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Overview of Helminths in Land Vertebrates from the Mordovia Nature Reserve, European Russia

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ABSTRACT

In this study, we summarized our own and literature data on the helminth fauna in amphibians, reptiles, birds, and mammals inhabiting the Mordovia Nature Reserve (European Russia). The history of research on parasitic worms in vertebrates has more than 70 years here. Nowadays, 242 species of helminths have been identified in vertebrates in this protected area: 54 cestodes, 87 trematodes, 98 nematodes, and 3 acanthocephalans. Of these, 169 helminth species have an indirect life cycle, while 73 develop directly. 217 revealed parasite species use vertebrates as definitive hosts and 21 as intermediate and/or parathenic hosts. Three species of trematodes, *Gorgoderina vitelliloba*, *Haplometra cylindracea*, and *Opisthioglyphe ranae* combine the larval and mature lifestyle stages in amphibians. The most diverse helminth fauna is in rodents (41 species), birds (38), artiodactyls (37), and insectivores (35). Less rich in amphibians (32), bats (32), reptiles (26), and carnivores (19). Only six parasite species are found in hares. Most of the helminth species recorded in the vertebrates of the Mordovia Nature Reserve belong to the Palearctic faunistic complex – 107 species. Fifty-eight species are cosmopolitan. The range of 39 species covers the Holarctic. The distribution of 37 species of helminths is limited to Europe. Seventy-three of 242 species found in the nature reserve's vertebrates have medical and veterinary importance as potential pathogens of dangerous zoonoses.

INTRODUCTION

Population growth, industrialization, expansion of transport communications, and tourism, combined with intensive agriculture, have led to increased exploitation of natural resources and loss of biodiversity caused by human activity. Nowadays, almost no natural ecosystems are left in Europe that have not been affected by anthropogenic activity (Poulin & Morand 2004, Kirillov et al. 2012). Protected areas are characterized by the undisturbed structure of biocenoses and minimal anthropogenic impact on them. Natural ecosystems with rich fauna and flora are often preserved only in nature reserves (Pringle 2017, Ghosh-Harihar et al. 2019, Afonina & Tashlykova 2021, Kaicheen & Mohd-Azlan 2022, Vasenkova et al. 2022). In this context, research in protected areas has always attracted the attention of parasitologists as areas where helminths can freely carry out their life cycles (Turner & Getz 2010, Kouassi et al. 2015, Herczeg, et al. 2016, Chikhlyaev et al. 2020, Kononova & Prisniy 2020, Bhat et al. 2022, Ieshko et al. 2022, Martinez-Sotelo et al. 2022).

An extensive study of the helminth fauna of different species of wild vertebrates is of general biological significance from the ecological, biocenotic, and zoogeographic aspects. Helminths, like other parasites, are a necessary component of a sustainable natural ecosystem, an integral part of the world's biodiversity (Poulin & Morand 2004, Horwitz & Wilcox 2005, Dobson et al. 2008).

The disappearance of parasites in biocenoses can lead to extensive and unforeseen consequences that will affect the condition and abundance of most animal species (Dobson et al. 2008, Orlova & Orlov 2019). On the other hand, interest in wild vertebrates from an applied aspect is determined primarily by their epidemiological and epizootological role as involvement in the preservation and distribution of natural focal zoonoses dangerous to humans, domestic and game animals (Georgopoulou & Tsiouris 2008, Froeschke & Matthee 2014, Bordes et al. 2015, Krucken et al. 2017, Recht et al. 2020, Romashov et al. 2021). As a rule, protected areas are surrounded by agricultural landscapes, livestock farms, and settlements. Wild vertebrates can move freely

from the reserve to the surrounding areas. The movement freedom of animals creates the possibility, if there are foci of zoonoses in the territory of reserves, to spread them to the surrounding territories. The reverse case is also possible. However, the main role in preserving and distributing natural focal helminthic zoonoses belongs to wild vertebrates.

The first helminthological studies in the Mordovia Nature Reserve began with the work of Nizhny Novgorod parasitologists in the late 1940s. The results of these studies were published in only a few publications on helminths in rodents, insectivores, bats, lagomorphs, carnivores, and ungulates (Shaldybin 1957, 1964, Matevosyan 1964a, 1964b, Shtarev 1967, 1971, Machinsky & Semov 1974, Nazarova 1974a, 1974b, Shtarev et al. 1978). Most attention was paid to the helminth fauna of introduced animals such as *Bison bonasus*, *Cervus nippon*, *Cervus elaphus,* and *Nyctereutes procyonoides*. Oliger (1952, 1957) published information on helminths of the tetraonid birds in European Russia, including data on this Nature Reserve. Since 2003, data about the parasitic worms in the animals of the protected area have increased quickly as a result of the partnership between staff of the Mordovia Nature Reserve, Mordovia State University (Saransk), and the Institute of Ecology of the Volga Basin of RAS (Togliatti). The first data on helminths of amphibians of Mordovia (Ryzhov et al. 2004, Chikhlyaev et al. 2009, Ruchin & Chikhlyaev 2013, Ivanov et al. 2019), reptiles (Ruchin & Kirillov 2012, Kirillov et al. 2015a), birds (Kirillov et al. 2023), and bats (Kirillov et al. 2015b) were published. Some parasitological manuscripts-reports are stored in the Mordovia Reserve, which began to be published only recently as Oliger's works (2016a, 2016b). Data on helminths in vertebrates of the reserve were partially included in some reviews and regional summaries (Bykhovskaya-Pavlovskaya 1962, Gvozdev et al. 1970, Ryzhikov et al. 1978, 1979, Kostyunin 2010, Kirillov et al. 2012, Chikhlyaev & Ruchin 2014, Chikhlyaev et al. 2015). In 2016, we published the first monographic summary of parasitic worms in terrestrial vertebrates of the Mordovia Nature Reserve, which contains information on helminth fauna of amphibians, reptiles, birds, and mammals (Ruchin et al. 2016). Nowadays, data on parasitic worms of vertebrates are contained in 41 papers and reviews.

The Mordovia Nature Reserve, one of the oldest in Russia, was organized in 1936. The territory of the protected area is part of the Temnikovsky district of the Republic of Mordovia, and currently, its area is 321.62 km^2. Its main task is to preserve the natural landscapes of the southern woodlands, extending along the border of mixed broadleafed forests and forest-steppe (Ruchin et al. 2016).

The Mordovia Nature Reserve is located in the northwestern part of the Volga Upland and occupies the wooded right bank of the Moksha River. From the North, the border runs along the Satis River, the right tributary of the Moksha River, and further to the East – along the Arga River, which flows into the Satis River. The western border goes along the Chernaya, Satis, and Moksha Rivers. Forest-steppe approaches from the south, naturally limiting the boundary of this protected area (Gafferberg 1960, 2015). In terms of climate, the territory of the reserve is included in the Atlantic-continental region of the temperate zone (Ruchin et al. 2016, Gafferberg 1960, 2015).

The water network of the nature reserve is represented by small rivers Pushta, Bolshaya Malaya Chernaya, Arga, and streams flowing into the Moksha River. Most of the territory is included in the catchment area of the Pushta River, which flows into the Satis River at the border of the protected area. The hydrology of rivers is significantly affected by beaver dams, which flood large areas. In dry years, the riverbed dries up to the very lower reaches. There are about two dozen lakes in the southwestern part of the nature reserve. These are the oxbows of the Moksha River, sometimes large and deep like Picherki, Bokovoe, Taratinskoe, Inorki, and Valza (Ruchin et al. 2016, Grishutkin 2013, Artaev & Grishutkin 2014). The fauna of the Mordovia Nature Reserve includes 10 species of amphibians, 7 reptiles, 219 birds, and 63 mammals (Ruchin et al. 2016, Artaev et al. 2012, Artaev & Smirnov 2016).

This work is based on the analysis of literature data and the results of our own studies of the helminth fauna of vertebrates in this protected area. Own material on helminths of amphibians, reptiles, insectivores, bats, birds and myomorph rodents, collected by the authors from various sites in the Mordovia Nature Reserve in 2008, 2009, 2011, 2014, 2021 and 2022. Fig. 1 shows the study localities of the helminth fauna in land vertebrates.

Helminthological studies of vertebrates were carried out in the vicinity of the Pushta village, on the cordons of the Nature Reserve and their vicinities. Only amphibians, insectivores, and myomorph rodents that fell into the pitfall traps of our fellow entomologists were studied in sites called "compartments". In site "440th compartment", only amphibians and reptiles were studied. In the works by Shaldybin (1964) and Oliger (1952, 1957, 2016a, 2016b), the study sites of the helminth fauna of vertebrates in the Mordovia Nature Reserve were not specified.

The international databases Scopus, Web of Science Core Collection, Google Scholar, and Russian scientific electronic library (eLIBRARY.ru) were used to search scientific literature on the helminths fauna in vertebrates from the Mordovia State Nature Reserve. We used both Russian and

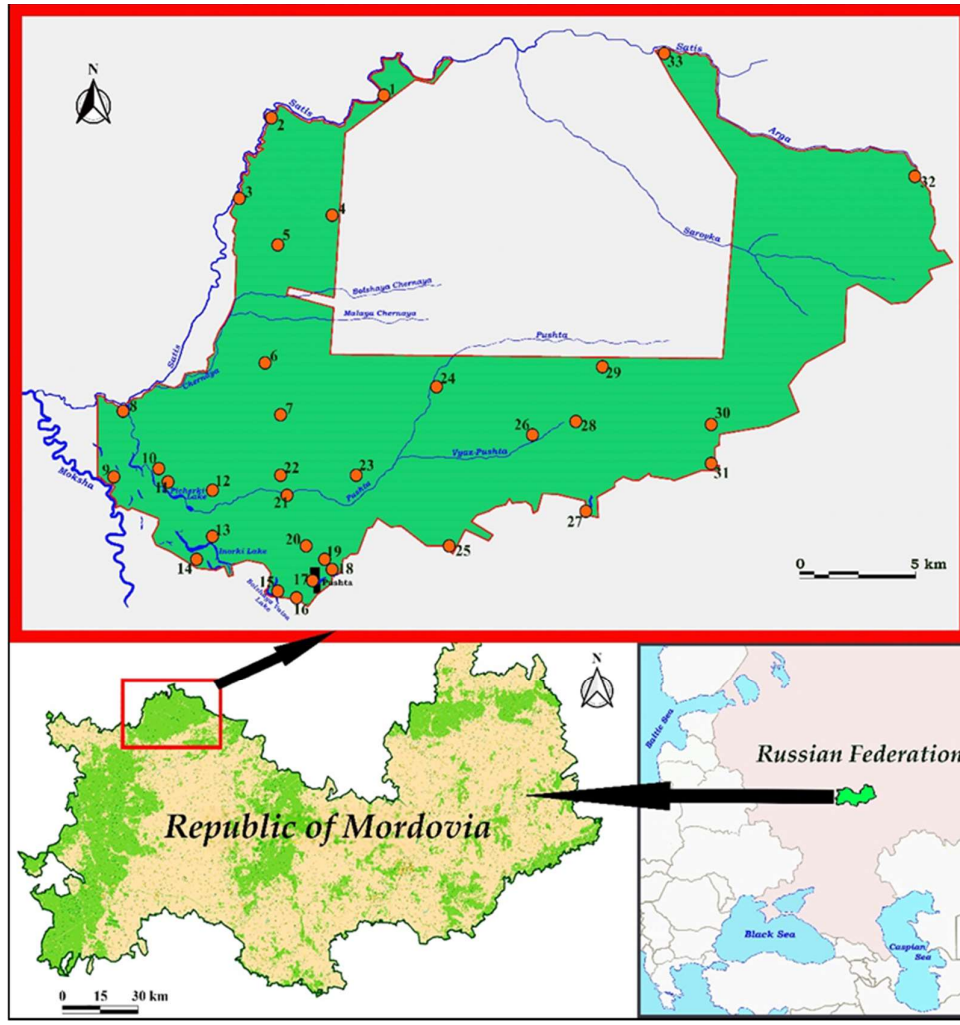

Fig. 1: A schematic map of the helminth studying sites in the Mordovia State Nature Reserve. Red circles in the map showed the places, where animal helminths were studied. 1 – Cordon "Srednyay Melnitsa", 2 – Cordon "Plotomoyka", 3 – Cordon "Pilna", 4 – 145th compartment, 5 – 170th compartment, 6 – 276th compartment, 7 – 330th compartment, 8 – Vorovskoy cordon, 9 – Taratinskiy cordon, 10 – 378th compartment, 11 – Picherki Lake, 12 – 405th compartment, 13 – Inorskiy cordon, 14 – 443rd compartment, 15 – Bolshaya Valza Lake, 16 – Novenkiy cordon, 17 – Pushta village, 18 – Valzenskiy cordon, 19 – 441st compartment, 20 – 440th compartment, 21 – Cordon "Dolgiy Most", 22 – 383rd compartment, 23 – 386th compartment, 24 – 308th compartment, 25 – Drozhdenovskiy cordon, 26 – Zhegalovskiy cordon, 27 – Pavlovskiy cordon, 28 – 342nd compartment, 29 – 290th compartment, 30 – 347th compartment, 31 – Polyanskiy cordon, 32 – Steklyanniy cordon, 33 – Novenkovskiy cordon.

English characters to enter our search strings in the Russian database eLIBRARY.ru. Most of the literature sources, including those not indexed in electronic databases, were taken from the library of the Mordovia Nature Reserve. The analysis of parasitological literature was conducted between 1950 and 2022.

