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Phylogenetic position of *Lecithodollfusia* (Trematoda: Microphalloidea) inferred from molecular data on *L. arenula* ex *Fulica atra* (Aves: Rallidae)

S.A. Vlasenkov[1], A.P. Kalmykov[2,3], S.G. Sokolov[1*]

[1] A.N. Severtsov Institute of Ecology and Evolution, RAS, Leninsky Prospect 33, Moscow, 119071 Russia.
[2] Astrakhan State Natural Biosphere Reserve, Naberezhnaya reki Tsarev 119, Astrakhan, 414021 Russia.
[3] Astrakhan State Joint Historical and Architectural Museum Preserve, Sovetskaya street 15, Astrakhan, 414000 Russia.
** Correspondence author: Sergey G. Sokolov, sokolovsg@mail.ru*
Sergei Vlasenkov: ORCID 0000-0002-5741-2255
Alexander Kalmykov: ORCID 0000-0003-0640-7963
Sergey Sokolov: ORCID 0000-0002-4822-966X

ABSTRACT: *Lecithodollfusia* Odening, 1964 is a small genus of microphalloid trematodes whose adults parasitize wetland birds. In this study, we assessed the taxonomic position and phylogenetic relationship of *Lecithodollfusia* based on newly obtained molecular data on its type species, *L. arenula*. The trematodes were isolated from the intestine of *Fulica atra* taken in Astrakhan Region, Russia. Morphological descriptions were made in addition to the molecular data. In our phylogenetic analysis based on 28S rRNA gene sequences, *Lecithodollfusia* was placed within the Pleurogenidae as a well-supported sister to *Leyogonimus*. The adults of *L. arenula* examined in our study were conspecific with the cercaria of Pleurogenidae gen. sp. previously found in *Bithynia tentaculata* from Germany. In addition, we transferred the genus *Collyriclum* into the Pleurogenidae and abolished the family Collyriclidae.
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KEY WORDS: *Collyriclum*, Collyriclidae, Pleurogenidae, River Volga delta.

Филогенетическое положение *Lecithodollfusia* (Trematoda: Microphalloidea) по молекулярным данным, полученным для *L. arenula* из *Fulica atra* (Aves: Rallidae)

С.А. Власенков[1], А.П. Калмыков[2,3], С.Г. Соколов[1*]

[1] Институт проблем экологии и эволюции им. А.Н. Северцова РАН, Ленинский проспект 33, Москва, 119071 Россия.
[2] Астраханский государственный природный биосферный заповедник Набережная реки Царев 119, Астрахань, 414021 Россия.
[3] Астраханский государственный объединенный историко-архитектурный музей -заповедник, ул. Советская15, Астрахань, 414000 Россия.
** Автор для корреспонденции: Sergey G. Sokolov, sokolovsg@mail.ru*

РЕЗЮМЕ: *Lecithodollfusia* Odening, 1964 — бедный видами род микрофаллоидных трематод, мариты которых паразитируют у водно-болотных птиц. В данной работе мы оценили таксономическое положение и филогенетические связи *Lecithodollfusia* на основе молекулярных данных, полученных из его типового вида *L. arenula*. Трематоды были выделены из кишечника лысухи *Fulica atra*, добытой в Астраханской области (Россия). В дополнение к молекулярным данным были сделаны морфологические описания собранных червей. В ходе филогенетического анализа, основанного на последовательностях генов 28S рРНК, *Lecithodollfusia* была отнесена к семейству Pleurogenidae, в качестве сестринского таксона к роду *Leyogonimus*. Мариты *L. arenula*, исследованные в нашей работе, были конспецифичны с церкариями Pleurogenidae gen. sp., ранее отмеченными у *Bithynia tentaculata* в Германии. Кроме того, результаты нашего анализа позволили перенести род *Collyriclum* в семейство Pleurogenidae и упразднить семейство Collyriclidae.
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КЛЮЧЕВЫЕ СЛОВА: *Collyriclum*, Collyriclidae, Pleurogenidae, дельта Волги.

Introduction

Lecithodollfusia Odening, 1964 is a small genus of microphalloid trematodes. It is characterised by a transversely or obliquely arranged cirrus sac, a marginal genital pore located at the level of the ventral sucker or just posterior to it, virgulate xiphidiocercariae with four pairs of penetration glands and several other features (Khotenovskii, 1970; Sharpilo, Iskova, 1989; Besprozvannykh, 2003).

