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Phylogenetic analysis of coccidia (Apicomplexa: Eimeriorina) in the belica *Leucaspius delineatus* (Heckel, 1843)

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ABSTRACT. This study was aimed to carry out a comparative analysis and reconstruction of the phylogenetic position of coccidia from the intestine of the belica *Leucaspius delineatus* (Heckel, 1843) from the Irkutsk Reservoir. Determination and comparative analysis of the nucleotide sequences of the *cox1* gene fragment, obtained and available in genetic databases, demonstrated paraphilia of the genera *Eimeria* and *Goussia*. The sequences in the phylogenetic tree formed a distinct cluster at the base of the tree. Thus, the hypothesis that fish coccidia were ancestors of coccidia of other vertebrates was indirectly confirmed. The need for additional research and revision of coccidia in fishes from the Angara River and Lake Baikal is discussed.

Keywords: Eimeriorina, *Leucaspius delineatus*, gene *cox1*, Irkutsk Reservoir, Baikal Region

1. Introduction

The efforts of human economic activities aimed at altering and regulating of natural watercourses, recreational developing of the coastal zone and aquaculture growth have increased significantly over the past 100 years. The side effect of this process has been the expansion outside of natural habitats and introduction of various hydrobiont species (Băncilă et al., 2022; Bernery et al., 2022; Zhu et al., 2022; Truter et al., 2023).

In addition to the obvious consequences of interactions between native fauna and invasive species (competition and predation; genetic influences, hybridization and introgression), there is a threat of introducing associated parasites and other pathogens (Ellender and Weyl, 2014; Truter et al., 2023). Significant epizootics have been described in populations of various fish species caused by viruses, imported with aquacultural species, oomycetes, and protozoa (Kaminskas, 2021). For example, a significant damage to the ichthyofauna of Europe and America was caused by *Sphaerothecum destruens* Arkush, Mendoza, Adkison & Hedrick, 2003 – an intracellular parasite of the stone moroco *Pseudorasbora parva* (Temminck & Schlegel, 1846) introduced from China (Andreou et al., 2012). In this regard, molecular genetic studies are particularly in demand when describing the distribution of invasive fish species as well as their parasites (Ali et al., 2022; Alyamkin et al., 2022; Dos Santos and Avenant-Oldewage, 2022).

All representatives of the protists of Sporozoa or Apicomplexa, belonging to the group Alveolata, are unicellular obligate parasites of multicellular animals and are also considered one of the most successful parasites in the world (Morrison, 2009). More than 6000 species described are thought to represent only 0.1% of their total diversity (Morrison, 2009). Representatives of Apicomplexa, which belong to the genera *Cryptosporidium*, *Plasmodium*, *Toxoplasma*, and *Babesia*, are pathogens of humans and animals. In addition, coccidia cause significant damage to agricultural production (Conoidasida: Eimeriorina). However, despite their widespread distribution and economic importance, research on the evolutionary relationships within this group is in its infancy (Arisue and Hashimoto, 2015; Xavier et al., 2018). The taxonomy of coccidia is in the developmental stage, and many genera are paraphyletic that call into question the value of strict morphological and ecological characters

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for parasite classification (Ogedengbe et al., 2018; Xavier et al., 2018). Moreover, representatives of the suborder Eimeriorina have been much less studied in aquatic animals than in terrestrial animals. However, even the poor data available for the small subunit ribosomal RNA (SSU rRNA) sequences suggest that these are the basic groups within the families (Jirků et al., 2009; Xavier et al., 2018).

The belica *Leucaspius delineatus* (Heckel, 1843), which historically was a representative of the Ponto-Caspian ichthyofauna, has significantly expanded its habitat through accidental introduction and further self-distribution (Slynko and Tereschenko, 2014; Reshetnikov et al., 2017). Molecular genetic studies of the belica from the Irkutsk Reservoir confirmed the information about accidental introduction of the species from the European part of Russia (Kulakova et al., 2022). Representatives of coccidia have been found in the native habitat of the belica (Jastrzębski, 1984; Belova and Krylov, 2006; Pugachev et al., 2012). There are few data on parasite fauna of the belica from the Irkutsk Reservoir (Denikina et al., 2023). Therefore, the study was aimed to carry out a comparative analysis and reconstruction of the phylogenetic position of coccidia from the intestine of the belica.

