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A chromosome-level reference genome of the surf parrotfish (*Scarus rivulatus*)

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The parrotfish, *Scarus rivulatus*, is a widely distributed herbivorous species, that helps maintain reef resilience by controlling algal growth. However, overfishing and reef degradation threaten its populations, and the lack of genomic resources limits studies on its adaptive potential and conservation strategies. In this study, we successfully assembled a high-quality chromosome-level genome for *S. rivulatus* using a combination of Illumina, Nanopore, and Hi-C technologies. The assembled genome is 1.58 Gb in size, with scaffold N50 lengths reaching 67.2 Mb. Hi-C contact maps anchored approximately 96.2% of the assembled sequences onto 24 chromosomes. Repetitive sequences accounted for 48.84% of the genome. The BUSCO assessment revealed that 97.8% of the expected conserved genes were complete. Integrating three lines of evidence, we predicted 41,823 protein-coding genes, of which 73.91% were functionally annotated in at least one protein database. This chromosome-level genome assembly filled a critical gap in genomic resources for *S. rivulatus*, providing a valuable foundation for elucidating its adaptive mechanisms in response to coral reef degradation and facilitating genetic breeding.

Background & Summary

Coral reefs are among the most biologically diverse and productive marine ecosystems in the world, providing an ideal habitat for marine life¹. As key consumers, coral reef fishes play a crucial role in cycling carbon (C), nitrogen (N), and phosphorus (P), as well as in processes such as biomass production, herbivory, and piscivory (secondary consumption)². These functions are intrinsically linked, with the synergistic actions of reef fishes collectively enhancing ecosystem resilience and supporting the maintenance of ecological balance. However, due to the combined effects of marine heatwaves, ocean acidification, pollution, and overfishing, global coral reef coverage has declined significantly in recent decades^{3,4}. The degradation of coral reefs has led to the decrease of coral fish biomass and the change of community structure⁵. For instance, in Australia's Great Barrier Reef, a massive coral bleaching event in 2016 led to the widespread death of about 30% of coral communities and a continuing decline in local fish species richness⁶. Recent studies have demonstrated that the spatial covariation patterns of herbivore functional roles can significantly affect coral reef resilience. Following coral mortality events, browsers, in contrast to grazers, play a more critical role in removing established macroalgae from reef substrates⁷. As the transition of corals to macroalgae gradually becomes the norm, herbivorous corals have received increasing attention for their role in regulating competition between corals and algae⁸.

Herbivorous fishes are considered key contributors to maintaining coral reef health, as they regulate the competition between algae and scleractinian corals for substrate space by controlling benthic algae, thereby enhancing reef resilience and preventing phase shifts^{9–11}. Among them, Acanthuridae and Scaridae are prominent herbivores in coral reef ecosystems¹². *Acanthurus nigrofasciatus* is recognized for its broad dietary range, which enables it to thrive under various environmental conditions, including degraded coral reefs¹³. In contrast,

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Ctenochaetus striatus primarily feeds on detritus; however, the accumulation of fine sediments can inhibit its feeding efficiency, thereby diminishing its critical role in sediment removal and redistribution within coral reef ecosystems^{14,15}. Species such as *S. rivulatus* and *S. taeniopterus* exhibit a preference for feeding on crustose coralline algae and the epilithic algal matrix associated with these substrates. This feeding behavior effectively suppresses the accumulation of tall filamentous and late-successional macroalgae, maintaining early-stage algal communities dominated by short filamentous algae and crustose coralline algae, which do not inhibit coral growth^{16,17}. The study found that the growth rate of Caribbean coral reefs declined in both prehistoric and historical periods as parrotfish declined¹⁸. Thus, parrotfish play a critical role in maintaining coral-dominated reef habitats, and there is an urgent need to restore parrotfish populations for reef persistence.

