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Evolution

The first complete mitochondrial genome of a trichodactylid crab: *Rodriguezia adani* (Brachyura: Trichodactyloidea: Trichodactylidae) from Mexico

Primer genoma mitocondrial completo de un cangrejo tricodactílido: Rodriguezia adani *(Brachyura: Trichodactyloidea: Trichodactylidae) de Mexico*

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Abstract

We report for the first time the complete mitochondrial genome of a crab in the family Trichodactylidae, that of the stygobitic *Rodriguezia adani* Álvarez and Villalobos, 2018. The mitogenome is 17,561 bp of length with a GC composition of 26.4% and comprises 13 protein coding genes (PCGs), 2 ribosomal subunits and 19 transfer RNA (tRNAs) genes; its ribosomal subunits are separated by 10 genes (5 PCGs and 19 tRNAs). Its phylogenetic position was obtained through Maximum Likelihood and Bayesian Inference analyses, both placed this species inside the subsection Heterotremata and as the sister group of the family Orithyiidae. Changes in the number of tRNAs could be the result of the adaptation to a stygobitic lifestyle. This is the first genomic resource for the Trichodactylidae and could be the initial step for future phylogenomic studies of this group.

Keywords: Stygobitic; Freshwater crab; Cave; Mitochondrion

Resumen

Reportamos el primer genoma mitocondrial completo de un cangrejo de la familia Trichodactylidae, el de la especie estigobítica *Rodriguezia adani* Álvarez y Villalobos, 2018. El mitogenoma tiene 17,561 pb de longitud, una composición de GC de 26.4% y contiene 13 genes codificantes de proteínas (PCGs), 2 subunidades ribosomales y 19 genes de RNA de transferencia (tRNAs); sus subunidades ribosomales están separadas por 10 genes (5 PCGs y 19 tRNAs). La posición filogenética obtenida a través de máxima verosimilitud e inferencia bayesiana ubica a esta especie dentro de la subsección Heterotremata y como grupo hermano de la familia Orithyiidae. Los cambios en el número de tRNAs podrían ser el resultado de la adaptación a un estilo de vida estigobítico. Este es el primer recurso genómico para los Trichodactylidae y posiblemente el paso inicial para futuros estudios filogenómicos de este grupo.

Palabras clave: Estigobítico; Cangrejo dulceacuícola; Cueva; Mitocondria

Introduction

The family Trichodactylidae H. Milne-Edwards, 1853, the single family in the superfamily Trichodactyloidea, is one of the 3 families of freshwater crabs in the American Continent (Álvarez et al., 2020). *Rodriguezia* Bott (1969) one of the 2 genera of Trichodactylidae found in Mexico; these are primary freshwater crabs distributed in southern Mexico (Álvarez & Villalobos, 2018; Magalhães & Türkay, 1996). The genus *Rodriguezia* comprises 3 species, 2 of them stygobitic; from them, *Rodriguezia adani* Álvarez & Villalobos, 2018 was the last one to be described (Fig. 1). Most of the research on this family has focused on its distribution, taxonomy, ecology, conservation and anatomy (Collins et al., 2009, 2011; Cumberlidge et al., 2014; Lima-Gomes et al., 2017; Magalhães et al., 2016; Magalhães & Türkay, 1996; Weihrauch et al., 2004; Williner & Collins, 2013). However, few attempts have been made to understand its phylogenetic relationships, except for few molecular analyses performed to solve species complex issues in the genera *Avotrichodactylus* Pretzmann, 1968, *Trichodactylus* Latreille, 1828 and *Dilocarcinus* Milne Edwards, 1853 (Caetano-França et al., 2024; Ojeda et al., 2013; Souza-Carvalho et al., 2017). Studies using genomic sequencing for this family are lacking, only recently a study on the genome size of *Trichodactylus fluviatilis* Latreille, 1828 was published (Barioto et al., 2024). To further advance our knowledge on the phylogeny and evolution of the Trichodactylidae, we present the first complete mitochondrial genome for the family.

Figure 1. Photograph of the specimen of *Rodriguezia adani* Álvarez & Villalobos, 2018 used in this study (CNCR 36762).