2. Materials and methods

The capture site with coordinates 52°12'37" N, 104°25'28"' E was located in the Irkutsk Reservoir on the Angara River. The fish were caught from a depth of 2-3 m with hooked gear in July and August 2019. Fish were euthanized with an overdose of anesthetic (GOST 33219-2014, 2016) using a 2% lidocaine solution (Lidocaine Bufus, Renewal, Russia). A total of 20 adults were caught. Specimens were transported in ice and stored at – 20°C. The weight and standard length of fish studied (mean ± SE) were 2.6 ± 0.2 g and 5.8 ± 1.4 cm, respectively (Kulakova et al., 2022; Denikina et al., 2023).

To isolate DNA from all individuals, the intestines and their content were removed and combined into a single sample. According to the manufacturer's instructions, total DNA was isolated using an AmpliSense DNA-sorb-AM extraction kit (Russia). A fragment of the cytochrome c oxidase (cox1) subunit 1 gene was amplified with MiSeq primers: COIintF 5´tcgtcggcagcgtcagatgtgtataagagacagGGWACWGGWTGAACWGTWTAYCCYCC and dgHCO2198 5´gtctcgtgggctcggagatgtgtataagagacagTAIACYTCIGGRTGICCRAARAAYCA (Leray et al., 2013). A library from the purified amplicon pool was constructed using the Nextera XT kit (Illumina, Hayward, CA, USA), and nucleotide sequences were determined with Illumina NextSeq. After bioinformatic processing, the resulting overlapping paired reads (contigs) were filtered according to the quality of the reads and their length. The data obtained were deposited into the NCBI international database with the bioproject registration number PRJNA648490 (Denikina et al., 2023).

Primary processing and translation of the nucleotide sequences obtained and data on representatives of the suborder Eimeriorina in the GenBank database (Table) were performed using the BioEdit program and aligned with the ClustalW software. Phylogenetic analysis was performed using MEGA7 software (Kumar et al., 2016).

The evolutionary history based on nucleotide sequences was inferred with the Maximum Likelihood Estimation (MLE) method using the Tamura-Nei model (Tamura and Nei, 1993). The evolutionary history based on amino-acid sequences was derived with the Le-Gascuel method (Nei and Kumar, 2000; Le and Gascuel, 2008). In both cases, the discrete gamma distribution was applied to model differences in evolutionary rates among sites. Statistical support for branch nodes was assessed using bootstrap analysis, 2000 replicates.

3. Results and discussion

Analysis of metagenomic DNA sequencing data from the intestine of the belica resulted in the determination of coccidia sequences. Eimeriorina accounted for more than 6.4% of the total pool of sequences obtained. Polymorphism of the parasite population was detected: there were 9 genotypes, with 99% of the sequences belonged to four (76.14; 10.65; 7.95 and 4.3%). The genotypes differ from each other by point mutations, only three sites resulted in amino acid replacements with similar charge and radical (V to I). The results obtained do not allow a clear conclusion about the abundance of Eimeriorina species in the analyzed material and require further research.

Fish coccidia are relatively understudied and nucleotide data for them are extremely scarce (at best, SSU rRNA genes have been identified). This fact is due to the lack of taxon-specific conserved regions in the SSU rRNA gene, which makes direct molecular genetic diagnosis of Eimeriorina more difficult. The *cox1* mtDNA gene sequences of fish coccidia are not available in the GenBank database. Sequences of Eimeriorina representatives of birds, rodents, primates, marsupials, and reptiles were used in the analysis; the *cox1* mtDNA gene sequence of *Toxoplasma gondii* was presented as an out-group (Table, Fig. 1).

In the dendrogram, the nucleotide sequences of coccidian of the belica formed a distinct cluster Eimeriorina* located at the base of the tree (Fig. 1). In this case, the tree is not resolved, and the support of the major branches is extremely low (from 0%). The phylogenetic reconstruction based on the analysis of the corresponding amino acid sequences (Fig. 2) is much more reliable: the Eimeriorina* cluster is formed with a more significant support (85%). The branching within the coccidia cluster from terrestrial vertebrates is weakly and unreliably supported, as in the case of the nucleotide sequences (Fig. 2).

On the one hand, this fact is evidence of a significant gap in our knowledge of the mitochondrial genomes of these parasites because the cox1 mtDNA gene sequences of fish coccidia are not available in the GenBank database. Moreover, there is no correlation of branching order with genus affiliation, and a very relative affiliation with a host in the phylogenetic tree constructed on the basis of SSU rRNA gene sequences

Table. Characterization of the nucleotide sequences of the *cox1* gene of the representatives of the suborder Eimeriorina from the GenBank database.