By different accounts, *Lecithodollfusia* contains two (Khotenovskii (1967, 1970) or three (Niewiadomska, Pojmańska, 2018) species. According to Khotenovskii (1967, 1970), it comprises *Lecithodollfusia arenula* (Creplin, 1825) (type) and *L. anatina* Khotenovskii, 1967. *L. arenula* has originally been described from *Fulica atra* Linnaeus, 1758 in Germany (Creplin, 1825). Since that time, this trematode species has been found in Europe, Central Asia and Western Siberia (e.g. Creplin, 1825; Dollfus, 1956; Odening, 1964; Filimonova, Shalapina, 1975; Belyakova, 1981; Sharpilo, Iskova, 1989; Serbina, 2014). *Lecithodollfusia anatina* has been described from *Anas* sp. and *Mergellus albellus* (Linnaeus, 1758) taken in Yakutia, Russia (Khotenovskii, 1967). Since the original description, there has been only one new report of this parasite. Besprozvannykh (2003) found it in the bithyniid mollusc *Boreoelona ussuriensis* (Ehrmann, 1927) in the Primorsky Region of Russia, identifying the species by adults experimentally reared in chicken. *Lecithodollfusia arenula* and *L. anatina* differ from each other in the position of the uterine loops (protruding into forebody *vs* not protruding) and the cirrus sac (not protruding beyond right margin of ventral sucker *vs* protruding) (Khotenovskii, 1967, 1970).

Niewiadomska and Pojmańska (2018) consider *Laterotrema vexans* (Braun, 1901) as *Lecithodollfusia vexans* without any explanation. *Laterotrema vexans* has an elongate-fusiform body shape, lacks the oesophagus and its genital pore is positioned antero-laterally to the ventral sucker (compare with Sharpilo, Iskova, 1989; Niewiadomska, Pojmañska, 2018). This means that this species is strikingly different from *L. arenula* and *L. anatina*, and we do not consider it as belonging to *Lecithodollfusia*.

Lecithodollfusia was recognised as a member of the Phaneropsolidae in the system of the Microphalloidea by Lotz and Font (2008a). However, the morphology of its cercariae, namely, the presence of four pairs of penetration glands (Besprozvannykh, 2003), indicates that this genus belongs to the Pleurogenidae (Shchenkov *et al*., 2020). In this paper, we consider *Lecithodollfusia* within the framework of the pleurogenic concept. To note, Khotenovskii (1970) also thought that *Lecithodollfusia* was a pleurogenid.

The taxonomy of the Pleurogenidae has recently been clarified with the use of molecular methods. In particular, the pleurogenid concept has been confirmed for *Collyricloides* Vaucher, 1969*, Cortrema* Tang, 1951, *Gyrabascus* Macy, 1935, *Leyogonimus* Ginetsinskaya, 1948, *Macyella* Neiland, 1951, *Parabascus* Looss, 1907 and *Urotrema* Braun, 1900, which were previously recognized as members of six distinct families (Tkach *et al*., 2002, 2003, 2019; Blair, Barton, 2008a, b; Lotz, Font, 2008a–d; Kanarek *et al*., 2014, 2015, 2017; Sokolov *et al*., 2020; Kirillova *et al*., 2022). Moreover, *Collyriclum* Kossack, 1911 (type genus of Collyriclidae) appears in the recent phylogenetic reconstructions as a member of the Pleurogenidae + Collyriclidae clade, in which the pleurogenids form a paraphyletic assemblage (Shchenkov *et al*., 2020, 2022; Sokolov *et al*., 2020; Kirillova *et al*., 2022).

The position of *Leyogonimus* within the Pleurogenidae + Collyriclidae clade is noteworthy. Its type species, *Leyogonimus polyoon* (Linstow, 1887), is a common parasite of rallid birds, similarly to *L. arenula*. This circumstance suggests that *Lecithodollfusia* might be phylogenetically close to *Leyogonimus.*

The aim of this study was to make a phylogenetic assessment of the genus *Lecithodollfusia* based on the data on its type species, *L. arenula.*

Materials and Methods

SAMPLING AND MORPHOLOGICAL STUDY. Gravid and sub-adult specimens of *L. arenula* were collected from two specimens of *F. atra* taken in the hunting grounds near Poldnevoe village (45º82' N, 47º91' E) in the River Volga delta, Astrakhan Region, Russia. Trematode specimens were initially relaxed in fresh water and fixed in 70% ethanol, and after a few minutes transferred into 96% ethanol. Three of these specimens were used as hologenophores. Small fragments of the bodies were extracted from the hologenophores using needles and subsequently used for the molecular genetic analysis. Hologenophores and the paragenophore were stained with acetocarmine, dehydrated in a graded ethanol series, cleared in dimethyl phthalate, and mounted in Canada balsam. Additionally, we examined slides with four adult specimens of *L. arenula* ex *F. atra* from Novosibirsk Region of Russia (collector: Dr. L.V. Filimonova) deposited in the Museum of Helminthological Collections at the Center of Parasitology of the Severtsov Institute of Ecology and Evolution (IPEE RAS; Moscow, Russia) under number 1282/Tr.

Drawings were made with the aid of a camera lucida. Photographs were made using a compound microscope Zeiss Axio Imager Z1 equipped with a camera Zeiss AxioCam HRc. All measurements are in micrometers. Hologenophores of *L. arenula* are stored in the personal collection of the first author. Unfortunately, the paragenophore was damaged during the final stage of the drawing.