The Scaridae family comprises 10 genera and 90 recognized species, with the genus *Scarus* emerging as the largest and most diverse, accounting for about 50 of these species¹⁹. Parrotfishes of the genus *Scarus* are primarily scrapers due to their special mouth structure, the fused dentate plate. Their beaks are strong and effective enough to grind up hard corals and rocks²⁰. Among them, *S. rivulatus* is a widely distributed species in Indo-Pacific coral reefs, recognized for its crucial ecological functions and increasing commercial exploitation²¹. Due to rising demand for fisheries and the aquarium trade, populations of *S. rivulatus* are facing mounting pressure from overfishing, which could compromise their ecological role in reef systems²². Despite its ecological and economic importance, genetic and genomic resources for *S. rivulatus* remain limited, constraining our understanding of its adaptive capacity in the face of ongoing coral reef decline.

In recent years, genomics has become an increasingly important tool in conservation biology for understanding the genetic diversity of threatened species. For economically significant species, high-quality reference genomes are essential foundational genetic resources, which also hold considerable value for applications in aquaculture. In this study, we constructed a high-quality, chromosome-level genome assembly of *S. rivulatus* by integrating Illumina short-read sequencing, Nanopore long-read sequencing, and high-throughput chromosome conformation capture (Hi-C) technology. The final assembly consisted of 24 chromosomes, with a total length of 1.58 Gb and a scaffold N50 of 67.2 Mb. We annotated 41,823 protein-coding genes, of which 73.91% (30,910 genes) were functionally annotated. Repetitive elements accounted for 48.84% of the genome, with DNA and LTR elements being particularly abundant. This reference genome fills an important gap in *S. rivulatus* genomic resources, providing a fundamental basis for exploring the genetic mechanisms underlying the adaptation of parrotfish to current reef degradation and supporting the conservation and restoration of both parrotfish populations and coral reef ecosystems.

Methods

Sample collection and DNA extraction. A single adult female *S. rivulatus* specimen was collected from Xincun Harbor, Hainan Province, China, in May 2019. Muscle tissue was excised and immediately snap-frozen in liquid nitrogen before storage at -80°C . High-quality genomic DNA (gDNA) was extracted from freshly harvested muscle using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol²³. The integrity of the DNA was verified by 1% agarose gel electrophoresis, and DNA concentrations were quantified using the Quant-iTTM PicoGreen[®] dsDNA assay (Thermo Fisher Scientific, Waltham, MA, USA).

Short-read library construction and sequencing. According to the method described previously²⁴, gDNA was sheared to an average fragment size of 300–500 bp using a Covaris 2000 Ultrasonicator (Covaris, USA) for short-read sequencing. Fragmented DNA was size-selected, end-repaired, and PCR-amplified to produce sequencing libraries. The prepared libraries were sequenced on an Illumina HiSeq 2500 platform (Illumina, San Diego, CA, USA) in paired-end mode (150 bp), generating approximately 96 Gb of raw data.

Long-read library construction and sequencing. For long-read sequencing, high-molecular-weight genomic DNA was size-selected (~ 20 kb) using the BluePippin system (Sage Science, USA). Library preparation followed the 1D Ligation Sequencing Kit (SQK-LSK109) protocol (Oxford Nanopore Technologies, UK). The final library concentration was measured using a Qubit 3.0 fluorometer (Thermo Fisher Scientific). Sequencing was carried out on a single flow cell of the PromethION platform (Oxford Nanopore Technologies), yielding approximately 196 Gb of raw data.

Hi-C library construction and sequencing. A Hi-C library was also prepared from the same genomic DNA sample to enable chromosome-level scaffolding. Following a previously described standard protocol with specific modifications²⁵, we digested the DNA with MboI and enriched the resulting biotin-labeled Hi-C fragments using streptavidin C1 magnetic beads. Subsequent library preparation involved adding A-tails to the fragment ends and ligating them with Illumina PE sequencing adapters. The final libraries were amplified by PCR and sequenced on the Illumina HiSeq X Ten to generate 150 bp paired-end reads. In total, 63 Gb of Hi-C sequencing data were obtained.

