MITOCHONDRIAL DNA PART B: RESOURCES
2025, VOL. 10, NO. 4, 292–297
https://doi.org/10.1080/23802359.2025.2478128

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MITOGENOME REPORT

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The complete mitochondrial genome of medicinally important wood-decaying fungus *Tyromyces fissilis* within the family Incrustoporiaceae, Polyporales

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ABSTRACT

Tyromyces fissilis (Berk. & M.A.Curtis) Donk 1933, a globally renowned white-rot basidiomycete belonging to the Polyporales order, holds significant potential for lignin degradation, yet its mitochondrial genome has received comparatively little attention. Our study concentrates on a specimen designated *T. fissilis* NEFU_01, sourced from the Forest Botanical Garden in Heilongjiang Province, China. Utilizing next-generation sequencing (NGS) technology, we have successfully delineated the complete mitochondrial genome of this *T. fissilis* isolate. The genome is composed of 15 protein-coding genes (PCGs), an array of 24 transfer RNAs (tRNAs), and a pair of ribosomal RNAs (rRNAs), encompassing a total of 163,380 base pairs (bp). Additionally, the genome encodes 28 LAGLIDADG- and 10 GIY-YIG-homing endonucleases. The nucleotide composition is characterized by adenine (A) at 37.02%, cytosine (C) at 12.91%, guanine (G) at 13.04%, and thymine (T) at 37.03%, culminating in a GC content of 25.95%. Subsequently, we undertook a phylogenetic analysis, employing a dataset of 25 mitochondrial genomes to construct a phylogenetic tree. This research represents the first comprehensive foray into understanding the phylogenetic relationships of *T. fissilis* with its Basidiomycete kin, particularly its sister-group relationship with *Phlebia radiata* Fr. (1821), thereby laying a substantive groundwork for subsequent evolutionary and taxonomic studies within this mycological cohort.

ARTICLE HISTORY
Received 5 July 2024
Accepted 6 March 2025

KEYWORDS
White-rot fungi; phylogenetic analysis; next-generation sequencing

Introduction

Tyromyces fissilis, a species of fungus belonging to the phylum Basidiomycota and the order Polyporales, is a member of the family Polyporaceae and the genus *Tyromyces* (GBIF 2024b). It is also known by the synonym *Pappia fissilis* (Berk. & M.A. Curtis) Zmitr 2018, which is a homotypic synonym. According to Global Biodiversity Information Facility (GBIF) records, the name *T. fissilis* was first published by Donk in 1933, while the name *P. fissilis* was proposed by Zmitr in 2018 (GBIF 2024a). As a wood-decaying fungus, it possesses a formidable ability to cause white rot in the heartwood of various trees (Mitomo et al. 2019). Studies have indicated that substances extracted from the fruiting bodies of *T. fissilis* have potential medicinal value, such as serving as xanthine oxidase inhibitors (Mitomo et al. 2019), which could be of significant importance in drug development. Furthermore, *T. fissilis* has been found to be rich in lanostane and rearranged lanostane carboxylic acids (Quang et al. 2003, 2004).

The mitochondrial genome plays a pivotal role in phylogenetic analysis, providing crucial insights into evolutionary relationships. Its maternal inheritance pattern and high conservation across species make it a reliable marker for tracing ancestry and divergence. The genome's unique characteristics, such as rapid mutation rates and lack of recombination, facilitate accurate phylogenetic reconstructions, offering a robust framework for evolutionary studies (Fonseca et al. 2021; Formaggioni et al. 2021; Kulik et al. 2021; Feng et al. 2024). In light of the burgeoning interest in *T. fissilis* within the spheres of ecology and biotechnology, it is imperative to acknowledge the paucity of information regarding its genetic endowment. This study addresses this oversight by elucidating the mitochondrial genome of *T. fissilis* through comprehensive sequencing and annotation. Furthermore, to delineate the genetic composition's profound implications for forest ecology and the taxonomy of fungi, we have meticulously analyzed its phylogenetic affiliations with cognate species via the application of two distinct evolutionary tree construction methodologies. This research underscores the essential need for further investigation into the genetic tapestry of *T. fissilis*, thereby enhancing our understanding of its pivotal role within the ecological and taxonomic frameworks.