MOLECULAR DATA AND PHYLOGENETIC ANALYSIS. Genomic DNA was isolated from three hologenophores using QIAamp DNA Mini Kit (QIAGEN). BIO-RAD T100 Thermal Cycler amplified the fragments. PCR reactions were performed in a total volume of 25 µl using the Encyclo Plus PCR kit (Eurogene) according to the manufacturer's instructions. Partial 28S rRNA gene sequences were amplified with ZX1aF (5'-ACCCGCTGAATTTAAGCATAT-3') (Palm *et al*., 2009) and 1500R (5'-GCTATCCTGAGGGAAACTTCG-3') (Snyder, Tkach, 2001) primers. The following protocol was used: initial denaturation at 95ºC (5 min); 40 cycles of 30 s at 95ºC; 30 s at 55ºC; 2 min at 72ºC; and 7 min at 72ºC for the final extension. In addition, we amplified ITS2 locus of nuclear DNA and cox1 gene of mitochondrial DNA. To amplify the complete sequences of the ITS2 locus, we used 3S (5'-GTACCGGTGGATCACGTGGCTAGTG-3') (Morgan and Blair, 1995) and ITS2.2 (5'-CCTGGTTAGTTTCTTTTCCTCCGC-3') (Cribb *et al*., 1998) primers, according to the following protocol: cycle 1 was 95°C for 3 min, 45°C for 2 min and 72°C for 150 s; this was followed by 4 shorter cycles, 95 °C for 45 s, 50°C for 45 s and 72 °C for 90 s, then further 30 cycles of 95 °C for 20 s, 52 °C for 20 s and 72 °C for 90 s and 5 min at 72°C for the final extension. Partial cox1 gene sequences were amplified with JB3 (5'-TTTTTTGGGCATCCTGAGGTTTAT-3') and JB4.5 (5'-TAAAGAAAGAACATAATGAAAATG-3') (Bowles *et al*., 1992) primers. The following protocol was used: initial denaturation at 95°C for 5 min, then 95°C for 20 s, 55°C for 30 s, 72°C for 30 s extension for 35 cycles, and 5 min at 72°C for the final extension.

The amplicons were purified using Cleanup S-Cap (Eurogene) and sequenced directly using PCR primers. In addition, internal primers 300F (5'-CAAGTACCGTGAGGGAAAGTTG-3') and ECD2r (5'-CTTGGTCCGTGTTTCAAGACGGG-3') were used to sequence 28S rRNA gene. DNA sequencing was performed using the ABI PRISM® BigDye™ Terminator v. 3.1 followed by the analysis of the reaction products on an Applied Biosystems 3730 DNA Analyzer automated sequencer at the "Genome" Shared Resource Centre (Engelhardt Institute of Molecular Biology, Moscow, Russia).

To assess the phylogenetic relationships of *Lecithodollfusia*, Bayesian inference analyses based on the 28S rRNA gene and the ITS2 locus sequences were performed. The main purpose of the 28S rRNA analysis was to molecularly verify the family affiliation of *Lecithodollfusia* and to identify closely related genera. The aim of the ITS2-based analysis was to find the conspecific isolates. We did not perform a phylogenetic analysis using cox1 sequence data because cox1 sequences of only three species belonging to the Pleurogenidae are currently available.

For the phylogenetic reconstructions based on the 28S rRNA gene and the ITS2 locus datasets newly obtained sequences were aligned with those of 46 and 12 microphalloid species, respectively (Table S1). Alignments were performed using the Muscle algorithm (Edgar, 2004) as implemented in SeaView Version 4.0 (Gouy *et al*., 2010), after which the alignment was adjusted manually. Bayesian algorithm was performed in MrBayes 3.2.7a (Ronquist *et al*., 2012) with the GTR+G+I model for both alignments. The evolutionary model was estimated with as suggested by jModeltest 2.1.7 (Darriba *et al*., 2012). In the analysis, 15 000 000 generations of the Markov chain Monte Carlo were simulated and selection was performed at a frequency of once every 100 generations.

The phylogenetic 28S tree was rooted to *Plagiorchis elegans* (Rudolphi, 1802) (Plagiorchioidea, Plagiorchiidae) based on the findings of Olson et al. (2003). For the ITS2 tree, *Renschetrema* sp. (Microphalloidea, Cryptotropidae) was used as an outgroup, in agreement with the data of Tkach *et al*. (2023) on phylogenetic relationships of the microphallod digeneans. Estimates of evolutionary divergence (p-distances) were made with MEGA 11.0.13 software (Tamura et al. 2021).

Results

Taxonomy

Family Pleurogenidae Looss, 1899
Genus *Lecithodollfusia* Odening, 1964
Lecithodollfusia arenula (Creplin, 1825)
Fig. 1A, B.

HOST: *Fulica atra* Linnaeus, 1758 (Aves, Rallidae).