RNA library construction and sequencing. Total RNA was extracted from ten tissues (fins, gonads, heart, intestines, blood, liver, muscles, brain, spleen, and kidneys) and treated with DNase I (Thermo Fisher Scientific, Wilmington, DE, USA) to remove any genomic DNA contamination²⁴. The integrity of the RNA from each tissue was verified using a Bioanalyzer 2100 (Agilent Technologies, Santa Clara, USA). RNA-sequencing libraries with a 300 bp insert size were constructed for each sample, and sequencing was carried out on the Illumina HiSeq platform using 150 bp PE mode. The result was 90 Gb of raw data.

Sequencing data processing and genome survey. The Illumina short-read data were first assessed for quality using FastQC (v0.11.9)²⁶, and low-quality reads and adapters were removed with SOAPnuke (v2.X)²⁷. After filtering, the clean reads were used for genome size and heterozygosity estimation for *S. rivulatus*. K-mer

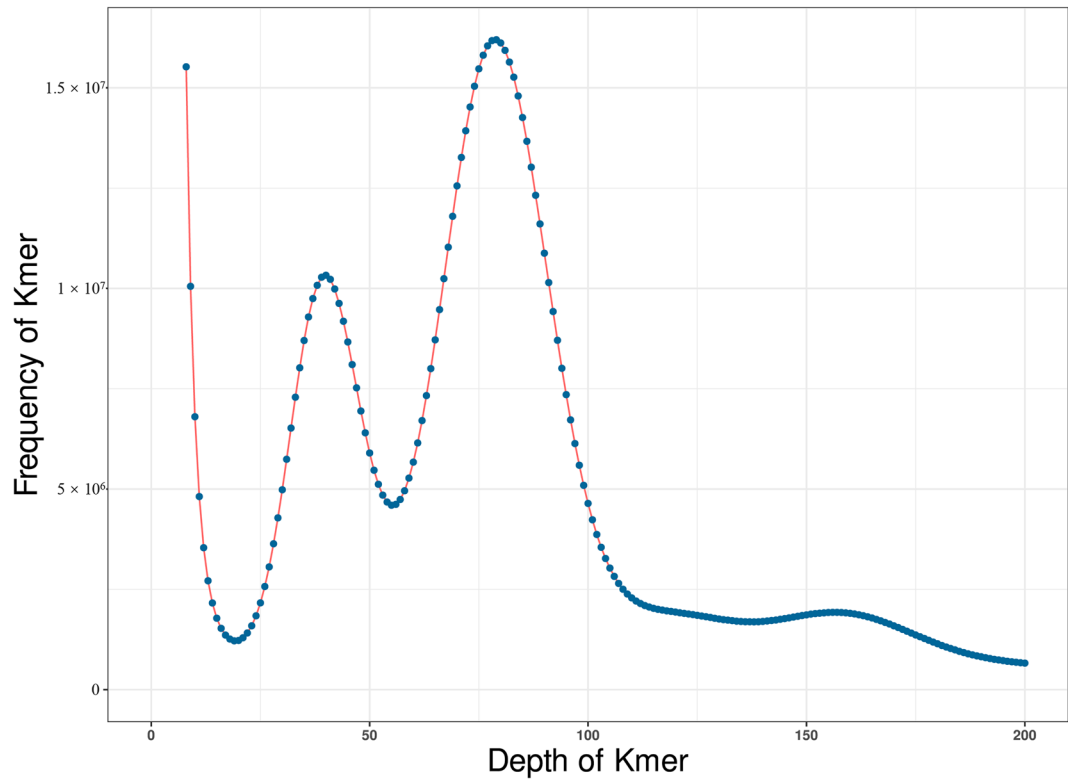


Fig. 1 K-mer frequency distribution of the *S. rivulatus* genome. 17-mer frequency distribution generated from *S. rivulatus* Illumina data, with k-mer depth plotted on the x-axis and frequency on the y-axis.