The helminth taxonomy is based on the Fauna Europaea (https://fauna-eu.org) and the Global Cestode Database (http://tapewormdb.uconn.edu). The voucher specimens of parasitic worms are stored in the Parasitological collection at the Institute of Ecology of Volga Basin of RAS, Togliatti, Russia.

PARASITIC WORMS OF VERTEBRATES IN THE MORDOVIA NATURE RESERVE

Nowadays, taking into account recent concepts on the helminth taxonomy, the list of parasitic worms in land vertebrates of the Mordovia Nature Reserve includes 242 species: 54 cestodes, 87 trematodes, 98 nematodes, and 3 acanthocephalans.

Helminths of Amphibians (Amphibia)

The helminth fauna in amphibians of the protected area includes 32 species: 25 trematodes and 7 nematodes

(Ryzhov et al. 2004, Ruchin et al. 2016, Chikhlyaev et al. 2009, Ruchin & Chikhlyaev 2013, Kirillov et al. 2012, Chikhlyaev & Ruchin 2014, Chikhlyaev et al. 2015) (Table 1).

Twenty-one helminth species in mature forms parasitize amphibians and use them as definitive hosts. While eight trematode species occur in amphibians at the larval stage. Three species (trematodes *Gorgoderina vitelliloba*,

Table 1: The list of helminths in amphibians (Amphibia) from the Mordovia Nature Reserve.

Species	D[1]	*Pelophylax ridibundus*	*Pelophylax lessonae*	*Rana arvalis*	*Rana temporaria*	*Bufo bufo*	*Pelobates vespertinus*	*Bombina bombina*	*Lissotriton vulgaris*	*Triturus cristatus*
Trematoda										
Halipegus ovocaudatus	E		+		+					
Diplodiscus subclavatus	P		+	+	+		+		+	+
Gorgodera cygnoides	P		+	+		+		+		
Gorgodera microovata	E		+	+	+	+				
Gorgodera pagenstecheri	P		+							
Gorgoderina vitelliloba	P			+	+	+				
Haplometra cylindracea	P			+						
Haematoloechus abbreviatus	E							+		
Haematoloechus asper	E		+							
Haematoloechus variegatus	P		+							
Skrjabinoeces similis	P		+							
Paralepoderma cloacicola, mtc.	P		+	+			+			
Opisthioglyphe ranae	P	+	+	+						
Pleurogenes claviger	C	+	+		+	+				
Pleurogenes intermedius	P			+						
Pleurogenoides medians	P		+	+		+				
Brandesia turgida	P		+							
Prosotocus confusus	P	+	+							
Strigea falconis, mtc.	C			+						
Strigea sphaerula, mtc.	P		+	+						
Strigea strigis, mtc.	P		+	+	+		+			
Alaria alata, msc.	C		+	+		+	+			
Neodiplostomum spathoides, mtc.	P			+			+			
Tylodelphys excavata, mtc.	E		+					+		
Astiotrema monticelli, mtc.	E		+			+	+			
Nematoda										
Amphibiocapillaria tritonispunctati	E									+
Rhabdias bufonis	P		+	+	+	+	+			
Oswaldocruzia filiformis	H		+	+	+	+	+			
Megalobatrachonema terdentatum	E								+	
Cosmocerca ornata	E		+	+	+	+	+	+		
Oxysomatium brevicaudatum	H					+	+			
Icosiella neglecta	C	+	+	+	+					
Total		4	23	18	10	11	10	4	2	2

[1] Here and in Tables 2–9, D – distribution, E – Europe, C – Cosmopolitan, H – Holarctic, P – Palaearctic.

Haplometra cylindracea, and *Opisthioglyphe ranae*) combine the larval and adult development stages in amphibians and characterize them as amphixenic hosts.

All found helminth species are obligate parasites of amphibians. According to the degree of host specificity, 30 species of trematodes and nematodes belong to parasites-generalists occurring in various amphibian species. Of these, 21 species are polyhostal parasites of amphibians. Nine more species (trematodes *Gorgodera pagenstecheri*, *G. microovata*, *Haplometra cylindracea*, *Haematoloechus asper*, *Skrjabinoeces similis*, *Pleurogenes intermedius*, *Brandesia turgida*, *Neodiplostomum spathoides*, mtc. and nematode *Icosiella neglecta*) are oligohostal parasites of frogs from the family Ranidae. The nematodes *Amphibiocapillaria tritonispunctati* and *Megalobatrachonema terdentatum* are host-specific parasites of newts from the genera *Triturus* and *Lissotriton*, respectively.

No helminth species was found to parasitize the entire range of infected amphibian species in the Mordovia Nature Reserve (Table 1). The trematode *Diplodiscus subclavatus* and the nematode *Cosmocerca ornata* have the widest host ranges (6 amphibian species each). Two nematodes *Rhabdias bufonis* and *Oswaldocruzia filiformis* were revealed in five amphibian species each. The trematodes *Gorgodera cygnoides*, *G. microovata*, *Pleurogenes claviger*, *Strigea strigis*, mtc., *Alaria alata*, msc. and the nematode

Table 2: The list of helminths in reptiles (Reptilia) from the Mordovia Nature Reserve.

Species	D	*Lacerta agilis*	*Zootoca vivipara*	*Anguis fragilis*	*Natrix natrix*	*Vipera berus*
Cestoda						
Spirometra erinaceieuropaei, plc.	P				+	
Ophiotaenia europaea	E				+	
Trematoda						
Plagiorchis elegans	H	+	+			
Plagiorchis molini	P	+	+			
Leptophallus nigrovenosus	P				+	+
Astiotrema monticelli	E				+	
Telorchis assula	P				+	
Macrodera longicollis	P				+	
Paralepoderma cloacicola	P				+	
Opisthioglyphe ranae	P				+	
Strigea falconis, mtc.	C				+	
Strigea sphaerula, mtc.	P				+	+
Strigea strigis, mtc.	P				+	+
Alaria alata, msc.	C				+	+
Neodiplostomum spathoides, mtc.	P				+	
Nematoda						
Rhabdias fuscovenosa	H				+	+
Strongyloides mirzai	P				+	
Oswaldocruzia filiformis	H	+	+	+		+
Entomelas entomelas	P			+		
Entomelas dujardini	P			+		
Oxysomatium brevicaudatum	H			+		
Physocephalus sexalatus, juv.	C				+	
Physaloptera clausa, juv.	H	+	+			+
Agamospirura minuta, juv.	E			+	+	+
Acanthocephala						
Centrorhynchus aluconis, juv.	P					+
Sphaerirostris picae, juv.	P		+			
Total		4	5	5	17	9

Icosiella neglecta were found in four host species each. The trematodes *Gorgoderina vitelliloba*, *Paralepoderma cloacicola*, larvae, *Opisthioglyphe ranae*, *Pleurogenoides medians*, *Astiotrema monticelli*, mtc. parasitize amphibians of three species each. For five trematode species (*Halipegus ovocaudatus*, *Prosotocus confusus*, *Strigea sphaerula*, mtc., *Neodiplostomum spathoides*, mtc., *Tylodelphys excavata*, mtc. and the nematode *Oxysomatium brevicaudatum*) the host range is limited to two species of anurans. Other 11 helminth species were found only in one host species (Table 1).

The most number of helminth species was found in *Pelophylax lessonae* (23 species). The helminth fauna of *Rana arvalis* (18), *Bufo bufo* (11), *Rana temporaria,* and *Pelobates vespertinus* (10 each) is less diverse. The smallest number of helminth species was identified in *Pelophylax ridibundus* and *Bombina bombina* (4 each), *Lissotriton vulgaris,* and *Triturus cristatus* (2 each) (Table 1).

Four species of parasitic worms found in amphibians in the Mordovia State Nature Reserve are cosmopolitans. Seventeen species of helminths have a Palearctic distribution. Two nematode species are distributed in the Holarctic. The distribution of nine species of trematodes and nematodes is limited to the territory of Europe (Table 1).

Helminths of Reptiles (Reptilia)

A total of 26 species of helminths were revealed in the reptiles of the Nature Reserve: 2 cestodes, 13 trematodes, 9 nematodes, and 2 acanthocephalans (Kirillov et al. 2012, 2015a, Ruchin & Kirillov 2012, Ruchin et al. 2016) (Table 2).

Fifteen species of helminths use reptiles as definitive hosts. Reptiles are paratenic hosts for other 11 species of parasites found at the larval stages. Most helminth species recorded are obligate parasites of reptiles. Only two species, the trematodes *Plagiorchis elegans* and *Opisthioglyphe ranae*, belong to occasional and facultative parasites of reptiles. The finding in *Natrix natrix* of a host-specific parasite of the amphibians, *O. ranae* is a case of post-cyclic parasitism. This trematode can be considered as a temporary transit inhabitant of the snake intestine, where the parasite came from tailless amphibians swallowed by reptiles. *Plagiorchis elegans* is a generalist parasite found in many vertebrates of different classes (birds, mammals, and reptiles), more common in passerine birds. The metacestode *Spirometra erinaceieuropaei* are parasitizing fish, amphibians, and reptiles. Seven species of parasitic worms (nematodes *Oswaldocruzia filiformis*, *Oxysomatium brevicaudatum*, trematodes *Strigea falconis*, mtc., *S. sphaerula*, mtc., *S. strigis*, mtc., *Neodiplostomum spathoides*, mtc. and *A. alata*, msc.) belong to amphibian and reptile generalists. Juveniles of nematodes *Physocephalus sexalatus*, *Physaloptera clausa*, *Agamospirura minuta,* and acanthocephalans *Centrorhynchus aluconis*, *Sphaerirostris picae* are reptile generalists. The cestode *Ophiotaenia europaea*, the trematodes *Leptophallus nigrovenosus*, *Astiotrema monticelli*, *Telorchis assula*, *Macrodera longicollis*, *Paralepoderma cloacicola*, the nematodes *Rhabdias fuscovenosa* and *Strongyloides mirzai* are generalist parasites in colubride snakes. The trematode *Plagiorchis molini* is a specific parasite of lacertid lizards, while *Entomelas entomelas* and *E. dujardini* belong to parasite specialists in *Anguis* slowworms.

We did not find a single helminth species that would be parasitized in all five studied reptile species in the Mordovia Nature Reserve. The nematode *Oswaldocruzia filiformis* was identified in four species of reptiles. The nematodes *Physaloptera clausa*, juv., *Agamospirura minuta* were found in three host species (Table 2). The trematodes *Plagiorchis elegans*, *P. molini*, *Leptophallus nigrovenosus*, *Strigea sphaerula*, mtc., *S. strigis*, mtc., *Alaria alata*, msc. and nematode *Rhabdias fuscovenosa* found in two host species each. Another 16 helminth species were registered only in one host species (Table 2).

The greatest helminth diversity was revealed in *Natrix natrix* – 17 species. The list of *Vipera berus* helminths includes 9 species. The helminth fauna of lizards is less diverse. So, in *Zootoca vivipara* and *Anguis fragilis*, five parasites were found, and in *Lacerta agilis* four helminth species were found (Table 2).

Most of the helminths of reptiles belong to the Palearctic complex (15 species). Five species of helminths are common in the Holarctic. Three parasite species are cosmopolitans. Distribution of three more species of parasitic worms restricted to Europe (Table 2).

Taxonomic remarks. *Agamospirura minuta*, juv. is a specific parasite of reptiles, usually parasitizing the slowworm *Anguis fragilis* and less common in other lizards and snakes (Sharpilo 1976). The final host is unknown. Lewin (1990) found similar nematode larvae in reptiles of Poland and identified them as Protostrongylidae sp. In his opinion, the identification by Sharpilo (1976) of *Agamospirura* larva as Spirurida is erroneous.

Helminths of Birds (Aves)

A total of 38 species of parasitic worms were revealed in the birds of the Mordovia Nature Reserve: 16 cestodes, 14 trematodes, and 8 nematodes (Oliger 1952, 1957, 2016a, Bykhovskaya-Pavlovskaya 1962, Kirillov et al. 2012, 2023, Ruchin et al. 2016) (Tables 3 and 4).

All of them parasitize birds at the mature stage and are their obligate parasites, with the exception of

Table 3: The list of helminths in passerine birds (Aves, Passeriformes) from the Mordovia Nature Reserve.