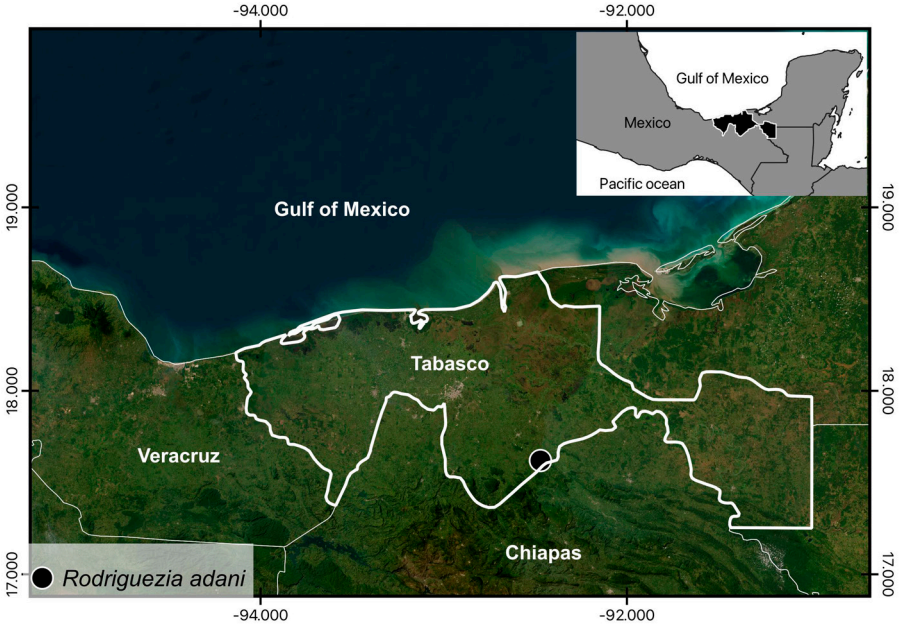

Figure 2. Geographic location of *Rodriguezia adani*.

Materials and methods

The organism used in this study was collected in the type locality, Aguas Blancas Cave, Tabasco, Mexico (17º36'22.06" N, 92º27'43.63" W, Fig. 2) and deposited in the Colección Nacional de Crustáceos (CNCR), of the Instituto de Biología, Universidad Nacional Autónoma de México (IB-UNAM), with catalog number CNCR 36762 (https://www.ib.unam.mx/ib/colecciones-biologicas/colecciones-zoologicas, Dr. Fernando Álvarez (falvarez@ib.unam.mx)). The organism was collected under license N° SGPA/DGVS/03775/22, provided by Semarnat. Its taxonomic identity was corroborated with Álvarez and Villalobos (2018) publication.

The DNA was purified from muscle tissue of the fifth pereopod with the Animal and Fungi DNA preparation kit, Jena Bioscience. Quality and concentration of DNA were determined with a NanoDrop 2000 spectrophotometer and Qubit 4 Fluorometer, respectively. The library used was prepared with Illumina DNA Prep Kit (Illumina, Inc.), following the Trevisan et al. (2019) protocol. The sequencing was conducted in an Illumina NextSeq 500 sequencer, using a 300-cycle cartridge in a Paired End (PE) 2X150 cycles configuration at the Massive Sequencing and Bioinformatic Unit of the Instituto de Biotecnología, UNAM.

A total of 11,090,166 raw sequences were obtained, its quality was measured with FastQC v. 0.11.9 (Andrews, 2010), and low quality reads (Q < 28) and adapters were removed with Trimmomatic v. 0.39 (Bolger et al., 2014). SPAdes v 3.15,1 (Bankevich et al., 2012) was implemented as assembler on Galaxy (The Galaxy Community, 2022) with k-mer values of 33, 55, 77, 105. The final sequence assembled was analyzed with MITOS (Bernt et al., 2013) to obtain the gene order and annotation. The framework of the Protein Coding Genes (PCGs) was corroborated with Geneious v. 2024.4 (Biomatters Inc., Auckland, New Zealand). To discard any issue during the assembly we performed the protocol of Vera-Paz et al. (2022). The depth average coverage was obtained with the online protocol of Ni et al. (2023). The final gene map was obtained with Chloroplot (Zheng et al., 2020).