Item	Contig genome	Chromosome-level genome
Total length (bp)	1,712,172,483	1,584,527,757
Total number (n, >)	495	24
GC (%)	39.36	39.31
N50 (bp)	18,517,359	67,170,024
N90 (bp)	1,065,493	56,837,962
Ave length (bp)	3,458,934	66,021,989
Max length (bp)	60,952,024	81,715,695

Table 1. Statistics of the assembled genome for *S. rivulatus*.

frequency analysis was conducted with GCE (v1.0.2)²⁸ using a *k*-mer size of 17. The resulting *k*-mer frequency distribution (Fig. 1) showed a major peak at a depth of 80. After excluding low-frequency *k*-mers, the genome size was estimated using the formula: genome size = total *k*-mer count/peak depth. The final estimated genome size was 1.55 Gb, with a heterozygosity rate of 0.77%.

De novo genome assembly. For *S. rivulatus*, de novo genome assembly was performed using Nanopore long-read data together with Illumina short reads. First, the assembly process using Nanopore data was carried out with NextDenovo (v2.5.0) (<https://github.com/Nextomics/NextDenovo>) under default parameters to generate an initial assembly. Then, to further improve the base-level accuracy, the assembly was polished using NextPolish (v1.4.1)²⁹ by the Illumina data. The final contig-level assembly comprised 495 contigs, with a total length of 1.71 Gb, an N50 of 18.5 Mb, and a GC content of 39.36%. The longest contig reached 60.9 Mb (Table 1).

The Hi-C sequencing data were utilized to achieve the chromosome-level assembly of the *S. rivulatus* genome. Initially, low-quality and duplicate Hi-C raw reads were removed using Trimmomatic (v0.39)³⁰. The resulting high-quality reads were aligned to the reference genome with Juicer (v1.6)³¹. Chromosome-level scaffolds were then generated by leveraging the genomic proximity information captured by the Hi-C data. To further scaffold the genome, the 3D-DNA³² pipeline was employed, followed by manual refinement of misassemblies using Juicebox (v1.11.08)³³. The final chromosome-level assembly reached a total size of 1.58 Gb, with a scaffold N50 of 67.17 Mb (Table 1). It comprised 24 chromosomes (Fig. 2), ranging from 36.08 Mb to 81.71 Mb in length, with an average chromosome size of 66.02 Mb (Table 2). The GC content of the final assembly was 39.31%. Notably, the total assembled genome size closely matched the estimated genome size from the genome survey, reflecting the high integrity and completeness of this assembly.

