

Helminths of the *Pelophylax esculentus* Complex (Anura, Amphibia) in the Middle Volga Region (Russia)

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Abstract

This paper presents an analysis of helminth diversity in green frogs of the *Pelophylax esculentus* complex from twelve provinces of the Middle Volga region (European Russia). The study relies on the occurrence dataset recently published in GBIF in the form of a Darwin Core archive. The database contains current information on helminth occurrences in these anurans, comprising records from our long-term helminthological survey conducted in 1997–2025. Our database includes 13,634 helminth occurrence records for three *Pelophylax* species residing in the Middle Volga region. Each helminth occurrence record is linked to georeferenced data. A total of 43 parasite species are documented in the dataset, including 29 species of trematodes, one cestode, 11 nematodes, and two acanthocephalans. The greatest helminth diversity was recorded in *Pelophylax ridibundus* (42 species), which is the most widespread and abundant amphibian species in European Russia. The helminth fauna is less diverse in *Pelophylax lessonae* (32 species) and their hybrid, *Pelophylax esculentus* (25). Most helminth species found in green frogs within the studied area belong to the Palearctic faunal complex (29 species). Five helminth species each have European and Holarctic distributions, while four species are cosmopolitan. Of the 43 species of helminths found, three (*Alaria alata*, *Spirometra erinacei*, *Ascarops strongylina*) are of medical and veterinary importance as causative agents of parasitic zoonoses, posing a threat to domestic animals and humans.

Keywords: biodiversity; database; green frogs; parasitic worms; amphibians; occurrence records; Ranidae; Europe



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1. Introduction

Amphibians (Amphibia) are found almost everywhere except Antarctica and the North Pole, and contribute significantly to global biodiversity [1,2]. They play a vital role in both aquatic and terrestrial ecosystems, being secondary consumers in many food chains, serving as prey items for vertebrates and even invertebrates, and facilitating energy transfer and nutrient cycling [3,4].

In recent decades, the study of amphibian parasites has gained increasing importance. This is driven, on the one hand, by the recognition of helminths as an essential component of global biodiversity and, on the other, by the ongoing extinction crisis facing amphibians. Amphibian ranges and populations are declining sharply worldwide [5–13]. Factors such

as diseases, habitat loss or degradation due to anthropogenic activity and pollution, and climate change are the primary causes of the decline in the distribution and abundance of many vertebrate species, including amphibians [9,14–22].

Given the global decline in amphibian populations, a comprehensive study of their biology and ecology, including their parasite fauna, is of significant interest. The involvement of amphibians (particularly anurans) in food chains within natural biocenoses determines their important role as intermediate, final, or paratenic hosts for various helminths with indirect life cycles [4,23–27]. Certain helminths infecting amphibians are of medical and veterinary importance as causative agents of parasitic zoonoses in humans and domestic and wild animals, posing global health and economic challenges. For example, amphibians can serve as a source of infection of fish with zoonotic agents [28]. A case of echinoccosis at a Ukrainian poultry farm, caused by the trematode *Echinocasmus beleocephalus* (Linstow, 1873), resulted in mass mortality among chickens [29]. The birds became infected after feeding on *Pelobates fuscus* (Laurenti, 1768) yearlings. Amphibians are also known to be involved in the life cycles of the nematodes *Gnathostoma spinigerum* Owen, 1836 and *G. hispidum* Fedtschenko, 1872, which cause gastric gnathostomiasis in wild animals [30–32]. The role of amphibians (specifically green toads) in the circulation of nematodes of the genera *Crenosoma* Molin, 1861 and *Spirocercia* Railliet & Henry, 1911, which cause pulmonary crenosomiasis and esophageal spirocercosis in canids and mustelids, has been established [31–34]. Similarly, the involvement of amphibians in the development of *Ascarops strongylina* (Rudolphi, 1819) and *Physocephalus sexalatus* (Molin, 1860), causing ascariasis and physocephalosis of the stomach in domestic mammals, has been documented [31,32,35–38]. The importance of marsh frogs in the spread of intestinal mesocestoidiasis, associated with tapeworms of the genus *Mesocestoides* Vaillant, 1863, in both wild and domestic mammals has been established [30,32,39–41].

Cases of fatal larval alariasis in humans merit special attention [42–44]. Such infections have been attributed to amphibians harboring mesocercariae of *Alaria americana* Hall & Wigdor, 1918. These are not isolated cases. In the Americas, Africa, and Asia, *G. hispidum* larvae, *Spirometra erinacei* (Rudolphi, 1819) plerocercoids, and tetrathyridia of *Mesocestoides* sp. have been repeatedly documented in humans. These infections resulted from the consumption of amphibians [38,45–47].

Amphibians deserve special attention as a source of potential human infection, particularly since several of the aforementioned helminth species have been recorded in Russia: the nematodes *G. hispidum* and *A. strongylina*, the cestodes *S. erinacei* and *Mesocestoides* sp. and the trematode *Alaria alata* (Goeze, 1782) [31,48–50]. The study of the helminth fauna of wild vertebrates and, in particular, amphibians aligns with the One Health concept to elucidate the interconnections among human, animal, and environmental health [51–53].

In recent decades, interest in studying amphibian parasites, including the helminth fauna of green frogs (*Pelophylax esculentus* complex) across Europe, has significantly increased [54–69]. Of particular note are studies addressing the “trematode hypothesis” of the morphological anomalies. Specifically, “P” syndrome has been attributed to trematode induction as confirmed in green frogs infected with *Strigea robusta* (Szidat, 1928) [70–72]. However, this type of morphological anomaly has not yet been identified in the Middle Volga basin [73].

The amphibian fauna of the Middle Volga region comprises 11 species. Of these, three species of green frogs inhabit the study region: the marsh frog *Pelophylax ridibundus* (Pallas, 1771), the pool frog *Pelophylax lessonae* (Camerano, 1882) and the edible frog *Pelophylax kl. esculentus* (Linnaeus, 1758) [74]. Despite the wide distribution of these anurans in European Russia, their parasitic worms remain insufficiently studied. The situation is somewhat

better in the Middle Volga region, where the history of amphibian helminthology spans over 75 years, beginning with the work of Sudarikov [75,76] in the Nizhny Novgorod Oblast.

Our research on amphibian helminths in the Middle Volga region, with a particular focus on green frogs (*Pelophylax* spp.), began in 1997. Over nearly three decades, we have examined the helminth fauna of *Pelophylax* spp. across 12 of the 14 administrative provinces of the Middle Volga region. Parasitic worms of green frogs have been studied unevenly in different provinces of the region, as our survey was conducted primarily in the Samara Oblast and the Republic of Mordovia. Our helminthological surveys were conducted on all three green frog species inhabiting the territory of the Middle Volga region [26,77–88]. Data on parasitic worms in the *Pelophylax esculentus* complex have been included in a number of regional reports [37,49,89–92].

The aim of our study is to describe the diversity of parasitic worms in green frogs (*Pelophylax esculentus* complex) from the Middle Volga region using our database recently published in the Global Biodiversity Information Facility (GBIF) in the form of a Darwin Core Archive [93]. This article follows the “data paper” concept [94,95], which facilitates the presentation of primary biodiversity data.

2. Materials and Methods

2.1. Study Area

The Middle Volga region is situated in the south-east of the Russian Plain, covering the middle flow of the Volga River and spanning the area between 52 and 57° northern latitude and 45–56° eastern longitude [96,97] (Figure 1). Administratively, the Middle Volga region consists of the territories of the Republics of Chuvashia, Mari El, Mordovia, and Tatarstan, western Bashkortostan, and the Samara, Ulyanovsk, Nizhny Novgorod, Penza, western Orenburg and northern Saratov Oblasts.