To corroborate the phylogenetic position of *R. adani*, we initially based our selection of taxa on Tsang et al. (2014) and Wolfe et al. (2023), whose partial sequence-based phylogenies recovered Trichodactylidae together with Orithyiidae, Chasmocarcinidae, and Bellidae as a sister group to all Heterotremata. However, the only available mitogenome from that group was *Orythia sinica* (Orithyiidae), so to give a general idea of the

phylogenetic position of *R. adani*, we selected other available mitogenomes from families and superfamilies representative of Heterotremata, species belonging to primary families of freshwater crabs, species of Thoracotremata, and *Ranina ranina* (Podotremata) as an outgroup (Table 1).

A total of 15 mitochondrial genes (13 PCGs and 2 rRNA) were individually aligned with Mafft v. 7 online service (Katoh et al., 2019). The final concatenated matrix was analyzed with a codon partition merging and a model selection analysis, implemented on IQ-tree (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017), resulting in

Table 1
Species included in the phylogenetic analysis and GenBank accession numbers.

Species	Accession number	Reference
Rodriguezia adani	PQ064124	This study
Ranina ranina	AB752308	Unpublished
Tzotzilthelphusa villarosalensis	OP295767	Moreno-Juárez et al., 2023
Longpotamon yangtsekiens	KY785879	Yuhui et al., 2017
Ocypode ceratophthalmus	LN611669	Tan et al., 2014
Eriocheir japonica	FJ455505	Wang et al., 2016
Pachygrapsus crassipes	KC878511	Yu et al., 2014
Orithyia sinica	MG840649	Zhong et al., 2018
Chionoecetes japonicus	MT750295	Kim et al., 2020
Maguimithrax spinosissimus	KM405516	Márquez et al., 2016
Maja crispata	KY650651	Basso et al., 2017
Maja squinado	KY650652	Basso et al., 2017
Segonzacia mesatlantica	KY541839	Mandon et al., 2017
Austinograea alayseae	KC851803	Kim et al., 2014
Gandalfus puia	KR002727	Kim et al., 2016
Echinoecus nipponicus	MG574831	Lee et al., 2018
Pilumnus vespertilio	MF457402	Tan et al., 2018
Atergatis floridus	MG792341	Karagozlu, Barbon et al., 2018
Etisus anaglyptus	MG751773	Karagozlu, Dihn et al., 2018
Epixanthus frontalis	MF457404	Tan et al., 2018
Leptodius sanguineus	KT896744	Sung et al., 2016
Myomenippe fornasiniiq	LK391943	Tan et al., 2016a
Myra affinis	MW192449	Zhang et al., 2022
Pyrhila pisum	KU343210	Park et al., 2017
Ashtoret lunaris	LK391941	Tan et al., 2016b
Matuta victor	MT416712	Huang et al., 2021
Calappa bilineata	MN562587	Lu et al., 2020
Chaceon granulatus	AB769383	Zhang et al., 2020
Ovalipes punctatus	MH802052	Unpublished
Scylla olivacea	FJ827760	Unpublished
Charybdis bimaculata	MG787408	Liu et al., 2018
Callinectes sapidus	AY363392	Place et al., 2005
Portunus sanguinolentus	KT438509	Ma et al., 2016

Table 2
Best partition scheme and model selection resulting from the analyses on IQ-Tree.

Partition	Nucleotide substitution model	Reference
12S	TVM + F + G4	
16S	TVM + F + I + G4	
ATP6 pos1, COX2 pos1, COX3 pos1, CYTB pos1, ND3 pos1	GTR + F + I + G4	Tavaré, 1986
ATP6 pos2, CYTB pos2, ND3 pos2	GTR+F+I+G4	Tavaré, 1986
ATP6 pos3, ATP8 pos3, COX1 pos3, COX2 pos3, COX3 pos3, CYTB pos3, ND3 pos3	GTR+F+I+G4	Tavaré, 1986
ATP8 pos1, ND2 pos1, ND6 pos1	GTR+F+I+G4	Tavaré, 1986
ATP8 pos2, ND2 pos2, ND6 pos2	GTR+F+I+G4	Tavaré, 1986
COX1 pos1	TIM2+F+I+G4	
COX1 pos2, COX2 pos2, COX3 pos2	TVM+F+I+G4	
ND1pos1, ND4 pos1, ND4L pos1, ND5 pos1	GTR+F+I+G4	Tavaré, 1986
ND1 pos2, ND4 pos2, ND4L pos2, ND5 pos2	GTR+F+I+G4	Tavaré, 1986
ND1 pos3, ND4 pos3, ND4L pos3, ND5 pos3	TN+F+I+G4	Tamura and Nei, 1993
ND2 pos3, ND6 pos	TN+F+G4	Tamura and Nei, 1993

