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Diversity of Helminths of Insectivorous Mammals (Mammalia: Eulipothyphla) from Large Forest Protected Areas of the Middle Volga Region (European Russia)

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Abstract: Insectivores (Eulypotiphla) are a substantial component of Russian forest ecosystems. The parasites of these animals also form an important part of natural biocenoses and act as one of the factors in the formation of biodiversity. The Mordovia Nature Reserve and National Park "Smolny" are large, forested areas located in the center of European Russia. We studied the helminth fauna of insectivores in these protected areas in 2018–2022. In total, using the method of complete helminthological necropsy, we examined 478 individuals of shrews, moles, and hedgehogs and recorded 34 species of parasitic worms, i.e., 8 trematode, 7 cestode, 1 acanthocephalan, and 18 nematode species. The most diverse helminth fauna was found in *Sorex araneus* (22 species). The composition of helminths in *S. isodon* (12), *Neomys fodiens* (9), *Sorex minutus*, and *Erinaceus roumanicus* (8 species each) turned out to be less diverse. The lowest species diversity of helminths was observed in *Neomys milleri* (3) and *Talpae europaea* (2 species). Taking into account the newly obtained data, we conducted a review of the helminth diversity in shrews, hedgehogs, and moles in the Middle Volga region. According to our literature data, the helminth fauna of insectivores in this region consists of 52 species, including 14 cestodes, 13 trematodes, 22 nematodes, and 3 acanthocephalans. Most of them belong to the Palearctic faunal complex (36 species). The helminth fauna of insectivores in the studied protected areas was compared with the helminth fauna of micromammals in other areas of the Middle Volga region. Our comparative analysis showed a high and average degree of similarity in the helminth fauna within individual species and genera of Eulipotyphla.

Keywords: protected areas; parasitic worms; shrews; moles; hedgehogs; biodiversity; overview; Volga region

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1. Introduction

The species diversity of small mammals in biocenoses is usually low. In terms of the number of species, they constitute hundredths of the total biodiversity of ecosystems, but their importance in natural communities is extremely diverse. This is determined by their high level of vital processes as well as their great activity [1–5]. Mammals are the main components of food chains and participate in the cycling of a significant amount of substances in terrestrial ecosystems [1,6–9].

Small mammals, such as Eulipotyphla and Rodentia, play a key role in regulatory processes that ensure the sustainability of natural ecosystems [6,7,10–16]. Widespread insectivores are an important component of Russian forest ecosystems. The significant role of insectivores in biocenoses is associated mainly with the regulation of the abundance of invertebrates. Thus, shrews consume up to 60–70% of the biomass of soil invertebrates [11,12,17–19]. Due to their high mobility, insectivores make a significant

contribution to the cycle of matter and energy in forest ecosystems [20]. Shrews, in particular, can carry micromycete spores on their fur, thereby promoting the decomposition of litter [21,22]. In addition, insectivorous mammals are the definitive and/or paratenic hosts of parasitic worms and participate in the circulation of the helminths of other vertebrates [23–25].

Helminths are one of the factors in the formation of global biodiversity [26–28]. In this regard, data on helminth communities are necessary to assess changes in the structure of the biocenosis, the functioning of food chains, and biodiversity [29–31].

The helminth fauna of insectivores has been studied in different parts of Europe. Thus, the most detailed studies were carried out in Germany, where 69 species of helminths were identified in 7 species of insectivores [32–37]. In addition, in Poland and Belarus, 64 helminth species were each found in 7 host species [36,38–51]. In Bulgaria, 62 species of helminths have been recorded in 8 species of insectivorous mammals [52,53], and in the territory of the former Czechoslovakia, 67 species of helminths have been recorded in 8 host species [36,54–59]. Regular helminthological studies of Eulipotyphla were also carried out in Spain [60–67], France [34,68–71], Switzerland [34,72–75], Hungary [76,77], Lithuania [78–80], Finland [81–84], Ukraine [85–88], and Moldova [89–93]. Data on the helminth communities in Eulipotyphla hosts were also obtained from the UK [94–98], Ireland [99], Belgium [100], Denmark [101], Portugal [102,103], Italy [104–106], Austria [107,108], Greece [109], Serbia [110], and Romania [111]. As a rule, studies were devoted either to individual taxonomic groups of helminths or to individual species or genera of hosts. Thus, the helminth fauna of hedgehogs [25,36,101] and moles [112] in Europe has been studied quite fully. Among shrews, the most common species, *Sorex araneus*, is the most studied [113]. In recent decades, reviews of the helminth fauna of individual species or genera of insectivores, as well as molecular genetic studies of cestodes from shrews, have appeared [25,36,101,112–119].

Despite the wide distribution of insectivorous mammals and the long history of studying their helminth fauna, in European Russia, there are still areas where the helminths of insectivores are almost unstudied. Systematic and long-term studies were carried out only on the territory of the Komi Republic [120,121], Karelia [122–127], and the Samara region [128–132]. Several studies of the helminths of various insectivorous mammals have been conducted on the territory of Tatarstan [133,134], Chuvashia [133], Mari El [133], Astrakhan [135,136], Vologda [137], Voronezh [138,139], Kursk [140,141], Leningrad [142], Nizhny Novgorod [143–145], and Tver [146] regions.

The article by Shaldybin [147] is the first and only study of the helminths of vertebrates in the Mordovia Nature Reserve. The author found 23 species of parasitic worms in four species of insectivores. This information was subsequently incorporated into review studies of the helminths of vertebrates in this protected area [148,149]. Such studies have not been carried out on the territory of the National Park "Smolny".

Here we present a study of the species diversity of parasitic worms in insectivorous mammals from the protected areas of Mordovia, with an overview of the helminth fauna of shrews, moles, and hedgehogs inhabiting the Middle Volga region (European Russia).

2. Materials and Methods

2.1. Study Area Description

The helminth fauna of insectivorous mammals was studied on the territory of the Federal State Budgetary Institution "Reserved Mordovia" ("Zapovednaya Mordovia"), which includes the Mordovia Nature Reserve and the National Park "Smolny". Both protected areas are located on the territory of the Republic of Mordovia and represent large forest areas.

The territory of the Mordovia Nature Reserve is located in the northwestern part of the Republic of Mordovia and occupies an area approximately within the range of 54°42′–54°56′ north latitude and 43°04′–43°36′ east longitude. The territory of the Mordovia Nature Reserve represents natural ecosystems of southern woodlands (southern taiga), located on

the border of mixed and broad-leaved forests and forest steppe and occupying the right bank of the Moksha River [150]. From the north and east, the territory of the reserve is limited by the Satis River (a tributary of the Moksha River) and the Arga River, which flows into the Satis. From the south, the forest steppe directly approaches the border of the reserve. The territory of the reserve is rich in small rivers, streams, and lakes, such as Pushta, Arga, Bolshaya Chernaya, Malaya Chernaya, Picherki, and Inorskoye. During dry years, rivers and streams in the reserve may dry up. The hydrological regime of small rivers often largely depends on beaver dams, which contribute to the flooding of large areas [151,152]. The fauna of the Mordovia Nature Reserve consists of 299 species, including 10 species of insectivores, i.e., northern white-breasted hedgehog *Erinaceus roumanicus* Barrett-Hamilton, 1900; European hedgehog *Erinaceus europaeus* Linnaeus, 1758; lesser white-toothed shrew *Crocidura suaveolens* (Pallas, 1811); common shrew *Sorex araneus* Linnaeus, 1758; Eurasian pygmy shrew *Sorex minutus* Linnaeus, 1766; masked shrew *Sorex caecutiens* Laxmann, 1788; taiga shrew *Sorex isodon* Turov, 1924; Eurasian water shrew *Neomys fodiens* Pennant, 1771; Mediterranean water shrew *Neomys milleri* Mottaz, 1907; and European mole *Talpa europaea* Linnaeus, 1758 [150,153].