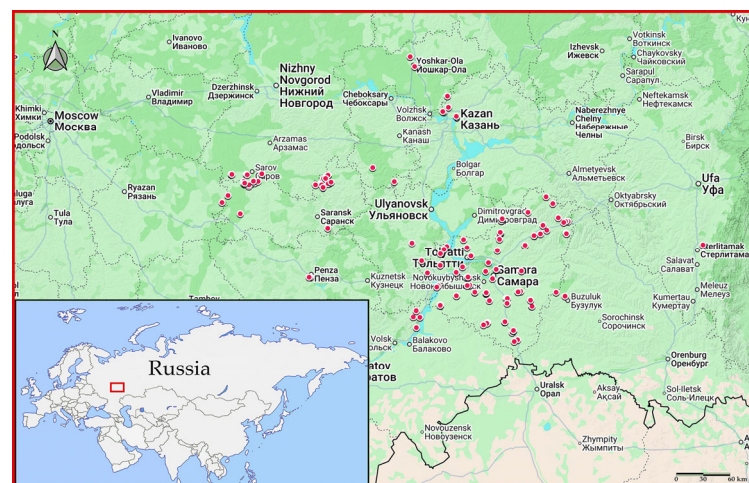


Figure 1. Sampling sites for helminths in amphibians in the Middle Volga region. Locations of parasite occurrence are marked by red circles. The red frame (bottom left) indicates the Middle Volga region. Map available online: <https://www.google.com/maps/d/edit?mid=1IGF1TCAKMgVahdnLILjId3zgXUx-084&usp=sharing> (accessed on 26 March 2026) and <https://www.gbif.org/dataset/f74a78e3-c619-4800-8c16-7ad4723b359f> (accessed on 26 March 2026).

In the middle part of the Volga basin, the forest biome gradually passes into forest-steppe landscapes, with steppe ecosystems becoming more prominent further south. A distinctive feature of this large area is its position across three natural zones: the forest zone with coniferous and mixed woods in the north, the extensive forest-steppe in the center, and the steppe in the south [98]. The transition of the Middle Volga region through forest, forest-steppe, and steppe zones accounts for the high diversity of its flora and

fauna. Consequently, the regional flora includes about 2050 plant species [99,100], and the fauna comprises 11 amphibian species, 14 reptiles, over 300 birds, and 85 species of mammals [101–105]. A more detailed description of the Middle Volga region is provided in our previous publication [106].

2.2. Description of Parasitological Data

The new dataset presents occurrence records obtained during our helminthological studies of green frogs in the Middle Volga region, spanning a 28-year period (1997–2025). This database is based on field research conducted by the Laboratory for Zoology and Parasitology of the Institute of Ecology of the Volga River basin (Togliatti) and the Joint Directorate of the Mordovia State Nature Reserve and National Park “Smolny” (Saransk).

The dataset includes information on the helminth fauna of green frogs from 12 of the 14 administrative provinces of the Middle Volga region. Additionally, it contains data on parasitic worms in *Pelophylax* spp. from the Ryazan Oblast, which borders the Republic of Mordovia. While the Ryazan Oblast is part of the Upper Volga, the Moksha River floodplain, where the research was conducted, is also situated within the Middle Volga area.

Most of the data on parasitic worms in green frogs from the studied area have been published previously, but lack geographic coordinates [26,77–88]. In our dataset, each occurrence of helminths in green frogs is georeferenced for the first time. Coordinates were determined using GPS Navigator (Garmin GPS MAP 65, Garmin Ltd., USA) and Google Maps service (<https://www.google.ru/maps/>, accessed on 14 January 2026) [107], with an accuracy of 10 m. All records are provided with a precision of four decimal places and use the WGS-84 coordinate system.

Green frogs were examined using the complete helminthological dissection method [108]. Only mature amphibians were used for the study. Parasitic worms were collected from amphibians and preserved in 70% ethanol for further evaluation and storage. Specimens of cestodes and trematodes were stained with aceto-carmin, dehydrated in a graded ethanol series (70–96%), cleared in clove oil and finally mounted in Canada balsam. Specimens of nematodes and acanthocephalans were cleared in lactic acid and preserved in Glycerin-Jelly mounts [109–111].

Identification of green frogs was based on morphological characteristics (male resonators color, overlap of ankle joints, shape and size of the internal calcaneal tuberosity, length of the first toe of the hind leg) in study areas where triploid individuals were absent [112]. In areas where *Pelophylax* spp. co-occur, DNA flow cytometry [113] and molecular genetic methods [114–116] were used. Two markers were used to assess molecular genetic variability: for mitochondrial DNA, a fragment of the first subunit of the cytochrome oxidase gene (COI), and for nuclear DNA, intron 1 of the serum albumin gene (SAI-1) [114,117,118]. The spatial distribution of green frog species in the Middle Volga region has been previously published [11,74,115,116,119,120].

The identification of helminths was performed according to Ryzhikov et al. [31], Sharpilo and Iskova [121], Sudarikov et al. [122], and Kirillov et al. [49]. In our dataset, all parasitic worms were identified to the species level. The helminth taxonomy follows the GBIF (<https://www.gbif.org/> (accessed on 26 March 2026)) [123].

Data visualization was carried out using the “R” (R Core Team, Vienna, Austria) [124] with the “treemapify” [125], “ggplot2” [126], “dplyr” [127], and “readxl” [128] packages. Venn diagrams were generated at “<https://bioinformatics.psb.ugent.be/webtools/Venn/>, accessed on 15 February 2026” [129].

Shannon’s diversity (H') and Berger–Parker (d) indices were used to determine the helminth species diversity [130]. The Shannon index comparisons were based on 95% bootstrap confidence intervals (10,000 resamples). The similarity of parasite fauna was

assessed using Morisita's overlap index (Cm). Similarity values were interpreted as low (0–0.33), medium (0.34–0.66), and high (0.67–1). A similarity dendrogram of the helminth fauna in green frogs was generated using the UPGMA (unweighted pair group method with arithmetic average) and the Morisita index as a distance measure (bootstrap support 1000 replicates). Statistical treatment of the data was performed using the PAST 2.16 (University of Oslo, Norway) [131].

It should be noted that both the number of amphibian species and the sample sizes per species vary in each province of the Middle Volga region. Given that data from certain areas are limited, the results of this comparative analysis of helminth diversity should be interpreted with caution. The majority of the parasite specimens obtained from green frogs as well as other amphibians of the Middle Volga region are preserved in the parasitological collection in the Institute of Ecology of Volga Basin of RAS, Togliatti (IEVB RAS), and in the personal collections of I.V. Chikhlyaev, N.Yu. Kirillova and A.A. Kirillov. The examined amphibian specimens are also held in the IEVB RAS herpetological collection.

3. Results

3.1. Structure of Dataset

In general, the dataset includes 17,191 records of helminth occurrences in green frogs (*Pelophylax esculentus* complex) inhabiting the Middle Volga region (European Russia). It comprises 13,634 records from the Samara Oblast, 2083 from the Republic of Mordovia, 284 from the Republic of Tatarstan, 273 from the Republic of Mari El, 199 from the Saratov Oblast, 190 from the Nizhny Novgorod Oblast, 171 from the Penza Oblast, 124 from the Orenburg Oblast, 74 from the Republic of Chuvashia, 99 from the Republic of Bashkortostan, 56 from the Ryazan Oblast, and four records from Ulyanovsk Oblast. Data are provided for *P. ridibundus*, *P. lessonae*, and *P. kl. esculentus*. Overall, our database contains occurrence records for 283,124 helminth specimens [93].

In our dataset, we used the standard terms provided in Darwin Core (<https://dwc.tdwg.org/list/#2-use-of-terms>, accessed on 8 February 2026) to describe each record [132]. Each helminth occurrence record contains basic information regarding the parasite species, its taxonomy, hosts, and infection site. Additionally, it provides data on the location and region of helminth detection with geographic coordinates, the number of helminth specimens per occurrence, the date of occurrence, and the authors who recorded and identified the helminth species (Table S1). The helminth taxa included in our dataset are shown in Table S2.

3.2. Dataset Data Description

The dataset comprises 43 helminth species parasitizing green frogs (*Pelophylax esculentus* complex) in the Middle Volga region, including 29 trematodes, one cestode, 11 nematodes, and two acanthocephalans (Table 1) [93].

According to the database, trematodes dominate in the helminth fauna of green frogs in the Middle Volga region both qualitatively and quantitatively (29 species/26,6125 specimens) and are represented by 12 families (Figure 2). In terms of species richness, the most represented families are Gorgoderidae (7 species) and Diplostomatidae (5). The family Pleurogenidae includes four species, while the families Haematoloechidae and Strigeidae each contain three species of flukes. Seven other trematode families are represented by a single species each (Figure 2).

Table 1. List of helminths of green frogs (*Pelophylax esculentus* complex) from the Middle Volga Region (Russia) included in the dataset (1997–2025).