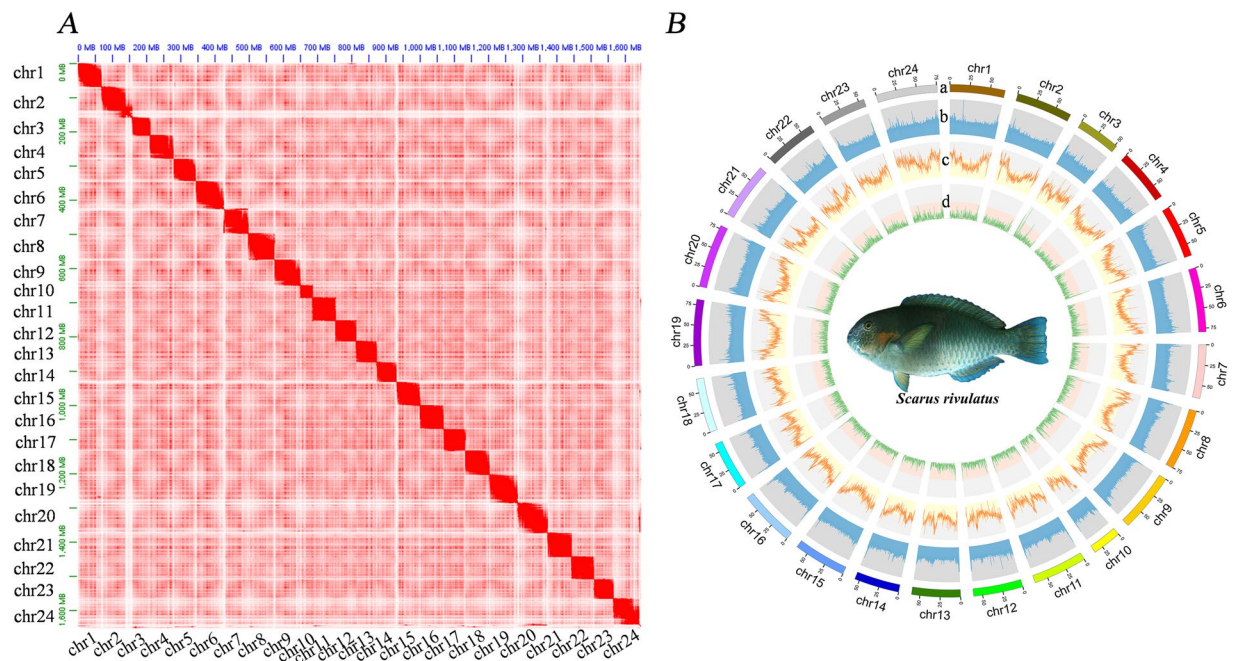


Fig. 2 Assembly results of the *S. rivulatus* genome. (A) Heat map of interactive intensity between chromosome sequences anchored by Hi-C. The width of each column reflects the relative length of the corresponding chromosome, while the intensity of the red color indicates the contact density. (B) Circos plot of the genome features. From the outermost to the innermost rings: (a) chromosomes, (b) GC content, (c) repeat content, and (d) gene density. The chromosome lengths were calculated, and the corresponding positions and lengths were used to create the outermost ring in the Circos plot. GC content was estimated by dividing the genome into 100 KB windows and calculating the GC ratio within each window, with the distribution of GC content displayed in the second ring. Repeat content was estimated by calculating the overlap between each window and known repetitive regions, represented in the third ring of the Circos plot. Gene density was estimated by counting the number of genes within each window and is shown in the innermost ring, reflecting the distribution of genes across the genome.

Repetitive sequences annotation. Prior to annotating protein-coding genes, repetitive regions in the genome were masked using a combined approach of *De Novo* and homology-based methods. We constructed an *S. rivulatus* specific repeat library using RepeatModeler (v2.0.3)³⁴. Initially, this library contained 3,173 consensus sequences, among which 2,510 were categorized as unknown transposable element (TE) families. These unknown sequences were subsequently classified using DeepTE³⁵, resulting in a reduction to 566 consensus sequences.

With this refined consensus sequence library, we annotated repetitive regions in the *S. rivulatus* genome using RepeatMasker (v4.1.2)³⁶. This approach revealed that 48.84% of the genome consists of TE. The most prevalent DNA transposon family was hobo-Activator comprising 8.09% of the genome, followed by the Tc1 family (7.77%). The Gypsy/DIRS1 retrotransposons accounted for 7.41% of LTR (Table 3). Overall, *S. rivulatus* possesses a notably high proportion of TE.

Additionally, we calculated the Kimura two-parameter divergence (K divergence) using the calcDivergence-FromAlign.pl script from RepeatMasker (v4.1.2). The insertion time for each consensus sequence was estimated using the formula $T = K/2r$, where K denotes the divergence calculated by the script, and r represents the neutral mutation rate for teleost (2.5×10^{-9} substitutions/site/year). Our findings indicated that although *S. rivulatus* has a high overall TE content, most of these transposable elements underwent significant expansions approximately 10 million years ago (Mya) (Fig. 3A). Currently, active TE expansions appear to be limited.

Gene prediction and functional annotation. A repeat sequence library was built using RepeatModeler (v2.0.3) and applied with RepeatMasker (v4.1.2) to identify repetitive elements in the *S. rivulatus* genome. Redundant and overlapping sequences were removed to improve accuracy. The resulting masked genome was used for subsequent gene annotation.