The National Park "Smolny" is located in the northeastern part of the Republic of Mordovia and occupies an area approximately within the range of 54°43′–54°53′ north latitude and 45°04′–45°37′ east longitude. The National Park is located on the border of mixed and broad-leaved forests and forest steppe [154]. The protected area is characterized by a fairly dissected relief with an extensive network of ravines in the northeastern part. The rivers of the park belong to the Sura River basin and include the small rivers Kalysha and Yazovka, as well as many streams. The lakes are concentrated mainly in the floodplain of the Alatyr River in the south of the National Park "Smolny" [152]. The diversity of natural conditions determines the richness of the flora and fauna of the National Park "Smolny". The fauna of this protected area consists of 282 species of animals, including 9 species of Eulipothyphla, i.e., *E. roumanicus*, *E. europaeus*, *C. suaveolens*, *S. araneus*, *S. minutus*, *S. caecutiens*, *S. isodon*, *N. fodiens*, and *T. europaea* [154–157].

2.2. Parasite Collection and Examination

Parasitic worms in insectivores were studied during the 2018–2022 field seasons. The material for parasitological research was obtained as a result of work on counting the number of small mammals. They are counted regularly according to research topics of the Mordovia Nature Reserve and the National Park "Smolny", approved by the Ministry of Natural Resources and Ecology of Russia. In total, 478 mammals of eight species were examined on the territory of the Mordovia Nature Reserve and the National Park "Smolny" (Table 1). Sampling sites for shrews, moles, and hedgehogs are presented in Table S1.

Table 1. List of insectivorous mammals examined in protected areas of Mordovia.

Species	Mordovia Nature Reserve	National Park "Smolny"
Sorex araneus	118	247
Sorex minutus	64	12
Sorex isodon	12	–
Neomys fodiens	3	3
Neomys milleri	1	–
Crocidura suaveolens	3	–
Talpa europaea	1	6
Erinaceus roumanicus	3	5
Total	205	273

Data on the helminth fauna of shrews were additionally obtained when studying the abundance of myomorph rodents in protected areas of Mordovia. Shrews were captured using spring metal snap traps (120 × 55 mm). Trap lines with 20 snap traps, at 10 m intervals, were installed along the banks of small rivers and streams, forest edges, fields,

and meadows. Pieces of rye bread fried in sunflower seed oil were placed in the snap traps. Capturing was carried out for 5 days in each locality. Some of the shrew specimens were obtained during the study of insects using pitfall traps and were kindly provided by entomologists of the Mordovia Nature Reserve. We also examined roadkill specimens of *E. roumanicus* and moles that died naturally and were provided by local residents.

The animals were examined using a complete helminthological necropsy, according to Ivashkin et al. [158] and Anikanova et al. [125]. Parasitic worms were recovered and fixed in 70% ethanol. Flukes and flatworms were stained with aceto-carmine, cleared with clove oil, and then mounted in Canada balsam. Nematodes were cleared with lactic acid and mounted in glycerin jelly [125,158,159]. Identification of parasites was carried out at the Laboratory for Zoology and Parasitology of the Institute of Ecology of the Volga Basin of the Russian Academy of Sciences (Togliatti).

2.3. Data Analysis

To characterize helminth infection in insectivorous mammals, the following indices were used: infection prevalence (P, %) and mean abundance (MA). The dominance of species in the helminth fauna was determined using the Palia–Kovnatsky index (D) [160]. Parasite dominance groups were considered as follows: 10–100—dominants, 1–10—subdominants, 0.001–1.000—adominants.

The similarity of helminth compositions was evaluated using Morisita's overlap index (C_m). The degree of similarity is as follows: 0–0.33—low; 0.34–0.66—medium; 0.67—1—high. Statistical data processing was performed using the PAST 2.16 [161] and Microsoft Excel 2003 software packages.

3. Results

3.1. Parasitic Worms of Insectivorous Mammals in the Protected Areas of Mordovia (European Russia)

In total, 34 species of helminths were found in shrews, hedgehogs, and moles from two protected areas of Mordovia, including 8 digenean, 7 cestode, 1 acanthocephalan, and 18 nematode species. On the territory of the Mordovia Nature Reserve (MNR), 28 species of helminths were recorded in insectivorous mammals, and 31 species of parasites were found on the territory of the National Park "Smolny" (NP "Smolny") (Table 2).

Table 2. Parasite–host checklist of helminths from insectivorous mammals in the protected areas of Mordovia.

Species	Host	Site	MNR		NP "Smolny"	
			P, %	MA	P, %	MA
Family Dilepididae *Dilepis undula* (Schrank, l788), larvae	*Sorex araneus*	small intestine	1.7	0.1	4.5	0.4
Family Hymenolepididae *Hymenolepis erinacei* (Gmelin, 1789) (=*Rodentolepis erinacei* (Gmelin, 1789), *Rodentolepis steudeneri* (Janicki, 1904))	*Erinaceus roumanicus*	small intestine	66.7 (in 2 of 3 examined)	36.3	80.0 (in 4 of 5 examined)	8.0
Ditestolepis diaphana (Cholodkowsky, 1906)	*Sorex araneus* *Sorex isodon* *Sorex minutus*	small intestine	28.8 41.7 50.8	2.1 1.7 1.3	21.1 – 41.7	1.1 1.6
Monocercus arionis Siebold, 1850 (=*Molluscotaenia crassiscolex* (von Linstow, 1890))	*Sorex araneus* *Sorex isodon* *Sorex minutus*	small intestine	78.0 58.3 34.9	3.4 2.5 0.8	74.5 – 75.0	5.8 3.5
Neoskrjabinolepis schaldybini Spasskii, 1947	*Sorex araneus* *Sorex isodon*	small intestine	28.8 8.3	1.0 0.3	25.1 –	1.8
Staphylocystis brusatae (Vaucher, 1971)	*Crocidura suaveolens*	small intestine	66.7 (in 2 of 3 examined)	4.0	–	
Vigisolepis spinulosa (Cholodkowsky, 1906)	*Sorex araneus*	small intestine	–		5.7	0.2
Family Brachylaimidae *Brachylaima fulvum* Dujardin, 1843 (=*Brachylaemus oesophagei* Shaldybin, 1953)	*Sorex araneus* *Sorex isodon*	small intestine	4.2 16.7	0.9 0.3	3.2 –	0.1