LOCALITY: Vicinity of Poldnevoe village (45º82′ N, 47º91′ E), Astrakhan Region, Russia.

PREVALENCE AND INTENSITY OF INFECTION: 2 of 4 host specimens; 10–14 worms per host specimen (4 gravid and 20 sub-adult *L. arenula* specimens).

ACCESSIONS: Two partial sequences of the 28S rRNA gene GenBank No OR233628; OR233629, two complete sequences of the ITS2 locus of nuclear DNA GenBank No OR233630; OR233631, and three partial sequences of the cox1 gene of mitochondrial GenBank No OR230528–OR230530.

DESCRIPTION (based on four gravid specimens — three hologenophores and one paragenophore; measurements on hologenophores only): Body oval to broadly fusiform, 497–541 × 284–344; length to width ratio 1:0.55–0.67 (Fig. 1A). Tegument spinose. Oral sucker subspherical, 50–63 × 65–70; mouth opening subterminal. Ventral sucker rounded, recessed into body, 70–83 × 73–85. Sucker-width ratio 1:1.03–1.30. Forebody 28.6–35.2% of body length. Prepharynx short, up to 6 in length. Pharynx 38–43 × 40–48. Oesophagus 25–50 long. Intestinal bifurcation at about level of anterior margin of ventral sucker. Caeca terminate blindly close to posterior extremity (Fig. 1A).

Testes two, entire, slightly diagonal from each other; right testis anterior to left testes or vice versa, anterior testis partly overlaps with ventral sucker area: right testis 101–104 × 89–92, left testis 94–98 × 66–86 (Fig. 1A, B). Post-testicular region 34.8–41.0% of body length. Cirrus sac claviform, almost rectilinear or curved posteriorly, transversally oriented or oblique; proximal end not protruding beyond right margin of ventral sucker (in three specimens) or slightly extends beyond this margin (in one specimen), 141–207 × 46; contains tubular looped internal seminal vesicle, tubular pars prostatica, surrounded by prostatic cells, ejaculatory duct and unarmed cirrus (Fig. 1A, B). Genital atrium shallow (Fig. 1B). Genital pore sinistro-marginal, at midlevel of or just posterior to ventral sucker (Fig. 1A, B).

Ovary lobed or slightly indented, antero-median to each testis, overlaps with ventral sucker, 94–123 × 76–205 (Fig. 1A, B). Seminal receptacle median, between testes, posterior to ovary (Fig. 1A). Mehlis' gland and Laurer's canal not observed. Metraterm thick-walled, opens into genital atrium dorsally to male duct (Fig. 1, mt). Uterus extensive, not extending into forebody (Fig. 1A). Eggs numerous, operculate, 22 × 12. Vitellarium follicular (Fig. 1, vf); numerous follicles, distributed between midlevels of pharynx and ventral sucker; common vitelline reservoir median (Fig. 1A), posterior to ovary. Excretory pore terminal. Excretory vesicle Y-shaped, with short stem (Fig. 1A).

PHYLOGENETIC RELATIONSHIPS. We managed to obtain partial sequences of the 28S rRNA gene from only two hologenophores of *L. arenula*. Each of the sequences was 1272 bp long. Complete sequences of the ITS2 locus (448–456 bp) and partial sequences of the cox1 gene (427–430 bp)