Helminth Species	Distribution	Host Species
Trematoda		
<i>Alaria alata</i> (Goeze, 1782), msc.	Cosmopolitan	<i>Pelophylax ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Astiotrema monticellii</i> Stossich, 1904, mtc.	Europe	<i>P. ridibundus</i> , <i>P. lessonae</i>
<i>Brandesia turgida</i> (Brandes, 1888)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i>
<i>Codonocephalus urniger</i> (Rudolphi, 1819), mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i>
<i>Diplodiscus subclavatus</i> (Goeze, 1782)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Encyclometra colubrimurorum</i> (Rudolphi, 1819), mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i>
<i>Gorgodera asiatica</i> Pigulewski, 1943	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Gorgodera cygnoides</i> (Zeder, 1800)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Gorgodera microovata</i> Fuhrmann, 1924	Europe	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Gorgodera pagenstecheri</i> Sinitzin, 1905	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Gorgodera varsoviensis</i> Sinitzin, 1905	Europe	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Gorgoderina vitelliloba</i> (Olsson, 1876)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Haematoloechus asper</i> Looss, 1899	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Haematoloechus similis</i> (Looss, 1899)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Haematoloechus variegatus</i> (Rudolphi, 1819)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Halipegus ovocaudatus</i> (Vulpian, 1859)	Europe	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Haplometra cylindracea</i> (Zeder, 1800)	Palearctic	<i>P. ridibundus</i>
<i>Neodiplostomum spathoides</i> Dubois, 1937, mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i>
<i>Opisthioglyphe ranae</i> (Frölich, 1791)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Paralepoderma cloacicola</i> (Lühe, 1909), mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Pharyngostomum cordatum</i> (Diesing, 1850), mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Phyllodistomum angulatum</i> Linstow, 1907	Palearctic	<i>P. ridibundus</i>
<i>Pleurogenes claviger</i> (Rudolphi, 1819)	Holarctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Pleurogenoides medians</i> (Olsson, 1876)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Prosotocus confusus</i> (Looss, 1896)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Strigea falconis</i> Szidat, 1928, mtc.	Cosmopolitan	<i>P. ridibundus</i> , <i>P. lessonae</i>
<i>Strigea sphaerula</i> (Rudolphi, 1803), mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Strigea strigis</i> (Schränk, 1788), mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Tylodelphys excavata</i> (Rudolphi, 1803), mtc.	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
Cestoda		
<i>Spirometra erinacei</i> (Rudolphi, 1819), plc.	Cosmopolitan	<i>P. ridibundus</i>
Nematoda		
<i>Aplectana acuminata</i> (Schränk, 1788)	Palearctic	<i>P. ridibundus</i>
<i>Ascarops strongylina</i> (Rudolphi, 1819), juv.	Cosmopolitan	<i>P. ridibundus</i>
<i>Camallanus truncatus</i> (Rudolphi, 1814)	Palearctic	<i>P. ridibundus</i>

Table 1. Cont.

Helminth Species	Distribution	Host Species
<i>Cosmocerca ornata</i> (Dujardin, 1845)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Eustrongylides excisus</i> Jagerskiold, 1909, juv.	Palearctic	<i>P. ridibundus</i>
<i>Icosiella neglecta</i> (Diesing, 1851)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Oswaldocruzia filiformis</i> (Goeze, 1782)	Palearctic	<i>P. ridibundus</i> , <i>P. lessonae</i> , <i>P. esculentus</i>
<i>Oxysomatium brevicaudatum</i> (Zeder, 1800)	Holarctic	<i>P. lessonae</i> , <i>P. esculentus</i>
<i>Rhabdias bufonis</i> (Schrunk, 1788)	Holarctic	<i>P. ridibundus</i> , <i>P. lessonae</i>
<i>Spiroxys contortus</i> (Rudolphi, 1819), juv.	Holarctic	<i>P. ridibundus</i>
<i>Strongyloides spiralis</i> Grabda-Kazubska, 1978	Palearctic	<i>P. ridibundus</i>
Acanthocephala		
<i>Acanthocephalus falcatus</i> (Frölich, 1789)	Europe	<i>P. ridibundus</i>
<i>Acanthocephalus ranae</i> (Schrunk, 1788)	Holarctic	<i>P. ridibundus</i>

Note: msc.—mesocercaria, mtc.—metacercaria, juv.—juvenile, plc.—plerocercoid.

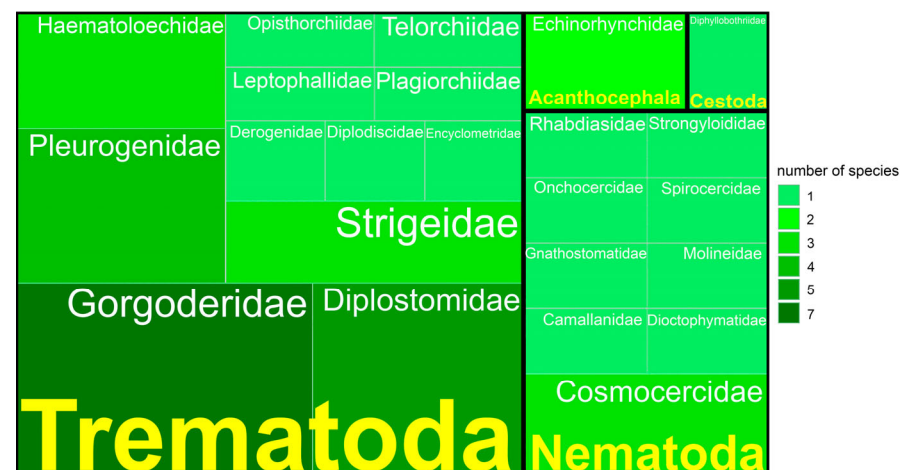


Figure 2. Taxonomic distribution of helminths across different families in the dataset.

The most abundant trematodes belong to the families Diplostomatidae (80,098 specimens), Pleurogenidae (77,860), and Telorchidae (77,195) (Figure 3). Trematodes are represented by both adult (18 species) and larval (12) stages. Notably, along with the adults of *Opisthioglyphe ranae* in the intestine, amphibians are also parasitized by its metacercariae, which are localized in the mesentery, serous membranes, and muscles. Mature trematodes predominated in both frequency of occurrence (11,324 records) and abundance (163,626 specimens). Larval stages accounted for 2449 records, and their abundance was 102,499 specimens. According to the Berger–Parker index, *O. ranae* dominates among adult trematodes ($d = 0.41$), and *Tylodelphys excavata* is the dominant among larval stages (0.26).

Nematodes are less represented in the helminth fauna of *Pelophylax* spp. in the Middle Volga region (11 species/16,994 specimens), comprising 9 families (Figures 2 and 3). Among these, members of the family Cosmocercidae predominate in both species richness (3 species) and abundance (7026 specimens). Each of the remaining roundworm families is represented by a single species (Figure 2). Nematodes in green frogs are represented by both adult (8 species) and larval (4) stages. Notably, *Cosmocerca ornata* has been recorded in amphibians in both adult (rectum) and larval (lower eyelid conjunctiva) stages. Adult nematodes predominate in both occurrence and abundance (3106 records/14,406 specimens),

while larval stages account for 307 occurrence records and 2588 specimens. The species *C. ornata* dominates among both adult and larval nematodes (0.34 and 0.79, respectively).

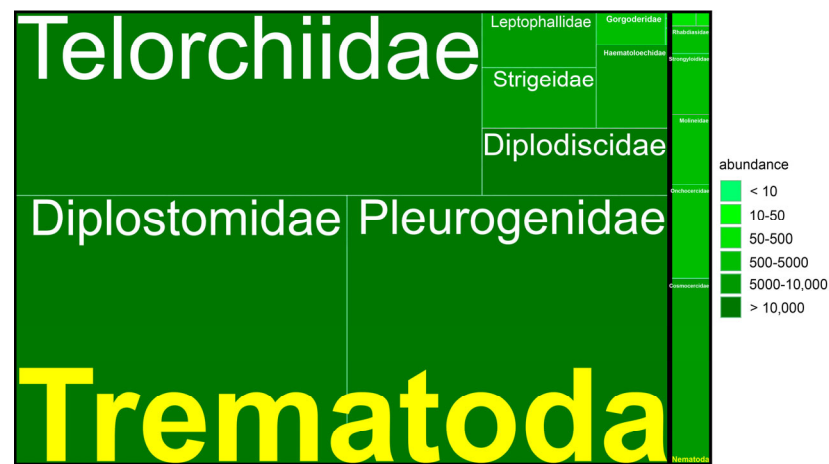


Figure 3. Distribution of helminth abundance amongst families in the dataset.