Table 2. *Cont.*

Species	Host	Site	MNR		NP "Smolny"	
			P, %	MA	P, %	MA
Family Panopistidae *Pseudoleucochloridium soricis* (Soltys, 1952) (=*Leucochloridium skrjabini* (Shaldybin, 1953))	*Sorex araneus*	stomach, small intestine	6.8	0.2	5.0	0.2
	Sorex isodon		8.3	0.1	–	
	Sorex minutus		1.6	0.02	–	
	Neomys fodiens		100 (in 3 examined)	3.7	66.7 (in 2 of 3 examined)	1.7
Family Strigeidae *Strigea strigis* (Schrank, 1788), mtc.	*Erinaceus roumanicus*	fat tissue between esophagus and trachea	–		40.0 (in 2 of 5 examined)	1.2
	Talpa europaea		–		1.6	0.03
Family Echinostomatidae *Isthmiophora melis* (Schrank, 1788) (=*Euparyphium melis* (Schrank, 1788))	*Erinaceus roumanicus*	small intestine	–		40.0 (in 2 of 5 examined)	1.4
Family Omphalometridae *Neoglyphe locellus* (Kossack, 1910) (=*Opistioglyphe oschmarini* Shaldybin, 1953)	*Neomys fodiens*	small intestine	33.3 (in 1 of 3 examined)	1.0	66.7 (in 2 of 3 examined)	0.7
Neoglyphe sobolevi Schaldybin, 1953	*Sorex araneus*	small intestine	5.9	0.8	1.6	0.5
Rubenstrema exasperatum (Rudolphi, 1819)	*Sorex araneus*	stomach	21.2	0.9	7.0	0.2
	Sorex isodon		16.7	0.9	–	
	Sorex minutus		34.9	1.4	58.3	1.2
	Neomys fodiens		66.7 (in 2 of 3 examined)	1.0	–	
	Neomys milleri		in one examined	1.0	–	
Rubenstrema opisthovitellinus (Soltys, 1954).	*Sorex araneus*	small intestine	–		1.2	0.03
	Neomys fodiens		33.3 (in 1 of 3 examined)	1.0	–	
Family Centrorhynchidae *Centrorhynchus aluconis* (Müller, 1780), larvae	*Sorex araneus*	liver	0.8	0.02	1.2%	0.02
	Sorex isodon		8.3	0.2	–	
Family Capillariidae *Aonchotheca erinacei* (Rudolphi, 1819) (=*Capillaria erinacei* (Rudolphi, 1819))	*Erinaceus roumanicus*	small intestine	100 (in 3 examined)	7.7	100 (in 5 examined)	24.8
Aonchotheca exigua (Dujardin, 1845)	*Sorex minutus*	stomach	6.4	0.2	–	
	Neomys fodiens		–		100 (in 3 examined)	1.7
Aonchotheca kutorii (Ruchljadeva, 1964)	*Sorex araneus*	stomach	2.5	0.1	9.3	0.4
	Neomys fodiens		–		100 (in 3 examined)	2.3
Calodium soricicola (Yokogava et Nishigori, 1924) (=*Hepaticola soricicola* (Yokogava et Nishigori, 1924))	*Sorex araneus*	Liver parenchyma	5.1	2.3	2.8	0.1
	Sorex isodon		8.3	0.8	–	
Eucoleus oesophagicola (Soltys, 1952) (=*Thominx blarinae* (Ogran, 1953))	*Sorex araneus*	mucous membrane of esophagus	3.4	0.2	17.4	0.5
	Sorex isodon		8.3	1.2	–	
Liniscus incrassatus Diesing, 1851 (=*Capillaria incrassata* (Diesing, 1851))	*Sorex araneus*	bladder	12.7	0.8	15.0	0.9
	Sorex isodon		50.0	3.9	–	
	Neomys fodiens		33.3 (in 1 of 3 examined)	0.7	–	
	Neomys milleri		in one examined	1.0	–	
Family Soboliphymidae *Soboliphyme soricis* Baylis et King, 1932	*Sorex araneus*	stomach	0.8	0.01	5.3	0.1
Family Metastrongylidae *Crenosoma striatum* Zeder, 1800	*Erinaceus roumanicus*	bronchi	–		40.0 (in 2 of 5 examined)	6.0
Paracrenosoma skrjabini (Pologentsev, 1935)	*Sorex minutus*	bronchi	1.6	0.03	–	
Family Heligmosomidae *Longistriata paradoxi* Schaldybin, 1964	*Sorex araneus*	small intestine	70.3	4.0	71.7	10.8
	Sorex isodon		75.0	7.7	–	
	Sorex minutus		55.6	1.9	75.0	3.2
Longistriata neomi Lubarskaja, 1962	*Neomys fodiens*	small intestine	100 (in 3 examined)	10.3	–	
	Neomys milleri		in one examined	3.0	–	
Tricholinstowia linstowi Travassos, 1918 (=*Longistriata vigisi* Petrov et Savinov, 1959)	*Talpa europaea*	small intestine	in one examined	20.0	50.0 (in 3 of 6 examined)	15.8
Family Anisakidae *Porrocaecum depressum* (Zeder, 1800), juveniles	*Sorex araneus*	mesentery, serous integument of gastrointestinal tract	11.0	0.3	11.7	0.5
	Sorex isodon		8.3	0,2	–	
	Talpa europaea		in one examined	11.0	83.3 (in 5 of 6 examined)	15.7
Family Habronematidae *Hadjelia truncata* (Creplin, 1825), juveniles	*Sorex araneus*	small intestine	1.7	0.02	1.2	0.1

Table 2. *Cont.*

Species	Host	Site	MNR		NP "Smolny"	
			P, %	MA	P, %	MA
Family Physalopteridae *Physaloptera clausa* Rudolphi, 1819	*Erinaceus roumanicus*	stomach (adults)	66.7 (in 2 of 3 examined)	7.0	100 (in 5 examined)	9.4
	Sorex araneus	gastric mucosa (juveniles)	5.1	0.1	1.2	0.01
Pseudophysaloptera soricina Baylis, 1934 (=*Physaloptera soricina* (Baylis, 1934))	*Sorex araneus*	stomach	–		2.0	0.1
	Sorex minutus		3.2	0.1	–	
	Neomys fodiens		–		33.3 (in 1 of 3 examined)	0.3
Family Spirocercidae *Physocephalus sexalatus* (Molin, 1860), juveniles	*Erinaceus roumanicus*	walls of stomach and small intestine	–		80.0 (in 4 of 5 examined)	61.8
Species insertae sedis *Agamospirura minuta* (Sharpilo, 1963), juveniles	*Erinaceus roumanicus*	walls of stomach and small intestine	–		40.0 (in 2 of 5 examined)	1.0

Most of the parasites found in insectivores were represented by adult forms (26 species). The larval stages of seven helminth species were also identified. Nematodes of the species *Physaloptera clausa* were represented by both adult and larval stages.

The studied insectivorous mammals are obligatory hosts of the majority of identified helminths (28 species). The same mammalian species serve as paratenic hosts for four helminth species (*S. strigis*, *Ph. sexalatus*, *A. minuta*, and *C. aluconis*) and abortive hosts for two species (*H. truncata* and *D. undula*). For the last two species, insectivores represent a so-called parasitic impasse.

The helminth fauna of *S. araneus* in the "Reserved Mordovia" includes 22 species of parasites. Of these, 11 helminth species (*D. diaphana*, *M. arionis*, *N. schaldybini*, *V. spinulosa*, *P. soricis*, *Neoglyphe sobolevi*, *R. exasperatum*, *R. opisthovitellinus*, *A. kutorii*, *S. soricis*, and *L. paradoxi*) are host-specific parasites of shrews of the family Soricidae. The cestode *D. diaphana* is a host-specific parasite of *Sorex* spp., and the five helminths (*B. fulvum*, *C. soricicola*, *L. incrassatus*, *E. oesophagicola*, and *P. soricina*) are generalist species that parasitize a variety of soricomorphs. The larvae of *P. depressum* are a common parasite of shrews, moles, and hedgehogs. The larvae of *D. undula*, *S. strigis*, *Ph. clausa*, *H. truncata*, and *C. aluconis* are occasional parasites of the common shrew. The total infection rate of *S. araneus* with helminths was 100%, MA = 21.3.

The helminth fauna of *S. araneus* is dominated by nematodes, represented by both adult (7 species) and larval forms (3 species). The infection rate of shrews with nematodes reaches 76.7%, 11.5. The trematode fauna of *S. araneus* includes six species; the total infection with digeneans was 17.5%, 1.3. Among them, five species of trematodes are represented by adult worms, and only one species (*S. strigis*) occurs at the larval stage. A total of five species of cestodes were identified in *S. araneus*, of which four are represented by the mature stage and one species (*D. undula*) is represented exclusively by juvenile individuals. The total infection with cestodes was 97.0%, 8.5. Of the acanthocephalans, larvae of only one species were recorded—*C. aluconis* (0.8%, 0.01).

According to the Palia–Kovnatsky dominance index, the helminth fauna of *S. araneus* was dominated by *L. paradoxi* (D = 28.7) and *M. arionis* (17.9). The subdominants were the cestodes *D. diaphana* (1.6) and *N. schaldybini* (1.9). The remaining 19 species of parasitic worms were classified as adominants. In two protected areas of Mordovia, eighteen shared species of helminths were found in shrews, and four species of parasites (*V. spinulosa*, *S. strigis*, *R. opistovitellinus*, and *P. soricina*) were found only in *S. araneus* from the National Park "Smolny".

The helminth fauna of *S. minutus* includes eight species of parasites, which are represented by adult individuals. All of them are host-specific parasites of insectivores from the family Soricidae. The total infection rate of *S. minutus* was 100%, 6.3. Like in *S. araneus*, the species composition of helminths in *S. minutus* is dominated by nematodes (4 species). The total infection of the pygmy shrew with nematodes was 64.0%, 2.4. Cestodes and trema-

todes in the helminth fauna of *S. minutus* are represented by two species each. Infection of *S. minutus* with cestodes was 78.7%, 2.5, and with trematodes—41.3%, 1.4.

The composition of dominant and subdominant helminth species in the pygmy shrew turned out to be the same as in *S. araneus*, but the order of dominance was different. The helminth fauna of *S. minutus* was dominated by *D. diaphana* (10.2) and *L. paradoxi* (19.6); the subdominants were *R. exasperatum* (8.6) and *M. arionis* (8.0). The remaining four parasite species were adominants.