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/23802359.2025.2478128.

Materials

The specimen of *T. fissilis*, depicted in Figure 1(A), was sourced from the Forest Botanical Garden in Heilongjiang Province, located in Harbin City, Heilongjiang Province, China, at the geographical coordinates of 126°65′16.89″E, 45°70′78.90″N. The fresh fruiting bodies were carefully tissue cultured on potato dextrose agar (PDA) medium in a sterile environment to produce viable mycelium as shown in Figure 1(B). This mycelium was then archived at the Shaanxi Key Laboratory of Natural Products & Chemical Biology (https://npcb.nwafu.edu.cn), within the College of Chemistry & Pharmacy at Northwest A&F University. It has been catalogued under the voucher number NEFU_01 and Dr Jianzhao Qi is available for further enquiries at qjz@nwafu.edu.cn. The authenticity of the specimen was confirmed by morphological characteristics as shown in Figure 1(A) and by ITS sequence with GenBank accession number PP892648.1, as detailed in Figure S1. It is noteworthy that no special permits were required for this collection, as the species in question is neither endangered nor protected.

Methods

Total genomic DNA was meticulously extracted from the fresh mycelial tissue, employing the CTAB protocol. DNA quality was assessed by spectrophotometric measurement of the absorbance ratio at 260/280 nm and the qualified DNA samples were stored at 4 °C. The DNA was subsequently sequenced by Biozeron Co., Ltd. (Shanghai, China), to secure high-quality reads. For the assembly of the sequences, we utilized the GetOrganelle software (Jin et al. 2020), leveraging the fungal mitochondrial database with the parameter '-F fungus_mt' to accurately identify, filter, and assemble the reads pertaining to the target organelle. The assembled sequences were annotated with the MITOS Web Server (Donath et al. 2019), applying the genetic code 4 for accurate prediction. The predicted protein-coding genes (PCGs) were subjected to further refinement using the open reading frame (ORF) finder tool provided by the National Center for Biotechnology Information, accessible at NCBI ORFfinder (www.ncbi.nlm.nih.gov/orffinder/). The identification of transfer RNA (tRNA) genes was accomplished using tRNAscan-SE v1.3.1 (Chan and Lowe 2019). The types of introns present were meticulously verified with the RNAweasel v5.2.1 software (Lang et al. 2007). To conclude the process, the gene map was elegantly visualized using the PMGmap tool, available at PMGmap (www.1kmpg.cn/pmgm).

A comprehensive dataset of 25 mitochondrial genomes has been obtained from the NCBI database, encompassing a diverse range of fungal species. This dataset notably includes 16 representative species from the Polyporaceae family, along with additional species from several other families: two from the Phanerochaetaceae, as well as one species each from five other families. Notably, *Inonotus hispidus* (Bull.) P. Karst. from the Hymenochaetaceae family is designated as the outgroup. From this genomic reservoir, a quintet of 15 core PCGs were meticulously identified and aligned employing the MAFFT v7.526 software suite (Rozewicki et al. 2019), with adherence to default parameters to ensure methodological consistency and fidelity in the alignment procedure. Subsequently, these discrete protein sequences were amalgamated into a unified dataset through the auspices of the PhyloSuite v1.2.2 platform (Zhang et al. 2020). The concatenated alignment was then subjected to rigorous phylogenetic scrutiny via two complementary methodologies: Bayesian inference (BI) and maximum likelihood (ML). The BI was meticulously executed with MrBayes v3.2.7 (Ronquist et al. 2012), allowing the analysis to evolve for a million generations with cessation upon reaching a plateau where the average standard deviation of the split frequencies descended below the 0.01 threshold. For the ML analysis, IQ-Tree v 2.0.3 (Minh et al. 2020) was the instrument of choice, with bootstrap support (BS) ascertained through an ultra-fast bootstrap approximation encompassing 1000 replicates, thereby providing a stringent evaluation of the phylogenetic nodes' robustness. The methodologies and parameter configurations for the construction of the evolutionary trees, as well as the scholarly justification for the selected analytical strategies, are elucidated with scholarly precision in the pertinent literature (Li Z-c et al. 2023).

