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Cestode Diversity of Shrews on the Kamchatka Peninsula and Paramushir Island

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Abstract: The aim of this study was to assess the taxonomic diversity and prevalence of shrew cestodes on the Kamchatka Peninsula and Paramushir Island on the basis of current understanding of cestode taxonomy. The diversity of shrew cestodes included 22 species from three families: Hymenolepididae, Dilepididae, and Mesocestoididae. In Paramushir, the diversity of shrew cestodes was substantially lower than in Kamchatka (14 and 22, respectively). In Kamchatka, three genera of cestodes (*Novobrachylepis*, *Mathevolepis*, *Ditestolepis*) were not found, but three species from genera *Lineolepis*, *Staphylocystis*, and *Monocercus* are possibly new species. The potential for endemic species and the unique characteristics of the cestode fauna on Kamchatka suggest that the peninsula may have been a refugium for shrews and their parasites in the last glacial maximum. In Kamchatka and Paramushir, two Nearctic species (*Lineolepis parva* and *L. pribilofensis*) were found, which indicates potential dispersal from North America. Most cestode species in Kamchatka were associated with the host shrew *Sorex caecutiens*, while in Paramushir most cestodes were associated with *Sorex isodon*. In Paramushir, shrews had higher prevalence of infection with cestodes than in Kamchatka. The dominant cestode taxa in shrews on Paramushir Island were species rare in Kamchatka. Conversely, the most abundant cestode species in shrews on Kamchatka were absent from the island fauna.

Keywords: parasite; diversity; cestodes; shrews; *Sorex*; Kamchatka Peninsula; Paramushir Island

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1. Introduction

Kamchatka Peninsula, located in the extreme northeast of Asia, is distinguished by distinct geographical, climatic, and faunistic features [1]. Of the 12 shrew species recorded in the Russian Far East (*Sorex caecutiens* Laxmann, 1788; *S. camtschaticus* Yudin, 1972; *S. daphaenodon* Thomas, 1907; *S. gracillimus* Thomas, 1907; *S. isodon* Turov, 1924; *S. jacksoni* Hall et Gilmore, 1932; *S. leucogaster* Kuroda, 1933; *S. minutissimus* Zimmermann, 1780; *S. mirabilis* Ognev, 1937; *S. roboratus* Hollister, 1913; *S. tundrensis* Merriam, 1900; *S. unguiculatus* Dobson, 1890) [2], less than half of them have been found in Kamchatka (*S. caecutiens*, *S. camtschaticus*, *S. daphaenodon*, *S. isodon*, *S. minutissimus*) [3]. Paramushir Island was part of the Kamchatka Peninsula at the maximum of the last glaciation. Currently, only three shrew species inhabit the island (*S. caecutiens*, *S. isodon*, *S. leucogaster*) [4].

Parasitological research on shrews in Kamchatka was carried out at the end of the last and the beginning of the current century. These studies were mainly faunistic reviews [5–8] only partly surveying certain species of shrew cestodes [9,10]. Most Palearctic shrew cestodes belong to the families Hymenolepididae and Dilepididae. Recent updates to the taxonomic structure of these families based on both morphological and molecular genetic methods [11–23] have made it possible to revise our understanding of the species diversity of Palearctic shrew cestodes. The aim of our study was to summarize and revise the data on shrew cestodes in Kamchatka and Paramushir Island, and to evaluate the

richness and prevalence of infection of shrew cestodes in these territories on the basis of current taxonomy.

2. Materials and Methods

The shrews (203 specimens) were collected in July–August 2002, 2007, and 2009 and examined by the method of incomplete helminthological dissection [24]. The animals were from the following locations in the Kamchatka Peninsula: in the vicinities of settlements Esso (55°56′ N, 158°42′ E), Yelizovo (53°11′ N, 158°22′ E), Pinachevo (53°21′ N, 158°23′ E), in the caldera Uzon (54°30′ N, 160°01′ E), and on Paramushir Island (50°41′ N, 156°07′ E). As Yelizovo and Pinachevo are located less than 20 km from each other, data on these points were combined. A collection of shrew cestodes (from 197 shrews) gathered in 1982 by S.V. Karpenko [5] in the area of Azhabachye Lake (56°10′ N, 161°55′ E) was included in the analysis (Figure 1). The skulls of the shrews are stored in the Mammal Collection of the Institute of Biological Problems of the North FEB RAS (IBPN, Magadan, Russia) with field number labels NED No/Year (N.E. Dokuchaev) and VDG No/Year (V.D. Gulyaev), and in the Mammal Collection of the Institute of Systematics and Ecology of Animals (ISEA SB RAS, Novosibirsk, Russia) with field number labels SVK No (S.V. Karpenko) (Appendix A).