13 partitions and nucleotide substitution models (Table 2). Two phylogenetic inference methods were implemented, the maximum likelihood (ML) analysis was performed in IQ-Tree with 10,000 ultrafast bootstrap analysis (Hoang et al., 2018; Trifinopoulos et al., 2016). The Bayesian Inference (BI) analysis was performed with Exabayes (Aberer et al., 2014) with 20 million generations, sampling every 10,000 generations, standard deviation of split frequencies convergence value of 0.01 and 25% of burn-in.

Results

The complete mitochondrial genome of *R. adani* (GenBank: PQ064124; associated BioProject, SRA, and Bio-Sample numbers are PRJNA1139182, SRR29931217, and SAMN42764363, respectively) was obtained in only 1 contig with a length of 17,561 bp, an average depth of 125.8X and a GC composition of 26.4% (Fig. 3). It comprised 13 PCGs, 2 ribosomal RNA (rRNA) genes and 19 confirmed transfer RNA (tRNA) genes (Fig. 4, Table 3). Twenty-three genes are in the antisense strand: 9 PCGs (*COX1*, COX*2*, *COX3*, *CYTB*, *ATP6*, *ATP8*, *ND1*, *ND3*, *ND6*), and 14 tRNAs (tRNA-L1, K, D, G, A, R, N, S1, E, T, I, S2, M, W); and 11 are in the sense strand, 4 PCGs (*ND1*, *ND4*, *ND4L*, *ND5*), both rRNA genes (12S and 16S) and 5 tRNAs (tRNA-P, H, Q, Y, V); 1 tRNA-C is missing and tRNA-L2 and F are not confirmed. PCGs starting codons were ATG (*COX1*, *COX2*, *COX3*, *ATP6*, *CYTB*, *ND2*, *ND4*, *ND4L*), ATT (*ATP8*, *ND5*, *ND6*), ATC (*ND3*) and ATA (*ND1*). Most of the PCGs terminate with TAA, except for *ND4* (TAG). Both phylogenetic analyses (ML, BI) recovered *R. adani* as the sister group of the family Orithyiidae with a high branch support (92/1) (Fig. 5).

Discussion

The family Trichodactylidae has been poorly studied molecularly and genomic sequencing of its species is non-existent, so this study contributes with the first mitochondrial genome sequenced from a stygobitic species. The gene order and topology found in *R. adani* is quite different from other crab mitochondrial genomes reported, this is due to the ribosomal subunits that are separated by several PCGs (5) and tRNAs (5). According to the mitochondrial patterns reported by Tan et al. (2019) this gene arrangement is not found in any other crab so far reported. Most decapod mitochondrial genomes present ribosomal subunits one next to the other or separated by tRNA-V or/and tRNA-Q, few decapod species (e.g., the crayfish *Parastacus brasiliensis* and *Engaeus quadrimanus*, reported in Tan et al., 2019) present ribosomal subunits separated by PCGs like *R. adani*. With respect to the tRNAs, although in mitochondrial genomes the most common number is 22, *R. adani* just presents 19 confirmed; several species could present more or less tRNAs, depending on their evolutionary history

Table 3
Comparative table of the differences between *R. adani* and other brachyuran species.