Species	D	*Turdus philomelos*	*Turdus viscivorus*	*Turdus merula*	*Parus major*	*Cyanistes caeruleus*	*Fringilla coelebs*	*Carduelis carduelis*	*Pyrrhula pyrrhula*	*Sylvia nisoria*	*Ficedula hypoleuca*	*Muscicapa striata*	*Hippolais icterina*	*Phylloscopus collybita*	*Erithacus rubecula*	*Motacilla alba*	*Hirundo rustica*
Cestoda																	
Dilepis undula	H	+	+	+													
Emberizotaenia reductorhyncha	P				+	+											
Passerilepis crenata	H	+	+				+	+		+	+				+		
Wardium farciminosa	C										+		+				
Monorcholepis dujardini	P	+															
Trematoda																	
Urogonimus macrostomus	H	+			+		+		+			+					+
Leucochloridium holostomum	C			+													
Leucochloridium phragmitophila	P														+		
Mosesia amplavaginata	P						+										
Plagiorchis elegans	H				+									+			
Plagiorchis maculosus	C												+			+	
Morishitium polonicum	P	+		+													
Brachylecithum fringillae	P						+										
Brachylecithum attenuatum	P			+													
Nematoda																	
Aonchotheca exilis	H	+	+														
Acuaria subula	P												+				
Hadjelia truncata	P	+	+												+		
Porrocaecum ensicaudatum	H	+	+														
Physocephalus sexalatus, juv.	C		+														
Diplotriaena henryi	P					+											
Total		8	6	4	3	2	4	1	1	1	2	1	3	1	3	1	1

the nematode *Physocephalus sexalatus*. Birds serve as paratenic hosts for these nematode larvae. The trematode *Plagiorchis elegans* is a parasite generalist found in a wide range of vertebrates (birds, mammals and reptiles) and more common in passerines. The cestodes *Dilepis undula*, *Passerilepis crenata*, trematodes *Mosesia amplavaginata*, *Plagiorchis maculosus*, *Prosthogonimus ovatus*, *Eumegacetes triangularis*, *Cotylurus cornutus* s.l., nematodes *Acuaria subula*, *Hadjelia truncata* and *Diplotriaena henryi* are bird generalists, parasitising a wide range of birds from different orders. Six species (the cestodes *Emberizotaenia reductorhyncha*, *Wardium farciminosa*, trematodes *Urogonimus macrostomus*, *Phaneropsolus micrococcus*, are specific parasites of Passeriformes birds. The cestodes *Liga crateriformis* and *Raillietina frontina* are helminths specialists of woodpeckers. The trematodes *Brachylecithum attenuatum*, *Morishitium polonicum,* and cestode *Monorcholepis dujardini* are specialist parasites in thrushes. Only waders are parasitized by the cestodes *Anomolepis glareola*, *Anomotaenia citrus*, *Kowalewskiella cingulifera*, and the trematode *Leucochloridium perturbatum*. The trematode *Leucochloridium holostomum* is a specific parasite of Rallidae birds, less common in waders and thrushes. The trematode *Leucochloridium phragmitophila* is a specialist parasite of birds from the family Passeridae, and the trematode *Brachylecithum fringillae* is a specific parasite of finches. Eight species of helminths (the cestodes *Choanotaenia infundibulum*, *Paroniella urogalli*, *Raillietina penetrans*, *Skrjabinia cesticillus*, *S. polyuterina*, *Rhabdometra tomica*, nematodes *Trichostrongylus medius*

Table 4: The list of helminths in non-passerine birds from the Mordovia Nature Reserve.

Species	D	*Lyrurus tetrix*	*Tetrao urogallus*	*Tetrastes bonasia*	*Actitis hypoleucos*	*Dendrocopos major*	*Picus canus*	*Caprimulgus europaeus*
Cestoda								
Dilepis undula	H					+		
Choanotaenia infundibulum	C	+						
Anomolepis glareola	P				+			
Anomotaenia citrus	H				+			
Kowalewskiella cingulifera	P				+			
Liga crateriformis	P					+	+	
Passerilepis crenata	H					+		
Monorcholepis dujardini	P							
Paroniella urogalli	H	+	+					
Raillietina frontina	P					+		
Raillietina penetrans	P		+					
Skrjabinia cesticillus	C	+	+	+				
Skrjabinia polyuterina	P	+	+					
Rhabdometra tomica	P	+						
Trematoda								
Urogonimus macrostomus	H					+		
Leucochloridium perturbatum	H				+			
Phaneropsolus micrococcus	P							+
Plagiorchis elegans	H							+
Eumegacetes triangularis	P							+
Morishitium polonicum	P							
Prosthogonimus ovatus	C	+						
Cotylurus cornutus s.l.	C				+			
Nematoda								
Aonchotheca exilis	H					+		
Trichostrongylus medius	E	+						
Porrocaecum ensicaudatum	H						+	
Ascaridia compar	C	+	+	+				
Hadjelia truncata	P							
Total		8	5	2	5	6	2	3

and *Ascaridia compar*) are specialist parasites in galliform birds.

No helminths were found in 8 of 31 studied bird species in the Mordovia Nature Reserve: *Anthus trivialis*, *Aegithalos caudatus*, *Alcedo atthis*, *Carduelis chloris*, *Poecile montanus*, *Sylvia atricapilla*, *Luscinia luscinia* and *Phoenicurus phoenicurus*. No parasite species would be identified in all five studied bird species in the protected area (Tables 3 and 4). The cestode *Passerilepis crenata* and the trematode *Urogonimus macrostomus* have the widest range of hosts, parasitizing 8 and 7 bird species, respectively. The cestode *Dilepis undula* was identified in four species of birds. The host range of the cestode *Skrjabinia cesticillus*, the trematode *Plagiorchis elegans*, and the nematodes *Aonchotheca exilis*, *Ascaridia compar* and *Hadjelia truncata* includes 3 bird species each. Eight parasite species (*Emberizotaenia reductorhyncha*, *Wardium farciminosa*, *Morishitium polonicum*, *Liga crateriformis*, *Paroniella*

Table 5: The list of helminths in insectivores (Eulipotyphla) from the Mordovia Nature Reserve.

Species	D	*Desmana moschata*	*Sorex araneus*	*Sorex minutus*	*Crocidura suaveolens*	*Neomys fodiens*	*Neomys anomalus*	*Erinaceus roumanicus*
Cestoda								
Dilepis undula	H		+					
Hymenolepis erinacei	E							+
Ditestolepis diaphana	P		+	+		+		
Insectivorolepis infirma	P		+	+				
Molluscotaenia crassiscolex	P		+	+		+		
Neomylepis magnirostellata	P					+		
Neoskrjabinolepis schaldybini	P		+	+		+		
Pseudobothrialepis mathevossianae	P		+	+				
Spasskylepis ovaluteri	P		+	+		+		
Staphylocystis brusatae	E				+			
Staphylocystis furcata	P		+	+				
Staphylocystoides stefanskii	P		+					
Vigisolepis spinulosa	P		+	+				
Trematoda								
Brachylaima fulvum	P		+	+		+		
Pseudoleucochloridium soricis	P		+	+		+		
Metorchis bilis	H					+		
Rubenstrema exasperatum	H		+	+		+	+	
Rubenstrema opisthovitellinus	P					+		
Neoglyphe locellus	H					+		
Neoglyphe sobolevi	H		+	+				
Omphalometra desmanae	E	+						
Nematoda								
Soboliphyme soricis	P					+		
Paracrenosoma skrjabini	P			+				
Aonchotheca erinacei	P							+
Aonchotheca kutorii	P		+	+		+		
Calodium soricicola	P		+					
Eucoleus oesophagicola	P		+			+		
Liniscus incrassatus	P		+			+	+	
Longistriata paradoxi	P		+	+				
Longistriata neomi	E					+	+	
Physaloptera clausa	H		+					+
Pseudophysaloptera soricina	H			+				
Porrocaecum depressum, juv.	C		+					
Hadjelia truncata, juv.	P		+					
Acanthocephala								
Centrorhynchus aluconis, juv.	P		+					
Total		1	23	16	1	16	3	3

urogalli, *Skrjabinia polyuterina*, *Plagiorchis maculosus* and *Porrocaecum ensicaudatum*) were each found in two host species. Another 22 species of parasitic worms were found only in a single bird species (Tables 3 and 4).

Among birds, the most diverse fauna of helminths is in *Turdus philomelos* and *Lyrurus tetrix*, in which 8 species of parasites each were found. The helminth fauna of *Turdus viscivorus* and *Dendrocopos major* has six species of helminths each, while *Tetrao urogallus* and *Actitis hypoleucos* have five species of parasitic worms each. Fewer helminth species were found in *Turdus merula* and *Fringilla coelebs* (4 species each); *Parus major*, *Hippolais icterina*, *Erithacus rubecula* and *Caprimulgus europaeus* (3 species each). Two species of parasites were noted in *Tetrastes bonasia*, *Picus canus*, *Cyanistes caeruleus,* and *Ficedula hypoleuca*. Another six species of birds have only one helminth species each (Tables 3 and 4).

Half of the helminth species found in the birds of the protected area have a Palearctic distribution – 19 species. The Holarctic faunistic complex includes 9 species of parasitic worms. Also, 9 species of parasites have a cosmopolitan distribution. The distribution range of one helminth species is limited to Europe (Tables 3 and 4).

Helminths of Insectivores (Eulipotyphla)

The helminth fauna in insectivores of the reserve includes 35 species: 13 cestodes, 8 trematodes, 13 nematodes, and one acanthocephalan (Shaldybin 1964, Kostyunin 2010, Kirillov et al. 2012, Ruchin et al. 2016) (Table 5).

Most parasites (32 species) use insectivores as final hosts. Insectivores serve as paratenic hosts for two species (acanthocephalan *Centrorhynchus aluconis* and nematode *Porrocaecum depressum*). The nematode juveniles of *Hadjelia truncata* is an occasional parasite of insectivores. This nematode is a specific avian parasite that only transits the intestinal tract of shrews and does not reach maturity in these hosts. The trematode *Metorchis bilis* is an occasional and facultative parasite of insectivores.

Thirty-two species of helminths use insectivores as obligate hosts and are their specialist parasites. The cestode *Dilepis undula* is a generalist parasite in bird insectivores and less common in rodents. The nematodes *Calodium soricicola*, *Eucoleus oesophagicola*, *Liniscus incrassatus,* and *Physaloptera clausa* are specialist parasites in insectivores, found in a wide range of species. Sixteen species of helminths, namely the cestodes *Molluscotaenia crassiscolex*, *Neoskrjabinolepis schaldybini, Spasskylepis ovaluteri, Staphylocystis furcata, Staphylocystoides stefanskii, Vigisolepis spinulosa,* trematodes *Brachylaima fulvum, Pseudoleucochloridium soricis, Rubenstrema exasperatum, R. opisthovitellinus, Neoglyphe locellus, N. sobolevi,* nematodes *Soboliphyme soricis, Aonchotheca kutorii, Longistriata paradoxi* and *Pseudophysaloptera soricina*, are specific parasites in mammals of the family Soricidae, while the cestodes *Ditestolepis diaphana*, *Molluscotaenia crassiscolex*, *Pseudobothrialepis mathevossianae* and nematode *Paracrenosoma skrjabini* are specialist parasites in *Sorex* shrews. The cestode *Hymenolepis erinacei* and the nematode *Aonchotheca erinacei* are host-specific parasites of hedgehogs of the genus *Erinaceus*. The cestode *Staphylocystis brusatae* parasitizes only shrews of the genus *Crocidura*. The cestode *Neomylepis magnirostellata* and nematode *Longistriata neomi* are specific parasites in *Neomys* shrews. The trematode *Omphalometra desmanae* is a host-specific parasite of *Desmana moschata* and is a threatened species like its host.

We did not identify a single parasite species that would be found in all seven studied species of Eulipotyphla in the Mordovia Nature Reserve (Table 5). The trematode *Rubenstrema exasperatum*, revealed in four animal species, is most often found in the insectivores of the reserve. The host range of cestodes *Molluscotaenia crassiscolex*, *Neoskrjabinolepis schaldybini*, *Spasskylepis ovaluteri*, *Ditestolepis diaphana*, trematodes *Brachylaima fulvum*, *Pseudoleucochloridium soricis*, nematodes *Aonchotheca kutorii* and *Liniscus incrassatus* includes three species of insectivores. The cestodes *Insectivorolepis infirma*, *Pseudobothrialepis mathevossianae*, *Staphylocystis furcata*, *Vigisolepis spinulosa*, trematode *Neoglyphe sobolevi*, nematodes *Eucoleus oesophagicola*, *Longistriata paradoxi*, *L. neomi* and *Physaloptera clausa* use as hosts two insectivore species each. Another 17 helminth species were identified only in one host species (Table 5).

Among the studied species of insectivores, the largest number of helminths was found in *Sorex araneus* (23 species). The helminth fauna of *Neomys fodiens* and *Sorex minutus* is less diverse, with 16 species of parasites each. The helminth fauna in *Neomys anomalus* and *Erinaceus roumanicus* is poor (3 species each). *Desmana moschata* and *Crocidura suaveolens* have only one helminth species each (Table 5).

Most of the helminths (23 species) in insectivores belong to the Palearctic complex. Seven species are distributed in the Holarctic. For four species of parasites, distribution is limited to Europe. And only one species is cosmopolitan (Table 5).

Taxonomic remarks. The article by Shaldybin (1964) should be considered the first essential work on helminths in vertebrate animals from the Mordovia Nature Reserve. This work contains several problematic helminth species. Shaldybin (1964) described nematode *Capillaria reni*

Shaldybin, 1964, from the kidneys of *Neomys fodiens*. But since the time of the original description, no one else has found this helminth species. Therefore, we classify this nematode as a species inquirenda. The species *Aonchotheca petrovi*

Table 6: The list of helminths in bats (Chiroptera) from the Mordovia Nature Reserve.