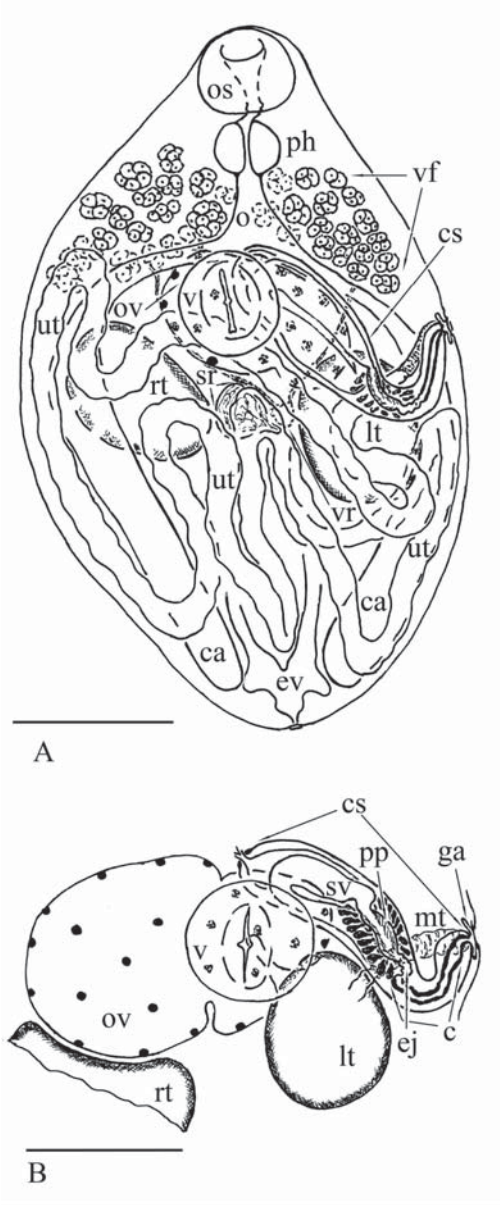

Fig. 1. *Lecithodollfusia arenula* ex *Fulica atra* from Astrakhan Region, Russia: A — paragenophore, whole ventral view; B — fragment of hologenophore body with ventral sucker and elements of male and female systems, ventral view. Scale bars: 100 μm.
Abbreviations: c — invaginated cirrus; ca — caeca; cs — cirrus sac; ej — ejaculatory duct; ev — excretory vesicle; ga — genital atrium; lt — left testis; mt — metraterm; o — oesophagus; os — oral sucker; ov — ovary; ph — pharynx; pp — pars prostatica; rt — right testis; sr — seminal receptacle; sv — internal seminal vesicle; ut — uterine loops; v — ventral sucker; vf — vitelline follicles; vr — common vitelline reservoir.
Рис. 1 *Lecithodollfusia arenula* из *Fulica atra*, Астраханская область России. A — парагенофор, общий вид, вентрально; B — фрагмент тела гологенофора с брюшной присоской и элементами мужской и женской половых систем, вентрально. Масштабные линейки: 100 μm.
Обозначения: c — инвагинированный циррус; ca — кишечные ветви; cs — сумка цирруса; ej — семеизвергательному канал; ev — экскреторный пузырь; ga — половой атриум; lt — левый семенник; mt — метратерм; o — пищевод; os — ротовая присоска; ov — яичник; ph — глотка; pp — простатическая часть; rt — правый семенник; sr — семяприемник; sv — внутренний семенной пузырек; ut — петли матки; v — брюшная присоска; vf — желточные фолликулы; vr — общий желточный резервуар.

were obtained for two and three hologenophores, respectively. The final alignment lengths were 1040 bp and 287 bp for the 28S rRNA gene and the ITS2 locus, respectively.

Analysis based on the 28S rRNA gene sequences combined two *L. arenula* specimens together with cercaria of Pleurogenidae gen. sp. 2 of Schwelm *et al*., 2020 ex *Bithynia tentaculata* (Linnaeus, 1758) from Germany into one strongly supported clade, and placed this clade (referred to below as *Lecithodollfusia*) into the large Pleurogenidae + Collyriclidae clade as a strongly supported sister to *Leyogonimus* (Fig. 2). All specimens of the *Lecithodollfusia* clade had identical sequences. The *Leyogonimus* + *Lecithodollfusia* clade had a strongly supported sister relationship with the clade containing the genera *Collyricloides*, *Cortrema* and *Macyella*. In turn, the group of these five genera was nested in the strongly supported clade, which also includes *Gyrabascus*, *Collyriclum* and *Loxogenes* Stafford, 1905. The latter two genera were strongly supported sister taxa within the group. The remaining pleurogenids were distributed between the two early-branching and highly-supported sister clades that had a poorly supported sister relationship. The clade uniting *Collyricloides*, *Collyriclum*, *Cortrema*, *Gyrabascus*, *Loxogenes*, *Lecithodollfusia*, *Leyogonimus* and *Macyella* was sister to the large clade comprising the other pleurogenids. In turn, the highly supported Pleurogenidae + Collyriclidae clade was a poorly supported sister to the strongly supported Prosthogonimidae clade.

Two recently obtained complete sequences of the ITS2 locus were identical. They were also very similar (p-distance 0.2–0.3%) to the sequences of Pleurogenidae gen. sp. 2 of Schwelm *et al*. (2020). An analysis based on the partial sequences of ITS2 locus also combined adult specimens of *L. arenula* together with the cercaria of Pleurogenidae gen. sp. 2 from Schwelm *et al*. (2020) into a single clade. Overall, the phylogenetic tree based on this locus had an unresolved topology (Fig. 3).