Four species of helminths (*D. diaphana*, *M. arionis*, *R. exasperatum*, and *L. paradoxi*) were found in *S. minutus* in both studied protected areas of Mordovia. The remaining four species (*P. soricis*, *P. soricina*, *A. exigua*, and *P. skrjabini*) were found in the pygmy shrew only in the Mordovia Nature Reserve.

Sorex isodon was studied only in the Mordovia Nature Reserve, where 12 species of helminths, also typical of *S. araneus*, were found. The total infection rate of *S. isodon* with parasites reaches 100%, 19.6. The helminth fauna of *S. isodon*, like other shrew species, was dominated by nematodes (5 species). The infection rate of *S. isodon* with these parasites was 100%, 13.8. Cestodes and trematodes are represented by three species each. Infection with cestodes was 83.3%, 4.4, and with digeneans—41.7%, 1.3. Acanthocephalans are represented by larvae of one species, *C. aluconis* (8.3%, 0.2). Among the helminths of *S. isodon*, the nematode *L. paradoxi* (29.4) dominated. The subdominants were the cestodes *M. arionis* (7.4), *D. diaphana* (3.6), and the nematode *L. incrassatus* (10.0). The remaining eight species of helminths were adominants.

The helminth fauna of *N. fodiens* includes nine species of parasites, represented by adult worms (Table 1). Six species (*R. exasperatum*, *R. opisthovitellinus*, *P. soricis*, *A. exigua*, *A. kutorii*, and *P. soricina*) are host-specific parasites of shrews from the family Soricidae, while the trematode *N. locellus* and the nematode *L. neomi* are associated with representatives of the genus *Neomys*. The nematode *L. incrassatus* parasitizes a wide range of soricomorphs. All six examined water shrews were infected with helminths (100%, 12.2). Five species of nematodes were found in all studied *N. fodiens* individuals (MA = 7.7). Trematodes in *N. fodiens* were represented by four species and were found in all shrews (100%, 4.5). In both protected areas, four helminth species (*P. soricis*, *N. locellus*, *R. opisthovitellinus*, and *A. kutorii*) were recorded for the water shrew. The nematodes *P. soricina* and *A. exigua* were found in *N. fodiens* only in the National Park "Smolny", while the trematode *R. exasperatum*, the nematodes *L. incrassatus*, and *L. neomi* were recorded only in the Mordovia Nature Reserve. The most common helminth species identified in *N. fodiens* was the trematode *P. soricis*, found in five of six shrews studied (83.3%, 2.7).

Three species of parasitic worms were found in the only studied specimen of *N. milleri* in the Mordovia Nature Reserve, i.e., *R. exasperatum*, *L. incrassatus*, and *L. neomi* (a total of five helminth specimens). In three studied individuals of *C. suaveolens* from the Mordovia Nature Reserve, one parasite species was recorded, the cestode *S. brusatae*, which is a host-specific parasite of the lesser white-toothed shrew.

The helminth fauna of *T. europaea* is represented by two species of nematodes, i.e., *T. linstowi* and *P. depressum*, juv. *Tricholinstowia linstowi* is a specific monohostal parasite of the European mole. At the same time, *P. depressum*, juv. is a common parasite of insectivorous mammals. The total infection rate of moles with parasites was 85.7%, 31.4. These nematode species were found in moles in both protected areas. The most common parasite found in moles is *P. depressum*, juv. (85.7%, 15.0).

The helminth fauna of *E. roumanicus* includes eight species of helminths. Of these, four species (*H. erinacei*, *A. erinacei*, *C. striatum*, and *Ph. clausa*) are host-specific parasites of hedgehogs. The remaining four helminth species are facultative or occasional parasites of hedgehogs (*I. melis*, *S. strigis*, mtc., *Ph. sexalatus*, juv., and *A. minuta*, juv.). In our study, all eight hedgehogs were infected with helminths (100%, 90.3). In the helminth community of *E. roumanicus*, nematodes predominate both in the number of species (4) and in terms of infection rates. Roundworms were found in all hedgehog specimens (MA = 69.9). Nematodes are represented by both adults (*A. erinacei*, *P. clausa*) and larval

forms (*Ph. sexalatus*, *A. minuta*). Trematodes in *E. roumanicus* are represented by two species and were found in two of eight examined hedgehogs (25.0%, 1.8). The trematode *I. melis* was recorded at the mature stage, and *S. strigis* was recorded at the metacercarial stage. Cestodes were represented by only one species—*H. erinacei*. In both protected areas, *E. roumanicus* has three species of parasites (*H. erinacei*, *A. erinacei*, and *P. clausa*). The remaining five helminth species (*I. melis*, *A. minuta*, juv., *C. striatum*, *S. strigis*, mtc., and *Ph. sexalatus*, juv.) were found in hedgehogs only in the National Park "Smolny".

No shared parasites were identified in all the species of insectivores we studied. Only *S. araneus* shares parasite species with other animals studied. The largest host range was recorded for the trematode *R. exasperatum* (five species). The trematode *P. soricis* and the nematode *Liniscus incrassatus* each use four species of insectivores as hosts. Three host species each were found for *D. diaphana*, *M. arionis*, *L. paradoxi*, *P. soricine*, and *P. depressum*, juv. The host range of 11 species of helminths (*B. fulvum*, *R. opisthovitellinus*, *S. strigis*, mtc., *N. schaldybini*, *A. exigua*, *A. kutorii*, *C. soricicola*, *E. oesophagicola*, *L. neomi*, *P. clausa*, and *C. aluconis*, larvae) includes two species of insectivores. The remaining 15 species of parasitic worms are each found in only one host.

Only one of the 34 species of helminths found in insectivores from the protected areas of Mordovia has veterinary significance as a causative agent of dangerous helminthiasis. This is a nematode, *Ph. sexalatus*, juv., that causes physocephalosis in wild boars and domestic pigs.

3.2. List of Helminths of Insectivorous Mammals in the Middle Volga Region

Previous studies of parasitic worms in insectivorous mammals were carried out in six of the 11 regions of the Middle Volga region, i.e., Chuvashia, Mari El, Mordovia, Tatarstan, Nizhny Novgorod, and Samara regions (Figure 1).

Figure 1. Map of the Middle Volga region showing regions with cases of detection of helminth species in insectivorous mammals (dark red—more than 30 species of helminths detected; red—10 or more helminth species; pink—less than 10 species; white—no helminthological studies). The numbers show the number of helminth species identified.

Taking into account the results of our study, the helminth fauna of insectivores includes 52 parasite species found in 9 species of soricomorphs and hedgehogs; these are 14 cestode, 13 trematode, 22 nematode, and 3 acanthocephalan species (Table 3).

Table 3. List of helminths found in insectivorous mammals of the Middle Volga region (European Russia).

Helminth Species	D	Hosts	Locality	References
Family Hymenolepididae *Hymenolepis erinacei* (Gmelin, 1789)	Palaearctic	*Erinaceus roumanicus*	Mordovia (MNR, NP "Smolny") Samara region (Zhiguli Reserve)	this study [128,130–132]
Monocercus arionis Siebold, 1850	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Sorex minutus*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147], this study
		Sorex araneus, *Sorex minutus*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Neoskrjabinolepis schaldybini Spasskii, 1947	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Sorex minutus*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147], this study
		Sorex araneus	Nizhny Novgorod region	[145]
		Sorex araneus, *Sorex minutus*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Ditestolepis diaphana (Cholodkowsky, 1906)	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Sorex minutus*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147], this study
		Sorex araneus, *Sorex minutus*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Insectivorolepis infirma Zarnowski, 1955	Palaearctic	*Sorex araneus*, *Sorex minutus*	Mordovia (MNR)	[147]
Neomylepis magnirostellata (Baer, 1931)	Palaearctic	*Neomys fodiens*	Mordovia (MNR)	[147]
Pseudobothrialepis mathevossianae Schaldybin, 1957	Palaearctic	*Sorex araneus*, *Sorex minutus*	Mordovia (MNR)	[147]
		Sorex araneus	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Soricinia soricis (Baer, 1928)	Palaearctic	*Sorex araneus*, *Sorex minutus*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Spasskylepis ovaluteri Schaldybin, 1964	Palaearctic	*Sorex araneus*, *Sorex minutus*, *Neomys fodiens*	Mordovia (MNR)	[147]
Staphylocystis brusatae (Vaucher, 1971)	Europe	*Crocidura suaveolens*	Mordovia (MNR), Samara region (NP "Samarskaya Luka")	[128,130], this study
Staphylocystis furcata (Stieda, 1862)	Palaearctic	*Sorex araneus*, *Sorex minutus*	Mordovia (MNR), Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132,147]
Staphylocystoides stefanskii (Zarnowski, 1954)	Palaearctic	*Sorex araneus*	Mordovia (MNR)	[147]
Vigisolepis spinulosa (Cholodkowsky, 1906)	Palaearctic	*Sorex araneus*, *Sorex minutus*	Mordovia (MNR, NP "Smolny")	[147], this study
		Sorex araneus	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Family Dilepididae *Dilepis undula* (Schrank, l788), larvae	Palaearctic	*Sorex araneus*	Mordovia (MNR, NP "Smolny")	this study
Family Brachylaimidae *Brachylaima fulvum* Dujardin, 1843	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Sorex minutus*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147,162], this study
		Sorex araneus	Nizhny Novgorod region	[145]