Species	Host	Location of sampling site	№№ GenBank
Caryospora bigenetica Wacha and Christiensen, 1982	*Sistrurus catenatus* (Say, 1823)	USA	KF859856
Cyclospora cayetanensis Ortega, Gilman & Sterling, 1994	*Homo sapiens* Linnaeus, 1758	USA	MN260359; MN260361; MN260362; MN260363; MN260364; MN260366; MN316534; MN316535
Eimeria acervulina Tyzzer, 1929	*Gallus gallus* (Linnaeus, 1758)	PRC	EF158855
Eimeria anseris (Kotlan, 1932)	*Anser albifrons* (Scopoli, 1769)	PRC	MH758793
Eimeria brunetti Levine, 1942	*G. gallus*	Canada	HM771675
Eimeria falciformis (Eimer, 1870)	*Mus musculus* Linnaeus, 1758	Germany	MH777557
Eimeria flavescens Marotel & Guilhon, 1941	*Oryctolagus cuniculus* (Linnaeus, 1758)	PRC	KP025693
Eimeria furonis Hoare, 1927	*Mustela putorius* Linnaeus, 1758	Canada	MF774035
Eimeria gaimardi Barker, O'Callaghan, and Beveridge, 1988	*Bettongia gaimardi* (Desmarest, 1822)	Australia	MK202809
Eimeria maxima Tyzzer, 1929	*G. gallus*	USA	FJ236459
Eimeria meleagrimitis Tyzzer 1929	*Meleagris gallopavo* Linnaeus, 1758	Canada	KJ526131
Eimeria mephitidis Andrews 1928	*Mephitis mephitis* (Schreber, 1776)	Canada	KT203398
Eimeria mitis Tyzzer, 1929	*G. gallus*	Chech Republic	FR796699
Eimeria mundayi Barker, O'Callaghan, and Beveridge, 1988	*Potorous tridactylus* (Kerr, 1792)	Australia	MK202808
Eimeria necatrix Johnson, 1930	*G. gallus*	Canada	HM771680
Eimeria papillata Ernst, Chobotar, & Hammond, 1971	*M. musculus*	Canada	KT184377
Eimeria piriformis Kotlan & Pospesch, 1934	*O. cuniculus*	Chech Republic	JQ993698
Eimeria potoroi Barker, O'Callaghan, and Beveridge, 1988	*P. tridactylus*	Australia	MK202807
Eimeria praecox Johnson, 1930	*G. gallus*	Canada	JQ659301
Eimeria tenella (Railliet & Lucet, 1891) Fantham, 1909	*G. gallus*	Sudan	MF497440
Eimeria subspherica Christensen, 1941	*Bos taurus* Linnaeus, 1758	Turkey	KU351704
Eimeria trichosuri O'Callaghan & O'Donoghue, 2001	*Trichosurus caninus* (Ogilby, 1835)	Australia	JN192136
Eimeria vermiformis Ernst, Chobotar and Hammond, 1971	*Apodemus flavicollis* (Melchior, 1834)	Germany	MK257110
Eimeria woyliei Northover et al., 2019	*Bettongia anhydra* Finlayson , 1957	Australia	MK202806
Eimeria zuernii (Rivolta, 1878) Martin, 1909	*B. taurus*	Canada, PRC, Australia	HM771687; KX495130; OL770312
Eimeria sp.	*Coturnix coturnix* (Linnaeus, 1758)	Egypt	MF496271