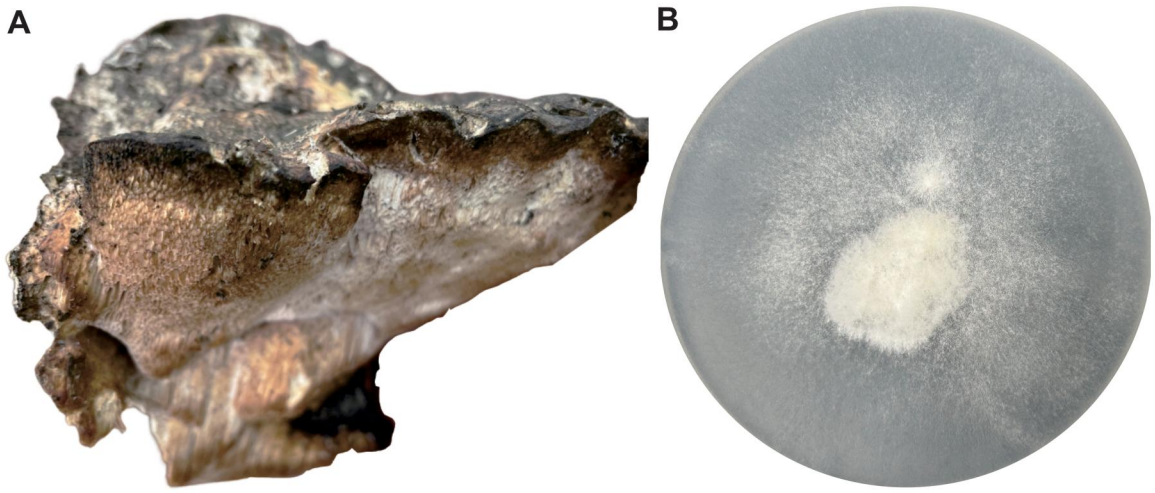

Figure 1. The fruit body of *Tyromyces fissilis* collected from Heilongjiang Province, China. The specimen is parasitic on a dead branch of oak. Photograph by Jianzhao Qi (A) and Mycelium growing on PDA medium (B).

Results

The complete mitochondrial genome sequence of *T. fissilis* (GenBank Accession No. OR701840) was determined to span 163,380 base pairs (bp) in length with a mean coverage of 7398.74×, as illustrated in Figure S2, and is graphically represented in Figure 2. This genome is composed of 15 PCGs, namely *atp6*, *atp8*, *atp9*, *cob*, *cox1*, *cox2*, *cox3*, *nad1*, *nad2*, *nad3*, *nad4*, *nad4L*, *nad5*, *nad6*, and *rps3*, along with 24 tRNA genes and a pair of ribosomal RNA (rRNA) genes. Genome annotation revealed 38 introns distributed across seven genes including *cox1*, *cox2*, *cox3*, *nad1*, *nad2*, *nad5*, and *cob*. However, no cis-splicing or trans-splicing genes were detected in any of the annotated genes. The base composition of the mitochondrial genome is as follows: A (37.02%), C (12.91%), G (13.04%), and T (37.03%), culminating in a GC