Species	D	*Myotis daubentonii*	*Myotis dasycneme*	*Myotis brandtii*	*Myotis nattereri*	*Vespertilio murinus*	*Nyctalus noctula*	*Nyctalus leisleri*	*Pipistrellus nathusii*	*Pipistrellus pygmaeus*
Cestoda										
Vampirolepis balsaci	P			+						
Vampirolepis spasskii	P					+	+	+		
Trematoda										
Plagiorchis elegans	H	+					+			
Plagiorchis koreanus	C	+	+	+		+	+	+	+	
Plagiorchis muelleri	H						+			
Plagiorchis vespertilionis	P	+	+			+	+	+		
Lecithodendrium linstowi	P	+					+		+	
Lecithodendrium rysavyi	E					+	+	+	+	+
Lecithodendrium skrjabini	E					+	+	+	+	+
Paralecithodendrium skrjabini	E					+				
Prosthodendrium ascidia	P	+	+	+					+	
Prosthodendrium chilostomum	C	+	+	+		+	+	+		
Prosthodendrium hurkovaae	P	+	+							
Prosthodendrium ilei	E						+			
Prosthodendrium longiforme	C	+	+	+						
Parabascus duboisi	P	+	+	+						
Parabascus joannae	E								+	
Parabascus lepidotus	P	+	+			+	+	+	+	
Parabascus semisquamosus	E						+	+	+	+
Gyrabascus amphoraeformis	E	+	+							
Gyrabascus oppositus	E						+	+	+	
Pycnoporus heteroporus	P					+	+		+	+
Pycnoporus megacotyle	P							+		
Symmetricatesticula symmetrica	E	+	+	+		+				
Nematoda										
Aonchotheca eubursata	P						+			
Pterothominx neopulchra	P	+	+		+		+		+	
Molinostrongylus skrjabini	P		+			+	+		+	
Molinostrongylis spasskii	P	+								
Molinostrongylis vespertilionis	P							+	+	
Litomosa filaria	P					+				
Physaloptera clausa, juv.	H								+	
Physocephalus sexalatus, juv.	C		+				+			
Total		14	13	7	1	12	18	11	14	4

(Ruchljadeva 1946) (= *Capillaria petrovi* Ruchljadeva, 1946) is a synonym of *Aonchotheca kutorii* (Ruchlyadeva 1946). The finding by Shaldybin (1964) of the muskrat parasite *Eucoleus marii* (= *Thominx marii*) in the nasal cavity of shrews was erroneous. Most likely, the author dealt with the unusual localization of the common parasite of the shrew' esophagus the nematode *Eucoleus oesophagicola*. The species *Longistriata paradoxi* Schaldybin, 1964 described by Shaldybin (1964) from the shrew intestine is close to *Longistriata pseudodidas* Vaucher et Durette-Desset, 1973. In accordance with Genov (1984), they are identical species. At the same time, the finding by Shaldybin (1964) of *L. paradoxi* in *Neomys fodiens* is erroneous. The author dealt with a specific parasite of *Neomys* spp. *Longistriata neomi* Lubarskaja, 1962. The cestode species *Vampirolepis heleni* described by Shaldybin (1964) from *Neomys fodiens* is a synonym of *Neomylepis magnirostellata* (Baer, 1931). According to Genov (1984), *Ditestolepis secunda* Shaldybin, 1964 from shrews is a synonym for *Insectivorolepis infirma* Zarnovski, 1955.

Helminths of Bats (Chiroptera)

A total of 32 species of helminths were identified in bats of the protected area: 2 cestodes, 22 trematodes, and 8 nematodes (Shaldybin 1964, Kostyunin 2010, Kirillov et al. 2012, 2015b, Ruchin et al. 2016) (Table 6).

Of these, only two species of nematodes, *Physaloptera clausa,* and *Physocephalus sexalatus* were recorded in bats at larval stage. Bats are paratenic hosts for these parasites. Adult forms represent all other species of parasites. Most of the helminth species (29 species) recorded are bat specialists. Of these, the trematodes *Plagiorchis vespertilionis* and *Prosthodendrium chilostomum* can facultatively parasitize other species of mammals. Three helminth species, *Plagiorchis elegans*, *Physaloptera clausa*, juv. and *Physocephalus sexalatus*, juv. are generalist parasites, occurring in a wide range of vertebrate hosts from different classes.

No helminth species was found to parasitize the entire range of bat species in this protected area (Table 6). The species diversity of helminths is greater in *Nyctalus noctula*, in which 18 species of parasites are revealed in the nature reserve. The helminth communities of *Myotis daubentonii* (14), *Myotis dasycneme* (13), and *Pipistrellus nathusii* (14) are also representative. In *Vespertilio murinus* and *Nyctalus leisleri* were recorded 12 and 11 species of helminths, respectively. The fauna of the helminths of Brandt's bat (7) and the *Pipistrellus pygmaeus* (4) is less diverse. *Myotis nattereri* has only one species of helminth (Table 6).

Three species of parasites have a wide host range in the nature reserve, namely *Plagiorchis koreanus* which is found in 8 bat species: *Prosthodendrium chilostomum* and *Parabascus lepidotus* – each in six species of bats. Four helminth species, *Plagiorchis vespertilionis*, *Lecithodendrium skrjabini*, *Lecithodendrium rysavyi,* and *Pterothominx neopulchra* each have five bat species (Table 6).

The host ranges of trematodes *Symmetricatesticula symmetrica*, *Prosthodendrium ascidia*, *Pycnoporus heteroporus,* and the nematode *Molinostrongylus skrjabini* include four bat species each. The cestode *Vampirolepis spasskii* and the trematodes *Lecithodendrium linstowi*, *Prosthodendrium longiforme*, *Parabascus duboisi,* and *Gyrabascus oppositus* recorded in three bat species each are relatively rare in the bats of the nature reserve. The trematodes *Plagiorchis elegans*, *Prosthodendrium hurkovaae*, *Gyrabascus amphoraeformis*, nematodes *Molinostrongylis vespertilionis* and *Physocephalus sexalatus*, juv. revealed in two host species. The other 10 helminth species are recorded in one bat species each (Table 6). No helminths were found in the Mordovia Nature Reserve in one of 10 studied bat species, *Plecotus auritus*.

Half of the helminth species (16 species) found in the bats of the protected area are distributed in the Palearctic. The distribution ranges of nine parasite species are limited to Europe. Four helminth species have a cosmopolitan distribution. Three species of helminths belong to the Holarctic faunistic complex (Table 6).

Helminths of Rodents (Rodentia)

A total of 41 species of helminths were revealed in rodents from the protected area: 14 cestodes, 11 trematodes, and 16 nematodes (Shaldybin 1964, Ryzhikov et al. 1978, 1979, Kostyunin 2010, Kirillov et al. 2012, Ruchin et al. 2016) (Table 7).

Of these, 36 species parasitize rodents at the mature stage, and four cestode species are revealed at the larval stage. For them, rodents serve as the main intermediate hosts. All helminths found in rodents are their obligate parasites, with the exception of the trematode *Echinostoma revolutum*, which parasitizes micromammals facultatively.

The cestode *Dilepis undula* and the trematode *Plagiorchis elegans* are generalist parasites in a wide range of vertebrates from different classes, while the metacestodes *Taenia laticollis*, *Taenia martis*, *Versteria mustelae* и *Hydatigera taeniaeformis* s.l. the trematodes *Brachylaima recurva*, *Skrjabinoplagiorchis polonicus*, *Brachylecithum rodentini*, *Corrigia vitta*, nematodes *Mastophorus muris* and *Rictularia cristata* are rodent generalists. The nematodes *Aonchotheca murissylvatici*, *Carolinensis minutus* and *Heligmosomum*

Table 7: The list of helminths in rodents (Rodentia) and lagomorphs (Lagomorpha) from the Mordovia Nature Reserve.

Species	D	*Castor fiber*	*Arvicola amphibius*	*Microtus cf arvalis*	*Microtus agrestis*	*Microtus oeconomus*	*Clethrionomys glareolus*	*Apodemus flavicollis*	*Apodemus uralensis*	*Apodemus agrarius*	*Sicista betulina*	*Dryomys nitedula*	*Lepus europaeus*	*Lepus timidus*
Cestoda														
Mosgovoyia pectinata	H													+
Anoplocephaloides dentata	H			+	+	+	+							
Paranoplocephala omphalodes	P		+	+		+	+							
Eurotaenia gracilis	E						+							
Hymenolepis procera	H		+											
Rodentolepis asymmetrica	E				+									
Spasskijela lobata	P							+	+	+				
Catenotaenia henttoneni	E						+							
Catenotaenia sp.	E										+			
Dilepis undula	H									+				
Armadolepis dryomi	E											+		
Taenia laticollis, larva	C													
Taenia martis, larva	H						+		+					
Versteria mustelae, larva	H						+							
Hydatigera taeniaeformis s.l., larva	C							+	+					
Trematoda														
Brachylaima recurva	P					+	+							
Stichorchis subtriquetrus	H	+												
Psilotrema castoris	E	+												
Echinostoma revolutum	C		+											
Notocotylus noyeri	P		+				+							
Plagiorchis elegans	H						+		+					
Plagiorchis arvicolae	P		+											
Skrjabinoplagiorchis polonicus	E							+	+					
Dicrocoelium dendriticum	C													+
Brachylecithum rodentini	P						+							
Corrigia vitta	P								+					
Macyella apodemi	E								+					
Nematoda														
Aonchotheca murissylvatici	P						+		+					
Trichuris arvicolae	E			+	+	+	+							
Trichostrongylus colubriformis	C												+	
Trichostrongylus retortaeformis	C													+
Carolinensis minutus	P				+		+							
Heligmosomoides polygyrus	P							+	+	+				
Heligmosomoides glareoli	P						+							
Heligmosomoides laevis	P			+	+	+								

Table cont....

Species	D	*Castor fiber*	*Arvicola amphibius*	*Microtus cf arvalis*	*Microtus agrestis*	*Microtus oeconomus*	*Clethrionomys glareolus*	*Apodemus flavicollis*	*Apodemus uralensis*	*Apodemus agrarius*	*Sicista betulina*	*Dryomys nitedula*	*Lepus europaeus*	*Lepus timidus*
Heligmosomum mixtum	P						+							
Protostrongylus kamenskyi	P													+
Protostrongylus terminalis	E												+	+
Heterakis spumosa	[illegible]								+					
Syphacia agraria	E									+				
Syphacia obvelata	C							+	+					
Syphacia nigeriana	H			+		+								
Syphacia stroma	P							+	+					
Syphacia petrusewiczii	H						+							
Mastophorus muris	C						+	+	+					
Rictularia proni	P							+	+					
Rictularia cristata	E											+		
Total		2	5	5	6	5	17	8	14	4	1	2	2	5

mixtum are specialist parasites in rodents of the families Cricetidae and Muridae, and the cestodes *Anoplocephaloides dentata*, *Paranoplocephala omphalodes*, *Eurotaenia gracilis*, *Hymenolepis procera*, *Rodentolepis asymmetrica*, trematodes *Notocotylus noyeri*, *Plagiorchis arvicolae*, nematodes *Trichuris arvicolae* and *Heligmosomoides laevis* are specialist parasites in members of the subfamily Arvicolinae. The cestode *Spasskijela lobata*, trematode *Macyella apodemi*, nematodes *Heligmosomoides polygyrus* and *Rictularia proni* are specific parasites of mice from the family Muridae. The nematode *Syphacia agraria* parasitizes only *Apodemus agrarius*, while the nematodes *Syphacia obvelata* and *Syphacia stroma* parasitize only wood mice *Apodemus flavicollis* and *A. uralensis*. The trematodes *Stichorchis subtriquetrus* and *Psilotrema castoris* are host-specific parasites of beavers.

A number of rodent helminths have a high degree of specificity. Thus, the nematode *Syphacia nigeriana* is *Microtus* voles' specialist, the cestode *Catenotaenia henttoneni*, nematodes *Heligmosomoides glareoli* and *Syphacia petrusewiczii* are *Clethrionomys* voles' specialist and the cestode *Armadolepis dryomi* is a host-specific parasite of *Dryomis nitedula*.

We did not find a single helminth species that would parasitize all studied rodent species (Table 7). The cestode *Anoplocephaloides dentata* and the nematode *Trichuris arvicolae* have the widest host range among rodent parasites, found in four host species each. The cestode *Spasskijela lobata*, nematodes *Heligmosomoides polygyrus*, *Heligmosomoides laevis,* and *Mastophorus muris* each parasitize three rodent species. For 12 helminth species (the cestodes *Taenia martis*, larva, *Hydatigera taeniaeformis* s.l., larva, trematodes *Brachylaima recurva*, *Notocotylus noyeri*, *Plagiorchis elegans*, *Skrjabinoplagiorchis polonicus*, nematodes *Aonchotheca murissylvatici*, *Carolinensis minutus*, *Syphacia obvelata*, *S. nigeriana*, *S. stroma* and *Rictularia proni*) two species of rodents were recorded as hosts. Another 21 species of parasitic worms were revealed in a single host species (Table 7). No parasitic worms in the nature reserve were found in two of the 13 studied rodent species (*Rattus norvegicus* and *Micromys minutus*).

Among all the studied rodents, the largest trematode species were recorded in the bank vole *Clethrionomys glareolus* (17 species). *Apodemus uralensis* has 14 species of parasites. The helminth fauna of *Apodemus flavicollis* (8), *Microtus agrestis* (6), *M.* cf *arvalis* (5), *M. oeconomus* (5), *Arvicola amphibius* (5), and *Apodemus agrarius* (4) is less diverse. The parasite communities of *Castor fiber* (2), *Dryomis nitedula* (2), and *Sicista betulina* (1) are poor (Table 7).

Most of the helminth species (15) revealed in rodents have a Palearctic distribution. In Europe and the Holarctic, 11 and 9 species are distributed, respectively. Six species of parasitic worms are cosmopolitan (Table 7).

