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Review

Helminths of *Erinaceus roumanicus* (Eulipotyphla, Erinaceidae) in Mordovia (Russia) with an Overview of Helminth Fauna of *Erinaceus* spp. Inhabiting the Palaearctic Region

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Abstract: The helminth fauna of the Northern white-breasted hedgehog *Erinaceus roumanicus* was studied in the Republic of Mordovia (Russia) for the first time. In total, 9 species of helminths were found in 23 studied hedgehogs: Trematoda—*Isthmiophora melis*, *Strigea strigis* (metacercaria); Cestoda—*Hymenolepis erinacei*; Nematoda—*Aonchotheca erinacei*, *Physaloptera clausa*, *Crenosoma striatum*, *Physocephalus sexalatus* (juvenile), *Agamospirura minuta* (juvenile); and Acanthocephala—*Nephridiorhynchus major*. Four parasite species (the trematode *I. melis*, nematodes *P. sexalatus*, *A. minuta*, and the acanthocephalan *N. major*) were found in hedgehogs for the first time in Russia. An overview of the helminth fauna of four species of *Erinaceus* hedgehogs inhabiting the Palearctic region is given. A total of 54 parasite species were recorded across *Erinaceus europaeus*, *E. roumanicus*, *E. concolor* and *E. amurensis*: 14 trematodes, 6 cestodes, 27 nematodes, and 7 acanthocephalans. Among all the studied species of hedgehogs, *E. europaeus* (35 species) and *E. roumanicus* (36) have the richest helminth faunas. The diversity of the parasite communities of *Erinaceus* spp. is due to the wide distribution and varied diet of these mammals. Most of the helminths found in hedgehogs are transmitted along trophic chains. Hedgehogs are the final hosts for 39 species of parasites. For 15 helminth species, *Erinaceus* spp. are paratenic hosts. The majority of the hedgehog's helminth fauna is formed by host-specific parasites, of which there are 13 species. Most of the hedgehog's parasites in the Palaearctic are facultative (non-specific) species that parasitize in various vertebrate species. The helminth fauna of *Erinaceus* hedgehogs is most studied in Russia and Belarus, where 17 species of parasites are found in each country. The comparative analysis of the helminth faunas of *Erinaceus* spp. from various regions showed, on the one hand, the originality of the helminth fauna of each hedgehog species and, on the other, the similarity of the helminth fauna of these insectivores from various countries of the Palaearctic. These features are caused by similar lifestyles and diet peculiarities of every hedgehog species in various regions of the Palaearctic. A total of 12 of the 54 helminth species found in hedgehogs have medical and veterinary significance as causative agents of dangerous helminthiasis.

Keywords: *Erinaceus* spp.; parasitic worms; Western European hedgehog; Northern white-breasted hedgehog; Southern white-breasted hedgehog; Amur hedgehog; Palaearctic

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1. Introduction

Small terrestrial mammals, such as the Eulipotyphla and Rodentia, are important elements of ecosystems due to their high species diversity, fitness, and diet specializations. This animal group, due to its high abundance and wide distribution, is an integral part of any semi-aquatic or terrestrial biocenosis and it is of great practical importance [1–5]. Small wild animals are the main forage resource for predatory mammals, birds of prey, and some reptiles (mainly snakes) [6–8]. Small mammals are of great importance in rural environments as many are a source of parasites and some diseases of domestic animals and livestock [9–14].

Among Eulipotyphla, the Erinaceinae subfamily containing the well-known hedgehogs of Eurasia and Africa deserves special attention [15]. Hedgehogs are nocturnal and spend most of their active time foraging [16,17]. These omnivores have ecological plasticity that allows them to inhabit various biotopes. They are present in many habitat types (habitats) if their primary forage (invertebrates) and suitable nest sites are sufficiently available [18]. Hedgehogs are often found in urban and suburban environments [17].

Hedgehogs of the Erinaceidae family are widespread in the Palaearctic. Currently, four hedgehog species of the genus *Erinaceus* are known: *Erinaceus europaeus* Linnaeus 1758, *Erinaceus roumanicus* Barrett-Hamilton, 1900, *Erinaceus concolor* Martin, 1837 and *Erinaceus amurensis* Schrenk, 1858. *Erinaceus roumanicus* has only recently been defined as a valid species [15]. Three hedgehog species inhabit Western Palaearctic: *E. europaeus*, *E. roumanicus*, and *E. concolor* [19]. The Western European hedgehog *E. europaeus* inhabits the forest areas of Western and Central Europe (including the British Isles), Southern Fennoscandia, Estonia, and the north and central regions of European Russia [20–25].

The Northern white-breasted hedgehog *E. roumanicus* inhabits Central and Eastern Europe, the south of Western Siberia and the North Caucasus. *Erinaceus roumanicus* and *E. europaeus* are sympatric in central Europe (the Balkans, Poland, the Czech Republic, and Slovakia) and central regions of European Russia [22,23,25]. The northern border of the species range in Russia is at the level of 56° north latitude; in the south it is distributed to the Caucasus [25].

The Southern white-breasted hedgehog *E. concolor* is found in the Middle East, isolated from *E. roumanicus* by the Bosphorus Strait and the Caucasus Mountains [22,23]. Until recent times, *E. roumanicus* was considered to belong either to *E. europaeus* or to *E. concolor*, and it has only recently been identified as a valid species [18].

The only *Erinaceus* species inhabiting the Eastern Palearctic is the Amur hedgehog *E. amurensis*. Its range covers the Russian Far East, and northeastern China, Korea, and Japan [26].

Hedgehogs harbor a wide range of numerous zoonotic pathogens, parasitic infections, and bacterial diseases [15,27]. Species-specific endoparasites, such as lungworms *Crenosoma striatum* cause bronchitis and bronchopneumonia [28]. Nematodes (mainly *Eucoleus* spp. and *Aonchotheca* spp.) are prevalent lung and intestinal parasites [28,29].

Hedgehogs as final, intermediate, and paratenic hosts can be involved in the life cycles of helminths that parasitize other vertebrates. So, hedgehogs can be infected by *Alaria alata* (mesocercaria), *Spirometra erinacei* (plerocercoid), *Physocephalus sexalatus* (juvenile), and *Trichinella* spp., which are zoonotic parasites [30–33]. The epidemiological and epizootic potential of many parasites carried by hedgehogs determines the interest in their study of the parasite fauna of these animals.

The first attempts to collect data on the helminths of *Erinaceus* spp. inhabiting the Western Palaearctic were made by Pfaffle [34] and Rasmussen [35]. In these publications, there were almost no data about parasites of hedgehogs from Eastern Europe as much of that literature was not available via electronic databases. The purpose of this study is to review the helminth fauna of *Erinaceus* spp. inhabiting the Palaearctic region and systematize data about helminths of the hedgehogs according to recent conceptions.

2. Materials and Methods

2.1. Parasite Examination

For this study, we used road-killed specimens of Northern white-breasted hedgehog *E. roumanicus* collected in the Temnikov and Ichalki districts of the Republic of Mordovia (Russia) in the summer months of 2019–2021. All animal specimens were placed in 70% ethanol until they were used for dissection.