Organism	Size	Gene number	tRNAs	GC % composition	Reference
Rodriguezia adani	17,561	34	19	26.4	This study
Orithya sinica	15,568	37	22	30.5	Zhong et al., 2018
Chionoecetes japonicus	16,060	37	22	28.2	Kim et al., 2020
Callinectes sapidus	16,263	37	22	30.9	Place et al., 2005
Eriocheir japonica	16,352	37	22	28.4	Wang et al., 2016
Maja crispata	16,592	37	22	29.7	Basso et al., 2017
Myra affinis	15,349	37	22	29.4	Basso et al., 2017
Gandalfus puia	15,548	37	22	30.1	Kim et al., 2016
Pilumnus vespertilio	16,222	37	22	28.9	Tan et al., 2018
Epixanthus frontalis	15,993	37	22	34.1	Tan et al., 2018
Matuta victor	15,782	37	22	29.9	Huang et al., 2021
Calappa bilineata	15,606	37	22	31.3	Lu et al., 2020
Ovalipes punctatus	16,084	37	22	31.9	Unpublished

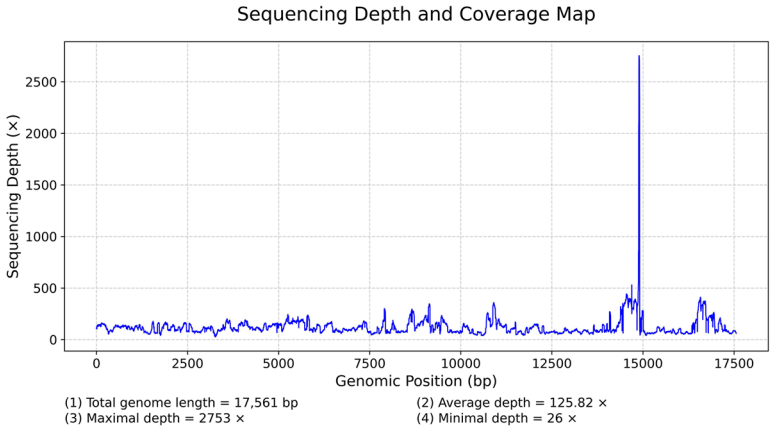

Figure 3. Coverage through the length of the mitochondrial genome of *Rodriguezia adani*, obtained with the protocol by Ni et al. (2023). The vertical axis indicates the depth (number of times that one nucleotide was read) and horizontal axis indicates the nucleotide position within the mitochondrial genome.

(Romanova et al., 2016, 2020, 2021; Tan et al., 2019). In the case of *R. adani*, its stygobitic condition could be related to physiological adaptations that enable survival in low food availability conditions and low oxygen concentrations (Hervant et al., 1999, 2001). It has been documented that in some instances metabolic changes can lead to the duplication or deletion of certain tRNAs, which can optimize the synthesis of enzymes or proteins that play an important role in these new metabolic processes (Romanova et al., 2021; Tan et al., 2019; Xing et al., 2025). Regarding tRNAs-L2 and F, both were recognized by MITOS and tRNAscan-SE but not supported by BlastN. It is possible that these tRNAs sequences are so novel that there is no sequence to compare them with, or an error