To comprehensively predict protein-coding genes in the assembled genome, three complementary strategies were employed. First, de novo gene prediction was conducted using the self-training mode of Augustus (v3.4.0)³⁷, with subsequent annotation refinement performed via the SNAP_to_GFF3.pl and augustus_GTF_to_EVM_GFF3.pl scripts from the Evidence Modeler (v1.1.1)³⁸. Second, transcriptome-based prediction involved aligning RNA-seq data to the *S. rivulatus* genome and assembling the transcriptome using HISAT2 (v2.1.0)³⁹ and StringTie (v2.1.4)⁴⁰. Subsequently, TransDecoder (v5.7.0, <https://github.com/TransDecoder/TransDecoder>) was used to predict the open reading frames (ORFs). Third, homology-based predictions were carried out by aligning protein sequences from *Labrus bergylta*, *Cheilinus undulatus*, *Notolabrus celidotus*, *Sparus aurata*, and *Acanthopagrus latus*, which were downloaded from the NCBI database (Table 4), to the *S. rivulatus* genome.

Chromosome ID	Length (bp)
chr1	68,135,665
chr2	69,493,850
chr3	52,320,324
chr4	66,394,857
chr5	65,105,775
chr6	79,654,674
chr7	65,922,457
chr8	75,545,670
chr9	72,853,727
chr10	36,087,154
chr11	66,384,164
chr12	61,177,400
chr13	60,364,500
chr14	55,849,752
chr15	65,126,414
chr16	69,334,684
chr17	60,693,957
chr18	67,170,024
chr19	81,715,695
chr20	79,135,578
chr21	69,705,093
chr22	63,982,278
chr23	56,837,962
chr24	75,536,103

Table 2. Chromosome length information of *S. rivulatus*.

Type of repeats	Length (bp)	% of genome
SINEs	12,707,630	0.80
LINEs	70,727,929	4.46
L2/CR1/Rex	47,210,726	2.98
R1/LOA/Jockey	605,581	0.04
R2/R4/NeSL	2,009,336	0.13
RTE/Bov-B	4,783,642	0.30
L1/CIN4	11,937,511	0.75
LTR	186,229,235	11.75
BEL/Pao	751,023	0.05
Ty1/Copia	14,710,829	0.93
Gypsy/DIRS1	117,490,550	7.41
Retroviral	17,081,635	1.08
DNA transposons	334,859,781	21.13
hobo-Activator	128,247,738	8.09
Tc1-IS630-Pogo	123,174,615	7.77
PiggyBac	197,626	0.01
Tourist/Harbinger	3,988,953	0.25
Rolling-circles	277,360	0.02
Unclassified	149,994,023	9.47
Simple_repeat	16,608,766	1.05
Low complexity	2,554,292	0.16
Total	773,959,016	48.84

Table 3. Repetitive element annotations in the genome of *S. rivulatus*.

These alignments were further analyzed using Genewise⁴¹ to precisely determine exon-intron structures. Finally, the gene predictions from all three strategies were integrated using EVM to generate a high-confidence, consensus set of protein-coding genes.

Functional annotation of the predicted protein-coding genes in the *S. rivulatus* genome was conducted by aligning these sequences to commonly used protein databases, including SWISS-PROT, NR, TrEMBL, COG,