In total, we examined 23 carcasses of hedgehogs. Animals were studied by the method of complete helminthological dissection according to Ivashkin [36] and Anikanova [37]. Parasitic worms were collected and fixed in 70% ethanol. Cestodes, trematodes, and acanthocephalans were dehydrated in a graded ethanol series (70–96%), stained with aceto-

carmine then cleared in clove oil, and mounted in Canada balsam. Nematodes were cleared in lactic acid and mounted in glycerin-jelly [36–38].

The identification of helminths was carried out at the Laboratory of Population Ecology of the Institute of Ecology of the Volga Basin of the Russian Academy of Sciences (Togliatti, Russia). The helminth species were identified according to publications of Genov [32], Sharpilo [39], Khokhlova [40] Moravec [41], and Kirillov [42]. The voucher specimens of parasitic helminths are stored in the helminth collection in the Institute of Ecology of Volga Basin of RAS—a branch of the Samara Federal Research Center of the Russian Academy of Sciences.

The recent helminth taxonomy is given according to Fauna Europaea (https://fauna-eu.org/, accessed on 22 January 2022) [43] and the Global Cestode database (http://out.easycounter.com/external/tapewormdb.uconn.edu, accessed on 22 January 2022) [44].

2.2. Literature Data Collection

A comparative review of the helminth fauna of *Erinaceus* spp. is based on the analysis of literature data on parasitic worms in hedgehogs inhabiting the Palearctic, as well as on the results of the authors' research in the Middle Volga region (Russia). We searched scientific literature on the hedgehog helminths using international databases: Web of Science Core Collection, Scopus, Google Scholar, and eLIBRARY.ru (Russian scientific electronic library). To find studies on hedgehog parasites, we used the following search strings: Topic: [("Helminths" or "Parasites" or "Trematodes" or "Cestodes" or "Nematodes" or "Acanthocephalans") and ("hedgehog" or "*Erinaceus*" or "*Erinaceus europaeus*" or "*Erinaceus roumanicus*" or "*Erinaceus concolor*" or "*Erinaceus amurensis*" or "Erinaceidae")]. We used both Russian and English characters to enter our search strings in the Russian database eLIBRARY.ru.

A certain number of articles for our review were taken from former USSR parasitological literature in Russian, not indexed in electronic databases. Literature sources were collected in public libraries: National Library of Russia (St. Petersburg), M. Gorky Scientific Library of St Petersburg University, and Samara Regional Universal Scientific Library. The analysis of literary sources was conducted between 1904 and 2021. We also used review papers on the helminths of the former USSR and adjacent countries [30,32,33,42,45–52].

2.3. Data Analysis

To characterize the infection of hedgehogs with parasitic worms, the following indices were used: the prevalence of infection (P, %), the intensity range (IR, specimens), and the mean abundance (MA).

The similarity between the helminth fauna of *Erinaceus* spp. was evaluated using the Jaccard similarity index (*Cj*) [53]. The degree of similarity is the following: 0–0.33—low; 0.34–0.66—medium; and 0.67–1—high. The similarity dendrogram of the helminth faunas of hedgehogs was created using the unweighted pair group method with arithmetic average (UPGMA) and the Morisita index as a distance measure in PAST 2.17 [54]. The cluster is representative when the cophenetic correlation coefficient is above 0.70. Statistical data processing was performed using the software package Microsoft Excel (2016).

3. Results

3.1. Helminths of Erinaceus roumanicus in Mordovia (Russia)

We found nine helminth species in twenty-three hedgehogs from the Republic of Mordovia, including two trematodes, one cestode, five nematodes, and one acanthocephalan (Table 1).

Table 1. Helminth fauna of *Erinaceus roumanicus* in Mordovia (Russia).

Helminth Species	Location in Host	P, %	IR, Spec.	MA
Trematoda *Isthmiophora melis* (Schrank, 1788)	small intestine	13.0	2–86	4.0
Strigea strigis (Schrank, 1788), metacercaria	mesentery around oesophagus and trachea	4.3	2	0.1
Cestoda *Hymenolepis erinacei* (Gmelin, 1789)	small intestine	52.2	1–97	7.8
Nematoda *Aonchotheca erinacei* (Rudolphi, 1819)	stomach, small intestine	56.5	1–149	19.5
Physaloptera clausa Rudolphi, 1819	stomach	100	9–420	77.4
Crenosoma striatum Zeder, 1800	bronchi	8.7	3–18	0.9
Physocephalus sexalatus (Molin, 1860), juv.	walls of stomach and small intestine	13.0	8–177	8.6
Agamospirura minuta Sharpilo, 1963	gastric mucosa and first third of small intestine	4.3	3	0.1
Acanthocephala *Nephridiorhynchus major* (Bremser, 1811)	small intestine	4.3	2	0.1

The overall infestation of hedgehogs by helminths was 100%, the index of helminth mean abundance was 118.5. The intensity range of hedgehog infection by helminths was from 17 to 514 specimens.

3.2. Checklist of Helminths of Erinaceus spp. *in the Palaearctic*

As a result of the analysis of the scientific literature, 125 articles and 9 monographs were identified, which contained data regarding the parasitic worms of the *Erinaceus* spp. inhabiting the Palaearctic region. Studies of the hedgehog helminth fauna were carried out in 30 countries. Currently, the helminth fauna of 4 hedgehog species of *Erinaceus* genus includes 54 records: 14 trematodes, 6 cestodes, 27 nematodes, and 7 acanthocephalans (Table 2).

Table 2. List of helminths of *Erinaceus* hedgehogs in the Palaearctic region.

Helminth Species	D	Host	Country	References
Trematoda				
Brachylaima recurva (Dujardin, 1845)	[1] E	*E. concolor*	Georgia	[55]
[2] *Brachylaima erinacei* Blanchard, 1847 (Syn.: *Brachylaima helicis* (Meckel, 1846))	[3] P	*E. europaeus*	UK	[28,56–61]
		E. europaeus	France	[62]
		E. europaeus	Germany	[59,63–72]
		E. europaeus	Italy	[73–76]
		E. europaeus	Spain	[77]
		E. europaeus	Switzerland	[29,78–80]
		E. europaeus, *E. roumanicus*	Czech Republic	[34,81]
		E. europaeus, *E. roumanicus*	Poland	[82,83]
		E. europaeus	Russia	[84]
		E. concolor	Iran	[85]
Brachylaima sp.	-	*E. europaeus*	Portugal	[86]
		E. europaeus	Denmark	[35]
		E. roumanicus	Greece	[87]
[2,4] *Isthmiophora melis* (Schrank, 1788) Syn.: *Euparyphium melis* (Schrank, 1788)	[5] H	*E. europaeus*	Czech Republic	[81,88]
		E. roumanicus	Moldova	[30,45]
		E. roumanicus	Belarus	[33,89,90]
		E. roumanicus	Ukraine	[91,92]
		E. roumanicus	Russia	this study
Nephrotrema truncatum (Leuckart, 1842)	E	*E. europaeus*	Austria	[93]
Dicrocoelium dendriticum (Rudolphi, 1819)	[6] C	*E. europaeus*	Italy	[73,75]
Dicrocoelium sp.	-	*E. europaeus*	Germany	[69]
Brachylecithum aetechini Dollfus, 1951	E	*E. europaeus*	Italy	[73,75]
Brachylecithum mackoi Casanova et Ribas, 2004	E	*E. europaeus*	Italy	[94]
Rubenstrema exasperatum (Rudolphi, 1819)	P	*E. roumanicus*	Ukraine	[92]
[2] *Alaria alata* (Goeze, 1782), msc.	C	*E. roumanicus*	Moldova	[30,45]
		E. roumanicus	Belarus	[33,89,90,95]
		E. europaeus	Russia	[84]
		E. roumanicus	Ukraine	[91,92]