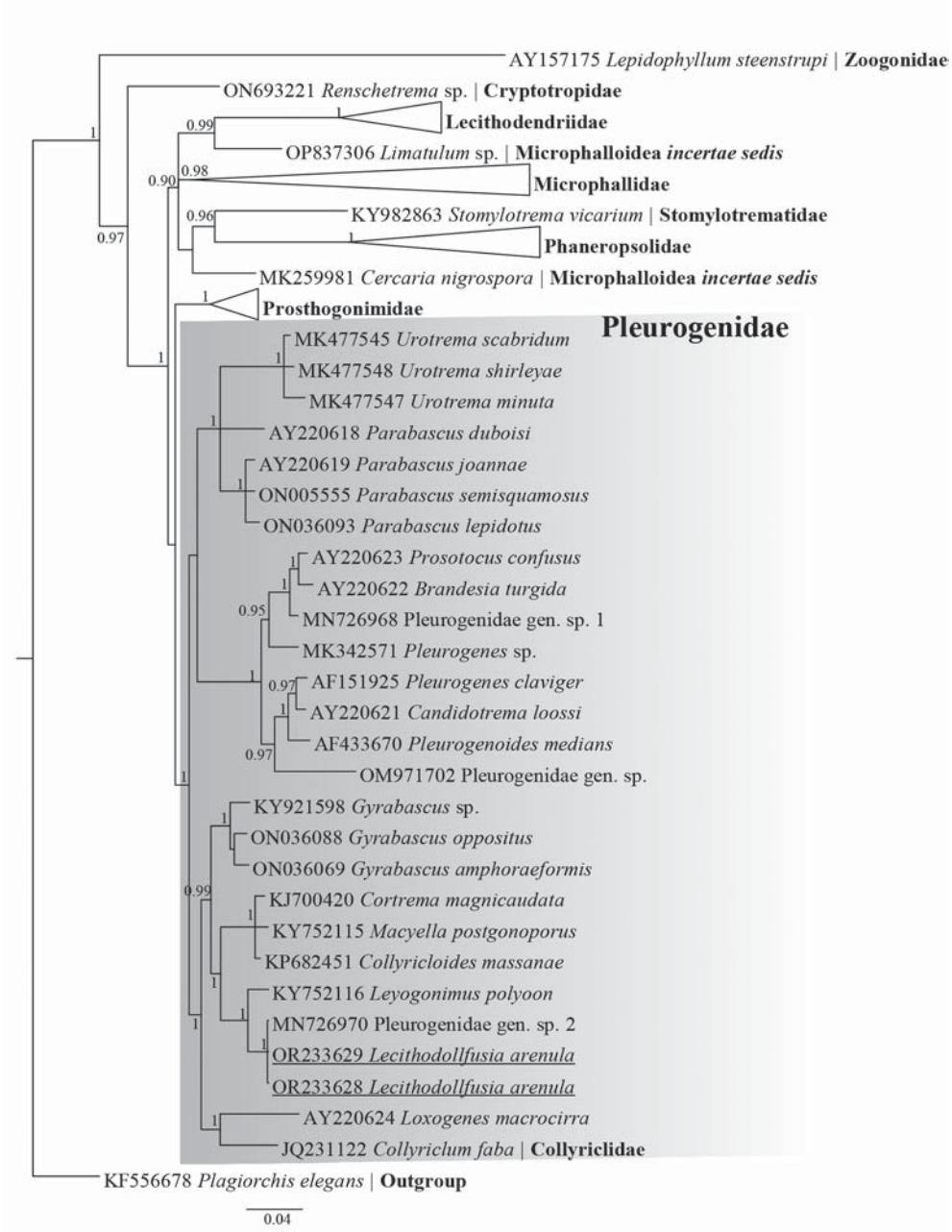

Fig. 2. Phylogenetic relationships of *Lecithodollfusia arenula* based on Bayesian inference analysis of sequences of 28S rRNA gene. Only significant values of the posterior probabilities (>0.9) are indicated. Newly obtained sequences are underlined.

Рис. 2. Филогенетические связи *Lecithodollfusia arenula,* реконструированные в ходе Байесовского анализа последовательностей гена 28S рРНК. Указаны только значимые поддержки апостериорных вероятностей (>0,9). Новые последовательности выделены подчеркиванием.