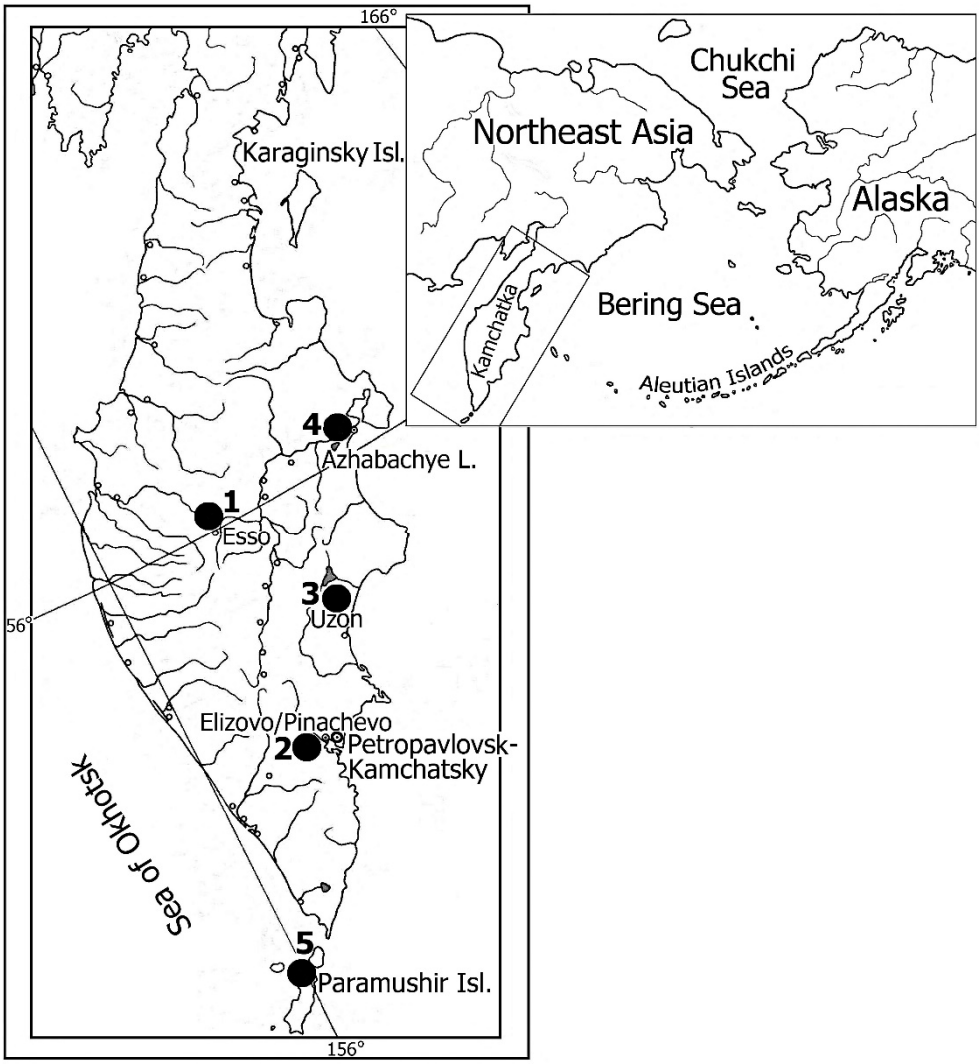

Figure 1. Collection sites of shrew cestodes on Kamchatka and Paramushir Island: 1—Esso, 2—Yelizovo/Pinachevo, 3—Uzon, 4—Azhabachye Lake area, 5—Paramushir Island.

Data on the species composition and number of shrews examined at each site (excluding S.V. Karpenko's data) are given in Figure 2.