Table 2. *Cont.*

Helminth Species	D	Host	Country	References
Strigea falconis Szidat, 1928, mtc.	C	*E. roumanicus*	Belarus	[33,95]
Strigea sphaerula (Rudolphi, 1803), mtc.	P	*E. roumanicus*	Belarus	[33,95]
[2,4] *Strigea strigis* (Schrank, 1788), mtc.	P	*E. roumanicus* *E. europaeus*, *E. roumanicus* *E. roumanicus*	Belarus Russia Ukraine	[89] [84], this study [92]
Cestoda				
[2,4] *Hymenolepis erinacei* (Gmelin, 1789) Syn.: *Rodentolepis erinacei* (Gmelin, 1789), *Rodentolepis steudeneri* (Janicki, 1904)	P	*E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus*, *E. roumanicus* *E. europaeus*, *E. roumanicus* *E. roumanicus* *E. roumanicus* *E. roumanicus* *E. roumanicus* *E. europaeus* *E. roumanicus* *E. roumanicus* *E. roumanicus* *E. concolor* *E. concolor* *E. concolor* *E. concolor*	UK Germany Switzerland Czech Republic Slovakia Serbia Poland Bulgaria Greece Lithuania Belarus Russia Ukraine Armenia Georgia Turkey Iran	[28,57,61,96,97] [63–65,67,69–72,98] [80] [34,81,99] [99] [100] [101] [32] [87] [102] [33,89,90,95,103] [49,104–108], this study [91,109] [47] [55] [110] [85,111]
Spirometra erinacei (Rudolphi, 1819), plc. (Syn.: *Diphyllobothrium erinacei* (Rudolphi, 1819))	C	*E. roumanicus* *E. roumanicus* *E. roumanicus*	Bulgaria Moldova Belarus	[32] [30,45] [33,89,90]
Taenia hydatigena Pallas, 1766, larvae (Syn.: *Taenia tenuicollis* Rudolphi, 1819)	C	*E. roumanicus*	Belarus	[90]

Table 2. *Cont.*

Helminth Species	D	Host	Country	References
Versteria mustelae (Gmelin, 1790), larvae (Syn.: *Taenia mustelae* Gmelin, 1790)	H	*E. roumanicus*	Belarus	[33]
Cladotaenia globifera (Batsch, 1786), larvae	H	*E. europaeus*	Portugal	[112]
Mesocestoides sp., larvae	-	*E. europaeus* *E. roumanicus*	Italy Bulgaria	[73,75,113] [32] as *M. lineatus* (Goeze, 1782)
Nematoda				
[2,4] *Aonchotheca erinacei* (Rudolphi, 1819) Syn.: *Capillaria erinacei* (Rudolphi, 1819), *Capillaria ovoreticulata* Laubmeier, 1985	P	*E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus*, *E. roumanicus* *E. europaeus*, *E. roumanicus* *E. roumanicus* *E. europaeus*, *E. roumanicus* *E. roumanicus* *E. roumanicus* *E. roumanicus* *E. europaeus*, *E. roumanicus* *E. roumanicus* *E. concolor* *E. concolor*	UK Ireland Italy Germany Switzerland Portugal Spain Czech Republic Slovakia Serbia Poland Bulgaria Moldova Belarus Russia Ukraine Armenia Turkey	[56–58,61,96] [114] [73–76] [67,70–72] [29] [112] [77] [41,81,99] as *Capillaria* sp 2 and 3 [99,115] [100] [82,83] [32] [30,45,116] [33,89,90,95,103] [49,107,108,117–119], this study [91] [50,120,121] [110]
Aonchotheca sp. + *Eucoleus* sp. (=*Capillaria* spp.)	-	*E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus* *E. europaeus*, *E. roumanicus* *E. roumanicus* *E. concolor*	UK Finland Denmark Germany Switzerland Czech Republic Greece Iran	[28,58–60] [16] [35] [59,64–69,98,122,123] [79,80] [34,124] [87] [85]
Capillariidae sp.	-	*E. europaeus* *E. amurensis*	France Japan	[62] [125]

Table 2. *Cont.*

Helminth Species	D	Host	Country	References
[2] *Eucoleus aerophilus* (Creplin, 1839) (Syn.: *Capillaria aerophila* (Creplin, 1839); *Thominx aerophilus* (Creplin, 1839))	C	*E. europaeus*	UK	[57–59,61,97]
		E. europaeus	Germany	[59,63–67,69–72]
		E. europaeus	Denmark	[35]
		E. europaeus	Switzerland	[29]
		E. europaeus, *E. roumanicus*	Czech Republic	[34]
		E. europaeus, *E. roumanicus*	Poland	[82,83]
		E. roumanicus	Belarus	[33,95,103]
		E. europaeus, *E. roumanicus*	Russia	[49,84,107,108,117–119]
		E. roumanicus	Ukraine	[91]
		E. concolor	Turkey	[110]
		E. concolor	Iran	[85]
[2] *Eucoleus tenuis* Dujardin, 1845	E	*E. europaeus*	UK	[96]
		E. europaeus, *E. roumanicus*	Czech Republic	[99]
		E. europaeus	Spain	[77]
		E. roumanicus	Bulgaria	[32]
		E. roumanicus	Russia	[106]
Pterothominx erinacei (Andrejko, 1969) (Syn.: *Thominx erinacei* Andrejko, 1969)	E	*E. roumanicus*	Moldova	[30,45,116]
Calodium hepaticum (Bancroft, 1893) (Syn.: *Hepaticola hepatica* (Bancroft, 1893))	C	*E. europaeus*	Denmark	[35]
		E. europaeus	Spain	[77]
		E. europaeus	Switzerland	[79,126]
		E. roumanicus	Ukraine	[127]
[2] *Trichinella spiralis* Owen, 1835	C	*E. europaeus*	Belgium	[31]
		E. europaeus	Czech Republic	[128]
		E. roumanicus	Bulgaria	[32]
		E. roumanicus	Belarus	[33]
		E. europaeus	Russia	[48,84]
[2] *Trichinella nativa* Britov et Boev, 1972, juveniles	H	*E. roumanicus*	Russia	[129]
Trichuris sp.	-	*E. europaeus*	Germany	[69]
		E. europaeus	Switzerland	[79,80]
Parastrongyloides winchesi Morgan, 1928	H	*E. roumanicus*	Belarus	[33]
		E. roumanicus	Ukraine	[91]