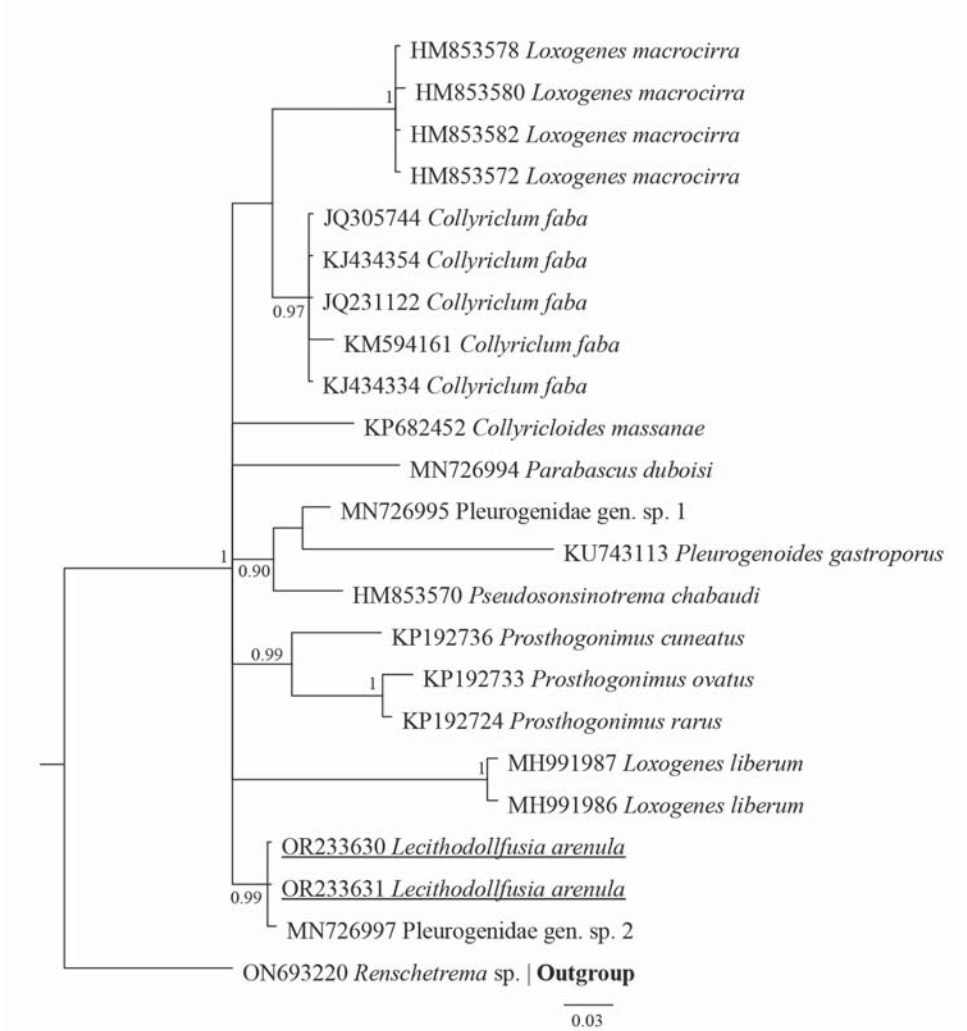

Fig. 3. Phylogenetic relationships of *Lecithodollfusia arenula* based on Bayesian inference analysis of sequences of ITS2 locus. Only significant values of the posterior probabilities (>0.9) are indicated. Newly obtained sequences are underlined.

Рис. 3. Филогенетические связи *Lecithodollfusia arenula,* реконструированные в ходе Байесовского анализа последовательностей ITS2 локуса рибосомной ДНК. Указаны только значимые поддержки апостериорных вероятностей (>0,9). Новые последовательности выделены подчеркиванием.

Given the limited data set on the cox1 gene sequences for the pleurogenids, we only compared the three specimens of *L. arenula* with each other. Three partial sequences of the cox1 gene obtained in this study showed a high degree of similarity (p-distance 0.2–0.4%).

Discussion

We identified the trematode specimens from *F. atra* taken in the River Volga delta examined in our study as *L. arenula* based on a combination of morphological characters (position of the cirrus sac in relation to the ventral sucker), ecological characters (host) and locality (Eastern Europe). However, it should be noted that the specimens examined in our study combine the features of *L. arenula* and *L. anatina*. Three of them have a relatively short cirrus sac (as does *L. arenula*), but their uterus does not protrude into the forebody (which is characteristic

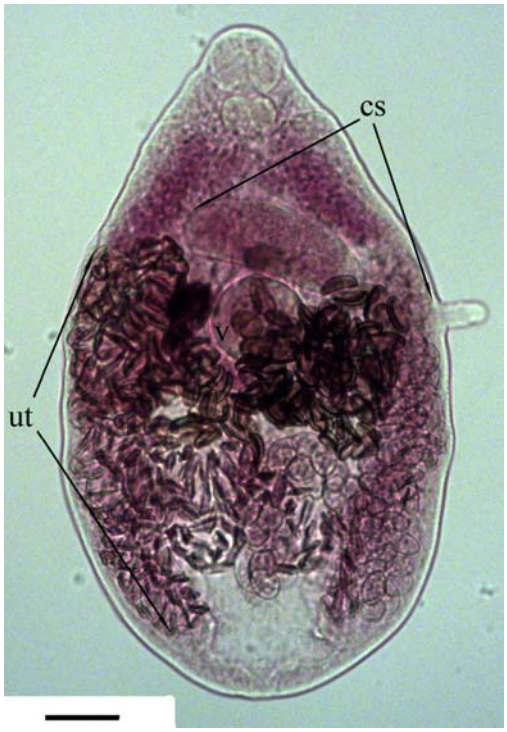

Fig. 4. Voucher specimen of *Lecithodollfusia arenula* ex *Fulica atra* from Novosibirsk Region, Russia, whole ventral view. Scale bar: 50 μm.
Abbreviations: cs — cirrus sac extending beyond the right margin of the ventral sucker; ut — uterine loops; v — ventral sucker.
Рис. 4. *Lecithodollfusia arenula* из *Fulica atra*, Новосибирская область России, общий вид, вентрально. Масштабная линейка: 50 μm.
Обозначения: cs — сумка цирруса, выступающая за правый край брюшной присоски; ut — петли матки; v — брюшная присоска.

of *L. anatina*). In one specimen from our material, the uterus also does not protrude into the forebody, and the cirrus sac extends beyond the right margin of the ventral sucker (both features as in *L. arenula*). Note that a relatively long cirrus sac was also present in the museum specimens of *Lecithodollfusia* from the same host collected in the Novosibirsk Region (IPEE RAS 1282/Tr), which we examined (Fig. 4), and in the syntype of *L. arenula* ex *F. atra* from Germany drawn by Braun (1902, fig. 99). We hypothesize that *L. anatina* is conspecific with *L. arenula*. However, a molecular study of *Lecithodollfusia* specimens from the Eastern Palearctic is needed to resolve this question.