Species	Host	Location of sampling site	№№ GenBank
Eimeria sp. 1	*Tiliqua rugosa* subsp. *rugosa* Gray, 1825	Australia	JX839284
Isospora amphiboluri Cannon, 1967	*Ctenophorus nuchalis* (De Vis, 1884)	Australia	KR108297; MW720599
Isospora butcherae Yang, Brice, Jian & Ryan, 2018	*Zosterops lateralis* (Latham, 1802)	Australia	KY801687
Isospora coerebae Berto et al., 2011	*Coereba flaveola* (Linnaeus, 1758)	Brazil	OK194672
Isospora coronoideae Liu et al., 2019	*Corvus coronoides* Vigors & Horsfield, 1827	Australia	MK867778
Isospora greineri Hafeez et al. 2014	*Lamprotornis superbus* Rüppell, 1845	Canada	KR108298
Isospora gryphoni Olson, Gissing, Barta & Middleton, 1998	*Carduelis tristis* (Linnaeus, 1758)	Canada	KC346355
Isospora lacazei (Labbé, 1893)	*Pavo cristatus* Linnaeus, 1758	PRC	MW775672
Isospora manorinae Yang, Brice, Jian & Ryan 2016	*Manorina flavigula* subsp. *wayensis* (Mathews, 1912)	Australia	KT224377
Isospora mayuri Patnaik, 1966	*P. cristatus*	PRC	MW775673
Isospora phylidonyrisae Yang, Brice, Berto & Ryan, 2021	*Phylidonyris novaehollandiae* (Latham, 1790)	Australia	MW423631
Isospora picoflavae Rejman, Hak-Kovacs & Barta, 2021	*Colaptes auratus* subsp. *luteus* Bangs, 1898	Canada	NC_065382
Isospora serini (Aragao, 1933)	*Serinus canaria* (Linnaeus, 1758)	Brazil	ON584773
Isospora serinuse Yang, Brice, Elliot & Ryan 2015	*S. canaria*	Australia	KX276860
Isospora superbusi Hafeez et al. 2014	*Lamprotornis superbus* Rüppell, 1845	Canada	KT203396
Isospora svecica Trefancová & Kvičerová, 2019	*Luscinia svecica* subsp. *cyanecula* (Wolf, 1810)	Chech Republic	MK573841
Isospora sp.	*Sturnus vulgaris* Linnaeus, 1758	USA	OL999169
Isospora sp. 1	*S. canaria*	Canada	KP658103
Isospora sp. 2	*M. gallopavo*	Canada	KC346356
Isospora sp. 3	*S. vulgaris*	USA	OL999161
Isospora sp. 4	*Carduelis carduelis* (Linnaeus, 1758)	Great Britain	OL999140
Lankesterella minima (Chaussat, 1850) Nöller, 1912	*Lithobates clamitans* (Latreille, 1801)	Canada	KT184381
Toxoplasma gondii (Nicolle & Manceaux, 1908)	Strain ME49, Center for tropical and emerging global diseases, University of Georgia, USA		MN077082

(Molnár et al., 2012; Couso-Pérez et al., 2019; Liu et al., 2021). On the other hand, it was previously hypothesized that it was the fish coccidia that gave rise to all known coccidia lineages in other vertebrates (Rosenthal et al., 2016; Xavier et al., 2018). Perhaps, our results are an indirect confirmation of this hypothesis, and the Eimeriorina* cluster (Figs. 1, 2) will be replenished when new nucleotide data on mitochondrial genomes of fish coccidia appear.

The obvious paraphilia of the genera *Eimeria* and *Goussia*, which was discussed many times and proven previously (Jirků et al., 2009; Ogedengbe et al., 2018; Xavier et al., 2018), is also reflected in our dendrograms. Undoubtedly, a revision of the main phenotypic characteristics, which determine the taxonomic affiliation of coccidia, is required.

Eimeria cyprinorum Stankovih, 1921 (Syn.: *Goussia carpelli* (Léger et Stankovith, 1921), *Goussia carpelli* (Léger et Stankovith, 1921) (Syn.: *Eimeria carpelli* Léger et Stankovith, 1921; *E. cyprini* Plehn, 1924; *E. cyprinorum* Stankovith, 1921; *E. wierzejskii* Hoer, 1904) and *Eimeria* sp. (Jastrzębski, 1984; Kirjušina and Vismanis, 2007; Belova and Krylov, 2006; Pugachev et al., 2012) were found in the belica in the native habitat (water bodies and watercourses of the Ponto-Caspian basin as well as the Baltic Sea basin).