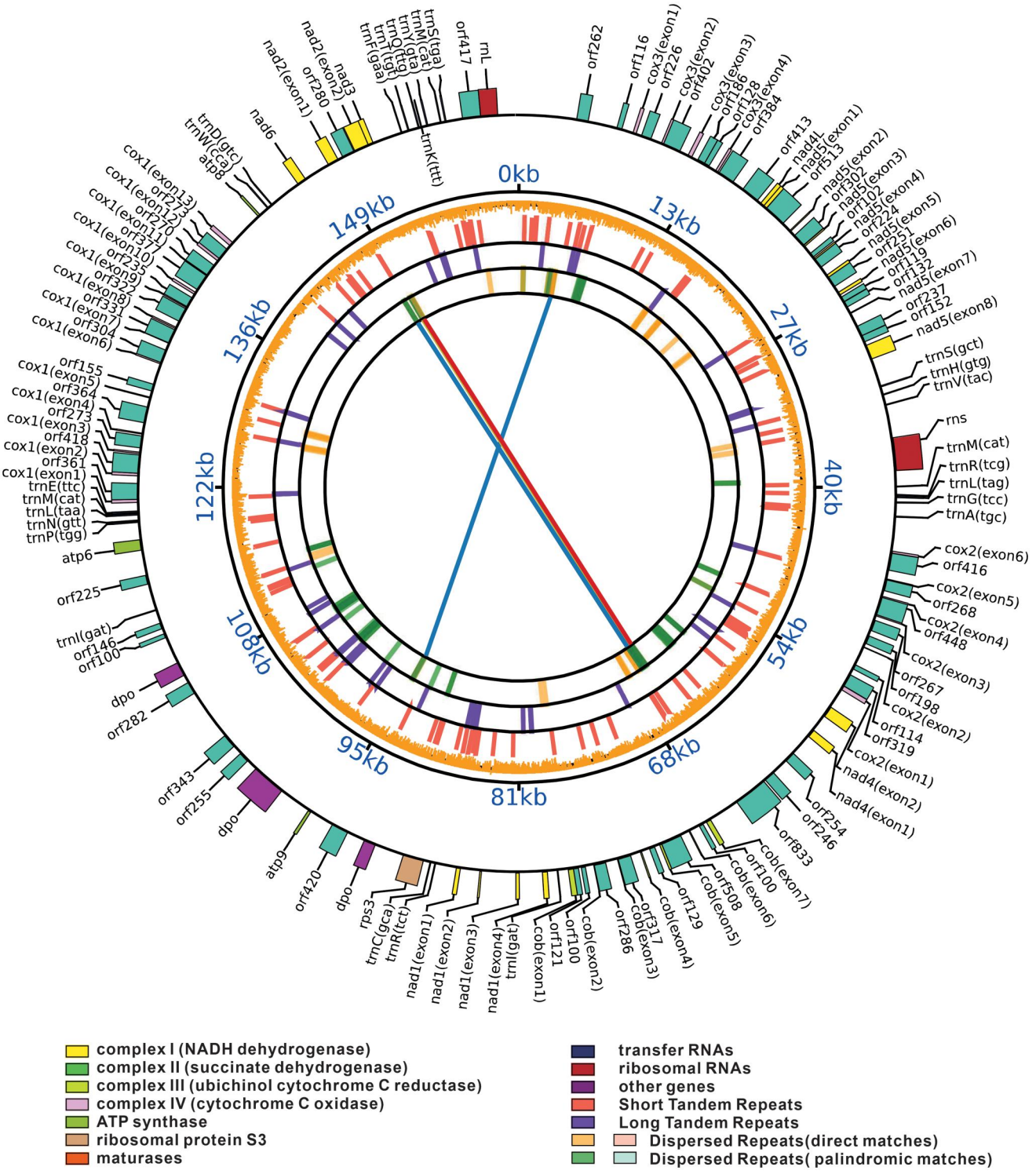

Figure 2. The diagram presents the mitochondrial genome of *T. fissilis* NEFU_01, with the outermost circle showing DNA elements containing ORFs. From the outside to the inside, the concentric circles represent the genome's scale, GC content, and the distribution of genetic elements, including short tandem repeats, long tandem repeats, and dispersed repeats. The central parabola, vividly colored, indicates the regions of dispersed repeats.

content of 25.95%. All 15 conserved PCGs initiate with the start codon ATG and terminate with the stop codon TAA, with the exception of the cox1 gene, which contains two introns; the remaining PCGs are devoid of introns. A total of 28 LAGLIDADG genes and 10 GIY-YIG genes were identified in the mitochondria, with eight LAGLIDADG genes and three GIY-YIG genes located in the *cox1* gene region.