Taxonomic remarks. The nematode *Trichuris muris* was identified in *Microtus agrestis* by Schaldybin (1964)

erroneously, just like the findings of the cestode *Catenotaenia pusilla* in *Clethrionomys glareolus* and *Sicista betulina*. Recent studies of *Trichuris* spp. from European mice and voles have revealed that arvicoline rodents parasitize by

Table 8: The list of helminths in artiodactyls (Artiodactyla) from the Mordovia Nature Reserve.

Species	D	*Cervus nippon*	*Cervus elaphus*	*Bison bonasus*	*Alces alces*
Cestoda					
Moniezia autumnalis	P			+	
Moniezia benedeni	C			+	+
Taenia hydatigena, larva	C	+		+	
Trematoda					
Fasciola hepatica	C	+		+	
Parafasciolopsis fasciolaemorpha	P	+			+
Paramphistomum cervi	C	+	+	+	+
Dicrocoelium dendriticum	C	+		+	+
Nematoda					
Aonchotheca bilobata	C			+	
Aonchotheca bovis	C	+		+	
Trichuris ovis	C			+	+
Camelostrongylus lyratus	C			+	
Cooperia oncophora	H			+	
Cooperia pectinata	C	+			
Cooperia punctata	C			+	
Cooperia zurnabada	P			+	
Haemonchus contortus	C			+	
Marshallagia marshalli	C	+			
Ostertagia ostertagi	C		+	+	+
Spiculopteragia alicis	E				+
Spiculopteragia asymmetrica	C	+		+	
Spiculopteragia spiculoptera	C	+			
Spiculopteragia panticola	P	+			
Spiculopteragia schulzi	P	+			
Trichostrongylus axei	C	+			
Dictyocaulus viviparus	C			+	
Nematodirella longissimespiculata	H	+			+
Nematodirus helvetianus	C			+	
Chabertia ovina	C			+	
Oesophagostomum asperum	C	+			+
Oesophagostomum radiatum	C	+		+	
Oesophagostomum sikae	C	+			
Oesophagostomum venulosum	C			+	
Schulzinema miroljubovi	P	+			
Bunostomum phlebotomum	C			+	
Elaphostrongylus panticola	P	+	+		+
Setaria labiatopapillosa	C			+	+
Thelazia rhodesi	C			+	
Total		19	3	24	11

Trichuris arvicolae Feliu et al., 2000 (Feliu et al. 2000, Cutillas et al. 2002). Studies of the morphological and genetic variability of *Trichuris* spp. have revealed that *T. arvicolae* parasitizes in rodents of the subfamily Arvicolinae, and *T. muris* parasitizes in mice (Feliu et al. 2000, Cutillas et al. 2002). Therefore, the nematodes found by Shaldybin (1964) in *Microtus agrestis* we assigned to *T. arvicolae*.

Recent studies have shown that *Catenotaenia* spp. possess a high degree of specificity. *Catenotaenia pusilla* is a host-specific parasite of *Mus musculus* and does not parasitize other rodent species (Haukisalmi et al. 2010). Therefore, the cestode found by Shaldybin (1964) in *Sicista betulina* is considered *Catenotaenia* sp. 1. Here, molecular genetic studies are needed to identify cestode from *S. betulina*. And *Clethrionomys glareolus* is parasitized by *Catenotaenia hentonneni*, a specific parasite of *Clethrionomys* voles (Haukisalmi et al. 2010).

The metacestode *H. taeniaeformis* s. l. is a common parasite of various rodent species. According to recent concepts, the cestode *H. taeniaformis* is a complex of species. There are three differentiated clades A (*H. taeniaformis* s.str.), B (*Hydatigera kamiyai* Iwaki 2016) and C (*Hydatigera* sp.) based on the results of molecular-based studies (Lavikainen, et al. 2015, Lavikainen et al. 2016).

Helminths of Lagomorphs (Lagomorpha)

In two species of lagomorphs of the reserve' fauna, a total of six species of helminths were found: one cestode, one trematode, and four nematodes (Shaldybin 1964, Gvozdev et al. 1970, Kirillov et al. 2012, Ruchin et al. 2016) (Table 7). Mature forms represent all of them. The trematode *Dicrocoelium dendriticum* and the nematode Trichostrongylus colubriformis are generalist parasites in mammals from various orders. *Dicrocoelium dendriticum* parasitizes mainly ungulates. The cestode *Mosgovoyia pectinata*, nematodes *Trichostrongylus retortaeformis*, *Protostrongylus kamenskyi,* and *Protostrongylus terminalis* are host-specific parasites of hares.

In both studied hare species, the nematode *P. kamenskyi* was found (Table 7). Only *Lepus timidus* is the host for the cestode *Mosgovoyia pectinata*, the trematode *Dicrocoelium dendriticum*, the nematodes *Trichostrongylus retortaeformis* and *P. terminalis*. The nematode *Trichostrongylus colubriformis* is identified only in *Lepus europaeus*. Thus, five species of helminths are registered in *Lepus timidus*, and two species in *L. europaeus* (Table 7).

Three species of parasites found in the hares of the reserve are cosmopolitan. Three more species are distributed in the Holarctic, Palearctic, and Europe (Table 7).

Helminths of Artiodactyls (Artiodactyla)

The list of the helminth fauna in artiodactyls of the nature reserve includes 37 species: 3 cestodes, 4 trematodes and 30 nematodes (Matevosyan, 1964a, Shaldybin 1964, Shtarev 1967, 1971, Machinsky & Semov 1974, Nazarova 1974a, 1974b, Shtarev et al. 1978, Kirillov et al. 2012, Oliger 2016b, Ruchin et al. 2016) (Table 8).

All helminth species found in ungulates use artiodactyls as definitive hosts, with the exception of the cestode *Taenia hydatigena*. For this metacestode, ungulates serve as the main intermediate hosts. All species of helminths identified in ungulates of the protected area are their obligate parasites.

The trematodes *Fasciola hepatica*, *Dicrocoelium dendriticum*, nematodes *Haemonchus contortus*, *Trichostrongylus axei,* and *Setaria labiatopapillosa* are generalist parasites in mammals from various orders. The nematode *Thelazia rhodesi* is a generalist parasite occurring in various species of the orders Artiodactyla and Perissodactyla. The nematodes *Aonchotheca bilobata*, *Ostertagia ostertagi,* and *Oesophagostomum venulosum* are specialist parasites in mammals from order Artiodactyla. *Ostertagia ostertagi* can also be found in primates. The cestodes *Moniezia autumnalis*, *M. benedeni*, nematodes from genus *Cooperia*, *Marshallagia marshalli*, *Spiculopteragia schulzi*, *Trichuris ovis*, *Camelostrongylus lyratus*, *Nematodirus helvetianus*, *Dictyocaulus viviparous*, *Bunostomum phlebotomum* and *Chabertia ovina* are specialist parasites in ungulates of the suborder Ruminantia.

Seven species of helminths (the trematodes *Parafasciolopsis fasciolaemorpha*, *Paramphistomum cervi*, nematodes *Aonchotheca bovis*, *Nematodirella longissimespiculata, Spiculopteragia spiculoptera*, *Oesophagostomum asperum* and *O. radiatum*) specific parasites of members from the families Cervidae and Bovidae, while six nematode species (*Oesophagostomum sikae*, *Spiculopteragia alicis*, *S. asymmetrica*, *S. panticola*, *Elaphostrongylus panticola* and *Schulzinema miroljubovi*) are specialist parasites in cervids.

Among four species of artiodactyls studied in the protected area, the largest number of helminths was found in *Bison bonasus* (24 species). Nineteen species of parasites were revealed in *Cervus nippon*. Less diverse is the helminth fauna of *Alces alces*, in which 11 species of helminths were registered. Only three helminth species were recorded in *Cervus elaphus* (Table 8).

The trematode *Paramphistomum cervi* found in all studied species of ungulates is the most common among hoofed mammals in the Mordovia Nature Reserve (Table 8). The trematode *Dicrocoelium dendriticum*,

nematodes *Elaphostrongylus panticola,* and *Ostertagia ostertagi* were revealed in three species of ungulates. The host range of ten helminth species (cestode *Moniezia benedeni*, trematodes *Fasciola hepatica*, *Parafasciolopsis fasciolaemorpha*, nematodes *Aonchotheca bovis*, *Trichuris ovis*, *Spiculopteragia asymmetrica*, *Nematodirella longissimespiculata*, *Oesophagostomum asperum*, *O. radiatum* and *Setaria labiatopapillosa*) includes two species of hoofed mammals each. Another 23 species of parasites were registered in one species of ungulates (Table 8).

Most of the helminth species recorded in artiodactyls from the Mordovia Nature Reserve are widely distributed in the world. Thus, 27 helminth species of 37 identified are cosmopolitan. The range of seven parasite species covers the Palearctic. In the Holarctic and Europe, two and one species of helminths are common, respectively (Table 8).

Helminths of Carnivores (Carnivora)

A total of 19 species of helminths were identified in carnivore mammals of the protected area: 6 cestodes, 2 trematodes, 10 nematodes, and one acanthocephalan (Shaldybin 1957, 1964, Matevosyan, 1964b, Kirillov et al. 2012, Ruchin et al. 2016) (Table 9).

All helminths found in carnivores parasitize at the mature stage and are obligate parasites of carnivores. The cestodes *Taenia multiceps*, *T. polyacantha*, trematode *Alaria alata,* and nematode *Uncinaria stenocephala* are specialist parasites in carnivores from the family Canidae, while the cestodes *Taenia krabbei*, *T. serialis*, *T. hydatigena*, nematodes *Toxascaris leonina* host-specific parasites in canids and felids. The nematodes *Skrjabingylus nasicola* and *Molineus patens* are specialist parasites in mammals from the family Mustelidae, and the nematode *Spirocerca lupi* is a specific parasite in canids, less common in Mustelids. The cestode *Mesocestoides lineatus*, trematode *Pseudamphistomum truncatum,* and nematodes *Aonchotheca putorii*, *Eucoleus aerophilus*, *Pearsonema plica*, *Toxocara canis,* and *Crenosoma vulpis* are generalist parasites in a wide range of carnivores from different families.

Table 9: The list of helminths in carnivores (Carnivora) from the Mordovia Nature Reserve.

Species	D	*Vulpes vulpes*	*Canis lupus*	*Mustela nivalis*	*Nyctereutes procyonoides*
Cestoda					
Taenia hydatigena	C		+		
Taenia krabbei	H		+		
Taenia multiceps	C	+	+		
Taenia polyacantha	H		+		
Taenia serialis	C	+	+		
Mesocestoides lineatus	P		+		
Trematoda					
Pseudamphistomum truncatum	H	+			
Alaria alata	C	+	+		
Nematoda					
Aonchotheca putorii	H			+	
Eucoleus aerophilus	H		+		
Pearsonema plica	H	+	+		
Molineus patens	C				+
Uncinaria stenocephala	H	+	+		
Crenosoma vulpis	H	+	+		
Skrjabingylus nasicola	H			+	
Spirocerca lupi	C		+		
Toxascaris leonina	C		+		
Toxocara canis	C	+			
Acanthocephala					
Macracanthorhynchus catulinus	P	+			
Total		9	13	2	1

Among the carnivores of the Mordovia Nature Reserve, the most diverse helminth fauna is *Canis lupis*, listed by 13 species of parasitic worms (Table 9). The less diverse parasite fauna of *Vulpes vulpes* includes nine helminth species. *Mustela nivalis* and *Nyctereutes procyonoides* have only two and one species of helminths, respectively. For six species of helminths (the cestodes *Taenia multiceps*, *Taenia serialis*, trematode *Alaria alata*, nematodes *Pearsonema plica*, *Uncinaria stenocephala,* and *Crenosoma vulpis*), two species of carnivores were recorded as hosts each. Another 13 helminth species parasitized one carnivore species in the Mordovia Nature Reserve (Table 9).

Most of the helminth species identified in the carnivores of the nature reserve are widespread and have a cosmopolitan and Holarctic distribution, with eight and nine species, respectively. Two species of parasites belonging to the Palearctic faunistic complex (Table 9).

Taxonomic remarks. Shaldybin (1964) described nematode *Metathelazia petrovi* Schaldybin, 1950 from the bronchi of *Canis lupus*. Since the time of the original description, no one else has found this parasite, as in the case of the shrew parasite *Capillaria reni*. We classify *Metathelazia petrovi* and *Capillaria reni* as species inquirenda.

STRUCTURE OF HELMINTH FAUNA IN VERTEBRATE ANIMALS IN THE MORDOVIA NATURE RESERVE

The fauna of nematodes represented by adult and larval forms is the most diverse in the Mordovia Nature Reserve vertebrates. Nematodes account for 40.5% of the parasite fauna in all studied animal species. Ninety-three species of nematodes were recorded at the mature stage and three species (*Physocephalus sexalatus*, *Porrocaecum depressum,* and *Agamospirura minuta*) only at the larval stage. The nematodes *Hadjelia truncata* and *Physaloptera clausa* parasitize animals in the protected area at the mature and larval stages. *Physaloptera clausa*, found in reptiles, insectivores, and bats, has the widest host range (Tables 2, 5 and 6). *Physocephalus sexalatus,* juv. was identified in reptiles, birds, and bats (Tables 2, 3, and 5); *Hadjelia truncata* occurs in birds and insectivores (Tables 3, 4, and 5); *Oswaldocruzia filiformis* and *Oxysomatium brevicaudatum* are common to the amphibians and reptiles in the nature reserve (Tables 1 and 2). Another 93 helminth species are identified only within one taxonomic group of vertebrates.