Earlier, *G. carpelli* was found in several species (Pugachev et al., 2012), including Lake Baikal hornbill fish: bighead sculpin *Batrachocottus baicalensis* (Dybowski, 1874), sand sculpin *Leocottus kesslerii* (Dybowski, 1874), and deepwater sculpin *Cyphocottus eurystomus* (Taliev, 1955) (Schulman and Zaika, 1964; Zaika, 1965). The spectrum of parasitic species of the common belica in a given water body depends on the conditions of the host habitat and the composition of the parasitic fauna of the dominant ichthyofauna species (Dorovskikh, 2019). The Irkutsk Reservoir is located along the Angara River basin from Lake Baikal to Irkutsk. Its total area is 15 thousand hectares, and almost 25% of it is accounted for by bays and shallow waters. The bighead sculpin can be found in the upper and middle areas of the Irkutsk Reservoir in stony-silty soils. The sand sculpin is spread in the Angara River from the source to the mouth; the highest abundance is found in the coastal zone of the reservoir with sandy, silty-sandy, and stony-sandy soils (Bogdanov, 2015). The belica prefers shallow and well heated stretches of water with silty and sandy bottoms. Nowadays, *G. carpelli* is considered to be a specific parasite of the carp *Cyprinus carpio* Linnaeus, 1758 (Molnár et al., 2005) and many fishes from its former host list have their own separate coccidia species (Sokolov and Moshu, 2014). In this regard, a complex morphological and molecular genetic study of these parasites, which are particularly widespread in different systematic groups of fish *G. carpelli*, is required.

Moreover, it was previously shown under experimental conditions it was hat feeding on fish by oligochaetes of the genera *Tubifex* and *Limnodrilus*, containing *G. carpelli* sporozoites, contributes to the infection of fish (Molnar and Ostoros, 2007). Representatives of these genera, dwelling in slow-flowing or stagnant silty and/or sandy bottoms, have been found in the zoobenthos composition of waters in the Baikal region (Semernoy, 2001). The Irkutsk Reservoir is subjected to anthropogenic impact: significant water level fluctuations (Bychkov and Nikitin, 2015) and recreational pressure. Previously, it was shown that environmental factors (increased input of biogenic elements into the reservoir, lowering of the water level, unfavorable temperature conditions, etc.) resulted in the greatest distribution of oligochaetes among other representatives of benthic fauna, which contributed to an increase in the infection of fish with parasites (Novokhatskaya et al., 2008; Jirsa et

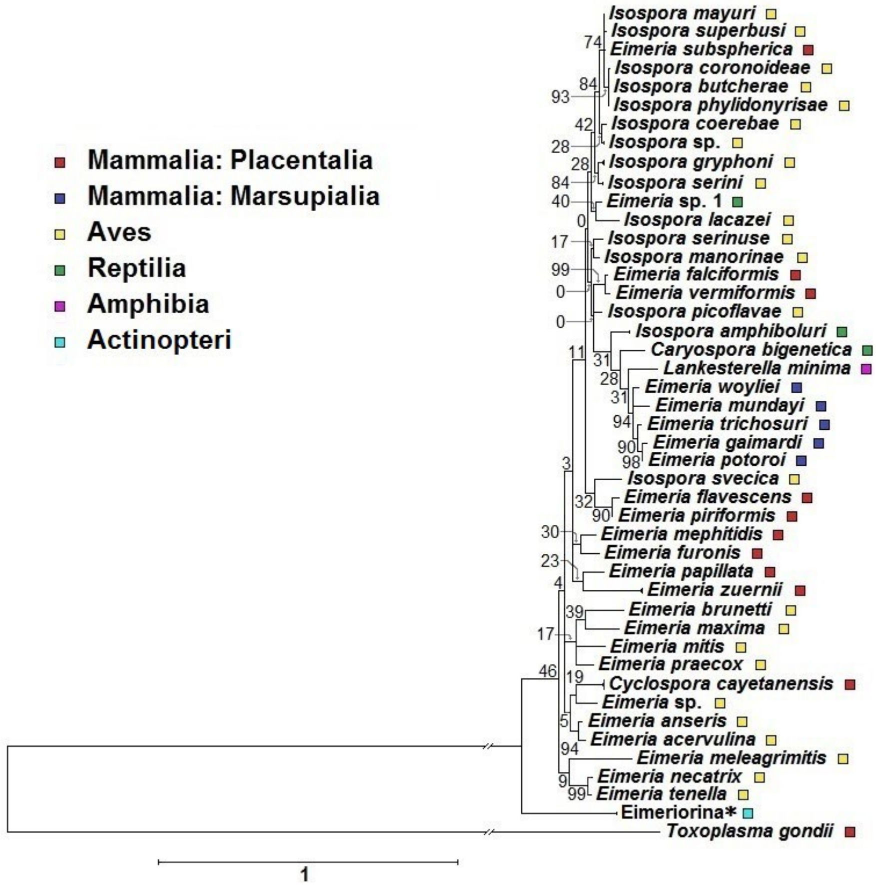

Fig.1. Phylogenetic tree of the representatives of the suborder Eimeriorina was derived with the Maximum Likelihood Estimation (MLE) method on the basis of nucleotide sequences of the *cox1* mitochondrial DNA gene fragments. Eimeriorina* – sequences from the belica.