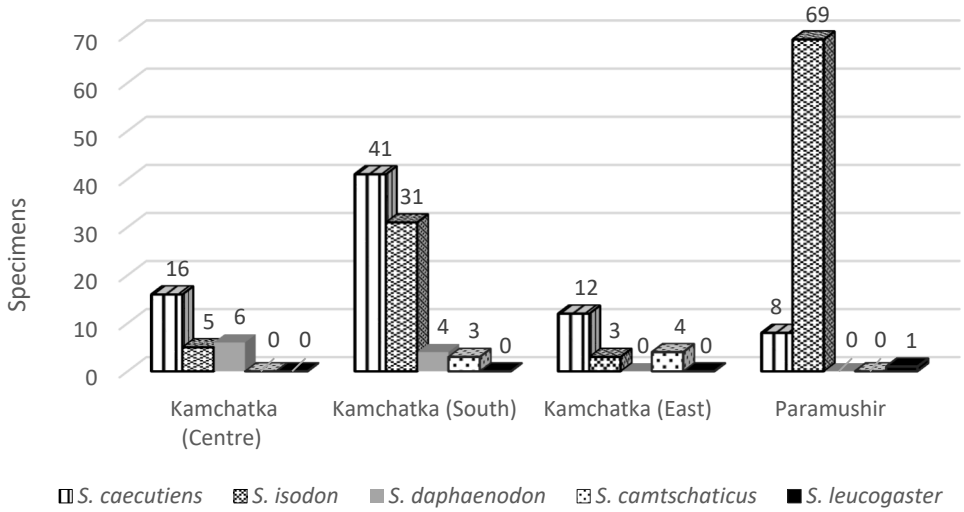

Figure 2. The number of shrews *Sorex* studied in Kamchatka and Paramushir Island.

Helminths found in the intestines of animals were fixed in 70% ethanol. Cestodes were stained with Ehrlich's hematoxylin and differentiated with a 3% aqueous solution of ferric ammonium sulphate 12-hydrate. Then, they were dehydrated in an ethanol series, cleared in clove oil, and mounted in Canadian balsam. Some fragments of strobila were mounted in Berlese's medium to facilitate detailed examination of the cirrus armature and the copulatory apparatus. The slides of the mounted specimens were studied using standard light and Axiolab phase-contrast microscopy at ×1000 magnification.

Total and voucher specimens of helminths (our collection, as well as 101 slides from the Karpenko' collection) were deposited in the helminthological collection of the Institute of Systematics and Ecology of Animals (ISEA SB RAS, Novosibirsk, Russia) (Appendix B).

The structure of dominance of the studied shrew cestode assemblages was assessed using the following indicators [25]: P—prevalence (percentage of individuals of host population infected with a certain helminth species) and its standard error (±E). The analysis did not assess prevalence for *S. daphaenodon*, *S. camtschaticus*, and *S. leucogaster* because of the small sample size.

3. Results

3.1. Species Diversity of Shrews Cestodes of Kamchatka Peninsula and Paramushir Island

The shrew communities from the studied sites of Kamchatka differ based on the distribution of different shrew species on the territory of the peninsula and their biotopic preferences. Two species of shrews dominate the shrew communities in Kamchatka: *Sorex caecutiens* and *S. isodon* (Figure 2). Only a few specimens of *S. daphaenodon* and *S. camtschaticus* were captured here, which does not allow us to evaluate the prevalence of infection or the importance of the species as hosts of cestode species on the peninsula. On Paramushir Island, *S. isodon* was the most abundant host species, and only eight specimens of *S. caecutiens* and one *S. leucogaster* were collected there.

As a result of the inventory of the shrew helminths in Kamchatka and Paramushir Island, cestodes of 22 species from 12 genera and three families (Hymenolepididae Perrier, 1897; Dilepididae Fuhrmann, 1907; and Mesocestoididae Perrier, 1897) were found (Table 1). Two species (*Dilepis undula* and *Mesocestoides lineatus*) were represented by larval stages of development. *D. undula* larvae were found in the intestine and *M. lineatus* in the body cavity.

Table 1. The occurrence of shrew cestodes at different sites in Kamchatka and Paramushir Island.