Acanthocephalans are rare parasites of amphibians in the Middle Volga region, represented by only two species (*Acanthocephalus falcatus* and *A. ranae*) from the family Echinorhynchidae. Only three records of these thorny-headed worms have been documented in green frogs. Both species parasitize amphibians as adults. Cestodes in *Pelophylax* spp. of the Middle Volga region are represented by a single species, *Spirometra erinacei* (Diphylobothriidae), which parasitizes amphibians at the plerocercoid stage. Only two occurrence records, each consisting of a single plerocercoid specimen, have been recorded.

Among the three studied species of green frogs, *P. ridibundus* possesses the most diverse helminth fauna. Thus, 42 of the 43 recorded helminth species are found in marsh frogs. The helminth fauna of *P. lessonae* includes 32 species of parasites. The helminth fauna of its hybrid form, *P. esculentus*, is less diverse, comprising 25 parasite species. Furthermore, 24 helminth species are common to all studied green frogs (Table 1, Figure 4) [93].

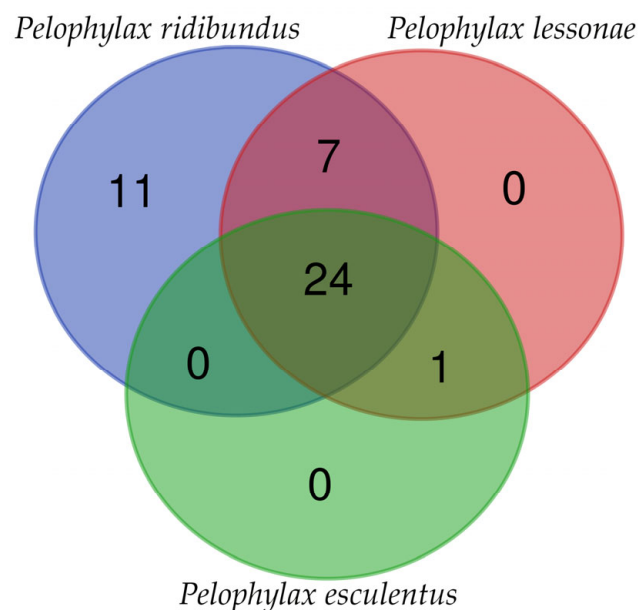


Figure 4. Number of helminth species in different *Pelophylax* spp. from the Middle Volga region. The blue circle indicates *P. ridibundus*, the red circle—*P. lessonae*, the green circle—*P. esculentus*. Over-lapping areas show the number of common helminth species.

Eleven helminth species were found only in *P. ridibundus*: the trematodes *Haplometra cylindracea* and *Phyllodistomum angulatum*; the cestode *S. erinacei*, plc.; the nematodes *Aplectana acuminata*, *Ascarops strongylina*, juv., *Camallanus truncatus*, *Eustrongylides excisus*, juv., *Spiroxys contortus*, juv., *Strongyloides spiralis*; and the acanthocephalans *A. falcatus* and *A. ranae* (Table 1). Seven helminth species were recorded in both *P. ridibundus* and *P. lessonae*: the trematodes *Astiotrema monticellii*, *Brandesia turgida*, *Codonocephalus urniger*, mtc., *Encyclometra colubrimurorum*, mtc., *Neodiplostomum spathoides*, mtc., *Strigea falconis*, mtc. and the nematode *Rhabdias bufonis*. The nematode *Oxysomatium brevicaudatum* was found in *P. lessonae* and *P. esculentus* (Table 1).

A comparison of the helminth fauna across the three amphibians revealed a high degree of similarity according to the Morisita index between *P. lessonae* and *P. esculentus* (0.78), as well as between *P. ridibundus* and *P. lessonae* (0.72). An average degree of similarity (0.56) was found between the helminth communities in *P. ridibundus* and *P. esculentus*.

The helminth fauna of green frogs varies across different provinces of the Middle Volga region. Only five helminth species (the trematodes *Diplodiscus subclavatus*, *O. ranae*, *Paralepoderma cloacicola*, mtc., *Pleurogenoides medians*, and *Prosotocus confusus*) were found in *Pelophylax* spp. across 11 studied areas. Two trematode species (*Haematoloechus similis* and *Pleurogenes claviger*) were recorded in 10 provinces (Table 2). The trematodes *B. turgida*, *Gorgoderina vitelliloba*, *Haematoloechus asper*, *Haematoloechus variegatus*, *Strigea strigis*, mtc. and the nematode *Icosiella neglecta* were recorded in 9 regions; the nematode *Oswaldocruzia filiformis* in 8 areas; and the trematodes *Gorgodera cygnoides*, *Gorgodera pagenstecheri*, the nematodes *C. ornata*, and *R. bufonis* in 7 provinces. In 6 studied oblasts, the trematodes *Gorgodera asiatica*, *Strigea sphaerula*, mtc. and *T. excavata*, mtc. were recorded in green frogs; in five provinces, the trematodes *Gorgodera microovata*, *Halipegus ovocaudatus*, and *Alaria alata*, msc. were identified (Table 2). The least common trematodes in the Middle Volga region include *Pharyngostomum cordatum*, mtc., found in three oblasts, and flukes *Gorgodera varsoviensis*, *A. monticellii*, mtc., *C. urniger*, mtc., *N. spathoides*, mtc. and *S. falconis*, mtc., each recorded in only two provinces, alongside the nematodes *O. brevicaudatum* and *S. spiralis*. Another 11 worm species were recorded in only one study area each; 10 of these were found exclusively in the Samara Oblast, while a single acantocephalan species, *A. ranae*, was recorded only in the Republic of Mordovia (Table 2).

Table 2. Helminths of the *Pelophylax esculentus* complex in different provinces of the Middle Volga Region (Russia) (1997–2025).

Province	Helminth Species Number	Helminth Species
Republic of Bashkortostan	16	<i>B. turgida</i> , <i>G. asiatica</i> , <i>G. cygnoides</i> , <i>G. microovata</i> , <i>G. vitelliloba</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , mtc., <i>Ph. cordatum</i> , mtc., <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. sphaerula</i> , mtc., <i>S. strigis</i> , mtc., <i>T. excavata</i> , mtc.
Republic of Chuvashia	12	<i>A. alata</i> , msc., <i>B. turgida</i> , <i>D. subclavatus</i> , <i>H. asper</i> , <i>H. variegatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , mtc., <i>P. medians</i> , <i>P. confusus</i> , <i>S. sphaerula</i> , mtc., <i>I. neglecta</i> , <i>O. filiformis</i>

Table 2. Cont.