Table 2. *Cont.*

Helminth Species	D	Host	Country	References
[2,4] *Crenosoma striatum* Zeder, 1800	P	*E. europaeus*	UK	[28,56,58–61,96,97,130,131]
		E. europaeus	Ireland	[114]
		E. europaeus	France	[62]
		E. europaeus	Denmark	[35]
		E. europaeus	Germany	[59,63–72,98,122,123]
		E. europaeus	Switzerland	[29,79,80]
		E. europaeus	Italy	[73,75,76]
		E. roumanicus	Greece	[87]
		E. europaeus	Finland	[16]
		E. roumanicus	Portugal	[86,112,132]
		E. europaeus	Spain	[77,133]
		E. roumanicus	Serbia	[100]
		E. europaeus, *E. roumanicus*	Czech Republic	[34,81,99,124,134]
		E. europaeus, *E. roumanicus*	Poland	[82,83,101]
		E. europaeus, *E. roumanicus*	Slovakia	[99,115,134]
		E. roumanicus	Belarus	[33,89,90,95,103]
		E. europaeus, *E. roumanicus*	Russia	[48,49,84,107,108,118,119,135], this study
		E. roumanicus	Ukraine	[91,109]
		E. concolor	Turkey	[110]
		E. concolor	Iran	[85,111,136]
Crenosoma lofocara Gerichter, 1951	P	*E. roumanicus*	Bulgaria	[32]
		E. concolor	Georgia	[137]
		E. concolor	Siria	[138]
Ancylostoma sp.	-	*E. europaeus*	Switzerland	[80]

Table 2. *Cont.*

Helminth Species	D	Host	Country	References
[2,4] *Physaloptera clausa* Rudolphi, 1819	H	*E. europaeus*	Germany	[67,70,72]
		E. europaeus	Italy	[75,76]
		E. europaeus	Spain	[77]
		E. roumanicus	Greece	[87]
		E. europaeus, *E. roumanicus*	Czech Republic	[34,81,99]
		E. europaeus, *E. roumanicus*	Slovakia	[99,115]
		E. roumanicus	Bulgaria	[32]
		E. europaeus, *E. roumanicus*	Poland	[82,83,101]
		E. roumanicus	Moldova	[30,45,116]
		E. roumanicus	Belarus	[33,89,90,95,103]
		E. europaeus, *E. roumanicus*	Russia	[49,104,105,107,108,118,119,135], this study
		E. roumanicus	Ukraine	[91,109,127]
		E. concolor	Turkey	[110]
		E. concolor	Iran	[85,111,139,140]
		E. amurensis	China	[141]
Haemonchus contortus (Rudolphi, 1803)	C	*E. europaeus*	Italy	[75]
Trichostrongylus retortaeformis (Zeder, 1800)	C	*E. europaeus*	UK	[142]
[2] *Porrocaecum* sp., juveniles	-	*E. europaeus*	Portugal	[112]
		E. europaeus	Spain	[77]
		E. roumanicus	Belarus	[95]
		E. roumanicus	Russia	[49,107,108,118,119] as *P. depressum* Zeder, 1800
		E. amurensis	Japan	[125]
[2,4] *Physocephalus sexalatus* (Molin, 1860), juveniles	P	*E. roumanicus*	Bulgaria	[32]
		E. roumanicus	Belarus	[33,90]
		E. roumanicus	Russia	this study
Ascarops strongylina (Rudolphi, 1819), juveniles	C	*E. roumanicus*	Bulgaria	[32]
Spirocerca lupi (Rudolphi, 1809), juveniles	C	*E. roumanicus*	Bulgaria	[32]
Gongylonema sp.	-	*E. europaeus*	Germany	[67]
		E. europaeus	Italy	[73]

Table 2. *Cont.*

Helminth Species	D	Host	Country	References
Spirura rytipleurites Deslongchamps, 1824	E	*E. europaeus* *E. roumanicus* *E. europaeus* *E. concolor*	Italy Slovakia Spain Armenia	[73,75] [99] [77] [50,120]
Spirura sp.	-	*E. europaeus*	Portugal	[112]
Rictularia plagiostoma (Wedl, 1861) (Syn.: *Pterygodermatites plagiostoma* Wedl, 1861)	E	*E. europaeus* *E. europaeus*	Spain Portugal	[77,143] [86]
[2,4] *Agamospirura minuta* Sharpilo, 1963, juveniles	P	*E. roumanicus*	Russia	this study
Monovaria sp.	-	*E. amurensis*	Japan	[125]
Acanthocephala				
[2,4] *Nephridiorhynchus major* (Bremser, 1811)	P	*E. europaeus* *E. europaeus*, *E. roumanicus* *E. europaeus* *E. roumanicus* *E. roumanicus* *E. concolor* *E. concolor* *E. concolor* *E. concolor*	Italy Czech Republic Spain Bulgaria Russia Armenia Georgia Turkey Iran	[73,75] [34,81,99] [77] [32] this study [50,120] [55,137,141] [110] [111,144]
Oligacanthorhynchus erinacei (Rudolphi, 1793)	P	*E. europaeus*	UK	[58]
[2] *Moniliformis moniliformis* (Bremser, 1811)	C	*E. roumanicus* *E. concolor*	Russia Georgia	[104] [55]
Plagiorhynchus cylindraceus (Goeze, 1782) (Syn.: *Plagiorhynchus formosus* Van Cleave, 1918), *Prosthorhynchus rosai* (Porta, 1910))	H, [7] NZ	*E. europaeus* *E. europaeus* *E. europaeus*, *E. roumanicus*	UK Germany Czech Republic	[59,61,145,146] [59,146] [34,81,99]
Plagiorhynchus gracilis (Petrotschenko, 1958), juv.	P	*E. roumanicus*	Ukraine	[147]
Plagiorhynchus sp. (Syn.: *Prosthorhynchus* Kostylev, 1915)	-	*E. europaeus* *E. europaeus*	UK Spain	[28] [77]
Sphaerirostris picae (Rudolphi, 1819) (Syn.: *Sphaerirostris teres* (Rudolphi, 1819)), juv.	P	*E. roumanicus*	Ukraine	[147]

Note: D—geographical distribution, [1]—Europe, [2]—helminth species found in Russia, [3]—Palaearctic, [4]—helminth species found in our study, [5]—Holarctic, [6]—Cosmopolitan, [7]—New Zealand.

In addition, Mariacher [76] noted in *E. europaeus* an unidentified acanthocephalan species in Italy. Liatis [87] registered unidentified species of trematode and acanthocephalan in *E. roumanicus* in Greece.

Thirteen species of parasites are host-specific parasites of hedgehogs: the trematodes *B. erinacei*, *B. aetechini*, *B. mackoi*, cestode *H. erinacei*, nematodes *A. erinacei*, *E. tenuis*, *P. erinacei*, *C. striatum*, *C. lofocara*, *P. clausa*, *R. plagiostoma*, acanthocephalans *N. major*, and *O. erinacei*.