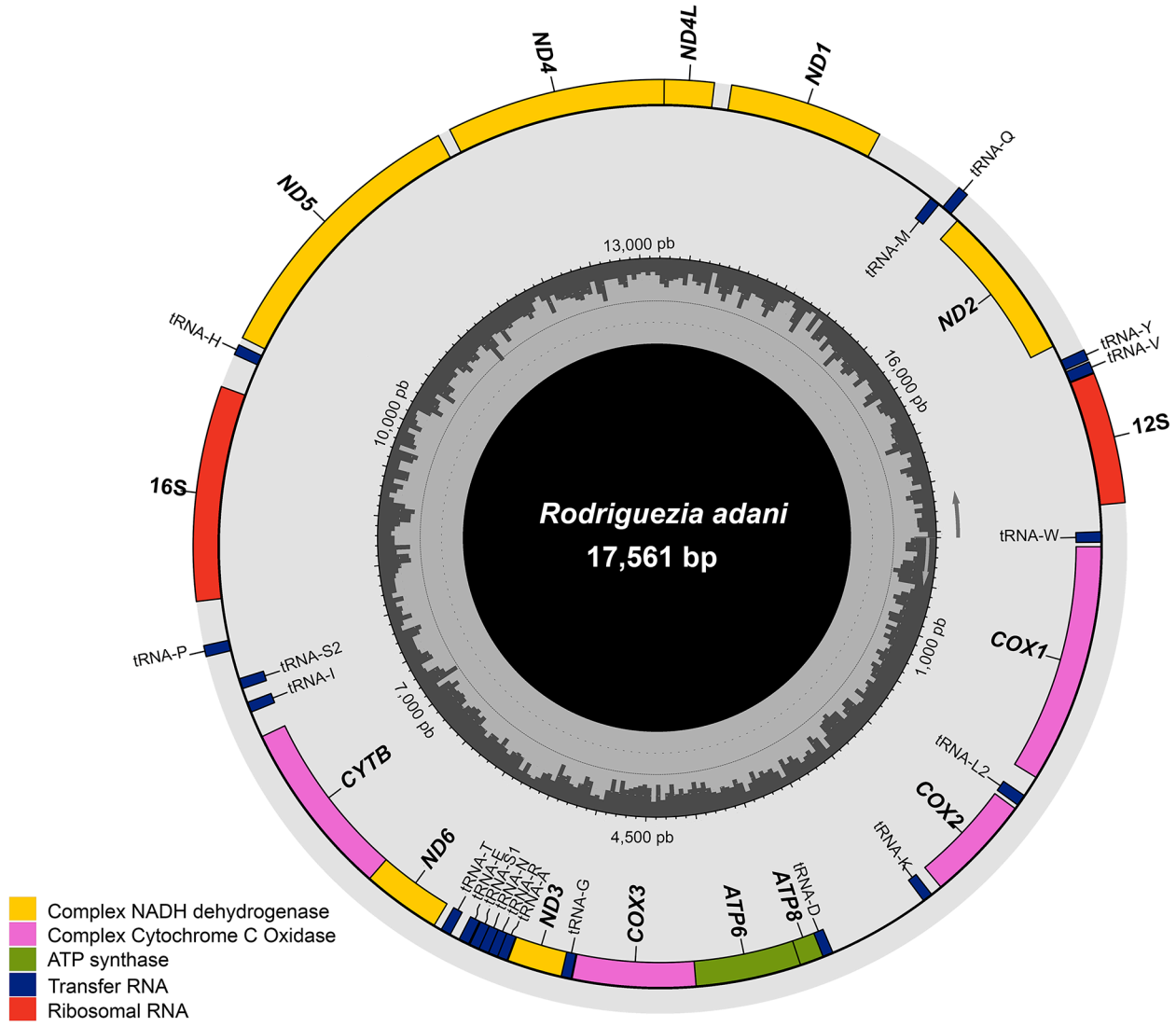

Figure 4. Diagram of the complete mitochondrial genome of *Rodriguezia adani* Álvarez & Villalobos, 2018 (PQ064124). Genes in the heavy strand are on the external side and the low strand are on the inner side. Colors: tRNAs in blue, rRNAs in red and PCGs in green, pink and yellow.

may have occurred during assembly or annotation; for these reasons we decided to leave them as unconfirmed until other mitogenomes of the family are reported to corroborate or invalidate their presence through Romanova et al. (2016, 2020) protocol.

Regarding the phylogenetic position of *R. adani*, it was recovered as the sister group of the Orithyiidae, forming a clade that is the sister group to the rest of the subsection Heterotremata (Fig. 4). Our results coincide with those of Wolfe et al. (2023), who using sequences of 10 genes, produced a phylogeny where the Orithyiidae and the Trichodactylidae are described as sister groups. Other coincidences with Wolfe et al. (2023) phylogenetic tree are the polyphyletic origin of primary freshwater crabs, Potamidae related to Thoracotremata, while Oregoniidae, Mithracidae, and Majidae are grouped in Majoidea and Portunidae, Ovalipidae and Geryonidae are grouped in Portunoidea. The phylogenetic relationships of the remaining species were not the aim of this work. The low branch supports for these clades, likely due to a