Province	Helminth Species Number	Helminth Species
Republic of Mari El	20	<i>B. turgida</i> , <i>D. subclavatus</i> , <i>G. asiatica</i> , <i>G. microovata</i> , <i>G. pagenstecheri</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>H. ovocaudatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , <i>mtc.</i> , <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. strigis</i> , <i>mtc.</i> , <i>T. excavata</i> , <i>mtc.</i> , <i>C. ornata</i> , <i>I. neglecta</i> , <i>O. filiformis</i>
Republic of Mordovia	30	<i>A. alata</i> , <i>msc.</i> , <i>A. monticellii</i> , <i>mtc.</i> , <i>A. ranae</i> , <i>B. turgida</i> , <i>D. subclavatus</i> , <i>G. asiatica</i> , <i>G. cygnoides</i> , <i>G. microovata</i> , <i>G. pagenstecheri</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>H. ovocaudatus</i> , <i>N. spathoides</i> , <i>mtc.</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , <i>mtc.</i> , <i>Ph. cordatum</i> , <i>mtc.</i> , <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. falconis</i> , <i>mtc.</i> , <i>S. sphaerula</i> , <i>mtc.</i> , <i>S. strigis</i> , <i>mtc.</i> , <i>T. excavata</i> , <i>mtc.</i> , <i>C. ornata</i> , <i>I. neglecta</i> , <i>O. brevicaudatum</i> , <i>Rh. bufonis</i>
Republic of Tatarstan	24	<i>A. alata</i> , <i>msc.</i> , <i>B. turgida</i> , <i>D. subclavatus</i> , <i>G. cygnoides</i> , <i>G. microovata</i> , <i>G. pagenstecheri</i> , <i>G. varsoviensis</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>H. ovocaudatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , <i>mtc.</i> , <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. sphaerula</i> , <i>mtc.</i> , <i>S. strigis</i> , <i>mtc.</i> , <i>T. excavata</i> , <i>mtc.</i> , <i>C. ornata</i> , <i>I. neglecta</i> , <i>O. brevicaudatum</i> , <i>O. filiformis</i>
Nizhny Novgorod Oblast	21	<i>A. alata</i> , <i>msc.</i> , <i>D. subclavatus</i> , <i>G. cygnoides</i> , <i>G. microovata</i> , <i>G. pagenstecheri</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>H. ovocaudatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , <i>mtc.</i> , <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. sphaerula</i> , <i>mtc.</i> , <i>S. strigis</i> , <i>mtc.</i> , <i>C. ornata</i> , <i>I. neglecta</i> , <i>O. filiformis</i> , <i>Rh. bufonis</i>
Orenburg Oblast	17	<i>B. turgida</i> , <i>D. subclavatus</i> , <i>G. cygnoides</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , <i>mtc.</i> , <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. strigis</i> , <i>mtc.</i> , <i>T. excavata</i> , <i>mtc.</i> , <i>C. ornata</i> , <i>Rh. bufonis</i> , <i>S. spiralis</i>
Penza Oblast	17	<i>B. turgida</i> , <i>D. subclavatus</i> , <i>G. asiatica</i> , <i>G. pagenstecheri</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , <i>mtc.</i> , <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. strigis</i> , <i>mtc.</i> , <i>I. neglecta</i> , <i>O. filiformis</i> , <i>Rh. bufonis</i>
Ryazan Oblast	11	<i>B. turgida</i> , <i>D. subclavatus</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , <i>mtc.</i> , <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>I. neglecta</i> , <i>Rh. bufonis</i>

Table 2. Cont.

Province	Helminth Species Number	Helminth Species
Samara Oblast	40	<i>A. alata</i> , msc., <i>A. falcatus</i> , <i>A. monticellii</i> , mtc., <i>B. turgida</i> , <i>C. urniger</i> , mtc., <i>D. subclavatus</i> , <i>E. colubrimurorum</i> , mtc., <i>G. asiatica</i> , <i>G. cygnoides</i> , <i>G. pagenstecheri</i> , <i>G. varsoviensis</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>H. cylindracea</i> , <i>H. ovocaudatus</i> , <i>N. spathoides</i> , mtc., <i>O. ranae</i> , <i>P. cloacicola</i> , mtc., <i>Ph. angulatum</i> , <i>Ph. cordatum</i> , mtc., <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. falconis</i> , mtc., <i>S. sphaerula</i> , mtc., <i>S. strigis</i> , mtc., <i>T. excavata</i> , mtc., <i>S. erinacei</i> , plc., <i>A. acuminata</i> , <i>A. strongylina</i> , juv., <i>C. truncatus</i> , <i>E. excisus</i> , juv., <i>I. neglecta</i> , <i>O. filiformis</i> , <i>S. contortus</i> , juv., <i>C. ornata</i> , <i>Rh. bufonis</i> , <i>S. spiralis</i>
Saratov Oblast	19	<i>C. urniger</i> , mtc., <i>D. subclavatus</i> , <i>G. asiatica</i> , <i>G. cygnoides</i> , <i>G. pagenstecheri</i> , <i>G. vitelliloba</i> , <i>H. asper</i> , <i>H. similis</i> , <i>H. variegatus</i> , <i>O. ranae</i> , <i>P. cloacicola</i> , mtc., <i>P. claviger</i> , <i>P. medians</i> , <i>P. confusus</i> , <i>S. strigis</i> , mtc., <i>C. ornata</i> , <i>I. neglecta</i> , <i>O. filiformis</i> , <i>Rh. bufonis</i>
Ulyanovsk Oblast	2	<i>D. subclavatus</i> , <i>H. variegatus</i>

The highest number of helminth species (40) was found in green frogs from the Samara Oblast (Table 2) [93]. The list of amphibian helminths from the Republic of Mordovia includes 30 species; in the Republic of Tatarstan—24; in the Nizhny Novgorod Oblast—21; in the Republic of Mari El—20; and in the Saratov Oblast—19. A smaller number of helminth species was recorded in green frogs from the Penza and Orenburg Oblasts (17 each), the Republic of Bashkortostan (16), the Republic of Chuvashia (12), and the Ryazan Oblast (11). Only two digenean species were found in amphibians from the Ulyanovsk Oblast (Table 1).

An analysis of helminth species diversity in green frogs across 12 provinces of the Middle Volga region revealed the greatest diversity in the Samara Oblast ($H = 2.439$). According to the Shannon index, helminth fauna is less diverse in the Nizhny Novgorod (2.177), Orenburg (1.998), Penza (1.685), Saratov (1.597) and Ryazan (1.587) Oblasts, as well as in the Republics of Mordovia (2.141), Mari El (2.032), Tatarstan (1.918), and Chuvashia (1.866). The lowest species diversity of helminths was recorded in the Republic of Bashkortostan (1.217) and Ulyanovsk Oblast (0.359). The Shannon index values for helminth fauna in green frogs differ significantly across various provinces of the Middle Volga region in most cases (Figure S1). Insignificant differences in the Shannon index were noted in the pairs Orenburg Oblast–Republic of Tatarstan, Orenburg Oblast–Republic of Mari El, Saratov–Ryazan Oblasts, Ryazan–Penza Oblasts, Republic of Chuvashia–Republic of Tatarstan, Republic of Chuvashia–Orenburg Oblast, and Republic of Mordovia–Nizhny Novgorod Oblast (Figure S1).

A comparative analysis of the helminth fauna of green frogs from different provinces of the Middle Volga region revealed two distinct clusters based on the species structure (Figure 5). In the comparative analysis, we did not include data on helminths in green frogs from the Ulyanovsk Oblast, where only two *P. ridibundus* individuals were studied.

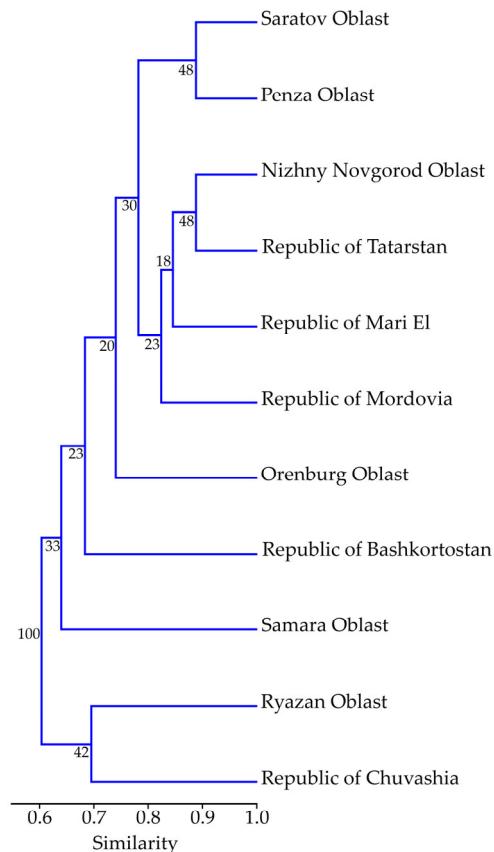


Figure 5. Similarity dendrogram of the helminth fauna in green frogs (*Pelophylax esculentus* complex) from the Middle Volga Region obtained using the Morisita index (UPGMA). Bootstrap support values are indicated at the nodes. Correlation coefficient: $r = 0.815$.