Other species of helminths are facultative (or accidental) parasites of hedgehogs. Thus, the trematodes *N. truncatum*, *R. exasperatum*, nematodes *P. winchesi*, *Porrocaecum* sp. (juv.) and *S. rytipleurites* parasitize other insectivore species. The nematode *T. retortaeformis* is a host-specific parasite of lagomorphs. Host-specific rodent parasites are the trematode *B. recurva*, the nematode *C. hepaticum*, and the acanthocephalan *M. moniliformis*. Small rodents are the obligate hosts of larval stages of the cestodes *V. mustelae* and *C. globifera*. The obligate hosts of the trematode *D. dendriticum*, the nematode *H. contortus* and the larval stage of the cestode *T. hydatigena*, are ungulates. Host-specific parasites of carnivores are the trematode *I. melis* and the nematode *E. aerophilus*. The nematode *T. spiralis* and larval stages of the trematode *A. alata*, cestodes *Mesocestoides* sp., *S. erinacei*, nematodes *T. nativa*, *P. sexalatus*, *A. strongylina*, *S. lupi* parasitize many species of vertebrates. The acanthocephalan *P. cylindraceus* is a common parasite of passerine birds. *Agamospirura minuta* is a common parasite of reptiles (mainly lizards). The metacercaria *S. falconis*, *S. sphaerula* and *S. strigis* commonly parasitize amphibians and colubrid snakes. The trematodes *Brachylaima* sp., *Dicrocoelium* sp., the nematodes *Trichuris* sp., *Monovaria* sp., *Ancylostoma* sp., *Gongylonema* sp., *Spirura* sp., the acanthocephalans *P. gracilis* (juv.), *Plagiorhynchus* sp. and *S. picae* (juv.) are accidental parasites of hedgehogs.

Most of the helminths (39 species) parasitize *Erinaceus* spp. in the Palearctic in mature forms. Fifteen species of parasites were noted in hedgehogs at the larval stage (Table 2). It should be noted here that the nematode *T. spiralis* was found in hedgehogs both at the adult (in the intestinal lumen) and larval (musculature) stages. Only one common helminth species, the nematode *P. clausa*, was found in all four hedgehog species studied in the Palearctic (Table 2). Nine species of helminths were found in three species of hedgehogs (the trematode *B. erinacei*, the cestode *H. erinacei*, the nematodes *A. erinacei*, *Aonchotheca* sp., *E. aerophilus*, *C. striatum*, *S. rytipleurites*, *Porrocaecum* sp., juv., and acanthocephalan *N. major*). Twelve helminth species parasitize two species of hedgehogs (the trematodes *Brachylaima* sp., *I. melis*, *A. alata* (msc.), *S. strigis* (mtc.), the metacestode *Mesocestoides* sp., the nematodes Capillariidae sp., *E. tenuis*, *C. hepaticum*, *T. spiralis*, *C. lofocara*, the acanthocephalans *M. moniliformis* and *P. cylindraceus*). Another 32 species of parasites are found in only a single hedgehog species (Table 2).

The greatest diversity was observed in hedgehog nematodes, represented by 28 species from 14 families: Capillariidae (7), Spirocercidae (3), Trichinellidae (2), Trichostrongylidae (2), Crenosomatidae (2), Spiruridae (2), Ascarididae (1), Trichuridae (1), Strongyloididae (1), Physalopteridae (1), Rictulariidae (1), Ancylostomatidae (1), Gongylonematidae (1), and Seuratidae (1) plus spirurid larva *A. minuta*. The trematode composition in *Erinaceus* spp. is less diverse, of which there are 14 species from 7 families: Dicrocoeliidae (4), Brachylaimidae (3), Strigeidae (3), Echinostomatidae (1), Plagiorchiidae (1), Troglotrematidae (1), and Diplostomidae (1). Cestodes and acanthocephalans are insignificantly represented in the helminth faunas of *Erinaceus* hedgehogs. Six species of cestodes from four families were registered in hedgehogs: Taeniidae (3), Diphyllobothriidae (1), Hymenolepididae (1), and Mesocestoididae (1). Acanthocephalans in the helminths of Palaearctic hedgehogs are represented by seven species from four families: Plagiorhynchidae (3), Oligacanthorhynchidae (2), Centrorhynchidae (1), and Moniliformidae (1).

Host-specific helminths of hedgehogs are widespread in the Palearctic region. The nematode *C. striatum* was found in *Erinaceus* spp. in 20 countries; the cestode *H. erinacei* and nematode *A. erinacei* in 17; the nematode *P. clausa* in 15; the trematode *B. erinaceid* in 10; the acanthocephalan *N. major* in 9. The parasite of carnivores *E. aerophilus*, which often parasitizes hedgehogs, was recorded in 11 countries (Table 2). Other parasite species are

less common in hedgehogs. A total of 22 species of helminths were recorded each in 2–8 countries. Twenty-five species of helminths are each found in only one country where hedgehog parasites were studied (Table 2).

3.3. Comparative Analysis of the Helminth Fauna of Erinaceus spp.

Among all the studied species of hedgehogs, *E. europaeus* and *E. roumanicus* have the richest helminth faunas. The helminth communities of the Northern white-breasted hedgehog in the Palaearctic include 36 species: 8 trematodes, 5 cestodes, 18 nematodes, and 5 acanthocephalans. The helminth fauna of *E. roumanicus* was studied in 10 European countries (Table 2). The helminth fauna of *E. europaeus* consists of 35 species: 10 trematodes, 3 cestodes, 18 nematodes, and 4 acanthocephalans. The parasitic worms of *E. europaeus* were studied in 17 countries. A significantly smaller number of parasite species was found in *E. concolor*: two trematodes, one cestode, seven nematodes, and two acanthocephalans. The helminths in *E. concolor* were studied in five countries. Only four nematode species were recorded in *E. amurensis*, inhabiting the eastern Palearctic. Parasites of this hedgehog species were studied in two countries (Table 2).

The helminth faunas of *E. europaeus* and *E. roumanicus* have an average degree of similarity according to the Jaccard index (0.37). The helminth compositions of *E. roumanicus; E. concolor*, *E. europaeus*; and *E. concolor* are less similar—0.30 and 0.24. The parasite fauna of *E. amurensis* has minimal similarity with the helminths of other *Erinaceus* hedgehogs: *E. europaeus* (0.08), *E. concolor* (0.07), and *E. roumanicus* (0.05).

The greatest richness of the helminth fauna in hedgehogs was in Russia and Belarus, where 17 species of parasites were found in each country (Table 2, Figure 1). Thirteen species of parasites were found in hedgehogs both in Italy and in Ukraine. Twelve species of parasitic worms were recorded in hedgehogs from the Czech Republic. Eleven helminth species were reported in hedgehogs in the UK, Germany, and Bulgaria, respectively; and, there were a reported 10 speciesin Spain and 9 speciesin Switzerland (Table 2, Figure 1).

The helminth communities in hedgehogs are relatively less diverse in Portugal, Greece, and Iran, where seven species of parasites were registered in each country. Six species of parasitic worms were noted in hedgehogs in Moldova, Turkey, and Poland, respectively; and, five helminth species were noted in Denmark, Slovakia, and Georgia. Four species of parasites were found in *E. concolor* from Armenia. Three helminth species were noted in hedgehogs in France, Serbia, and Japan, respectively. In the other seven countries, data on hedgehog parasites included only 1–2 species (Table 2, Figure 1).

Nematodes are found in *Erinaceus* spp. in all countries except Austria and Lithuania. Cestodes and trematodes were observed in hedgehogs in 20 and 18 studied regions, respectively. Acanthocephalans were found in *Erinaceus* spp. in 12 countries (Figure 1).