Phylogenetic analyses, meticulously conducted using BI and ML methods, have yielded robust evolutionary trees. These analyses position *T. fissilis* as a basal taxonomic unit within the Incrustoporiaceae family, as portrayed in Figure 3. *Phlebia radiata* is the closest species to *T. fissilis* under the family Meruliaceae. The families Incrustoporiaceae and Phanerochaetaceae are revealed as sister taxa within the Polyporales order. The reconstructed evolutionary tree clearly reveals the phylogenetic position of *T. fissilis*. This finding indicates that Incrustoporiaceae is the sister taxa of Meruliaceae, and will make a significant contribution to the ongoing discussion on the phylogeny and evolutionary narrative of Incrustoporiaceae and its related taxa.

Discussion

This study reports, for the first time, the complete mitochondrial genome sequence of the wood-rotting fungus *T. fissilis*. The family Incrustoporiaceae, within the order Polyporales, has long been a neglected group, with the few existing studies focusing on the discovery of new species based on DNA marker sequences (Rui and Yu-Cheng 2020). To our knowledge, this is the first report of a mitochondrial genome in the family Incrustoporiaceae.

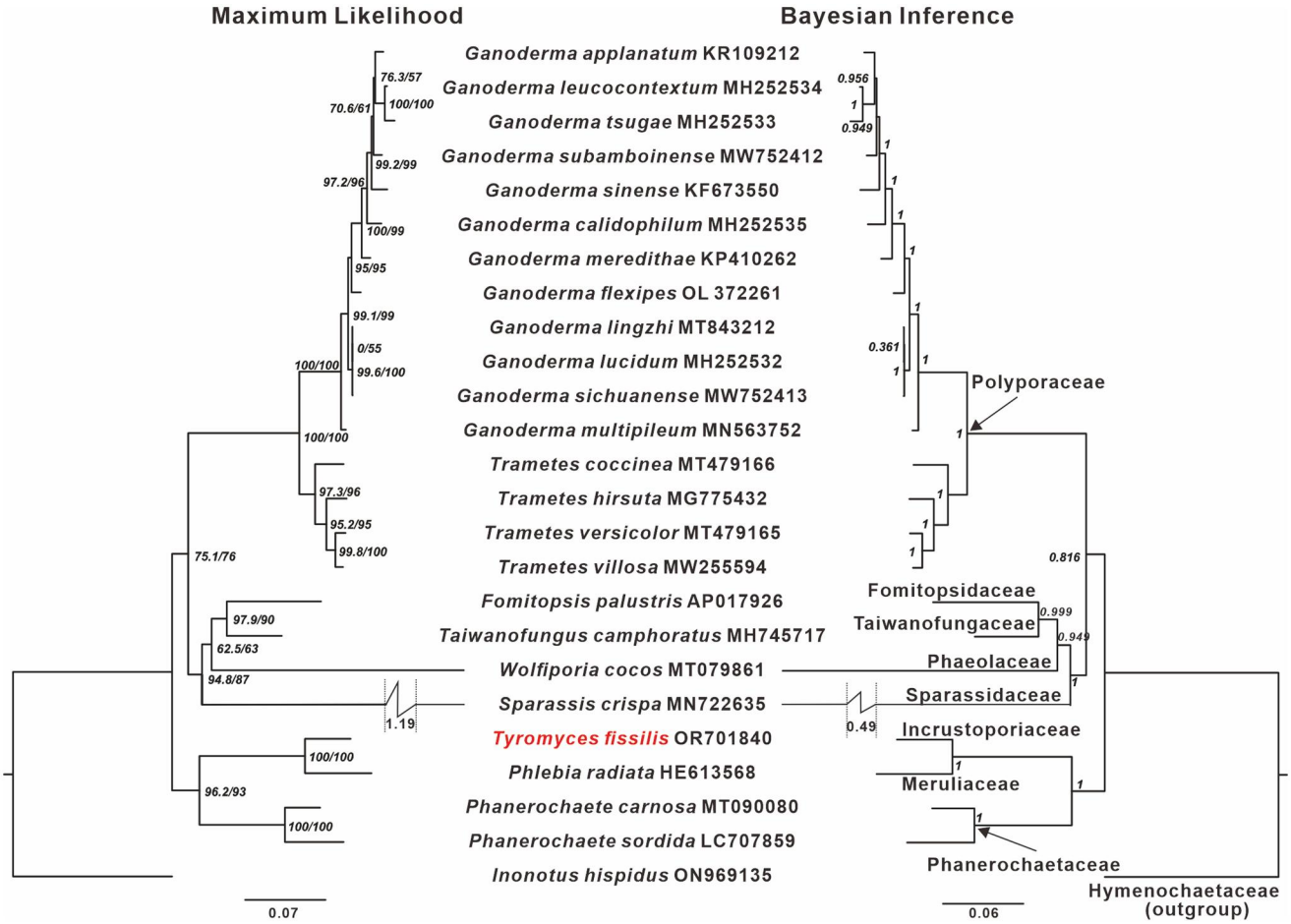

Figure 3. The phylogenetic tree based on ML (left) and BI (right) analyses of 15 mitochondrion-encoded core proteins. The 25 fungal mitogenomes were used in this phylogenetic analysis: *Ganoderma applanatum* (Pers.) Pat. (KR109212, Cho et al. 2023), *Ganoderma leucocontextum T.H.* Li, W.Q. Deng, Sheng H. Wu, Dong M. Wang & H.P. Hu (MH252534, Li et al. 2020), *Ganoderma tsugae* Murrill (MH252533, Li et al. 2019), *Ganoderma subamboinense* var. *laevisporum* Bazzalo & J.E. Wright. (MW752412, Ye et al. 2022), *Ganoderma sinense* J.D. Zhao, L.W. Hsu & X.Q. Zhang (KF673550, Li et al. 