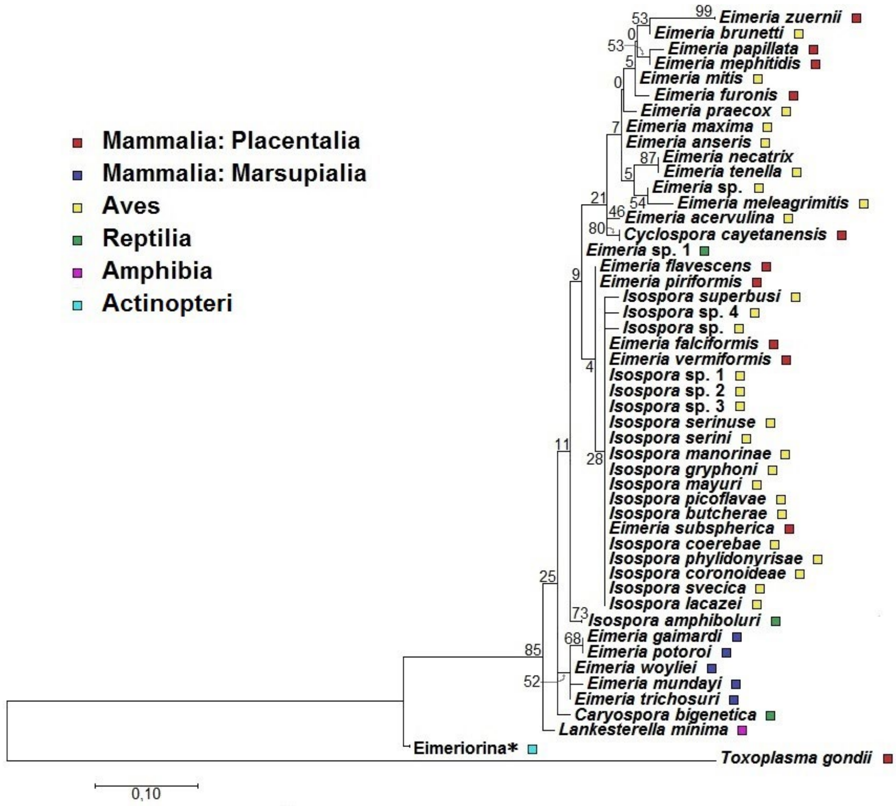

Fig.2. Phylogenetic tree of the representatives of the suborder Eimeriorina was derived with the Maximum Likelihood Estimation (MLE) method on the basis of amino acid sequences of the *cox1* gene fragments. Eimeriorina* – sequences from the belica.

al., 2008), for instance, with cestodes of the genus *Caryophyllaeus* (Denikina et al., 2023). Thus, the presence of the nucleotide sequences of the representatives of Eimeriorina in the intestines of fish could indicate feeding of the belica by infected oligochaetes. In this regard, the need for revision of parasites in fish of the Angara River and Lake Baikal and additional studies of their biology and ecology is considered.

4. Conclusion

The results of comparative analysis and reconstruction of the phylogenetic position of coccidia from the intestine of the belica from the Irkutsk Reservoir revealed a significant gap in the knowledge of their mitochondrial genomes expressed in the absence of the *cox1* mtDNA gene sequences of Eimeriorina representatives from fish in the GenBank database. Determination of the cox1 gene fragment and comparative analysis of the obtained nucleotide sequences and those available in genetic databases revealed paraphilia of the genera *Eimeria* and *Goussia*. In the dendrograms, the sequences of the belica coccidia formed a distinct cluster Eimeriorina*, located at the base of the tree. Polymorphism of the parasite population was detected, but the results obtained did not allow a clear conclusion about the abundance of Eimeriorina species in the analyzed material and required further investigations. Thus, the hypothesis that coccidia of fish were ancestors of coccidia of other vertebrates was indirectly confirmed. In this regard, the need for revision of parasites in fish of the Angara River and Lake Baikal and additional studies of their biology and ecology are considered.

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Conflict of interest

The authors declare that they have no competing interests.

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