Lecithodollfusia arenula has previously been recorded in the River Volga delta by of Ginetsinskaya (1952) and Ginetsinskaya and Dobrovolskii (1968). According to the fair observation of Odening (1964), trematode specimens from *F. atra* from the River Volga delta, found by Ginetsinskaya (1952, fig. 10) and identified by her as *Leyogonimus polyoon*, are actually *Lecithodollfusia arenula*.

Many authors have noted the low prevalence (<2%) of *L. arenula* in samles of *F. atra* (Bykhovskaya-Pavlovskaya, 1953; Smogorzhevskaya, 1976; Sitko, Heneberg, 2020). However, Filimonova and Shalapina (1975) found this parasite species in more than 30% of the *F. atra* specimens they examined (n=18). An adequate estimate of the prevalenc of *L. arenula* based on the number of host individuals we have investigated is not possible.

In this study, we obtained the first molecular data on *Lecithodollfusia*. Analysis of complete sequences of the ITS2 locus indicates that the adults of *L. arenula* are conspecific with cercariae of Pleurogenidae gen. sp. 2 of Schwelm *et al*., 2020 ex *B. tentaculata* from Germany. The morphology of the cercariae of *L. arenula* has first been described by Belyakova (1981), but the description lacks some important details, in particular, the number of penetration glands. The data of Schwelm *et al*. (2020) confirm the presence of four pairs of penetration glands in the cercaria of this species.

The analysis of the partial 28S rRNA gene sequences confirmed our hypothesis about the phylogenetic affinity of *Lecithodollfusia* to *Leyogonimus*. The Pleurogenidae appears as a paraphyletic taxon both in our study and in several previous reconstructions (Shchenkov *et al*., 2020; Sokolov *et al*., *2020*; Kirillova *et al*., 2022), since *Loxogenes*, the genus traditionally attributed to pleurogenids (or pleurogenines) (e.g., Yamaguti, 1971; Lotz, Font, 2008e), has a sister relationship with *Collyriclum*, the type genus of the Collyriclidae.

The Collyriclidae has often been recognized as a separate family (e.g., Ward, 1917; Yamaguti, 1958, 1971; Skrjabin, 1947; Blair, Barton, 2008a; Kanarek *et al*., 2014; Heneberg *et al*., 2015a). Until recently, it was represented by two genera, *Collyriclum* and *Collyricloides*. Kanarek *et al*. (2014) transferred the latter genus to the Pleurogenidae based on the phylogenetic

analysis. To note, they also synonymized *Collyricloides* with *Macyella*, but the results of the subsequent phylogenetic reconstructions did not support this synonymy (Shchenkov *et al*., 2020; Sokolov *et al*., 2020; Kirillova *et al*., 2022).

We abolish the family Collyriclidae and transfer *Collyriclum* Kossack, 1911 into the Pleurogenidae, thus resolving the non-monophyly of the pleurogenids. Our proposal is based on the molecular data on 28S rRNA gene and the morphology of *Collyriclum* at the cercaria stage. Cercariae of *Collyriclum*, like those of the pleurogenids, have a simple virgule and four pairs of penetration glands (Heneberg *et al*., 2015a; Shchenkov *et al*., 2020). Adults of *Collyriclum* differ from other pleurogenids only in the presence of a strongly elongated blind Laurer's canal and the absence of the ventral sucker (Kossack, 1911; Bykhovskaya-Pavlovskaya, Khotenovskii, 1964).

The revision of the Pleurogenidae is far from completion, with genera being constantly added to or removed from this family (Kanarek *et al*., 2014, 2015, 2017; Tkach *et al*., 2019, 2023). Therefore, it would be inappropriate to suggest an amended diagnosis of the Pleurogenidae at this stage.

Conclusions

Our molecular data combined with previous morphological data on the *Lecithodollfusia* cercariae support the pleurogenic concept of this genus. We also transferred the genus *Collyriclum* into the Pleurogenidae and abolished the family Collyriclidae. Further elucidation of the genus composition of the Pleurogenidae is necessary before a phylogenetically sound taxonomic model of this family can be suggested.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

Supplementary data. The following materials are available online.

Table S1. List of species, incorporated into phylogenetic analyses based on the 28S rRNA gene and ITS2 locus sequences

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