Table 3. *Cont.*

Helminth Species	D	Hosts	Locality	References
Ityogonimus talpae (Goeze, 1782)	Palaearctic	*Talpa europaea*	Nizhny Novgorod region	[144]
Family Panopistidae *Pseudoleucochloridium soricis* (Soltys, 1952)	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Sorex minutus*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147,162], this study
Family Opisthorchiidae *Metorchis bilis* (Braun, 1890)	Holarctic	*Neomys fodiens*	Mordovia (MNR)	[147]
Family Echinostomatidae *Isthmiophora melis* (Schrank, 1788)	Holarctic	*Erinaceus roumanicus*	Mordovia (NP "Smolny")	this study
Family Omphalometridae *Neoglyphe locellus* (Kossack, 1910)	Holarctic	*Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147,162], this study
Neoglyphe sobolevi Schaldybin, 1953	Holarctic	*Sorex araneus*, *Sorex minutus* *Sorex araneus* *Sorex araneus*, *Sorex minutus*	Mordovia (MNR, NP "Smolny") Nizhny Novgorod region Samara region (NP "Samarskaya Luka")	[147,162], this study [145] [128–132]
Rubenstrema exasperatum (Rudolphi, 1819)	Holarctic	*Sorex araneus*, *Sorex isodon*, *Sorex minutus*, *Neomys fodiens*, *Neomys milleri* *Sorex araneus* *Sorex araneus*, *Sorex minutus*	Mordovia (MNR, NP "Smolny") Nizhny Novgorod region Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[147,162], this study [145] [128–132]
Rubenstrema opisthovitellinus (Soltys, 1954)	Palaearctic	*Sorex araneus*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[162], this study
Omphalometra desmanae (Sobolev, Maschkov et Maschkov, 1939)	Europe	*Desmana moschata*	Nizhny Novgorod region Mordovia (MNR) Tatarstan Samara region	[163] [147] [164] [165]
Family Diplostomidae *Alaria alata* (Goeze, 1782), mesocercaria	Cosmopolitan	*Sorex araneus*	Samara region (NP "Samarskaya Luka")	[128–130]
Family Strigeidae *Strigea strigis* (Schrank, 1788), metacercaria	Palaearctic	*Erinaceus roumanicus*, *Sorex araneus*	Mordovia (NP "Smolny")	this study
Holostephanus desmanae	Europe	*Desmana moschata*	Nizhny Novgorod region	[166]
Family Capillariidae *Aonchotheca kutorii* (Ruchljadeva, 1964)	Palaearctic	*Sorex araneus* *Neomys fodiens* *Sorex araneus*	Mordovia (MNR, NP "Smolny") Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[147], this study [128–132]
Aonchotheca erinacei (Rudolphi, 1819)	Palaearctic	*Erinaceus roumanicus*	Mordovia (MNR, NP "Smolny") Samara region (Zhiguli Reserve)	[128,130–132], this study
Aonchotheca exigua (Dujardin, 1845)	Europe	*Sorex minutus*, *Neomys fodiens* *Sorex minutus*, *Crocidura suaveolens*	Mordovia (MNR, NP "Smolny") Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	this study [128,130–132]
Calodium soricicola (Yokogava et Nishigori, 1924)	Palaearctic	*Sorex araneus*, *Sorex isodon* *Sorex araneus*	Mordovia (MNR, NP "Smolny") Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	this study [128–132]

Table 3. *Cont.*

Helminth Species	D	Hosts	Locality	References
Eucoleus oesophagicola (Soltys, 1952)	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147], this study
		Sorex araneus, *Erinaceus roumanicus*, *Talpa europaea*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Liniscus incrassatus Diesing, 1851	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Neomys fodiens*, *Neomys milleri*	Mordovia (MNR, NP "Smolny")	[147], this study
		Neomys fodiens	Tatarstan	[134]
		Sorex araneus	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Nematoideum talpae Siebold, 1850	Palaearctic	*Talpa europaea*	Samara region (Zhiguli Reserve)	[128,130–132]
Family Soboliphymidae *Soboliphyme soricis* Baylis et King, 1932	Palaearctic	*Sorex araneus*, *Neomys fodiens*	Mordovia (MNR, NP "Smolny")	[147], this study
		Sorex araneus	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Family Metastrongylidae *Crenosoma striatum* Zeder, 1800	Palaearctic	*Erinaceus roumanicus*	Mordovia (NP "Smolny"), Samara region (Zhiguli Reserve), Nizhny Novgorod region	[128,130–132,143], this study
Paracrenosoma skrjabini (Pologentsev, 1935)	Palaearctic	*Sorex minutus*	Mordovia (MNR), Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128,130–132], this study
Family Heligmosomidae *Longistriata paradoxi* Schaldybin, 1964	Palaearctic	*Sorex araneus*, *Sorex isodon*, *Sorex minutus*	Mordovia (MNR, NP "Smolny")	[147], this study
		Sorex araneus, *Sorex minutus*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Longistriata codrus Thomas, 1953	Palaearctic	*Sorex araneus*, *Sorex minutus*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Longistriata neomi Lubarskaja, 1962	Palaearctic	*Neomys fodiens*	Tatarstan	[134]
		Neomys fodiens, *Neomys milleri*	Mordovia (MNR)	[147], this study
Tricholinstowia linstowi Travassos, 1918	Palaearctic	*Talpa europaea*	Mordovia (MNR, NP "Smolny"), Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128,130–132], this study
Tricholinstowia talpae (Morgan, 1928)	Palaearctic	*Talpa europaea*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128,130–132]
Family Anisakidae *Porrocaecum depressum* (Zeder, 1800), juveniles	Cosmopolitan	*Talpa europaea*	Chuvashia, Mari El	[133]
		Sorex araneus, *Sorex isodon*, *Talpa europaea*	Mordovia (MNR, NP "Smolny")	this study
		Neomys fodiens Talpa europaea	Tatarstan	[133,134]
		Talpa europaea	Nizhny Novgorod region	[144]
		Sorex araneus, *Talpa europaea*, *Erinaceus roumanicus*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]
Family Habronematidae *Hadjelia truncata* (Creplin, 1825), juveniles	Palaearctic	*Sorex araneus*	Mordovia (MNR, NP "Smolny")	this study
Family Physalopteridae *Physaloptera clausa* Rudolphi, 1819	Holarctic	*Erinaceus roumanicus* (adults), *Sorex araneus* (larvae)	Mordovia (MNR, NP "Smolny"), Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128,130–132], this study
		Erinaceus roumanicus	Nizhny Novgorod region	[143]