The first cluster is the largest and is formed by the helminth fauna of green frogs from nine provinces, subdivided into two groups. The first group comprises the helminth fauna from eight provinces. Here, high similarity was observed for the helminth fauna of amphibians between the Saratov and Penza Oblasts (0.89), as well as between the Nizhny Novgorod Oblast and the Republic of Tatarstan (0.89). High similarity was also recorded between the Republics of Mari El and Tatarstan (0.86), Mordovia and Tatarstan (0.85), Mari El and Nizhny Novgorod Oblast (0.83), Republic of Mordovia and Nizhny Novgorod Oblast (0.82), and the Republics of Mordovia and Mari El (0.80) (Figure 5). The Republic of Bashkortostan and the Orenburg Oblast occupy distinct positions within the first group of the first cluster. The second group of the first cluster consists solely of the helminth fauna from the Samara Oblast (Figure 5). Among the aforementioned provinces, high similarity was revealed between the Samara Oblast and the Republic of Mordovia (0.77); the Orenburg Oblast and the Republic of Mari El (0.76), the Nizhny Novgorod Oblast (0.74), the Republics of Tatarstan (0.73) and Bashkortostan (0.73). Additionally, significant similarity was noted between the Republic of Bashkortostan and the Republics of Tatarstan (0.70) and Mari El (0.72) (Figure 5).

The second cluster includes the Ryazan Oblast and the Republic of Chuvashia (0.70) as the provinces most similar in helminth species structure and abundance (Figure 5). The Republic of Chuvashia, in turn, showed high similarity with the Penza (0.69) and the Nizhny Novgorod (0.67) Oblasts. Similarly, the helminth fauna of frogs in the Ryazan Oblast closely resembles that of the Penza (0.79), the Orenburg (0.71), and the Saratov (0.67) Oblasts.

Of the 43 species of helminths found, three are of medical and veterinary concern as causative agents of parasitic zoonoses, posing a threat to domestic animals and humans (Table 3).

Table 3. Zoonotic helminths of the *Pelophylax esculentus* complex in the Middle Volga region (1997–2025).

Region	Host	<i>A. alata</i> , msc.	<i>S. erinacei</i> , plc.	<i>A. strongylina</i> , juv.
Republic of Chuvashia	<i>P. ridibundus</i>	–	1/2	54/202
	<i>P. lessonae</i>	2/5 *	–	–
Republic of Mordovia	<i>P. ridibundus</i>	2/7	–	–
	<i>P. lessonae</i>	83/4244	–	–
Republic of Tatarstan	<i>P. lessonae</i>	1/8	–	–
	<i>P. esculentus</i>	1/6	–	–
Nizhny Novgorod Oblast	<i>P. lessonae</i>	2/9	–	–
Samara Oblast	<i>P. ridibundus</i>	4/35	–	–
	<i>P. lessonae</i>	45/4293	–	–

Note: *—before the slash—number of occurrences, after the slash—abundance, specimens.

4. Discussion

In this study, we describe a recently published GBIF database on parasitic worms in green frogs (*Pelophylax esculentus* complex) from the Middle Volga region (European Russia) [93]. Based on our 28-year helminthological study of these anurans in the region, the list of helminth fauna has been expanded and currently includes 43 species (Table 1). Thus, we have recorded seven helminth species in green frogs for the first time in Russia: the trematodes *A. monticellii*, mtc. and *Ph. angulatum*; the nematodes *C. truncatus*, *S. spiralis*, and *S. contortus*, juv.; and the acanthocephalans *A. falcatus* and *A. ranae*. In addition to the aforementioned parasites, the nematode larva *A. strongylina* is recorded for the first time in amphibians within the Volga River basin.

Six parasite species were found for the first time in amphibians of the Middle Volga region: *G. asiatica*, *N. spathoides*, mtc., *P. cloacicola*, mtc., *Ph. cordatum*, mtc., *S. falconis*, mtc. and *E. excisus*, juv. Additionally, a new host for the acanthocephalan *A. falcatus* has been identified among amphibians of Russia, namely *Pelophylax ridibundus*.

Most of the helminth species registered in green frogs of the Middle Volga region (37 species) are obligate parasites of amphibians. Only two species, *Ph. angulatum* and *C. truncatus*, are accidental parasites of green frogs. The trematode *Ph. angulatum* parasitizes the bladder of freshwater fish, and the nematode *C. truncatus* parasitizes the intestines of fish [133]. In addition to the Middle Volga region, there are previously published reports of *Camallanus* sp. found in *Pelophylax ridibundus* tadpoles in Ukraine [134]. The larval stages of the cestode *S. erinacei* and the nematodes *A. strongylina*, *S. contortus*, *E. excisus* are found in vertebrate hosts of different classes and orders [45,135].

Plerocercoids of *S. erinacei* are often found in amphibians, reptiles, corvids, insectivores, and mustelids. The larval stage of *E. excisus* parasitizes various freshwater fish, while the adult nematode completes its life cycle in wetland birds [135,136]. The range of paratenic hosts of this nematode includes predatory fish, amphibians, and reptiles [137–139]. The larval stage of the nematode *S. contortus* is found in fish, newts, lizards, and snakes; its final host is the European pond turtle *Emys orbicularis* (Linnaeus, 1758) [31,135,140,141]. In its larval stage, the nematode *A. strongylina* parasitizes reptiles, most commonly lizards [135].

An analysis of the helminth fauna in green frogs of the *Pelophylax esculentus* complex in the Middle Volga region revealed predominance of trematodes (29 out of 43 identified

species). This taxonomic group significantly prevails in terms of species richness, abundance, and occurrences (Figures 1 and 2, Table 1) [93]. This is due to the semi-aquatic lifestyle and diet range of these amphibians. The diet of *Pelophylax* spp. includes both terrestrial and aquatic invertebrates, which serve as intermediate hosts for trematodes. Adult green frogs also prey on small fish, mammals, and birds, and exhibit cannibalistic behavior [74,80,90,142]. Most trematode species infect frogs through feeding on various freshwater arthropods. Thus, the presence of trematodes such as adults of *Gorgoderia* spp., *Haematoloechus* spp., *H. ovocaudatus*, *Ph. angulatum*, *P. claviger*, *P. medians*, *P. confusus* and, probably, *B. turgida* in *Pelophylax* frogs indicates that these amphibians consume larval and adult aquatic or semi-aquatic insects [49,121,122,143,144]. The trematode *O. ranae* infect amphibians through feeding on gastropods, which act as second intermediate hosts of this fluke. Green frogs become infected with *D. subclavatus* by ingesting the parasite's adolescariiae along with water, mud, or food items, such as mollusks and other amphibians, on which the larvae are encysted [31,122,144]. Furthermore, the life cycle of *O. ranae*, as well as *G. vitelliloba* and *H. cylindracea*, can also involve amphibian tadpoles and yearlings as second intermediate hosts. Therefore, the main route of infection for adult amphibians with these trematode species is cannibalism [122,145,146]. Infection of green frogs with all larval stages of trematodes (11 species + *O. ranae*) occurs mainly through percutaneous and/or oral penetration by cercariae [122].

The species structure of nematodes in green frogs is less diverse. Six of the 11 nematode species found in green frogs in the Middle Volga region are geohelminths. Thus, infection of amphibians with *S. spiralis*, *A. acuminata*, and *C. ornata* occurs in the aquatic environment through oral (for the first two species) and per-ocular (for *C. ornata*) penetration by invasive nematode larvae [31,147,148]. In contrast, infection of frogs with *O. brevicaudatum*, *O. filiformis*, and *R. bufonis* occurs in humid terrestrial environments via oral (for the first two species) and percutaneous (for *Rh. bufonis*) penetration by invasive helminth larvae [149–151]. It should be noted that water-developing geohelminths significantly predominate in occurrence and abundance over nematodes with terrestrial larval development, which is associated with the prolonged periods green frogs spend in water.

Amphibians become infected with nematodes that possess indirect life cycles when feeding on invertebrates. This applies to the larval stages of *S. contortus* and *A. strongylina*. Infection of frogs with *S. contortus* occurs through the ingestion of cyclops (intermediate hosts) or paratenic hosts of the parasite, such as dragonfly larvae and small fish [133]. In contrast, frogs become infected with *A. strongylina* by eating beetles of the family Scarabaeidae, the parasite's intermediate hosts [135,152]. Infection of green frogs with *C. truncatus* and the larvae of *E. excisus* occurs through the consumption of copepods and small fish [133,153]. The life cycle of *I. neglecta* involves intermediate hosts, biting midges of the family Ceratopogonidae, in which the infective larvae develop. Green frogs become infected through the bites of these dipterans [154].

Acanthocephalans and cestodes are rare parasites of green frogs, occurring only as individual specimens. Infection of *Pelophylax* frogs with spiny-headed worms *Acanthocephalus* spp. and the cestode *S. erinacei* occurs through the ingestion of crustaceans, specifically Isopoda and Cyclopoida [155,156].