Half of the helminth species found in hedgehogs are widely distributed in the world; parasites have a cosmopolitan (13 species) and Palaearctic distribution (14 species). The distribution of eight species is limited to Europe. Seven species of hedgehog helminths have a Holarctic distribution. For 12 helminths, identified only to the genus level, distribution has not been established (Table 2).

We carried out a comparative analysis of the helminth faunas of *Erinaceus* spp. from various regions of the Palaearctic. The similarity dendrogram of the helminth faunas in four hedgehog species from various countries is shown in Figure 2.

The cophenetic correlation coefficient is 0.875, which confirms the validity of the cluster. As a result of the clustering analysis, the considered hedgehog species were divided into 10 groups, with the most similar helminth fauna (Figure 2). The first group is formed by the helminth faunas of *E. europaeus* from Lithuania and *E. concolor* from Armenia and Georgia. The greatest similarity in the first group was observed in the helminth fauna of *E. concolor* from Armenia and Georgia (0.44). The second group is formed by the helminth fauna of *E. europaeus* from Finland, Ireland, and France. Here, the greatest similarity was noted for hedgehog parasites from Finland and Ireland (0.67).

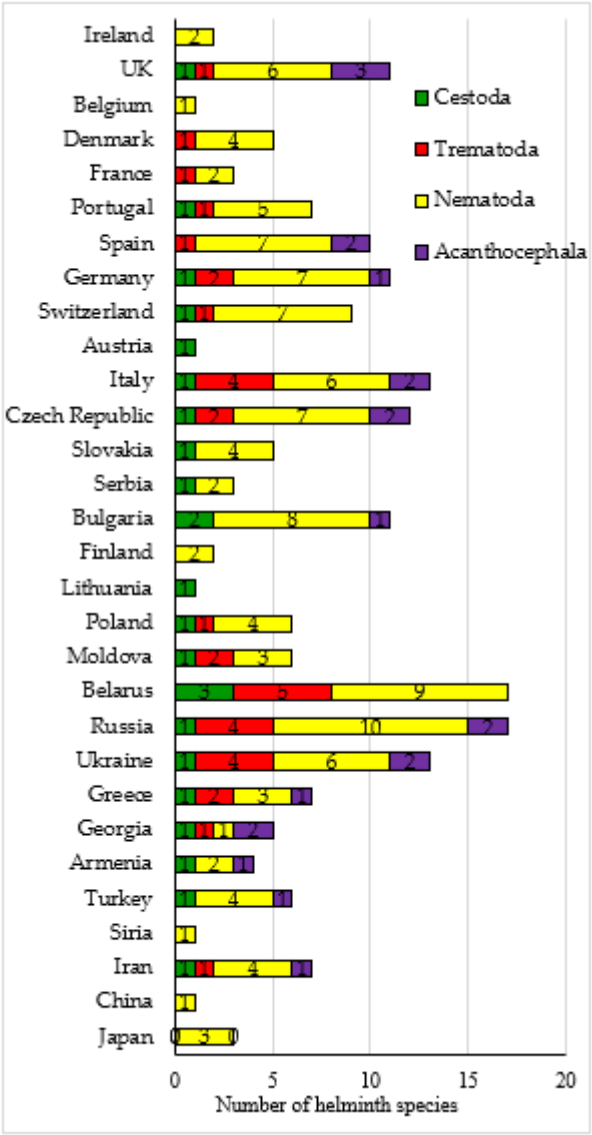

Figure 1. Species richness of helminths in hedgehogs of *Erinaceus* genus in Palaearctic region.

The third single-species group is formed by helminths of *E. roumanicus* from Moldova and Bulgaria (0.33). The fourth cluster is formed by the helminths of *E. europaeus* from the southern European countries: Spain, Portugal, and Italy. Between them, the greatest similarity was noted in the parasite composition of hedgehogs from Spain and Portugal (0.56) (Figure 2).

The fifth largest group is formed by the helminth faunas of three hedgehog species from 14 countries of the Western Palearctic (Figure 2). In this group, a high degree of similarity was noted for the parasite faunas of *E. roumanicus* and *E. europaeus*, from the same habitats in the Czech Republic (0.91), Poland (0.91), and Slovakia (0.89) (Figure 2).

The first five clusters are combined into one large group. Five separate single-species groups adjoin it (Figure 2). The sixth and the seventh clusters are formed by the helminth fauna of *E. amurensis* from China and Japan. The eighth cluster was formed by the parasite fauna of *E. europaeus* from Belgium. The ninth group is formed by *E. concolor* helminths in Syria. The helminth fauna of hedgehogs from clusters six to nine minimally overlaps with the parasite faunas of all other groups. The tenth and final cluster is formed by the helminth fauna of *E. europaeus* from Austria, which does not show any similarity with any others (Figure 2).

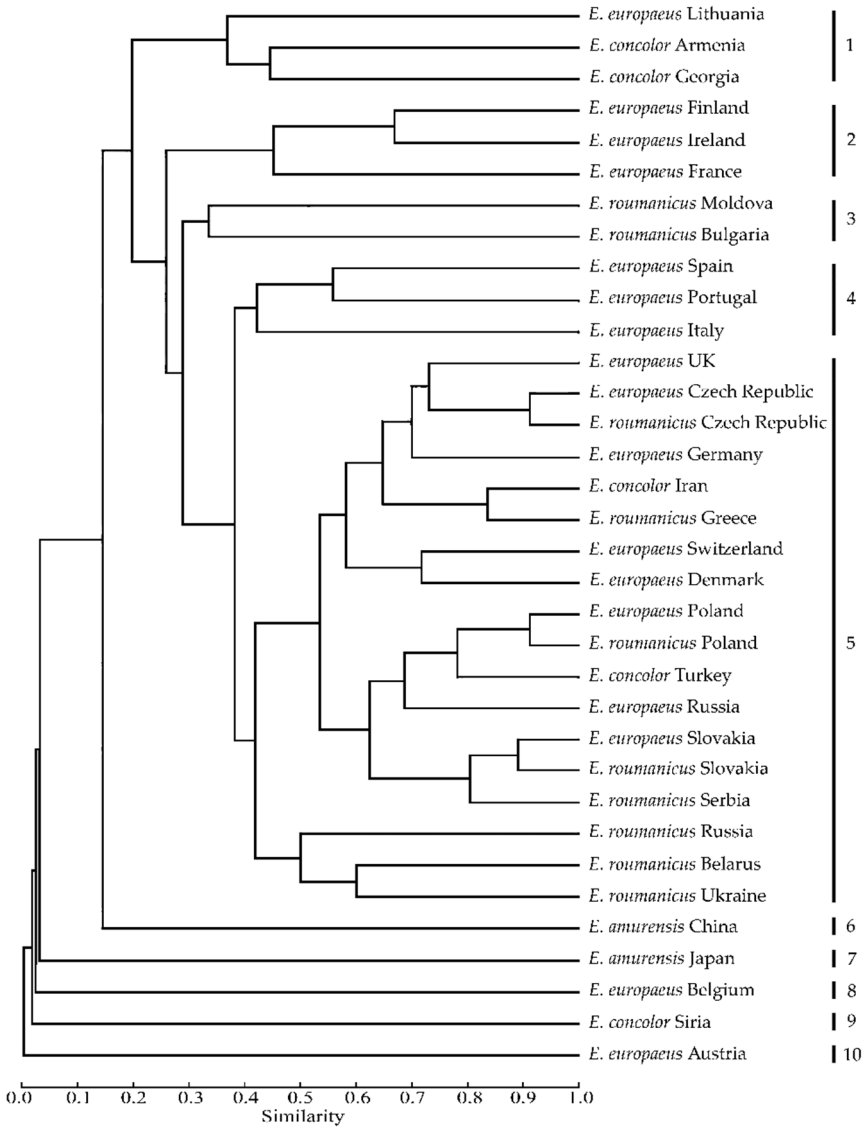

Figure 2. Similarity dendrogram of the helminth faunas in *Erinaceus* spp. from various countries, obtained by the Morisita index (UPGMA). Cophen. corr.: $r = 0.875$.