Cestode Species	Kamchatka				Paramushir
	Esso	Azhabachye	Uzon	Yelizovo/Pinachevo	
Family Dilepididae Fuhrmann, 1907					
Dilepis undula (larva) (Schrank, 1788) Weinland, 1858	+	-	-	+	+
Monocercus baicalensis (Eltyshev, 1971) Gulyaev and Kornienko, 1998	+	+	+	+	+
Monocercus sp.	+	+	-	+	+
Family Hymenolepididae Perrier, 1897					
Ecrinolepis collaris (Karpenko, 1984) Gulyaev, 1991	-	+	+	+	-
Lineolepis parva Rausch and Kuns, 1950	+	+	+	+	+
L. pribilofensis Olsen, 1969	+	-	-	+	+
L. skrjabini Spassky and Morosov, 1959	-	+	-	+	-
Lineolepis sp.	-	-	-	+	-
Neoskrjabinolepis corticirrosa Kornienko, Gulyaev and Melnikova, 2007	-	+	+	+	-
N. kedrovensis Kornienko, Gulyaev and Melnikova, 2007	+	+	-	+	+
N. longicirrosa Kornienko, Gulyaev and Melnikova, 2006	+	+	+	+	+
N. nadtochijae Kornienko, Gulyaev and Melnikova, 2006	+	+	-	+	+
Pseudobothrialepis mathevossianae Schaldybin, 1957	+	+	-	+	+
Soricinia bargusinica Eltyschev, 1975	-	+	-	+	-
S. infirma (Zarnowsky, 1955) Czaplinski and Vaucher, 1994	-	+	-	+	-
S. quarta (Karpenko, 1983) Karpenko, 1999	+	+	-	+	+
Spasskylepis ovaluteri Schaldybin, 1964	+	+	+	+	+
Staphylocystis sibirica (Morosov, 1957) Spassky and Andrejko, 1970	+	+	-	+	+
Staphylocystis sp.	+	-	-	+	-
Staphylocystoides spasskii (Karpenko, 1984)	+	-	-	-	+
Urocystis prolifer Villot, 1880	-	-	-	+	-
Family Mesocestoididae Perrier, 1897					
Mesocestoides lineatus (larva) (Goeze, 1782)	+	-	+	+	+
The number of species	15	15	7	21	14

Currently, out of the 50 species of the shrew cestodes registered in the Russian Far East, less than half (22 species) have been found in Kamchatka and Paramushir Island. This is also less than one third of the total species richness of tapeworms in the Palearctic, numbering about 70 species [11,26,27]. The reduced cestode richness is possibly related to the partial geographical isolation of the Kamchatka peninsula.

The core of the cestode fauna of Palearctic shrews in mainland Eurasia includes representatives of the hymenolepids of the tribe Ditestolepidini, which includes 24 species of eight genera of cestodes with serial and gradual maturation of strobila [20]. However, only two species of Ditestolepidini (*E. collaris* and *S. ovaliteri*) have been found in Kamchatka. Three other genera of Ditestolepidini (*Novobrachylepis*, *Mathevolepis*, *Ditestolepis*) are completely absent in Kamchatka, but are common in the population structure of the shrew cestodes in Yakutia, Western Siberia, and the south of the Russian Far East [5,6,20,28,29].

One of the speciose genera of tapeworms of the Palearctic shrew is the genus *Neoskrjabinolepis*. In the Far East of Russia, 9 out of the 16 currently known species in the genus are documented [13,15–17,28–32]. In Kamchatka, only four species (*N. corticorosa*, *N. longicirrosa*, *N. nadtochijae* and *N. kedrovensis*) have been recorded (Table 1). Of these, *N. corticirrosa* and *N. longicirrosa* are distributed throughout northeastern Asia, while *N. kedrovensis* is found only in the Far East and *N. nadtochijae* is found in the Far East and East Siberia [13,15–17,28,29,31]. Prior to the current study, *N. nadtochijae* was thought to be absent in Kamchatka [32].

Out of the nine species of the multispecies complex *Staphylocystoides*, a dominant genus in the cestode assemblages of Nearctic shrews [10,33,34], only one species, *S. spasskii*, was found in Kamchatka. Three species of the genera *Lineolepis* and *Soricinia* are recorded on the peninsula, and two of these species (*L. pribilofensis* and *L. parva*) are found on both sides of the Bering Strait, exhibiting a Holarctic distribution [32,35]. Earlier it was pointed out that only one species of the genus *Staphylocystis*, *S. furcata* (Stieda, 1862) Spassky, 1950, was previously known to parasitize shrews in Kamchatka [2,6,7,32]. We did not find this species in Kamchatka; instead, our survey identified the cestode *S. sibirica*.

In the studied area (Kamchatka and Paramushir) several cestodes representing the genera *Lineolepis*, *Monocercus,* and *Staphylocystis* differ morphologically from known taxa and appear to be new species, which will require confirmation by additional research.

The highest diversity of cestode taxa, 21 species belonging to 11 genera, was observed in the south of the Kamchatka peninsula. In the central part and on the eastern coast of the peninsula, species diversity was decreased to 15 species from 10 and 9 genera, respectively (Table 2).