2019), *Ganoderma calidophilum* J.D. Zhao, L.W. Hsu & X.Q. Zhang (MH252535, Li et al. 2019), *Ganoderma meredithae* Adask. & Gilb. (KP410262, Li et al. 2019), *Ganoderma flexipes* (Fr.) Zmitr. & Kovalenko (OL372261), *Ganoderma lingzhi* S.H. Wu, Y. Cao & Y.C. Dai (MT843212, Ye et al. 2022), *Ganoderma lucidum* Karst. 1881 (MH252532, Li et al. 2019), *Ganoderma sichuanense* J. D. Zhao & X. Q. Zhang (MW752413, Wu et al. 2023), *Ganoderma multipileum* Ding Hou (MN563752), *Trametes coccinea* (Fr.) Hai J. Li & S.H. He (MT479166, Chen C et al. 2021), *Trametes hirsuta* (Wulfen) Pilat (MG775432, Meng et al. 2022), *Trametes versicolor* (L.) Lloyd (MT479165, Chen C et al. 2021), *Trametes villosa* (Sw.) Kreisel (MW255594, Araújo et al. 2021), *Fomitopsis palustris* (Berk. & M.A. Curtis) Gilb. & Ryvarden (AP017926, Tanaka et al. 2017), *Taiwanofungus camphoratus* (M. Zang & C.H. Su) Sheng H. Wu, Z.H. Yu, Y.C. Dai & C.H. Su (MH745717, Wang, Jia, et al. 2020), *Wolfiporia cocos* (F.A. Wolf) Ryvarden & Gilb. (MT079861, Chen M et al. 2020), *Sparassis crispa* (Wulfen) Fr. (MN722635, Bashir et al. 2020), *Tyromyces fissilis* (Berk. & M.A. Curtis) Zmitr. (OR701840, this study), *Phlebia radiata* Fr., 1821 (HE613568, Yu et al. 2019), *Phanerochaete carnosa* (Burt) Parmasto (MT090080, Wang, Song, et al. 2020), *Phanerochaete sordida* (P. Karst.) J. Erikss. & Ryvarden (LC707859, Mori et al. 2022), and *Inonotus hispidus* (Bull.) P. Karst. (ON969135). Mitochondrial genome information for the four species for which only GenBank accession numbers are available is available through the corresponding GenBank accession numbers. The GenBank accession number from NCBI is provided after the species names. The newly sequenced mitogenome is marked in red. Numbers near the nodes indicate bootstrap support values (>50%) and posterior probabilities (>0.95).