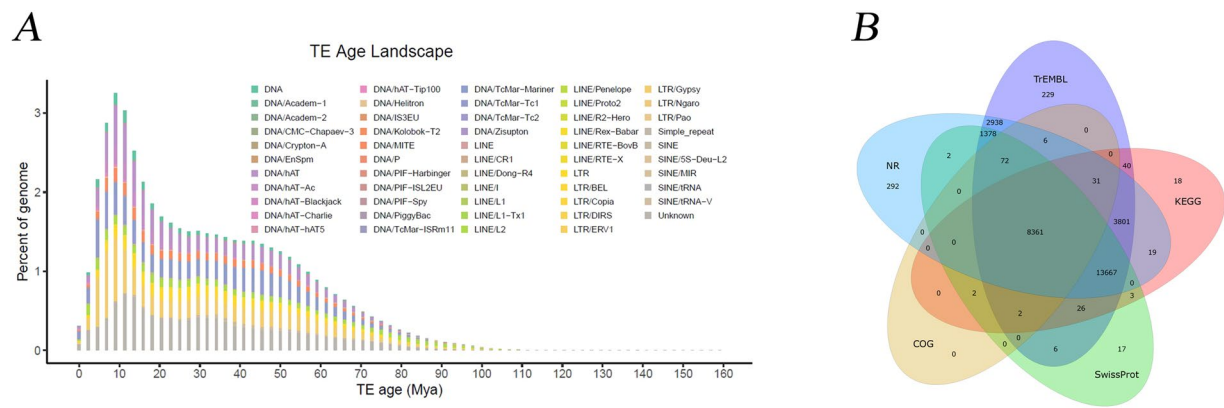


Fig. 3 Repeat and protein-coding genes annotations of the *S. rivulatus* genome. **(A)** Distribution of divergence rate for each type of TEs in the *S. rivulatus* genome. **(B)** Venn diagram of the functionally annotated protein-coding genes based on different databases.

Species	Assembly
<i>Scarus rivulatus</i>	This study
<i>Labrus bergylta</i>	fLabBer1.1
<i>Cheilinus undulatus</i>	ASM1832078v1
<i>Notolabrus celidotus</i>	fNotCel1.pri
<i>Sparus aurata</i>	fSpaAur1.1
<i>Acanthopagrus latus</i>	fAcaLat1.1

Table 4. Genomic information of the species used in annotation analysis.

Database	Number	Percent
COG	8,474	20.26%
KEGG	25,970	62.10%
NR	30,567	73.09%
SwissProt	23,536	56.28%
TrEMBL	30,557	73.06%
Overall	30,910	73.91%
Total genes	41,823	100.00%

Table 5. Statistics of gene functional annotation for *S. rivulatus*.

and KEGG, using BLAST (blastp) with an e-value cutoff of 1e-5. Motifs and domains were further annotated using InterProScan (v4.8)⁴², and partial non-coding RNAs were identified with Infernal (v1.1.2)⁴³.

A total of 41,823 protein-coding genes were predicted in the *S. rivulatus* genome, among which 30,910 genes (73.91%) were functionally annotated in at least one of the utilized databases (Table 5). Specifically, 30,567 genes (73.09%) were annotated in the NR database, 30,557 genes (73.06%) in TrEMBL, 23,536 genes (56.28%) in SwissProt, 25,970 genes (62.10%) in KEGG, and 8,474 genes (20.26%) in COG (Fig. 3B). In addition to protein-coding genes, non-coding RNAs were comprehensively identified, including 1,794 tRNAs, 284 rRNAs, 543 snRNAs, and 338 miRNAs (Table 6).

Data Records

The sequencing data and genome assembly have been submitted to the public databases. The Illumina short-read sequencing, Nanopore long-read sequencing, Hi-C sequencing, and RNA-seq data have been deposited in the NCBI Sequence Read Archive (SRA) database under the accession number SRP600033⁴⁴. The genome assembly has been deposited at the NCBI GenBank under the accession GCA_051912175.1⁴⁵. Moreover, data of the genome annotations, predicted coding sequences, and protein sequences have been deposited at Figshare (<https://doi.org/10.6084/m9.figshare.29642444.v1>)⁴⁶.

Technical Validation

Evaluation of the genome assembly. To assess the integrity and quality of the genome assembly, we used BUSCO (v5.4.4)⁴⁷ software and performed analyses based on the Actinopterygii database, which contains 3,640 conserved single-copy orthologs. The results showed that a total of 3,573 (98.16%) complete BUSCO genes

Non-code RNA Type	Copy Number	Avg Length (bp)	Total Length (bp)
tRNA	1,794	74.7341	134,073
rRNA	284	204.553	58,093
snRNA	543	130.092	70,640
miRNA	338	76.5888	25,887

Table 6. Statistics of gene Non-code RNA annotation for *S. rivulatus*.