Table 3. *Cont.*

Helminth Species	D	Hosts	Locality	References
Pseudophysaloptera soricina Baylis, 1934	Holarctic	*Sorex araneus*, *Sorex minutus*, *Neomys fodiens* *Sorex araneus*, *Sorex minutus*	Mordovia (MNR, NP "Smolny") Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	this study [128–132]
Family Spiruridae *Spirura talpae* (Gmelin, 1790)	Europe	*Talpa europaea*	Tatarstan	[133]
Family Spirocercidae *Physocephalus sexalatus* (Molin, 1860), juveniles	Cosmopolitan	*Erinaceus roumanicus*	Mordovia (NP "Smolny")	this study
Species insertae sedis *Agamospirura minuta* (Sharpilo, 1963), juveniles	Palaearctic	*Erinaceus roumanicus*	Mordovia (NP "Smolny")	this study
Family Centrorhynchidae *Centrorhynchus aluconis* (Müller, 1780), larvae	Palaearctic	*Sorex araneus*, *Sorex isodon* *Sorex araneus*, *Sorex minutus*	Mordovia (MNR) Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	this study [128–132]
Family Oligacanthorhynchidae *Oligacanthorhynchus citilli* (Rudolphi, 1806)	Palaearctic	*Crocidura suaveolens*	Samara region (NP "Samarskaya Luka")	[128,130]
Family Moniliformidae *Moniliformis moniliformis* (Bremser, 1811), larvae	Cosmopolitan	*Sorex araneus*, *Sorex minutus*, *Crocidura suaveolens*	Samara region (Zhiguli Reserve, NP "Samarskaya Luka")	[128–132]

Note: D—distribution.

In the Middle Volga region, the main part of the helminth fauna of insectivores consists of host-specific parasite species (42 species). Occasional and facultative parasites of insectivores are represented by nine species, i.e., *D. undula* (larvae), *M. bilis*, *A. alata* (msc.), *S. strigis* (mtc.), *Ph. clausa* (juv.) for *S. araneus*, *Ph. sexalatus* (juv.), *H. truncata* (juv.), *C. aluconis* (larvae), *O. citilli*, and *M. moniliformis* (larvae).

Shrews, moles, and hedgehogs are the definitive hosts of 42 species of parasitic worms. These insectivorous mammals serve as intermediate and/or paratenic hosts for nine species of helminths, i.e., *D. undula*, *A. alata*, *S. strigis*, *P. depressum*, *H. truncata*, *Ph. clausa* (juv.) (for *S. araneus*), *Ph. sexalatus*, *A. minuta*, *C. aluconis*, and *M. moniliformis*. Adult worms of *Ph. clausa* are host-specific parasites of hedgehogs. *Sorex araneus* serves as the paratenic host of the larval stage of this nematode.

The majority of helminths (40 species) recorded in insectivores have an indirect life cycle. Their definitive or intermediate/paratenic hosts are shrews, moles, and hedgehogs. Parasites with a direct life cycle include only 12 species of nematodes from the families Capillariidae and Heligmosomidae.

In the insectivores of the Middle Volga region, nematodes, which are represented by nine families, have the greatest species richness. Of these, the family Capillariidae (seven species) is the most represented. Five of the identified species belong to the family Heligmosomidae, and two species each belong to the families Metastrongylidae and Physalopteridae. The families Anisakidae, Habronematidae, Soboliphymidae, Spiruridae, and Spirocercidae are represented by only one species.

Trematodes in the studied insectivores are representatives of seven families. Among them, the family Omphalometridae (five species) predominates. Two species belong to the family Brachylaimidae. The remaining four families of trematodes (Diplostomidae, Panopistidae, Echinostomatidae, and Strigeidae) in the helminth fauna of insectivores are represented by one species each. Cestodes and acanthocephalans are the least represented helminths in the insectivores of the Middle Volga region. The observed tapeworms belong to only two families, i.e., the Hymenolepididae (13 species) and the Dilepididae (1). Three

species of acanthocephalans recorded in the shrews of the Middle Volga region belong to the families Centrorhynchidae, Moniliformidae, and Oligacanthorhynchidae.

Despite the high species richness of helminths (42 species) found in insectivores in the protected areas of Mordovia, it has not yet reached its maximum. In total, 52 species of parasitic worms are currently known for 9 studied species of insectivores in the Middle Volga region (Table 3). In the Samara region, six species of these small mammals were studied, of which 33 species of helminths were registered. In particular, in the Zhiguli Nature Reserve and the National Park "Samarskaya Luka", we previously found 28 species of helminths each. The helminth fauna of the Nizhny Novgorod region turned out to be much poorer, since among four insectivorous hosts, 10 species of parasites were identified here. The least studied is the helminth fauna of insectivores in Tatarstan (5 species), as well as in Chuvashia and Mari El, where one parasite species (*P. depressum*, juv.) was found in the common mole (Table 3).

Most species of helminths (36) found in insectivores of the Middle Volga region belong to the Palearctic faunal complex (Table 3). Seven species (*R. exasperatum*, *P. soricina*, *M. bilis*, *I. melis*, *N. locellus*, *N. sobolevi*, and *P. clausa*) have a Holarctic distribution. Four species of helminths (*A. alata*, *P. depressum*, *Ph. sexalatus*, and *M. moniliformis*) are cosmopolitan. The distribution of five species (*O. desmanae*, *H. desmanae*, *S. brusatae*, *A. exigua*, and *S. talpae*) is limited to Europe.

Three of the 52 species of helminths found in insectivorous mammals in the Middle Volga region are of veterinary importance as causative agents of dangerous helminthiases. These are the trematodes *A. alata* and *M. bilis* and the nematode *Ph. sexalatus*, juv. that cause alariosis (affects canids and mustelids), metorchosis (piscivorous animals), and physocephalosis (wild boars and domestic pigs), respectively.

We conducted a comparative analysis of the species structure of helminths in insectivores from different areas of the Middle Volga region. A dendrogram of the similarity of the helminth fauna of various insectivorous species is presented in Figure 2.

As a result of clustering, the studied insectivores were divided into five groups with the closest species composition of helminths. The first single-species group consists of parasites of *D. moschata*. In this group, complete similarity of the helminth fauna was revealed for *D. moschata* from the Samara region, Tatarstan, and the Mordovia Nature Reserve. The highest degree of similarity in the composition of helminths was found in *D. moschata* from the Nizhny Novgorod region and other territories (0.67).

The second group is also single-species and is represented by the helminth fauna of *C. suaveolens*. In this group, an average degree of similarity in the composition of helminths was revealed for the lesser white-toothed shrew from the Zhiguli Nature Reserve and the National Park "Samarskaya Luka" (0.40). The helminth fauna of *C. suaveolens* from the Mordovia Nature Reserve is also close to them (0.40).

The third group is the largest and has five species. It includes the parasitic fauna of shrews of the genera *Sorex* and *Neomys*. A high degree of similarity here was revealed for *S. minutus* from the Zhiguli Reserve and the NP "Samarskaya Luka" (0.93), *S. araneus* from the Zhiguli Reserve and the NP "Samarskaya Luka" (0.90), *S. araneus* from the Mordovia Reserve and the NP "Smolny" (0.80), *S. minutus* and *S. araneus* from the Mordovia Reserve (0.72), *S. araneus* from the NP "Smolny" and *S. isodon* from the Mordovia Reserve (0.71), *S. araneus* from the NP "Smolny" and the NP "Samarskaya Luka" (0.70), *S. araneus* and *S. isodon* from the Mordovia Reserve (0.69), *S. araneus* from the NP "Smolny" and the Zhiguli Reserve (0.68), *S. araneus* from the Mordovia Reserve and the NP "Samarskaya Luka" (0.68), *S. araneus* from the Zhiguli Reserve and the Mordovia Reserve (0.67), *N. fodiens* from Tatarstan and *N. milleri* from the Mordovia Reserve (0.67). The remaining pairs in the third group showed an average and low degree of similarity.

