et al. (2022). The obtained length of *T. brevis* in the present study was 188 bp longer than the reported sequences, which was caused by the absence of tRNA for sequence MW694877. Although the absence of some fragments often occurs in the next high-throughput sequencing, it still was thought to be an effective method for developing the mitogenome sequences (Xu et al., 2019).

The ML phylogenetic tree constructed by 12 protein-coding genes showed a close relationship among *T. japonicus*, *T. nanhaiensis*, *T. brevis*, *L. savala*, and *E. muticus*, which was consistent with the previous results (Xiong et al., 2021; Yi, 2019; Cai, 2020). Trichiuridae fishes were often classified into two groups (scabbardfishes and hairtails) based on their tail characters. The five Trichiuridae species in the present study belong to the hairtail type and the other four species, *A. carbo*, *A. anzac*, *B. tenuis*, and *E. poeyi*, belong to scabbardfishes, which was also in accordance with the results of COI sequences (Cai, 2020). There are few reported mitochondrial genomes of Trichiuridae fish, which had an appreciable effect on the construction of their phylogenetic tree. More molecular and morphological data were required to reveal the phylogenetic relationship of Trichiuridae fish. Moreover, the genomic information of scabbardfishes is strongly demanded in the following studies.

The population history dynamic analysis based on the PSMC model showed that the effective population sizes of five Trichiuridae fish all increased before the last glacial maximum. However, they emerged with different changing trends during the last glacial maximum. The drastic climate change during the Pleistocene period has been reported to play an important role in the population size and habitat dynamic of marine organisms (Liu et al., 2007). In the present study, only *T. nanhaiensis* showed a continuing increase, while *T. japonicus* experienced a brief decreasing period and began to increase continuously. The effective population size of *T. brevis*, *L. savala*, and *E. muticus* failed to increase since the last glacial maximum. The recolonizing ability may be related to their original distribution and adaptability (Liu et al., 2007). Among the genus *Trichiurus*, *T. brevis* was the ancestral species. *T. japonicus* was the latest species, but it had the widest distribution (Yi et al., 2022). The process of species formation and evolution ability may correspond to its distribution area. The genome size of *T. japonicus* was the largest, and the ratio of the repeat sequence was the smallest in this study. This may be related to its strong adaptability and rapid expansion after the Pleistocene period (Lin et al., 2021).

In conclusion, this is the first report to sequence and characterize the whole genomes of five Trichiuridae fish, which opened up new horizons for this fish group. The genomes of five Trichiuridae fish ranged from 670 Mb to 913 Mb, which were relatively simple and suitable for further whole genome sequencing. The sequencing data will profit the following SSR development of the Trichiuridae fish and can provide useful genetic information for them.

## Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://www.ncbi.nlm.nih.gov/>, PRJNA825079.

## Ethics statement

The animal study was reviewed and approved by Animal Research and Ethics Committees of the Ocean University of China.

## Author contributions

TG conceived and managed the project. XZ and CC collected the sequencing samples. XZ performed the experiment and analysis. NS wrote the manuscript. TG and

XZ revised the manuscript. All authors contributed to the article and approved the submitted version.

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