Item	Number	Percent (%)
Complete BUSCOs (C)	3573	98.16
Complete and single-copy BUSCOs (S)	3455	94.92
Complete and duplicated BUSCOs (D)	118	3.24
Fragmented BUSCOs (F)	21	0.58
Missing BUSCOs (M)	46	1.26
Total BUSCO groups searched	3640	100.00

Table 7. BUSCO analysis statistics in the genome of *S. rivulatus*.

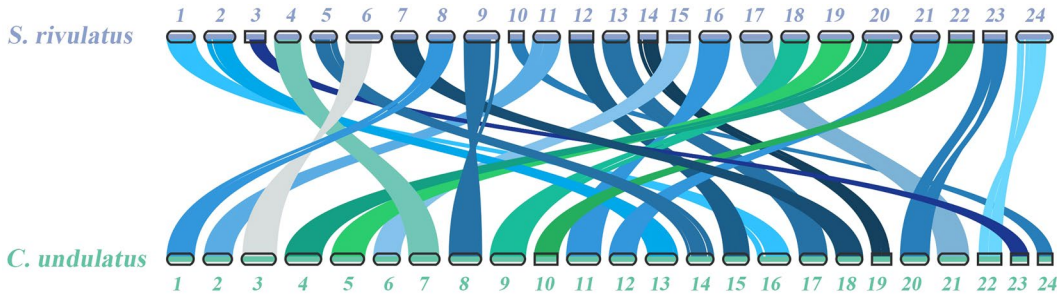


Fig. 4 The genome synteny analysis between *S. rivulatus* and *Cheilinus undulatus*.

were detected, including 3,455 complete single-copy genes and 118 complete duplicated genes. In addition, 21 (0.58%) fragmented genes were detected and only 46 (1.26%) missing genes (Table 7). Additionally, to evaluate the accuracy of our assembly, we aligned Illumina short reads to the assembled genome using BWA (v0.7.17)⁴⁸ and performed statistical analysis using SAMtools (v1.13)⁴⁹. The results showed that 99.66% of the short reads were successfully aligned, and 96.48% of them were correctly aligned, indicating that the assembly had high alignment consistency and accuracy. These results suggest that the *S. rivulatus* genome assembled in this study has high quality and strong integrity compared to other published teleost genomes.

Genome collinearity analysis. We performed genome synteny analysis between *S. rivulatus* and *C. undulatus*⁵⁰ using JCVI (v1.4.21)⁵¹. The results revealed a strong collinearity between the two species, highlighting the high quality of the *S. rivulatus* genome assembly (Fig. 4).

Ethics statement. The animal experiment was approved by the Committee of the South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences (Project No. 201810825825) SCSFRI96-253 and carried out according to applicable standards.

Data availability

The Illumina short-read sequencing, Nanopore long-read sequencing, Hi-C sequencing, and RNA-seq data are available in the NCBI SRA database under the accession number SRP600033⁴⁴. The genome assembly is deposited at NCBI GenBank under the accession GCA_051912175.1⁴⁵. Data on genome annotations, predicted coding sequences, and protein sequences are available at Figshare (<https://doi.org/10.6084/m9.figshare.29642444.v1>)⁴⁶.

Code availability

No custom scripts were developed in this study. All data analyses were conducted using publicly available bioinformatics tools, strictly following the manuals and standard protocols provided by their developers, as detailed in the Methods section along with the respective software versions.

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Author contributions

D.C.Z. conceived and designed the study. B.S.L. and N.Z. collected samples, K.C.Z. and H.Y.G. performed molecular work. Y.L., J.M.P. and X.L. performed bioinformatic analysis. Y.L. and J.M.P. wrote initial draft of the manuscript. D.C.Z., Y.L. and J.M.P. reviewed and edited the manuscript. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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