The group I intron-mediated trans-splicing phenomenon found in the mitochondrial genome of *Gigaspora rosea* provides important insights into the mechanism of splicing in fungal mitochondrial genomes. Cis-splicing in fungal mitochondrial genomes has been reported less frequently. Neither trans-splicing nor cis-splicing was found in the *T. fissilis* mitochondrial genome. LAGLIDADG and GIY-YIG types of homing endonuclease genes (HEGs) are typically found within the core PCGs of mitochondria. These HEGs can alter the organization and size of the mitochondrial genome, playing a crucial role in mitochondrial diversity (Belfort and Roberts 1997; Edgell 2009). Despite the close phylogenetic relationship between *T. fissilis* and *P. radiata*, and their similar mitochondrial genome sizes (163,380 bp for *T. fissilis* and 156,348 bp for *P. radiata*), a notable difference in the number of HEGs is observed between the two species.

Considering the important role of fungal mitochondrial genomes in the study of species evolution and phylogenetic relationships (Curole and Kocher 1999; Santamaria et al. 2009; Basse 2010; Li Z-c et al. 2023), the report of the *T. fissilis* mitochondrial genome not only reveals the general characteristics of mitochondrial genomes in the Incrustoporiaceae, but also enriches the diversity of basidiomycete mitochondrial genomes. A comprehensive analysis of the *T. fissilis* mitochondrial genome will contribute to a better understanding of the phylogenetic relationships and evolutionary history of Polyporales fungi. However, compared to the construction of phylogenetic trees based on single-copy genomic sequences, the precision of phylogenetic trees built with the limited number of mitochondrial genomes is constrained, particularly when analyzing the evolutionary relationships of species on a large scale.

Conclusions

In conclusion, this study presents the first complete mitochondrial genome of the family Incrustoporiaceae. Furthermore, based on the sequences of 15 PCGs, we performed a phylogenetic analysis with other related Polyporales fungi, and the results indicate a close relationship between *P. radiata* and *T. fissilis*.

Acknowledgments

Conceptualization, LZ and JZQ; methodology, LZ and JZQ; formal analysis and investigation, LZ; resources, JZQ; writing LZ; supervision, JZQ; funding acquisition, JZQ. All authors have read and agreed to the published version of the manuscript.

Author contributions

CRediT: **Ling Zhao**: Conceptualization, Formal analysis, Funding acquisition, Investigation, Software, Supervision, Validation, Visualization, Writing – review & editing; **Jianzhao Qi**: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was financially supported by the Key R&D Projects in Shaanxi Province of China (No. 2023-YBSF-164).

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Data availability statement

The genome sequence data that support the findings of this study are openly available in GenBank of NCBI at https://www.ncbi.nlm.nih.gov under the Accession No. OR701840. The accession no. of BioProject, BioSample, and SRA are PRJNA1120639, SAMN41705534, and SRR29304337, respectively.

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