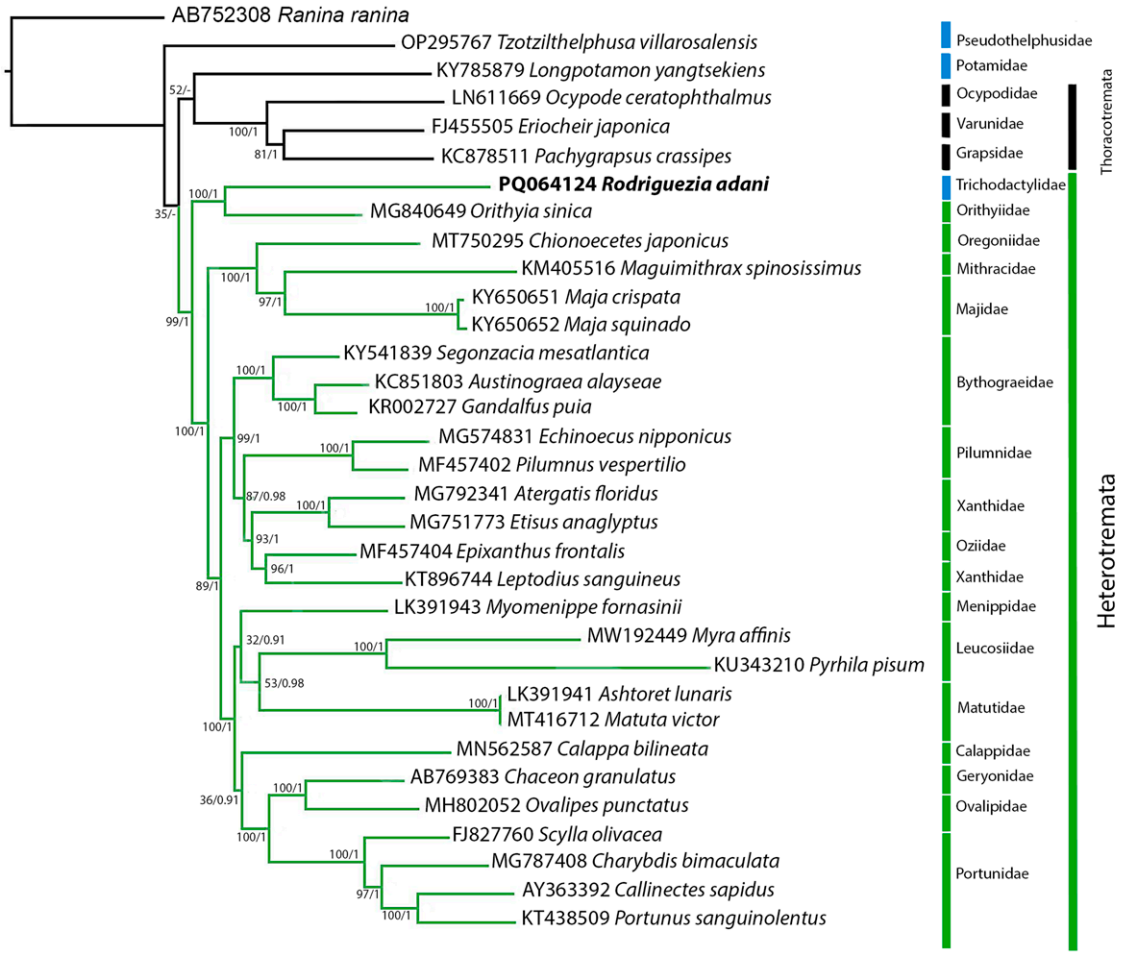

Figure 5. Phylogenetic tree resulting from the analysis of a concatenated matrix of 15 genes (13 PCGs and 2 ribosomal subunits) of the mitochondrial genome of *Rodriguezia adani* (GenBank: PQ064124). Branch supports bootstrap/posterior probability. Color of lateral lines, blue: freshwater groups; black: Thoracothremata; green: Heterotremata.

limited taxon sampling, preclude further interpretation. Future studies with more comprehensive sampling as in Tsang et al. (2014), Tan et al. (2019) or Wolfe et al. (2023), are needed to resolve these relationships with confidence (Nabhan & Sakar, 2012; Som, 2015).

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