Trematodes represent 36.0% of the total helminth species in vertebrates from the reserve's fauna. Both marites and larval forms represent trematodes. Seventy-six species of trematodes were revealed only in the adult stage. Five species (*Strigea falconis*, *S. sphaerula*, *S. strigis*, *Neodiplostomum spathoides*, and *Tylodelphys excavata*) were found only in the larval stage. Six species of trematodes (*Gorgoderina vitelliloba*, *Haplometra cylindracea*, *Opisthioglyphe ranae*, *Paralepoderma cloacicola*, *Alaria alata,* and *Astiotrema monticelli*) use vertebrates both as intermediate and definitive hosts. The trematodes *Plagiorchis elegans* (reptiles, birds, bats, and rodents) (Tables 2, 3, 4, 6, and 7) and *Alaria alata* (in amphibians, reptiles, and carnivores) have the widest range of hosts (Tables 1, 2 and 9).

Seven species of trematodes (*Paralepoderma cloacicola*, *Astiotrema monticelli*, *Opisthioglyphe ranae*, *Strigea falconis* mtc., *S. sphaerula* mtc., *S. strigis* mtc. and *Neodiplostomum spathoides*) parasitize both amphibians and reptiles (Tables 1 and 2). The trematode *Dicrocoelium dendriticum is* found in ungulates and hares (Tables 7 and 8). Another 77 trematode species parasitize within the same taxonomic group of vertebrates.

The cestodes account for 22.3% of the helminth fauna of the studied vertebrate species in the reserve, found in vertebrates as adult forms and larval stages. Forty-eight cestode species were identified at the mature stage, while five species (*Taenia laticollis*, *T. martis*, *Versteria mustelae,* and *Hydatigera taeniaeformis* s.l., *Spirometra erinaceieuropaei*) only as metacestodes. One species, *Taenia hydatigena*, was recorded in adult and larval stages in vertebrates.

Dilepis undula has the widest host range among the recorded cestode species and occurs in birds, insectivores, and rodents (Tables 3, 4, 5, and 7). *Taenia hydatigena* is a common species for carnivores and ungulates (Tables 8 and 9). Another 52 species parasitize within the same systematic group of vertebrates-hosts.

Only three species of acanthocephalans (1.2%) were recorded in the studied vertebrate species in the reserve. Two acanthocephalan species parasitize at the larval stage, and one occurs in adulthood. *Centrothynchus aluconis* is a common species for insectivores and reptiles (Tables 2 and 5). *Macracanthorhynchus catulinus* parasitizes only carnivores (Table 9), while *Sphaerirostris picae* is found only in reptiles (Table 2).

The helminth communities are represented in reptiles, insectivores, and carnivores. All taxonomic groups of parasites are recorded in reptiles: Trematoda-Nematoda-Cestoda-Acanthocephala (Fig. 2).

The predominance of trematodes is due to feeding mainly on anurans (snakes) and terrestrial invertebrates (lizards). The helminth fauna of insectivores is dominated equally by cestodes and nematodes: Cestoda-Nematoda-Trematoda-

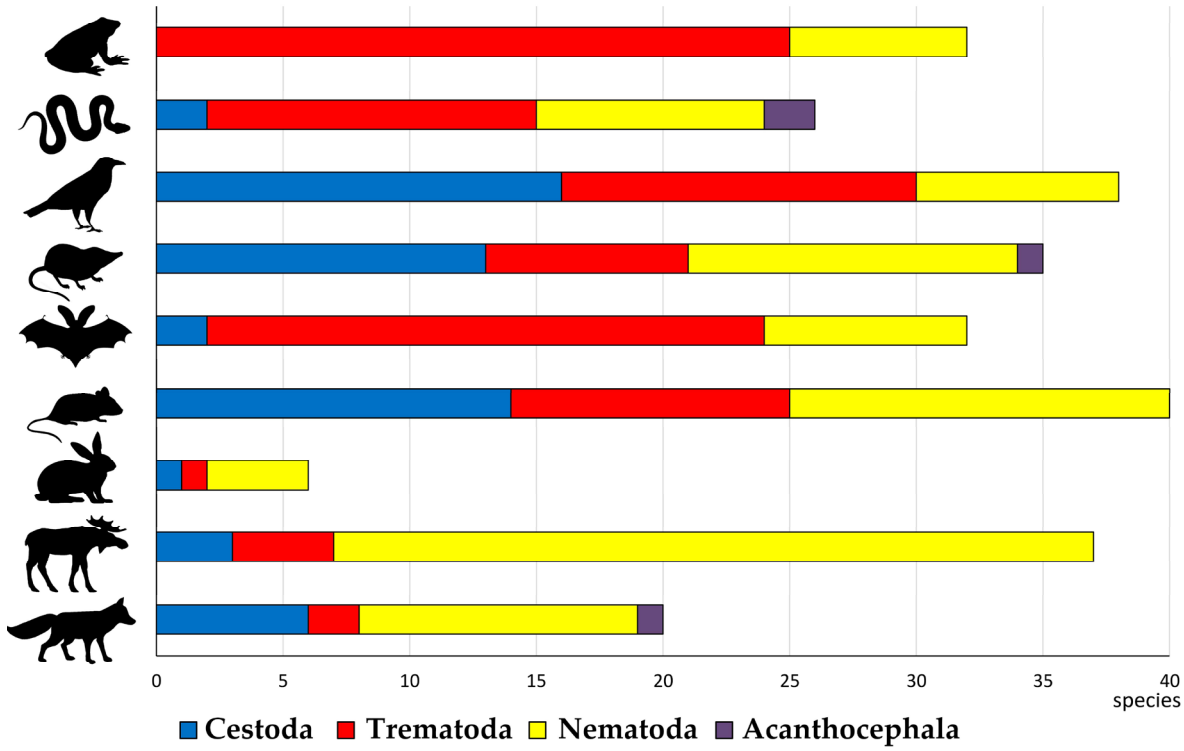

Fig. 2: The diversity of different taxonomic groups of helminths in vertebrates of the Mordovia Nature Reserve.

Acanthocephala. Feeding on terrestrial invertebrates and close contact of insectivores with soil litter play an important role here. The structure of the helminth fauna of carnivore animals is similar to insectivores: Nematoda-Cestoda-Trematoda-Acanthocephala, but with a predominance of nematodes, among which half of the species have an indirect life cycle. Birds, rodents, bats, hares, and artiodactyls do not have acanthocephalans in the helminth fauna. In the structure of the community of bird parasites, cestodes and trematodes prevail: Cestoda-Trematoda-Nematoda (Fig. 2), which is primarily due to feeding on terrestrial and semi-aquatic invertebrates.

In rodents, hares, and artiodactyls, the structure of the helminth fauna is similar in the dominance of nematodes (mainly with a direct life cycle) due to the nutrition of plant food, along with which animals obtain invasive eggs and larvae of nematodes. In rodents and hares, the helminth community structure looks like Nematoda-Cestoda-Trematoda, and in artiodactyls Nematoda-Trematoda-Cestoda. In bats, the predominance of trematodes in the helminth fauna (Trematoda-Nematoda-Cestoda) is due to feeding mainly on peri-aquatic insects. The structure of the helminth fauna of amphibians is represented only by nematodes and trematodes, with a predominance of the latter (Trematoda-Nematoda), which is also associated with feeding on aquatic and semi-aquatic insects and gastropods.

Thus, the helminth species composition in vertebrates is strongly influenced by the diet and lifestyle of animals. Vertebrates obtain most of the parasite species through food. Thus, 169 of 242 parasite species recorded in the nature reserve's vertebrates have an indirect life cycle. Infection of animals with them occurs through various food objects intermediate and paratenic hosts of helminths. If animals' dietary range is more varied, their helminth fauna is more varied, too. Thus, the largest number of helminth species with a complex life cycle was recorded in birds, 35 of 38 (92.1%). Fewer helminth species with indirect lifestyle were found in bats – 27 of 32 recorded (84.4%), in insectivores – 28 of 35 (80.0%), in amphibians – 25 of 32 (78.1%), in reptiles – 20 of 26 (76.9%), in carnivores – 14 of 19 (73.7%). %), in rodents – 28 of 41 (68.3%), and in hares – 4 of 6 (66.7%). The smallest number of helminth species with an indirect life cycle was found in ungulates (10 of 37, 27.0%), whose diet includes animal food only occasionally swallowed together with plant food.

Another 73 species of parasites found in the reserve's vertebrates have a direct life cycle. Infection with helminths occurs directly from the environment. In the infection of

different vertebrates with the soil-transmitted helminths, feeding on plant foods and the degree of contact of the animals with wet forest litter play a decisive role. The largest number of helminth species with a direct lifestyle is observed in animals whose diet includes mainly green parts of plants. Thus, 27 such species of 37 recorded (73.0%) were found in ungulates of the reserve, 2 of 6 (33.3%) in hares, and 13 of 41 (31.7%) in rodents. Fewer helminths with an indirect life cycle were recorded in amphibians of the reserve, 7 of 32 (21.9%), and in reptiles, 6 out of 26 (23.1%). And in carnivores, 5 out of 19 (26.3%). The least number of parasites with a complex lifestyle is in bats (5 of 32, 15.6%) and birds (3 of 38, 7.9%), animals with minimal contact with the soil litter.

Only 21 of 242 helminths found in vertebrates were revealed at the larval stage. A greater number of larval stages of helminths was recorded in reptiles (11 species) and amphibians (8), which are, in most cases, the paratenic hosts of parasites (Tables 1 and 2). Significantly fewer helminth larvae were observed in rodents (4), insectivores (3), and bats (2) (Tables 5, 6 and 7). One helminth species, the metacestode *Taenia hydatigena*, was found in ungulates, the second intermediate host of this parasite (Table 8). No larval helminth forms were found because the carnivore mammals complete the trophic chains.

The findings of helminth larvae in amphibians, reptiles, small mammals, and ungulates indicate an important role of these vertebrates in the circulation of parasites in animals at the highest trophic levels – birds of prey and carnivores. On the other hand, the findings of many larval forms in vertebrates indicate the biocenosis's integrity and the stability of parasitic systems in the study area. The involvement of paratenic hosts in the helminth life cycles plays an important role in the distribution and preservation of parasites in the wild. It increases the infection probability of the definitive hosts.

It should be noted that the nematode juveniles of *Hadjelia truncata* (in insectivores), *Physocephalus sexalatus* (in bats and birds), *Physaloptera clausa* (in bats and insectivores), *Agamospirura minuta* (in reptiles) are occasional parasites in these hosts. The probability of their transmission to the final hosts is extremely low. These vertebrate hosts represent a kind of "ecological dead end" for nematodes. While parasitisation of larvae of *Physocephalus sexalatus* and *Physaloptera clausa* in reptiles (parathenic hosts) provides an opportunity to complete their life cycle since reptiles are included in the diet of the final hosts of these nematodes (Bakiev 2007).

Comparison of the helminth fauna in vertebrates of different taxonomic groups according to the Jaccard index (*Cj*) showed a low degree of similarity in the composition of helminths (Table 10).

The helminth communities in amphibians and reptiles are the most similar (10 common species), which is primarily due to the use of trophic chains between these vertebrates by trematodes; to a lesser extent – by inhabiting the same habitats, which leads to infection of amphibians and reptiles by nematodes with a direct life cycle. In other cases, extremely low values of the Jaccard index are recorded, or there is no similarity of helminth fauna. In all pairs (where the Jaccard index is greater than 0), with the exception of Artyodactyla-Carnivora, the similarity in the parasite faunas in different taxonomic groups of vertebrates is associated with feeding (possibly occasional) on the same invertebrates, which are intermediate or paratenic hosts of parasites. It should be noted that these were single findings of common parasite species in vertebrates of various taxonomic groups. In the pair Artyodactyla-Carnivora, the trophic chain is used by the cestode *T. hydatigena*.

The similarity level between vertebrates of various taxonomic groups expected by us was not noted; for example,

Table 10: Similarity of helminth fauna in land vertebrates from the Mordovia Nature Reserve (*Cj*).