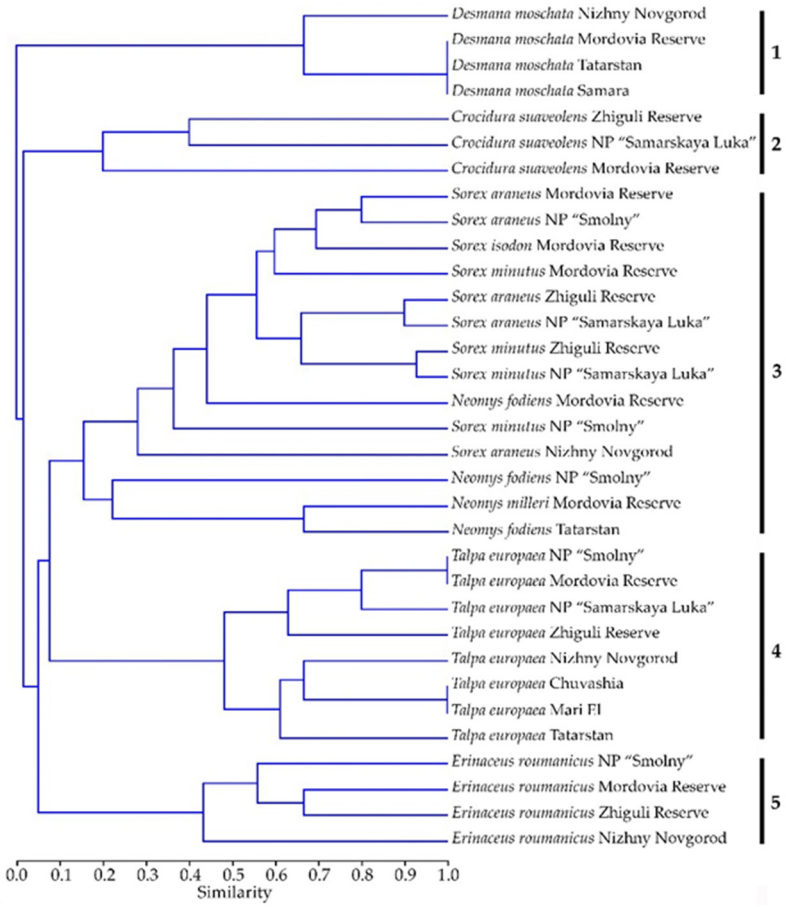

Figure 2. Dendrogram of the similarity of the helminth fauna of insectivores from different areas of the Middle Volga region, obtained using the Morisita index (UPGMA). 1–5—groups with the most similar helminth fauna. Correlation coefficient: r = 0.935.

The fourth group is formed by the helminth fauna of *T. europaea* from different regions of the Middle Volga region. This group is divided into two subgroups. The first subgroup is formed by helminths of moles from protected areas of Mordovia and the Samara region. Here, a complete similarity of helminths was revealed for *T. europaea* from the NP "Smolny" and the Mordovia Reserve. A high degree of similarity of the helminth fauna was noted in moles from the NP "Smolny" and the NP "Samarskaya Luka", from the Mordovia Reserve and the NP "Samarskaya Luka" (0.80 each), from the Zhiguli Reserve, and from the NP "Samarskaya Luka" (0.75). The second subgroup is formed by helminths of moles from the Nizhny Novgorod region, Chuvashia, Mari El, and Tatarstan, where complete similarity of the helminth fauna was revealed for Chuvashia and Mari El. A high degree of similarity was revealed for Tatarstan, Chuvashia, and Mari El (0.67 each).

The fifth group consists of the helminth fauna of hedgehogs from different regions of the Middle Volga region. The greatest similarity in this group was found between the Zhiguli Reserve and the Mordovia Reserve (0.67).

4. Discussion

Previously, 23 species of helminths were known to parasitize insectivorous mammals in Mordovia [148]. As a result of our research, 19 species of parasites were added to this list. Thus, the list of helminths of insectivores in Mordovia now includes 42 species.

Analysis of the helminth fauna of insectivores from both protected areas of Mordovia showed that nematodes are characterized by the greatest species richness (18 species) (Table 2). The identified nematode species have different life cycles and different localizations in the host body. Host-specific nematodes (*A. kutorii*, *A. erinacei*, *A. exigua*, *C. soricicola*,

E. oesophagicola, *L. incrassatus*, *L. paradoxi*, *L. neomi*, and *T. linstowi*) develop directly, without the involvement of intermediate hosts. Infection with these parasites occurs through accidental ingestion of nematode eggs and infective larvae in close contact with the soil litter. In addition, infection can occur when insectivores feed on earthworms, which are reservoir hosts for these geohelminths [121,167,168].

Nine species of helminths found in the insectivores studied are parasites with an indirect life cycle. Being one of the main food items for shrews and moles, earthworms serve as intermediate hosts for the nematodes *S. soricis* and *P. depressum* [169–172]. Infection of shrews and hedgehogs with nematodes *Ph. clausa*, *P. soricina*, *Ph. sexalatus*, and *H. truncata* occurs when animals feed on beetles of the families Tenebrionidae and Scarabaenidae, which are intermediate hosts of these parasites [55,172–174]. The development of *C. striatum*, like, apparently, that of *P. skrjabini*, occurs with the participation of terrestrial gastropods (slugs and snails), through which hedgehogs and shrews become infected with nematodes [175]. Thus, gastropods *Radix balthica* (Linnaeus, 1758), *Morlina glabra* (Rossmassler, 1835), *Arion circumscriptus* Johnston, 1828, *Succinea putris* Linnaeus, 1758, *Urticicola umbrosus* (Pfeiffer, 1828), *Malacolimax tenellus* (Muller, 1774) and *Tandonia rustica* (Millet, 1843) are known as intermediate hosts of this nematode species [176].

Nematodes have different localizations in the bodies of their hosts. Most of these helminths parasitize in various parts of the gastrointestinal tract, i.e., the esophagus (*E. oesophagicola*), stomach (*Ph. clausa*, *P. soricina*, *S. soricis*), small intestine (*A. kutorii*, *A. erinacei*, *A. exigua*, *L. paradoxi*, *L. neomi*, *T. linstowi*, *H. truncata*, juv.), and liver (*C. soricicola*). Nematodes are also found in the bladder (*L. incrassatus*), lungs (*C. striatum*, *P. crenosoma*), and walls of the esophagus, stomach, and intestines (*P. depressum*, juv., *Ph. sexalatus*, juv., *A. minuta*, juv.).

The trematode fauna of insectivores in protected areas of Mordovia is represented by eight species (Table 2). Infection occurs exclusively when animals eat invertebrates, which are intermediate hosts of these parasites. Thus, the trematodes *B. fulvum* and *P. soricis* use terrestrial gastropods as intermediate hosts [44,177].

In North America, the intermediate host of the trematode *N. locellus* is the freshwater mollusk *Galba (Bakerilymnaea) bulimoides* (Lea, 1841) [178]. Metacercariae develop in gastropods, larvae, and adults of aquatic and semi-aquatic insects of the Coleoptera, Neuroptera, and Diptera [55,179,180]. The development of other representatives of the family Omphalometridae (*N. sobolevi*, *R. exasperatum*, and, apparently, *R. opisthovitellinus*) occurs with the participation of gastropods of the genera *Lymnaea* and *Planorbarius*. *Culex pipiens* Linnaeus, 1758 mosquito larvae, have been reported as second intermediate hosts [181,182]. *Isthmiophora melis* develops with the involvement of the gastropod *Lymnaea stagnalis* (Linnaeus, 1758). The second intermediate hosts of this parasite are amphibians and freshwater fish [183–185].

Infection of shrews and hedgehogs with the metacercariae of *S. strigis* probably occurs when the animals feed on amphibians, which are the second intermediate host of this parasite [186]. Infection of insectivores with this trematode species is less likely through aquatic gastropods, intermediate hosts of strigeids [25,186].

Most trematodes are localized in the gastrointestinal tract of insectivores. Five digenean species (*B. fulvum*, *I. melis*, *N. locellus*, *N. sobolevi*, and *R. opisthovitellinus*) parasitize only in the small intestine, and *R. exasperatum*—only in the stomach of shrews. *Pseudoleucochloridium soricis* was found in both the stomach and small intestine of shrews. Only the metacercariae of *S. strigis* are localized in the adipose tissue around the trachea and esophagus.