Overall, in the Middle Volga region, green frogs serve as definitive hosts for 28 species of parasitic worms. Helminth larvae account for 16 species (with the trematode *O. ranae* occurring in both adult and larval stages), for which amphibians act as second intermediate and/or paratenic hosts. The wide diversity of helminth species recorded at the larval stage indicates the widespread involvement of frogs in the circulation of parasitic worms infecting reptiles, birds and mammals. In particular, the final hosts of the trematodes *A. monticellii*, *E. colubrimurorum*, and *P. cloacicola*, as well as the nematode *S. contortus*, are reptiles [135].

Adults of *S. strigis* are found in owls, and *N. spathoides* and *S. falconis* parasitize diurnal birds of prey, while the final hosts of *S. sphaerula* are corvids [122,157,158]. *C. urniger* and *T. excavata* complete their life cycles in grebes and herons [159,160]. The definitive hosts of *A. alata* and *Ph. cordatum* are carnivores, primarily of the family Canidae [122,160,161]. Adult cestode *S. erinacei* parasitizes wild and domestic carnivores, as well as wild boars [45,135,155]. Wild boars are also definitive hosts of the nematode *A. strongylina* [135,152]. The nematode *E. excisus* completes its life cycle in piscivorous birds of the families Phalacrocoracidae, Ardeidae, and Anatidae [133,137,153]. Moreover, green frogs can participate in the infection of not only definitive but also paratenic hosts of the nematode, such as colubrid snakes [135].

Our data on the helminth fauna of green frogs in the Middle Volga region revealed that the greatest helminth species richness is characteristic of *P. ridibundus* (Table 1, Figure 4), the most numerous and widespread green frog species in the region [11]. It is also listed among the 100 most invasive species in Russia [162]. Our helminthological surveys of *P. ridibundus* were conducted in all studied provinces of the Middle Volga region, with the exception of the Republic of Chuvashia (Table 2).

At the same time, helminth infection is closely related to the host's lifestyle and diet. The marsh frog exhibits high ecological plasticity [74,90]. It inhabits open water bodies (rivers, lakes, streams, oxbow lakes, ponds, etc.), preferring floodplain areas. These habitats host a diverse fauna and flora; therefore, there is a high probability of amphibian infection with helminths transmitted through the food chain. Furthermore, the lakes are characterized by a wide range of prey, which, along with various invertebrates, includes small fish, amphibians (including their own species), and small mammals [74,90]. In contrast to the marsh frog, the pond frog *P. lessonae* prefers isolated forest water bodies (forested rivers, oxbow lakes, small forest ponds, etc.) [90,116]. Such ecological isolation often leads to the loss of certain species from the helminth fauna of these amphibians [74]. Differences in the helminth structure between *P. ridibundus* and *P. lessonae* primarily concern rare and/or occasional parasites. The diet of *P. lessonae* is similar to that of *P. ridibundus*. According to Fayzulin et al. [90], in the Middle Volga region, high similarity was observed between the diets of both anuran species regarding terrestrial prey, while low similarity was revealed for aquatic items. The edible frog *P. esculentus* harbors the fewest number of helminth species among green frogs inhabiting the Middle Volga region. *Pelophylax esculentus* is less abundant and widespread than *P. ridibundus* and *P. lessonae* in the studied region [11]. It inhabits the borders of forested and open floodplain zones, typically living in mixed-species groups with its parental species, *P. ridibundus* and *P. lessonae* [116]. The diet of this frog resembles that of other green frog species, although certain differences exist. Fayzulin et al. [90,116] noted that the diet of *P. esculentus* is similar to that of *P. ridibundus* in terms of aquatic prey and aligns with that of *P. lessonae* regarding terrestrial food objects.

Thus, the spatial and trophic niches of *P. esculentus* occupy an intermediate position, which is explained by the hybrid origin of this species of green frogs. Consequently, this also leads to differences in the helminth fauna of *P. esculentus* compared to those of the other two *Pelophylax* species.

Our dataset of helminths in *Pelophylax* spp. from 12 provinces of the Middle Volga region demonstrated differences in parasite species structure, abundance, and occurrence (Table 2, Figures 2 and 3) [93]. These differences are due to both diverse regional environmental conditions and the number of *Pelophylax* spp. examined, as well as the sample sizes for each amphibian species across the various areas. Over the course of the green frog survey in the Middle Volga region, the three *Pelophylax* species were studied to varying degrees. However, the core helminth fauna of each *Pelophylax* species was identified in all provinces of the Middle Volga region, with the exception of the Ulyanovsk Oblast. Further

helminthological studies of green frogs in the Middle Volga region may expand the known parasite diversity, primarily due to the findings of rare and/or accidental helminth species. Thus, the most complete data on green frog helminths were obtained from the Samara and Nizhny Novgorod Oblasts, the Republic of Mordovia, Tatarstan, and Mari El, where three *Pelophylax* species were investigated. Consequently, these provinces were found to have both the highest number of helminth species and the greatest similarity in the helminth fauna (Tables 1 and 2, Figure 5). Moreover, in the Samara Oblast, the highest number of helminth species was found in green frogs (Table 2). The area is situated at the boundary of two natural zones—forest-steppe and steppe, boasting a high diversity of landscapes that promote a rich flora and fauna [98,99]. The Zhiguli Mountains are located on the right bank of the Volga, around which the Volga forms the famous Samarskaya Luka. The Samara Oblast has many natural and artificial water bodies: large Kuibyshev and Saratov water reservoirs, small rivers, lakes, ponds, and streams. Diverse natural environments of near-water biocenoses create favorable conditions for amphibians and underlie the richness of their helminths. The diversity and abundance of vertebrates and invertebrates (intermediate, paratenic, and definitive hosts of parasitic worms) ensure a constant release of infectious eggs and larvae of helminths into the environment, facilitating the subsequent infection of amphibians.

At the same time, the Samara Oblast is experiencing increasing anthropogenic pressure on its natural ecosystems. While not the sole determining factor, this pressure has a significant impact on the diversity of invertebrates and vertebrates—potential hosts for helminths of various ranks. This process has a long-term dynamic, and the results of this study can serve as a basis for comparative assessment of changes across natural, disturbed, and heavily transformed habitats of green frogs.

In the Ryazan, Saratov, Orenburg, Penza, and Ulyanovsk Oblasts, as well as the Republic of Bashkortostan, only the helminth fauna of *P. ridibundus* was examined, while in the Republic of Chuvashia, only *P. lessonae* was studied. Therefore, less data on helminths in green frogs were obtained for these provinces, which also showed high similarity in their helminth fauna (Table 2, Figure 5). The Ulyanovsk Oblast was excluded from the comparative analysis, since only two *P. ridibundus* individuals were studied and two helminth species were found there (Table 2) [93].

Despite the high diversity of helminths found in green frogs of the Middle Volga region, it does not reach the maximum value. For instance, the highest helminth species diversity was revealed in *Pelophylax esculentus* complex in Ukraine (57 species) [65,121,134,163–169]. Similarly, 53 helminth species have been recorded in green frogs in the former Czechoslovakia (Czech Republic + Slovakia) [149,170,171]. The helminth species composition of *Pelophylax* spp. in the Middle Volga region is comparable to those reported in Poland (46) [58,61,170–172], Bulgaria (43) [170,171,173–177], and the Lower Volga region (42) [30,48,50,178], and is richer than that in Belarus [55,179,180], Georgia (35 each) [181–183], Turkey (33) [56,60,63,68,184–188], Germany (30) [170,171], France [170,171,189–191], Hungary (29 each) [64,170,171,192], Latvia (26) [42,193,194], the Upper Volga region (25) [195–197], Serbia (21) [54,198–201], and Austria (19) [202,203] (Figure 6).