	Amphibia	Reptilia	Aves	Eulipotyphla	Chiroptera	Rodentia	Lagomorpha	Artyodactyla	Carnivora
Amphibia	1	0.21	0	0	0	0	0	0	0.02
Reptilia	0.21	1	0.06	0.03	0.06	0.02	0	0	0.02
Aves	0	0.06	1	0.03	0.03	0.03	0	0	0
Eulipotyphla	0	0.03	0.03	1	0.02	0.01	0	0	0
Chiroptera	0	0.06	0.03	0.02	1	0.01	0	0	0
Rodentia	0	0.02	0.03	0.01	0.01	1	0	0	0
Lagomorpha	0	0	0	0	0	0	1	0.02	0
Artyodactyla	0	0	0	0	0	0	0.02	1	0.02
Carnivora	0.02	0.02	0	0	0	0	0	0.02	1

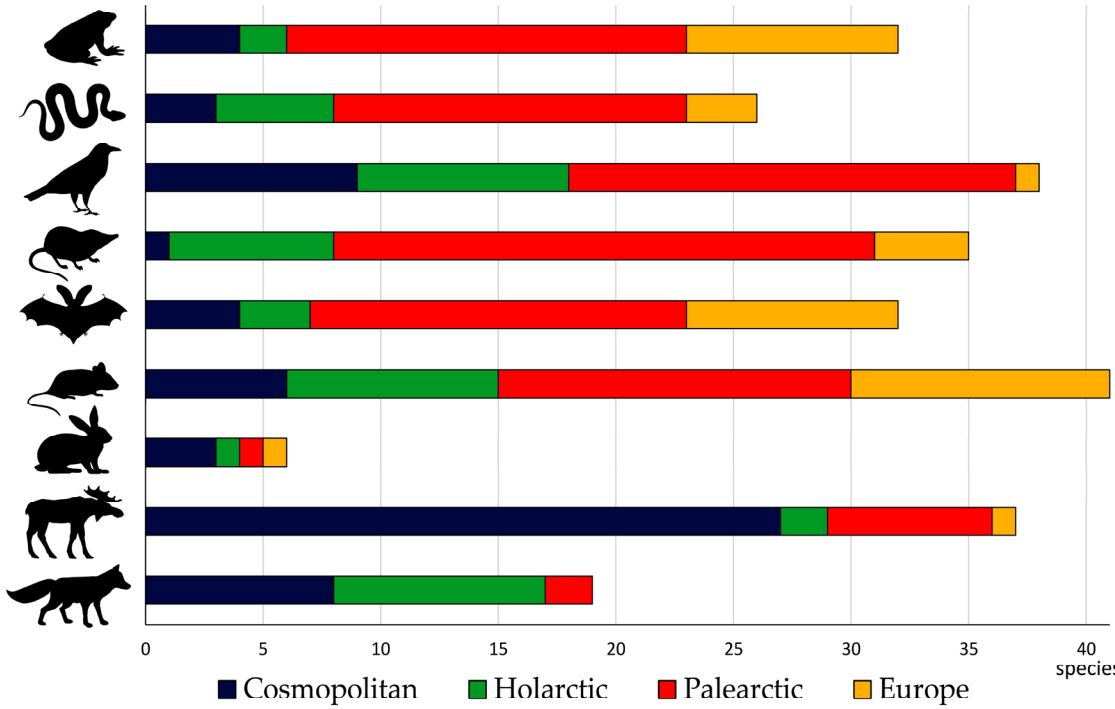

Fig. 3: The zoogeographical distribution of helminths found in vertebrate animals in the Mordovia Nature Reserve.

between rodents and carnivores, rodents and birds, ungulates, lagomorphs, and rodents. This is due to the insufficient knowledge of helminths in various taxonomic groups and species of vertebrates in the Mordovia Nature Reserve. In particular, the helminth fauna of ungulates, lagomorphs, and mustelids have been poorly studied, and the parasite study of birds of prey has not yet been carried out. This caused a low similarity of the helminth fauna of vertebrates from separate taxonomic groups.

The helminth fauna of land vertebrates in the Mordovia Nature Reserve is heterogeneous and is represented by parasites of different zoogeographic regions (Tables 1-9 and Fig. 3).

The broad distribution of parasites depends not so much on environmental conditions as on the distribution of their hosts, as in the case of ungulate helminths. The wider distribution range of those helminths that have adapted to habitation in several species or groups of hosts (intermediate or final) with different ranges, such as the trematodes *Fasciola hepatica*, *Dicrocoelium dendriticum*, *Alaria alata,* and nematode *Physocephalus sexalatus*. The bulk of the helminth fauna of the land vertebrates in the nature reserve are parasites belonging to the Palearctic complex (107 of 242 identified species). Most Palearctic species of helminths parasitize amphibians, reptiles, birds, insectivores, bats, and rodents (Fig. 3). The parasites of these taxonomic groups of vertebrates have a high degree of specificity for host species, genera, or subfamilies. Fifty-eight species of vertebrate helminths have a cosmopolitan distribution. About half of them are parasites of ungulates (Fig. 3). The number of helminths cosmopolitan is much less in other studied vertebrate groups. The Holarctic complex is represented by 39 species of helminths among the vertebrates of the Mordovia Nature Reserve. The parasite fauna of birds, rodents, and predators is more represented here (Fig. 3). The distribution of 37 helminth species, most found in amphibians, bats, and rodents, was limited to Europe and represented by species specialists.

CONCLUSION

Thus, 242 species of helminths were identified in the studied land vertebrates in the Mordovia Nature Reserve: 54 cestodes, 87 trematodes, 98 nematodes, and 3 acanthocephalans. Of these, 169 parasite species have an indirect life cycle, and 72 develop directly. Two hundred seventeen species of parasitic worms use vertebrates as definitive hosts and 21 as intermediate and/or parathenic hosts. Three more species of trematodes (*Gorgoderina vitelliloba*, *Haplometra cylindracea*, and *Opisthioglyphe ranae*) combine the larval and adult stages of the life cycle in amphibians and characterize them as amphixenic hosts. Seventy-three of 242 species found in the reserve's vertebrates are of

medical and veterinary importance as potential pathogens of zoonoses.

An analysis of the helminth fauna in vertebrates showed that it is the richest in rodents (41 species), birds (38), artiodactyls (37), and insectivores (35). Less diverse in amphibians (32), bats (32), reptiles (26), and carnivores (19). Very few species of parasites were found in the hares of the Nature Reserve – six species. Here, the degree of helminthological knowledge of individual vertebrate groups and species is of great importance. In addition, the diversity of various systematic vertebrate groups in the study area is important. Thus, the helminth fauna of 85 out of 299 species of land vertebrates inhabiting the Mordovia Nature Reserve were studied to some extent. The helminth fauna of bats, hares, amphibians, and reptiles were studied more fully and in detail. So, among bats, all 10 species of bats inhabiting the reserve and from lagomorphs, both species were studied. Also, 9 of 10 species of amphibians and 5 of 7 species of reptiles were subjected to parasitological research. To a lesser extent, rodents (13 out of 20), artiodactyls (4 out of 7), and predators (4 out of 13) have been studied. Of the vertebrate fauna of the reserve, birds are the most poorly studied. They harbored only 32 of 219 species of helminths found in vertebrates in the protected area.

Most of the helminth species (107) identified in the vertebrates from the Mordovia Nature Reserve belong to the Palearctic faunistic complex. Fifty-eight species of parasitic worms have a cosmopolitan distribution. The range of 39 species of parasites covers the Holarctic. The distribution of 37 species of helminths is limited to Europe.

Sixty-eight of 242 helminth species of recorded in vertebrates of the protected area are of epidemiological and epizootological significance, since they are potential pathogens of dangerous helminthiases in humans, wild and domestic animals: the trematodes *Fasciola hepatica*, *Paraphasciolopsis fasciolaemorpha*, *Paramphistomum cervi*, *Stichorchis subtriquetrus*, *Dicrocoelium dendriticum*, *Metorchis bilis*, *Pseudamphistomum truncatum*, *Alaria alata*, *Echinostoma revolutum*, *Prosthogonimus ovatus*, cestodes of genera *Taenia* and *Moniezia*, *Mosgovoyia pectinata*, *Versteria mustelae*, *Hydatigera taeniaeformis* s.l., *Mesocestoides lineatus*, acanthocephalan *Macracanthorhynchus catulinus*, nematodes of genera *Cooperia*, *Trichostrongylus*, *Spiculopteragia*, *Oesophagostomum*, *Protostrongylus*, *Ascaridia compar*, *Aonchotheca bilobata*, *A. bovis*, *A. putorii*, *Eucoleus aerophilus*, *Pearsonema plica*, *Trichuris ovis*, *Camelostrongylus lyratus*, *Haemonchus contortus*, *Marshallagia marshalli*, *Ostertagia ostertagi*, *Dictyocaulus viviparus*, *Molineus patens*, *Nematodirella longissimespiculata*, *Nematodirus helvetianus*, *Bunostomum phlebotomum*, *Chabertia ovina*, *Crenosoma vulpis*, *Uncinaria stenocephala*, *Elaphostrongylus panticola*, *Skrjabingylus nasicola*, *Physocephalus sexalatus*, *Spirocerca lupi*, *Setaria labiatopapillosa*, *Thelazia rhodesi*, *Toxascaris leonina*, *Toxocara canis* and *Syphacia obvelata*.

The data obtained help the implementation of prevention and the development of measures to combat natural focal helminthiases, in the maintenance of which wild vertebrates play an important role. When taking into account the epidemiological significance of parasites, it is necessary to know that the spread of a particular zoonosis is associated with the spread of its pathogens. These helminth diseases may not occur in this territory despite the presence of their pathogens.

The parasites found in the examined animals of the Mordovia Nature Reserve do not reflect overall helminth diversity in land vertebrates since a great number of animal species were not subjected to parasitological studies. In particular, there is still little data on helminths of birds and carnivore mammals and no information about fish parasites in the protected area. From the perspective of further research, on the one hand, the identification of the helminth fauna of unstudied species of vertebrates. On the other hand, the extension of research sites in the Mordovia Nature Reserve will greatly expand the list of helminth fauna in vertebrate animals.

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REFERENCES

Afonina, E.Yu. and Tashlykova, N.A. 2021. Torey Lakes, Daursky State Nature Biosphere Reserve, Russia: Long-term changes in environmental parameters. Nat. Conserv. Res., 6(2): 42-52. https://dx.doi.org/10.24189/ncr.2021.024

Artaev, O.N. and Grishutkin, O.G. 2014. Lakes of Mordovia. Mord. Res., 6: 20-23.

Artaev, O.N. and Smirnov, D.G. 2016. Bats (Chiroptera; Mammalia) of Mordovia: Specific structure and features of distribution. Nat. Conserv. Res., 1(1): 38-51. https://doi.org/10.24189/ncr.2016.004

Artaev, O.N., Ruchin, A.B., Bugaev, K.E., Grishutkin, G.F., Potapov, S.K. and Spiridonov, S.N. 2012. Vertebrates of the Mordovia State Nature Reserve. Flora and Fauna of Reserves, Vol. 120. Committee of RAS for the Conservation of Biological Diversity, pp. 64.

Bakiev, A.G. 2007. Snakes of the Volga River basin as nutrition objects for vertebrates. Cur. Stud. Herpetol., 7(1/2): 124-132.

Bhat, R.A., Tak, H., Bhat, B.A., Dar, J.A. and Ahmad, R. 2022. Gastrointestinal helminth parasites of wild ungulates in Hirpora Wildlife Sanctuary, Kashmir, India. J. Parasit. Dis., 46(3): 804–810. https://dx.doi.org/10.1007/s12639-022-01493-3

Bordes, F., Blasdell, K. and Morand, S. 2015. Transmission ecology of rodent-borne diseases: New frontiers. Integr. Zool., 10: 424-435. https://dx.doi.org/10.1111/1749-4877.12149

Bykhovskaya-Pavlovskaya, I.E. 1962. Trematodes of birds of the fauna of the USSR. Academy of Sciences of the USSR Publishers, Moscow, pp. 407.

Chikhlyaev, I.V. and Ruchin, A.B. 2014. The helminth fauna study of the European common brown frog (*Rana temporaria* Linnaeus, 1758) in the Volga basin. Acta Parasitol., 59(3): 459-471.

Chikhlyaev, I.V., Ruchin, A.B. and Lukiyanov, S.V. 2009. Helminthofauna of *Bufo bufo* (Amphibia: Anura) in Mordovia. Cur. Stud. Herpetol., 9(3/4): 153-158.

Chikhlyaev, I.V., Ruchin, A.B. and Fayzulin, A.I. 2015. Helminths of tailless amphibians (Amphibia, Anura) in the Mordovia State Nature Reserve. Proc. Mord. St. Nat. Res., 14: 376-388.

Chikhlyaev, I.V., Ruchin, A.B. and Kirillov, A.A. 2020. Ecological analysis of the helminth fauna of European common toad *Bufo bufo* (Amphibia: Anura) from various habitats. Nat. Conserv. Res., 5(2): 1-10. https://dx.doi.org/10.24189/ncr.2020.026

Cutillas, C., Oliveros, R., Rojas, M. and Guevarra, D.C. 2002. Determination of *Trichuris muris* from murid hosts and *T. arvicolae* (Nematoda) from arvicolid rodents by amplification and sequestration of the ITS1-5.8SITS2 segment of the ribosomal DNA. Parasitol. Res., 88: 574–582. https://doi.org/10.1007/s00436-002-0596-5

Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F. and Jetz, W. 2008. Homage to Linnaeus: How many parasites? How many hosts? Proc. Nat. Acad. Sci. USA, 105(1): 11482-11489. http://dx.doi.org/10.1073/pnas.0803232105

Feliu, C., Spakulova, M., Casanova, J.C., Renaud, F., Morand, S., Hugot, J.P., Santalla, F. and Durand, P. 2000. Genetic and morphological heterogeneity in small rodent whipworms in southwestern Europe: Characterization of *Trichuris muris* and description of *Trichuris arvicolae* n. sp. (Nematoda: Trichuridae). J. Parasitol., 86: 442-449. https://doi.org/10.1645/0022-3395(2000)086[0442:GAMHIS]2.0.CO;2

Froeschke, G. and Matthee, S. 2014. Landscape characteristics influence helminth infestations in a peri-domestic rodent - implications for possible zoonotic disease. Parasit. Vect., 7: 393. https://doi.org/10.1186/1756-3305-7-393

Gafferberg, I.G. 1960. Mordovia State Nature Reserve: A brief physical and geographical review of the nature in the Mordovia Reserve. Proc. Mord. St. Nat. Res., 1: 5-24.