The cestode fauna of insectivores in the protected areas of Mordovia includes seven species (Table 2). Like trematodes, all cestode species have an indirect life cycle. Shrews and hedgehogs become infected with species such as *N. schaldybini*, *D. diaphana*, *V. spinulosa*, and *H. erinacei* by feeding on the beetles, which serve as intermediate hosts for these tapeworms [55,187]. The development of *H. erinacei* cysticercoids can occur both in the intestinal villi of the definitive hosts (hedgehogs) and in the small intestine, where they

grow to maturity [188], with the participation of intermediate hosts—beetles of the genera *Oiceoptoma*, *Nicrophorus*, and *Geotrupes* [187]. The development of *M. arionis* occurs with the participation of terrestrial mollusks of the genus *Succinea* [125,189]. Infection of shrews with the cestode *D. undula* probably occurred when they ate the intermediate hosts of the cestode—oligochaetes [125]. The presence of acanthocephalan larvae of *C. aluconis* in shrews indicates that the animals consume the intermediate hosts of this parasite—beetles of the families Tenebrionidae and Scarabaeidae [190,191].

Findings of larval forms of helminths (*S. strigis*, *P. depressum*, *Ph. sexalatus*, and *C. aluconis*) in insectivores indicate the important role of these small mammals in the spread and circulation of parasitic worms of carnivores and birds of prey. Hedgehogs and shrews are paratenic hosts of these parasites.

In our opinion, the findings of larvae of the cestode *D. undula* and the nematode *H. truncata* in the intestines of shrews are cases of transit parasitism. These parasites do not reach maturity in the intestine of shrews and leave the host body without development.

Agamospirura minuta is an occasional parasite of insectivores. This juvenile nematode is a specific parasite of reptiles, usually parasitizing the slowworm *Anguis fragilis* Linnaeus, 1758, and less commonly other lizards and snakes [192]. The definitive hosts of this parasite are unknown. Lewin [193] found similar nematode larvae in reptiles in Poland and identified them as Protostrongylidae sp. Further studies using molecular genetic methods are required to accurately identify this parasite.

Despite the fact that the various species of insectivores under consideration often live in the same habitats, the strict specificity of their parasites to the species and genera of hosts is revealed. Our study showed that no shared parasite species was found among the studied hosts. The highest species richness of helminths was observed in the most numerous and eurytopic shrew, *S. araneus* (22 species). It is this species of shrew that shares parasites with all other studied insectivores. Compared to *S. araneus*, all other insectivores have a poorer composition of helminths. Apparently, this is due to the small sample size of the animals examined. In addition, the formation of helminth fauna is influenced by the lifestyle of the host. For example, *C. suaveolens* prefers to settle in open, dry habitats where the likelihood of infection with helminths is low. The underground lifestyle of *T. europaea* limits the range of food items as possible intermediate hosts of helminths, which reduces the diversity of the parasitic fauna. Due to its lifestyle, *E. roumanicus* has a specific composition of parasites. The enrichment of its helminth fauna occurs due to occasional parasites characteristic of other vertebrates [25].

It should be noted that all the species of insectivores we studied, due to their diet, behavioral characteristics, and lifestyle throughout their range, are characterized by a high infection with helminths [115,125,129,194,195].

According to our data and previous records, there are 52 species of parasites in the helminth fauna of insectivores in the Middle Volga region. A comparative analysis of the species composition of helminths in insectivores from different areas of the Middle Volga region showed both significant similarity in the helminth fauna of insectivorous species as well as its originality in a certain research area.

In *Sorex* spp., the majority of helminth species recorded are common and widespread parasites of shrews, occurring throughout their range. This explains the high and average degree of similarity of the helminth fauna of representatives of the genus *Sorex* from different areas of the Middle Volga region (Figure 2).

The helminth fauna of *E. roumanicus* in the Middle Volga region includes nine species, of which four were found only in the National Park "Smolny". Therefore, the similarity of the helminth fauna of hedgehogs in the NP "Smolny" with the helminth fauna in other regions is less. Only two species of helminths have been registered in hedgehogs of the Nizhny Novgorod region, which determines the low similarity of its helminth fauna with other regions (Figure 2).

The uniqueness of the helminth fauna of *N. fodiens* from the National Park "Smolny" is due to the presence of nematodes *A. exigua* and *P. soricina* (Tables 2 and 3). The water

shrew from the NP "Smolny" also lacks a number of parasites found in *N. fodiens* from the Mordovia Nature Reserve. This fact determines the low degree of similarity of the helminth fauna of water shrews from the NP "Smolny", the Mordovia Nature Reserve, and Tatarstan. We found an average degree of similarity in the composition of helminths in *Sorex* and *Neomys* species (Figure 2). At the same time, of the 19 species of parasites found in *N. fodiens* of the Middle Volga region, 14 are common with *S. araneus*, and 8 species each are shared with *S. isodon* and *S. minutus*.

Only four species of helminths have been registered in *C. suaveolens*, including one species in the Mordovia Nature Reserve and three species in both protected areas of the Samara region (Table 3). No shared species of helminths were identified in the lesser white-toothed shrew from the Zhiguli and Mordovia Nature Reserves. For *C. suaveolens* from the Zhiguli Nature Reserve and the National Park "Samarskaya Luka", as well as from the Mordovia Nature Reserve and the National Park "Samarskaya Luka", only one shared species of helminths was noted. Therefore, *C. suaveolens* from the Zhiguli Nature Reserve and the National Park "Samarskaya Luka" have an average degree of similarity (Figure 2).

In *D. moschata*, only two species of specific trematodes were noted, of which *O. desmanae* was found in four regions, which ensures complete similarity of the helminth community in the Mordovia Nature Reserve, Tatarstan, and the Samara region (Table 3, Figure 2).

In total, six species of helminths have been registered in *T. europaea* in the Middle Volga region (Table 3). Only two species of parasites were found in moles from the Mordovia Nature Reserve and the National Park "Smolny". This determines the complete similarity of their helminth fauna. One species (*P. depresum*, juv.) was found in moles in all studied areas of the Middle Volga region. This fact determines the complete similarity of the helminth fauna of *T. europaea* from Chuvashia and Mari El, where only this species of helminth was found in moles.

Differences in the helminth composition of insectivores from different areas of the Middle Volga region are mainly due to the degree of study of the helminth fauna of various Eulipotiphla species (Figure 2). On the other hand, differences in the helminth fauna of insectivores may depend on abiotic and biotic factors at each specific study site, such as microclimatic conditions of habitats, species composition and abundance of invertebrates (intermediate and/or paratenic hosts of helminths), and population density of insectivorous mammals.

5. Conclusions

As a result of our research, the list of helminths in insectivorous mammals in Mordovia was replenished with 19 species of parasites and currently includes 42 species. For the first time, we registered the nematodes *A. exigua* and *P. soricina* in *N. fodiens* from European Russia, as well as the trematode *Rubenstrema opisthovitellinus* in *S. araneus* from the Volga basin. The first data on the helminths of *S. isodon* in the Volga basin have been obtained.

According to our research and previous records, the helminth fauna of insectivores of Eulipotyphla from the Middle Volga region includes 52 species, i.e., 14 cestodes, 13 trematodes, 22 nematodes, and 3 acanthocephalans. Most of them belong to the Palearctic faunal complex (36 species). Among all insectivorous species, the richest helminth fauna was found in *S. araneus* (31 species), *S. minutus* (20), and *N. fodiens* (19). The composition of helminths is less diverse in *S. isodon* (12), *E. roumanicus* (9), and *T. europaea* (6). The least studied soricomorphs also have the fewest recorded parasite species. These species include *C. suaveolens* (4 species), *N. milleri* (3), and *D. moschata* (2).

Forty of the 52 helminth species found in the insectivores of Eulipotyphla have an indirect life cycle. Shrews, moles, and hedgehogs serve as definitive or intermediate/paratenic hosts for these parasites. The twelve species of nematodes observed are geohelminths.

Insectivorous mammals are the definitive hosts of 42 species of parasitic worms. For nine species of helminths, these animals serve as intermediate and/or paratenic hosts. In

addition, the adult worm of *Ph. clausa* is a specific parasite of hedgehogs, and *S. araneus* serves as the paratenic host of the larval stage of this nematode. The bulk of the helminth fauna of insectivores consists of host-specific species (42). Facultative and occasional parasites are represented by nine species.

A comparative analysis of the helminth fauna of various insectivorous species in the Middle Volga region showed a high and average degree of similarity among the helminth communities within individual species and genera of Eulipotyphla.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16050307/s1. Table S1: Sampling sites of helminths of insectivorous mammals, with coordinates.

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