4. Discussion

The first study of the helminth fauna of *E. roumanicus* in Mordovia has noted nine species of parasites (Table 1). Most of the helminths (6 species) found in the hedgehogs of Mordovia parasitize at the mature stage. Three species (the trematode *S. strigis*, the nematodes *P. sexalatus*, and *A. minuta*) were found at the larval stage. Hedgehogs are paratenic and/or intermediate hosts for these parasites. Five species are host-specific parasites of hedgehogs: the cestode *H. erinacei*, the nematodes *A. erinacei*, *P. clausa*, *C. striatum* and the acanthocephalan *N. major*. Another four species are accidental (or unusual) parasites of hedgehogs.

Before our research, 13 species of helminths were noted in hedgehogs (*E. europaeus* + *E. roumanicus*) in European Russia (Table 2). Our studies of the helminth fauna of *E. roumanicus* in the Republic of Mordovia have added four species to the list of parasites in Russian hedgehogs: the trematode *I. melis*, the nematodes *P. sexalatus* (juv.), *A. minuta* (juv.), and the acanthocephalan *N. major*. According to both authors' and literature data, 17 species of helminths parasitize *Erinaceus* hedgehogs in Russia [49,52,104,106–108], this study.

We have also added one species to the list of helminths of the Palearctic hedgehogs, *A. minuta* (juv.). At the present stage of research, the fauna of parasitic worms of *Erinaceus*

spp. in the Palaearctic includes 54 species. Analysis of the helminth faunas of *Erinaceus* spp. showed that the richest species composition is in *E. europaeus* and *E. roumanicus*, less diverse in *E. concolor*, and extremely few helminths were found in *E. amurensis*. The degree of helminthological study of various hedgehog species in a particular region of the Palaearctic is of great importance here. Most helminthological studies have been carried out in Europe on the parasites of *E. europaeus* and *E. roumanicus*. There are very few articles on the helminths of *E. concolor* and *E. amurensis* (Table 2).

The following are some remarks on the taxonomy of parasites found in hedgehogs. The species *Capillaria ovoreticulata* Laubmeier, 1985 is diagnosed predominantly in hedgehogs in Germany and the UK. As Pfaffle [59] rightly noted, *A. erinacei* (former *Capillaria erinacei*) and *C. ovoreticulata* are morphologically difficult to distinguish. Since both species are very hard to distinguish, most authors refer to them as *Capillaria* spp. Meanwhile, Moravec [41] classifies this species as invalid because the description of the species has not been published [148]. We agree with the opinion of Moravec [41]. Molecular genetic studies are needed to confirm the validity of *Capillaria ovoreticulata*.

The finding of the cestode *Mathevotaenia parva* (Janicki, 1904) in hedgehogs in the Czech Republic is erroneous [99]. The cestode has been described as *Davainea parva* Janicki, 1904 in *Erinaceus* sp. from Cyprus [149], but this is a mistake since only one hedgehog species, *Hemiechinus auritus* (Gmelin, 1770) inhabits this island. According to Binkiene [102], *H. erinacei* is the only known species of cestodes parasitizing hedgehogs of *Erinaceus* genus, while *Mathevotaenia* cestodes can be detected in *Hemiechinus, Paraechinus*, and *Atelerix* hedgehogs only.

The findings of Nematollahi [140] in *E. concolor*, a parasite of the lungs and bronchi of small ruminants *Mullerius capillaris* (Mueller, 1889) (Protostrongylidae) and host-specific rodent parasite, *Hymenolepis diminuta* (Rudolphi, 1819) (Hymenolepididae), are also erroneous. Most likely, the authors dealt with common hedgehog parasites *C. striatum* and *H. erinacei*, previously recorded in hedgehogs in northern and northwestern Iran [85].

The diet and lifestyle of hedgehogs affect their helminth species composition. Hedgehogs get most of their helminths through food. Hedgehogs are omnivorous animals. But invertebrates are important food sources, including beetles (adult and larvae), earthworms, caterpillars and moth larvae, slugs, and snails [57,150,151]. In addition, the diet of hedgehogs includes amphibians; small reptiles; small mammals; birds, their young, and their eggs; and carrion [57].

The revealed helminth fauna confirms the omnivorous diet of *Erinaceus* hedgehogs. Hedgehogs get all species of trematodes and cestodes (except parasite larvae), acanthocephalans, as well as most species of nematodes (except nematodes with a direct life cycle) by eating invertebrates, which are intermediate and paratenic hosts of helminths.

The trematode *I. melis* develops with the involvement of the gastropod *Lymnaea stagnalis* (Linnaeus, 1758). Amphibians and freshwater fish are additional hosts for the parasite [152,153]. Infection of hedgehogs can occur both through gastropods and by eating amphibians [42,49,153,154].

The development of *H. erinacei* cysticercoids can occur in the intestinal villi of the final hosts, hedgehogs, and then pass into the intestine, where they grow to maturity [155]; and with the involvement of intermediate hosts, beetles *Nicrophorus humator* (Gleditsch, 1767), *Nicrophorus vespillo* (Linnaeus, 1758), *Oiceoptoma thoracicum* (Linnaeus, 1758) and *Geotrupes stercorarius* (Linnaeus, 1758) [156].

The mesocercariae *A. alata* and *Strigea* spp. hedgehogs probably also survive by feeding on amphibians, which are mesocercarial hosts of parasites [157]. It is less likely that hedgehogs become infected with these trematodes through aquatic gastropods, the intermediate hosts of diplostomids and strigeids, because the probability of encounters with terrestrial frogs and toads is much higher than with mollusks inhabiting the water.

The infection of *Erinaceus* spp. by the metacestodes *V. mustelae, T. hydatigena, C. globifera, S. erinacei*, and *Mesocestoides* sp. occurs through accidental ingestion of cestode eggs along with food [158].

Hedgehogs, as intermediate and paratenic hosts, are involved in the life cycles of helminths and can transmit infective parasite larvae along the food chains to the final hosts, birds of prey, and mammals. They potentially can become prey to red foxes (*Vulpes vulpes* (Linnaeus, 1758)), badgers (*Meles meles* (Linnaeus, 1758)), and other species of mustelid, wild boars (*Sus scrofa* Linnaeus, 1758), eagle owls (*Bubo bubo* (Linnaeus, 1758)) and tawny owls (*Strix aluco* Linnaeus, 1758) [16,62,159–161]. The involvement of hedgehogs as intermediate and paratenic hosts in the helminth life cycles plays an important role in the distribution and conservation of parasites in the wild; and it increases the infection probability of the final hosts (carnivores and birds of prey).