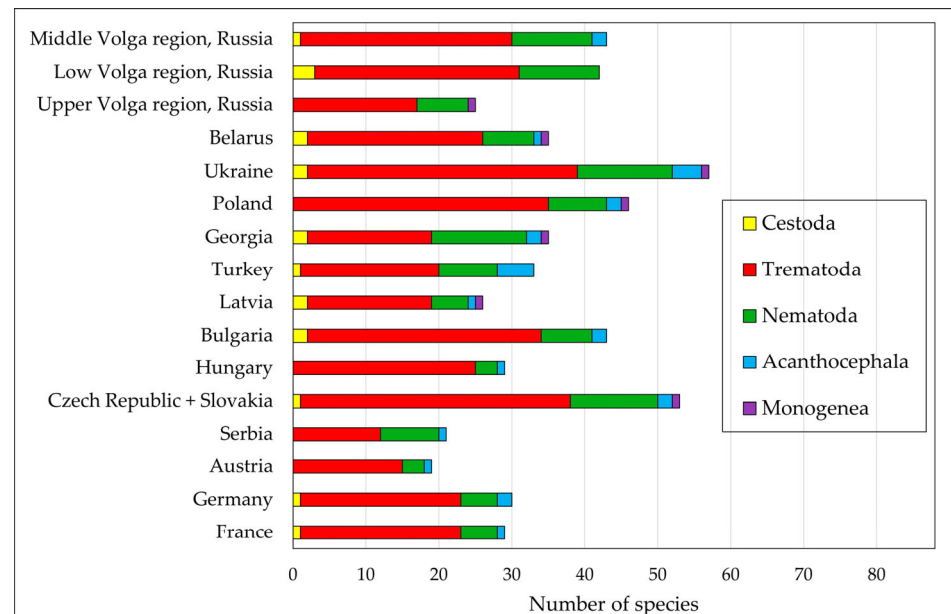


Figure 6. Number of helminth species found in amphibians across different European countries and regions of the Volga River basin.

Trematodes are the most diverse taxonomic group of helminths in *Pelophylax* species throughout their range [31]. The number of trematode species in green frogs across European countries and the Volga River region varies from 12 to 37 (Figure 6). The highest trematode species richness was observed in green frogs from Ukraine and the former Czechoslovakia (37 species each), while the lowest was recorded in Serbia (12). Nematode species diversity in these amphibians is low everywhere. The highest number of roundworm species was recorded in green frogs from Ukraine and Georgia (13 species each), with the lowest numbers found in Austria and Hungary (3 species each) (Figure 6). Acanthocephalans and cestodes are rare parasites of green frogs in Europe. The number of acanthocephalan species in the *Pelophylax esculentus* complex varies across European countries from one to five; in other regions of the Volga basin (Lower and Upper Volga), spiny-headed worms were not found (Figure 6). The greatest diversity of acanthocephalan species is found in Turkey (5). The number of cestode species in different European countries and Volga River regions varies from one to three (Figure 6). Cestodes were observed in 9 of the 13 European countries studied, as well as in the Lower Volga region (Russia). Tapeworms were not detected in green frogs in Poland, Hungary, Serbia, Austria, or the Upper Volga region. Monogeneans (*Polystoma integerrimum* (Frölich, 1791)) were found in green frogs only in Ukraine, Belarus, the former Czechoslovakia, Latvia, Poland, Georgia, and the Upper Volga region.

Thus, the species diversity of helminths in European green frogs varies across the individual regions studied. This is primarily due to the varying extent of study of the helminth fauna in different *Pelophylax* species. For example, the helminth fauna of green frogs is most extensive in Ukraine and the former Czechoslovakia, where all three frog species have been studied, as well as in Poland and the Middle Volga region.

The helminth fauna of green frogs in the Middle Volga region is dominated by helminths of the Palearctic faunal complex (Table 1). Parasitic worms of Holarctic and European origin are represented by five species each. Of the 43 helminth species found in green frogs, only four species are ubiquitous (cosmopolitan) (Table 1).

Our database indicates that green frogs in the Middle Volga region participate in life cycles of pathogenic parasite species, namely the trematode *A. alata*, the cestode *S. erinacei*, and the nematode *A. strongylina*, serving as second intermediate or paratenic hosts.

The trematode *A. alata* is the causative agent of alariasis, a dangerous disease affecting fur-bearing animals. This species is widespread throughout the Middle Volga region [49]. The first intermediate hosts of *A. alata* are mollusks of the genera *Planorbis* Müller, 1774 and *Anisus* Studer, 1820 [122]. The definitive hosts of the parasite are carnivores of the Canidae and Procyonidae families [27,122,135]. In the Middle Volga region, amphibians and colubrid snakes serve as the main paratenic hosts for *A. alata*, exhibiting high infection rates [49,87]. The parasite was identified in green frogs in five of the 11 administrative provinces studied (Tables 2 and 3). These findings are of particular importance for the prevention of dangerous helminthiasis in domestic dogs (especially in rural areas) and for the sustainability of fur farms located across the Middle Volga region.

The plerocercoid of *S. erinacei* causes sparganosis, a dangerous disease in both predators and humans. Human infections with the parasite, which typically resides in the subcutaneous tissue, have been documented [46,155]. Cyclops species serve as the primary intermediate host, while amphibians, reptiles, and rodents act as secondary intermediate hosts. Canids and felines represent the natural definitive hosts for the parasite. A wide range of vertebrates across various classes have been reported as paratenic hosts for *S. erinacei* [135,155]. This species was rarely found in *P. ridibundus* only in the Samara Oblast [93] (Tables 2 and 3), which indicates the low zoonotic potential of green frogs for this parasite.

The nematode *A. strongylina* causes ascariasis, a helminthiasis affecting domestic pigs and wild boars [32,36,152]. While the transmission of these zoonotic parasites from green frogs to humans and domestic animals is improbable, the involvement of anurans in their life cycles facilitates transmission to definitive hosts. Consequently, green frogs contribute to the conservation of zoonotic foci in the wild. Similar to *S. erinacei*, the nematode *A. strongylina* was recorded in *P. ridibundus* in the Samara Oblast with low occurrence [93] (Tables 2 and 3). Thus, green frogs are involved in the formation and spread of natural foci of dangerous zoonoses caused by these helminths in natural ecosystems of the Middle Volga region.

5. Conclusions

Our newly presented dataset demonstrates that the helminth fauna of *Pelophylax* frogs in the Middle Volga region currently includes 43 species. As a result of our helminthological studies, seven helminth species were documented in green frogs for the first time in Russia: *Astiotrema monticellii*, mtc., *Phyllodistomum angulatum*, *Camallanus truncatus*, *Strongyloides spiralis*, *Spiroxys contortus*, juv., *Acanthocephalus falcatus*, and *A. ranae*. The most diverse helminth fauna is found in the most common and abundant amphibian species, the marsh frog *Pelophylax ridibundus* (42 species). The helminth faunas of *P. lessonae* (32 species) and *P. esculentus* (25 species) are less diverse.

Among the helminths parasitizing green frogs in the Middle Volga region, trematodes exhibit the greatest species diversity, occurrence, and abundance. Nematodes are less represented in the helminth community of the *Pelophylax esculentus* complex in terms of species number, abundance, and occurrence records. Acanthocephalans and cestodes are rare parasites of *Pelophylax* spp. in the Middle Volga region, which is consistent with findings elsewhere.

The majority of helminth species found in green frogs of the Middle Volga region belong to the Palearctic faunal complex (29 species). Parasitic worms of Holarctic and European distribution are represented by five species each. Additionally, four species of helminths are considered cosmopolitan. Of the 43 helminth species found in green frogs, three (*Alaria alata*, *Spirometra erinacei*, and *Ascarops strongylina*) are of medical and veterinary importance as causative agents of zoonoses.

Despite the long-standing and fruitful parasitological studies of amphibians in the Middle Volga region, information on the diversity and distribution of helminths parasitizing the *Pelophylax esculentus* complex remains incomplete, as some areas are still unexplored and poorly studied. Our database, published in GBIF, can be further supplemented with new data on helminth occurrences in green frogs and updated in accordance with new records and taxonomic revisions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18050245/s1>, Table S1: Description of the data in the dataset according Darwin Core; Table S2: Helminth taxa included in the dataset, Figure S1. Comparison of Shannon diversity indices for the helminth fauna of green frogs from different provinces of the Middle Volga region; Supplementary Materials Codes.

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Data Availability Statement: The data are presented in our database at <https://doi.org/10.15468/tzkn7v> (accessed on 26 March 2026).

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Abbreviations

The following abbreviations are used in this manuscript:

GBIF	Global Biodiversity Information Facility
IEVB RAS	Institute of Ecology of the Volga River basin of the Russian Academy of Sciences
msc.	Mesocercaria
mtc.	Metacercaria
plc.	Plerocercoid
juv.	Juvenile
UPGMA	Unweighted pair group method with arithmetic mean

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