Gafferberg, I.G. 2015. Climate of the Mordovia State Nature Reserve. 1938. Proc. Mord. St. Nat. Res., 13: 5-20.

Genov, T. 1984. Helminths of Insectivores and Rodents in Bulgaria. Bulg. Acad. Sci., 16: 348.

Georgopoulou, I. and Tsiouris, V. 2008. The potential role of migratory birds in the transmission of zoonoses. Vet. Ital., 44(4): 671-677.

Ghosh-Harihar, M., An, R., Athreya, R., Borthakur, U., Chanchani, P., Chetry, D., Datta, A., Harihar, A., Karanth, K.K., Mariyam, D., Mohan D., Onial M., Ramakrishnan U., Robin V.V., Saxena A., Shahabuddin Gh., Thatte P., Vijay V., Wacker K., Mathur V.B., Pimm S.L. and Price T.D. 2019. Protected areas and biodiversity conservation in India. Biol. Conserv., 237: 114-124. https://doi.org/10.1016/j.biocon.2019.06.024

Grishutkin, O.G. 2013. Patterns of the distribution of swamps depending on the absolute marks of the relief on the territory of the Mordovia State Nature Reserve. Proc. Mord. St. Nat. Res., 11: 259-263.

Gvozdev, E.V., Kontrimavichus V.L., Ryzhikov, K.M. and Shaldybin L.S. 1970. Keys to the helminths of lagomorphs of the USSR. Nauka, 11: 232.

Haukisalmi, V., Hardman, L.M. and Henttonen, H. 2010. Taxonomic review of cestodes oft the genus *Catenotaenia* Janicki, 1904 in Eurasia and molecular phylogeny of the Catenotaeniidae (Cyclophyllidea). Zootaxa, 2489: 1-33.

Herczeg, D., Vörös, J., Vegvari, Z., Kuzmin, Y. and Brooks, D.R. 2016. Helminth parasites of the *Pelophylax esculentus* complex (Anura: Ranidae) in Hortobágy National Park (Hungary). Comp. Parasitol., 83(1): 36–48. https://doi.org/10.1654/1525-2647-83.1.36

Horwitz, P. and Wilcox, B. 2005. Parasites, ecosystems and sustainability: An ecological and complex systems perspective. Int. J. Parasitol., 35: 725-732. https://doi.org/10.1016/J.IJPARA.2005.03.002

Ieshko, E.P., Lebedeva, D.I., Anikieva, L.V., Gorbach, V.V. and Ilmast, N.V. 2022. Helminth communities of *Coregonus lavaretus* (Salmonidae: Coregoninae) from Lake Kamennoye (Kostomuksha State Nature Reserve, Russia). Nat. Conserv. Res., 7(3): 75-87. https://dx.doi.org/10.24189/ncr.2022.032

Ivanov, A.Y., Ruchin, A.B., Fayzulin, A.I., Chikhlyaev, I.V., Litvinchuk, S.N., Kirillov, A.A., Svinin, A.O. and Ermakov, O.A. 2019. The first record of the natural transfer of mitochondrial DNA from *Pelophylax cf. bedriagae* into *P. lessonae* (Amphibia, Anura). Nat. Conserv. Res., 4(2): 125-128. https://dx.doi.org/10.24189/ncr.2019.020

Kaicheen, S.S. and Mohd-Azlan, J. 2022. Community structures of mid-sized to large-bodied mammals in tropical lowland and lower montane forests in Gunung Pueh National Park, Western Sarawak, Borneo. Nat. Conserv. Res., 7(1): 70-79. https://dx.doi.org/10.24189/ncr.2022.009

Kirillov, A.A., Kirillova, N.Y. and Chikhlyaev, I.V. 2012. Trematodes of land vertebrates of the Middle Volga region. Cassandra, 11: 329.

Kirillov, A.A., Ruchin, A.B., Fayzulin, A.I. and Chikhlyaev, I.V. 2015a. Helminths of reptiles in Mordovia: preliminary data. Proc. Mord. St. Nat. Res., 14: 243-255.

Kirillov, A.A., Ruchin, A.B. and Artaev, O.N. 2015b. Helminths of bats (Chiroptera) from Mordovia. Bull. Univ. Tatishch., 4: 319-328.

Kirillov, A.A., Kirillova, N.Y. and Spiridonov, S.N. 2023. Trematodes of land birds from the Republic of Mordovia with a checklist of avian trematodes of the Middle Volga region (European Russia). Diversity, 15: 330. https://doi.org/10.3390/d15030330

Kononova, M.I. and Prisniy, Yu.A. 2020. Helminthes of mouse-like rodents in the Belogorye State Nature Reserve (Russia). Nat. Conserv. Res., 5(2): 11-18. https://dx.doi.org/10.24189/ncr.2020.036

Kostyunin, V.M. 2010. Helminth fauna of land vertebrates in the Middle Volga region. Nizhny Novgorod State Pedagogical University, pp. 225.

Kouassi, R.Y.W., McGraw, S.W., Yao, P.K., Abou-Bacar, A., Brunet, J., Pesson, B., Bonfoh, B., N'goran, E.K. and Candolfi, E. 2015. Diversity and prevalence of gastrointestinal parasites in seven non-human primates of the Taï National Park, Côte d'Ivoire. Parasite, 22: 1. https://dx.doi.org/10.1051/parasite/2015001

Krucken, J., Blumke, J., Maaz, D., Demeler, J., Ramunke, S., Antolova, D., Schaper, R. and von Samson-Himmelstjerna, G. 2017. Small rodents as paratenic or intermediate hosts of carnivore parasites in Berlin, Germany. PLoS ONE, 12: e0172829. https://dx.doi.org/10.1371/journal.pone.0172829

Lavikainen, A., Iwaki, T., Nakao, M. and Konyaev, S.V. 2015. Genetic Diversity of the Cryptic *Hydatigera taeniaformis* complex. In: Yurlova, N.I, and Konyaev, S.V. (eds.) New knowledge about parasites. Parasitological research in Siberia and the Far East. Materials of the V Interregional conference, Garamond.

Lavikainen, A., Iwaki, T., Haukisalmi, V., Konyaev, S.V., Casiraghi, M.; Dokuchaev, N.E., Galimberti, A., Haljian, A., Henttonen, H., Ichikawa-Seki, M., Itagaki T., Krivopalov AV., Meri S., Morand S., Näreaho A.,

Olsson G.E., Ribas A., Terefe Y. and Nakao M. 2016. Reappraisal of *Hydatigera taeniaeformis* (Batsch, 1786) (Cestoda: Taeniidae) sensu lato with description of *Hydatigera kamiyai* n. sp. Int. J. Parasitol., 46(5-6): 361-374.

Lewin, J. 1990. Parasitic worms in a slowworm (*Anguis fragilis* L.) population from the Bieszczady Mountains (Poland). Acta Parasitol. Polon., 35(3): 207-215.

Machinsky, A.P. and Semov, V.N. 1974. On the fauna of helminths of the sika deer in the Mordovia State Nature Reserve. Proc. Mord. St. Nat. Res., 6: 169-173.

Martinez-Sotelo, J., Sanchez-Jasso, J.M., Ibarra-Zimbron, S. and Sanchez-Nava, P. 2022. Zoonotic intestinal parasites in free-ranging dogs (*Canis lupus familiaris*): A risk to public health in a Mexican protected area. Nat. Conserv. Res., 7(2): 21-31. https://dx.doi.org/10.24189/ncr.2022.015

Matevosyan, E.M. 1964a. Helminth fauna of bison in the Mordovia State Nature Reserve. Proc. Mord. St. Nat. Res., 2: 181-189.

Matevosyan, E.M. 1964b. To the knowledge of the helminth fauna in the common raccoon dog *Nyctereutes procyonoides* Gray. Proc. Mord. St. Nat. Res., 2: 233-235.

Nazarova, N.S. 1974a. Helminth fauna of the sika deer of the Mordovia State Nature Reserve and its change depending on the host age. Proc. Mord. St. Nat. Res., 6: 174-179.

Nazarova, N.S. 1974b. Helminths of complicated hybrids of bison of the Mordovia Nature Reserve. Proc. Mord. St. Nat. Res., 6: 180-185.

Oliger, I.M. 1952. Parasite fauna of the tetraonid birds from the forest area of the European part of the RSFSR. Proc. Helminthol. Lab. Acad. Sci., 6: 411-412.

Oliger, I.M. 1957. Fauna of the parasites of the family Tetraonidae in the forest zone of the European part of the RSFSR. Zool. Zhurn., 36(4): 493-503.

Oliger, I.M. 2016a. Parasite fauna of wild galliform birds in the Mordovia State Nature Reserve. Report of 1941. Proc. Mord. St. Nat. Res., 16: 34-42.

Oliger, I.M. 2016b. Parasite fauna of acclimatized ungulates in the Mordovia State Reserve. 1941. Proc. Mord. St. Nat. Res., 16: 43-52.

Orlova, M.V. and Orlov, O.L. 2019. Conservation of animals' parasite species: problems and prospects. Nat. Conserv. Res., 4(1): 1-21. http://dx.doi.org/10.24189/ncr.2019.011

Poulin, R. and Morand, S. 2004. Parasite Biodiversity. Smithsonian Institution Press, Washington DC., pp. 216.

Pringle, R. 2017. Upgrading protected areas to conserve wild biodiversity. Nature, 546: 91-99. https://doi.org/10.1038/nature2290

Recht, J., Schuenemann, V.J. and Sanchez-Villagra, M.R. 2020. Host diversity and origin of zoonoses: The ancient and the new. Animals, 10(9): 1672. https://doi.org/10.3390/ani10091672

Romashov, B.V., Odoevskaya, I.M., Romashova, N.B. and Golubova, N.A. 2021. Ecology of trichinellosis transmission in the Voronezh State Nature Reserve and adjacent areas, Russia. Nat. Conserv. Res., 6(2): 51-65. https://dx.doi.org/10.24189/ncr.2021.023

Ruchin, A.B. and Chikhlyaev, I.V. 2013. Helminth fauna of the moor frog *Rana arvalis* Nilsson (Amphibia: Anura) in the Republic of Mordovia. Rus. J. Parasitol., 3: 27-34.

Ruchin, A.B. and Kirillov, A.A. 2012. The helminth fauna of the grass snake *Natrix natrix* L. from Republic of Mordovia. Biol. Sci. Kazakh., 4: 30-37.

Ruchin, A.B., Kirillov, A.A., Chikhlyaev, I.V. and Kirillova, N.Y. 2016. Parasitic worms of land vertebrates of the Mordovia State Nature Reserve. Flora and Fauna of Reserves. Vol. 124. Committee of RAS for the Conservation of Biological Diversity, pp. 72.

Ryzhikov, K.M., Gvozdev, E.V., Tokobaev, M.M., Shaldybin, L.C., Matsaberidze, G.V., Merkusheva, I.V., Nadtochiy, E.V., Khokhlova, I.G. and Sharpilo, L.D. 1978. Keys to the helminths of rodents in the USSR fauna: Cestodes and Trematodes. Nauka, 7: 232.

Ryzhikov, K.M., Gvozdev, E.V., Tokobaev, M.M., Shaldybin, L.C., Matsaberidze, G.V., Merkusheva, I.V., Nadtochiy, E.V., Khokhlova, I.G. and Sharpilo, L.D. 1979. Keys to the helminths of rodents in the USSR fauna: Nematodes and Acanthocephalans. Nauka, 14: 272.

Ryzhov, M.K., Chikhlyaev, I.V. and Ruchin, A.B. 2004. About helminths of the marsh frog (*Pelophylax ridibundus*) in Mordovia. Act. Probl. Herpetol. Toxinol., 7: 119-121.

Shaldybin, L.S. 1957. Parasitological worms of wolves in the Mordovia ASSR. Proc. Gorky St. Ped. Inst., 19: 65-71.

Shaldybin, L.S. 1964. Helminth fauna of mammals in Mordovia State Nature Reserve. Proc. Mord. St. Nat. Res., 2: 135-180.

Sharpilo, V.P. 1976. Parasitic worms of the reptilian fauna of the USSR. Naukova Dumka, 11: 376.

Shtarev, Y.F. 1967. The results of the acclimatization of the sika deer in the Mordovia ASSR. Proc. Mord. St. Nat. Res., 3: 55-125.

Shtarev, Y.F. 1971. The results of the acclimatization of the red deer in the Mordovia ASSR. Proc. Mord. St. Nat. Res., 5: 137-170.

Shtarev, Y.F., Potapov, S.K., Astradamov, V.I. and Machinsky, A.P. 1978. Ecology and Helminth Fauna of the Sika Deer in the Conditions of the Mordovia State Nature Reserve. In: Antsiferova, T.A. (ed.) Ecological and Faunistic Research in the Non-Chernozem Zone of the European Part of the USSR. Vol. 1. Mordovia State University.

Turner, W.C. and Getz, W.M. 2010. Seasonal and demographic factors influencing gastrointestinal parasitism in ungulates of Etosha National Park. J. Wildl. Dis., 46(4): 1108-1119. https://dx.doi.org/10.7589/0090-3558-46.4.1108

Vasenkova, N.V. and Kuznetsova, N.A. 2022. A multiscale approach to evaluate the structure of diversity of Collembola in boreo-nemoral forests of the Russian Plain. Nat. Conserv. Res., 7(1): 38-51. https://dx.doi.org/10.24189/ncr.2022.019

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