Hedgehogs become infected with the specific parasite *P. clausa* by eating the beetles of the family Scarabaenidae [32]. At the larval stage, *P. clausa* is a common parasite of reptiles, mainly lizards. Reptiles are paratenic hosts of the nematode. In the Middle Volga region, we found the parasite in the final host—*E. roumanicus*, in paratenic hosts—insectivores (*Sorex araneus* Linnaeus, 1758), and reptiles [51,108,162–165].

The common food of *Erinaceus* spp. is mollusks (mainly slugs and snails)—intermediate hosts of the highly specific parasite of hedgehogs, the nematode *C. striatum* [3,166]. So, the mollusks *Radix balthica* (Linnaeus, 1758), *Morlina glabra* (Rossmassler, 1835), *Succinea putris* Linnaeus, 1758, *Urticicola umbrosus* (Pfeiffer, 1828), *Arion circumscriptus* Johnston, 1828, *Malacolimax tenellus* (Muller, 1774) and *Tandonia rustica* (Millet, 1843) are registered as intermediate hosts of the nematode [167].

The close contact between hedgehogs and soil and forest litter causes their infection with capillariids, nematodes with a direct lifestyle. The nematode *E. aerophilus* can be transmitted to hedgehogs directly, as well as when eating earthworms [130]. The development of *A. erinacei* is associated with the terrestrial environment and it can happen both directly and with the involvement of paratenic hosts: terrestrial gastropods and earthworms *Lumbricus terrestris* Linnaeus, 1758 and *Aporrectodea rosea* (Savigny, 1826) [130,166,168].

The host-specific hedgehog's parasite, *N. major*, also develops with the involvement of intermediate hosts, represented by terrestrial Isopoda and Coleoptera. Paratenic hosts, such as fish, amphibians, reptiles, and mammals, may be involved in the life circle of acanthocephalans [40,169].

A comparative analysis of the helminth species composition in *Erinaceus* spp. from various countries showed, on the one hand, the originality of the parasite faunas of each hedgehog species and, on the other, the similarity of the helminth communities of *Erinaceus* spp. from various regions of the Palaearctic. The originality of the helminth fauna of hedgehogs is achieved by parasitizing them with accidental or non-specific helminths or locally distributed helminths. Thus, in *E. europaeus* and *E. roumanicus*, 15 species of parasites were noted in each, which are not found in other species of hedgehogs. The trematode *B. recurva* was found only in *E. concolor*, and the nematode *Monovaria* sp. in *E. amurensis* (Table 2). As a result, the average and low degree of similarity index of the helminth faunas of various species of *Erinaceus* was noted according to the Jaccard index.

The similarity of the helminth fauna of hedgehogs in certain studied regions is defined as a wide distribution of specific helminth species of *Erinaceus* spp. (*C. striatum*, *H. erinacei*, *A. erinacei*, *P. clausa*, and others) and the geographical proximity of study areas. Thus, the highest similarity was noted in the helminth composition of various hedgehog species from the same territory: *E. europaeus* and *E. roumanicus* from the Czech Republic, Poland, and Slovakia; as well as hedgehogs from Serbia and Slovakia (0.75–0.86), Germany and Switzerland (0.70), the Czech Republic and Germany (0.70) (Figure 2).

A high similarity in the helminth fauna of hedgehogs from countries far from each other was noted only when comparing the parasites of one species of hedgehogs (in *E. europaeus* from Finland and Ireland—0.67). As a rule, the helminth faunas of various species of hedgehogs from distant countries have a low similarity (*E. europaeus* from Spain and *E. roumanicus* from Russia—0.50, *E. europaeus* from Russia and *E. roumanicus* from Bulgaria—0.30) (Figure 2).

A total of 12 of the 54 helminth species found in hedgehogs in the Palaearctic have medical and veterinary significance as potential pathogens of dangerous helminthiasis. These include the trematodes *A. alata* (causes alariosis in humans and domestic animals), *D. dendriticum* (dicrocoeliosis in humans and domestic ruminants, dogs, and cats), the cestode *S. erinacei* (spirometrosis and sparganosis in humans and domestic animals), *Mesocestoides* sp. (mesocestidosis in domestic and wild carnivores), *T. hydatigena* (taeniasis and cysticercosis in dogs and wild carnivores), the nematodes *E. aerophilus* (pulmonary capillariasis in humans and wild carnivorous and omnivorous mammals), *T. spiralis* and *T. nativa* (trichinellosis in humans and domestic and wild mammals), *Ph. sexalatus* (physocephalosis in domestic pigs and wild boars), *H. contortus* (haemonchosis of ruminants), *A. strongylina* (ascaropsosis in domestic pigs and wild boars) and *S. lupi* (spirocercosis in domestic and wild carnivores) [170–177]. It should be noted that transmission of these parasites to humans and domestic animals from hedgehogs is unlikely. However, the involvement of hedgehogs in the life cycles of dangerous helminth species increases the possibility of transmission of parasites to their final hosts. In this way, hedgehogs contribute to the conservation of zoonotic foci in the wild.

5. Conclusions

The helminth fauna of the Northern white-breasted hedgehog *Erinaceus roumanicus* was studied for the first time in the Republic of Mordovia (Russia). In total, we found nine species of helminths in hedgehogs. Of them, four species were noted in Russian hedgehogs for the first time: the trematode *I. melis*, nematodes *P. sexalatus* (juv.), *A. minuta* (juv.), and the acanthocephalan *N. major*.

According to our research and literature data, the helminth fauna of *Erinaceus* spp. in the Palaearctic includes 54 species: 14 trematodes, 8 cestodes, 27 nematodes, and 7 acanthocephalans. Among all the studied species of hedgehogs, *E. europaeus* (35 species) and *E. roumanicus* (36) have the richest helminth faunas. The diversity of the parasite communities of *Erinaceus* spp. is due to the wide distribution and varied diet of these mammals. Most of the helminths found in hedgehogs are transmitted to them along trophic chains. Hedgehogs are the final hosts for 39 species of parasites. For 15 helminth species, *Erinaceus* spp. are paratenic and/or intermediate hosts. The base of the hedgehog helminth fauna is formed by host-specific parasites, of which there are only 13 species. Most of the hedgehog parasites in the Palaearctic are facultative (non-specific) species that parasitize in various vertebrates. The comparative analysis of the helminth faunas of *Erinaceus* spp. from various countries showed, on the one hand, the originality of the helminth fauna of each hedgehog species and, on the other, the similarity of the helminth fauna of these insectivores from various regions of the Palearctic. These features are caused by similar lifestyles and diet peculiarities of every hedgehog species in various regions. A total of 12 of the 54 helminth species found in hedgehogs in the Palaearctic region have medical and veterinary significance as causative agents of dangerous helminthiasis, including the trematodes *D. dendriticum*, *A. alata*, the cestodes *T. hydatigena*, *S. erinacei*, *Mesocestoides* sp., and the nematodes *E. aerophilus*, *T. spiralis*, *T. nativa*, *H. contortus*, *P. sexalatus*, *A. strongylina* and *S. lupi*.

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