Table 2. Distribution of cestodes in different shrew species in Kamchatka and Paramushir Island.

Cestode Species	Kamchatka				Paramushir		
	S. caecutiens	*S. isodon*	*S. camtschaticus*	*S. daphaenodon*	*S. caecutiens*	*S. isodon*	*S. leucogaster*
D. undula	+	+	-	+	-	+	-
E. collaris	+	+	-	+	-	-	-
L. parva	+	+	+	+	-	+	-
L. pribilofensis	+	-	+	-	+	+	+
L. skrjabini	+	+	+	+	-	-	-
Lineolepis sp.	+	-	-	-	-	-	-
M. lineatus	-	-	+	-	+	-	-
M. baicalensis	+	+	-	+	+	+	-
Monocercus sp.	-	-	-	+	-	+	-
N. corticirrosa	+	-	-	-	-	-	-
N. kedrovensis	+	-	-	+	+	+	-
N. longicirrosa	+	+	-	+	+	+	-
N. nadtochijae	+	+	-	-	+	+	-
P. mathevossianae	+	+	-	-	-	+	-
S. bargusinica	+	-	-	-	-	-	-
S. infirma	+	-	-	-	-	-	-
S. quarta	+	+	-	-	+	+	-
S. ovaluteri	+	+	-	-	+	+	-
S. sibirica	+	-	-	-	+	+	-
Staphylocystis sp.	+	-	-	+	-	-	-
S. spasskii	+	-	-	-	+	+	-
U. prolifer	+	+	-	-	-	-	-
The number of species	20	11	4	9	10	13	1

Several species, *S. ovaluteri*, *P. mathevossianae*, *M. baicalensis*, and *S. sibirica*, were found at all surveyed locations. At the same time, some species were only documented at single locations. For example, *U. prolifer* was only collected in the south, and *S. spasskii* was only collected in the central part of Kamchatka. Cestode *U. prolifer* is a transpalearctic species with high prevalence and abundance [36]. The low prevalence in Kamchatka was possibly related to the area border. It should be noted that the same genus of tapeworms in different parts of the peninsula can be represented by different species. For example, out of the three species of the genus *Lineolepis*, all three taxa (*L. parva*, *L. pribilofensis*, *L. skrjabini*) were found in the south of Kamchatka, while *L. pribilofensis* was not collected in the east and *L. skrjabini* was absent in the central part of peninsula. Additionally, three species of the genus *Soricinia* were represented in Kamchatka, but only *S. quarta* was recorded at all locations surveyed on the peninsula. Of the four species of the genus *Neoskrjabinolepis*, three species were recorded everywhere on the peninsula, but *N. corticirrosa* was absent from the central area.

On Paramushir Island, 10 out of the 12 genera of tapeworms reported from the region were found, and their species richness was one-third poorer than in Kamchatka (Table 1) due to the absence of six species: *E. collaris*, *L. skrjabini*, *N. corticirrosa*, *S. bargusinica*, *S. infirma*, and *U. prolifer*. These species, except for *L. skrjabini*, are ubiquitous in Siberia and the Russian Far East [6,28,29,37], while two species (*U. prolifer* and *S. infirma*) have a transpalearctic distribution [19,36]. On the island, the multispecies genus *Neoskrjabinolepis* was represented by three species (*N. longicirrosa*, *N. nadtochijae*, and *N. kedrovensis*), and the genus *Lineolepis* only by the North American species *L. pribilofensis* and *L. parva*.

The distribution of cestodes between different shrew species in the community of definitive hosts deserves special attention. Cestodes of shrews are characterized by wide host specificity, but at the same time, some species are only found in a particular species of shrews. In Kamchatka, the highest number of cestode species (20) was found in *S. caecutiens*, while *S. isodon* and *S. daphaenodon* had half as many species of cestodes (11 and 9, respectively) (Table 2). In *S. caecutiens* on Paramushir Island, there were half as many cestode species as in the same species in Kamchatka (10). The checklist of tapeworms in *S. caecutiens* in Kamchatka and Paramushir Island differs not only in the number of species but also in their taxonomic diversity. For example, cestodes of the genera *Lineolepis* and *Soricinia* are represented by three species each in *S. caecutiens* in Kamchatka, but only one species each on Paramushir (Table 2). In *S. isodon*, an almost equal number of cestode species were found in Kamchatka and Paramushir (11 and 13, accordingly) but the species were different. On Paramushir, representatives of the genus *Staphylocystis* were not found; out of four species of the genus *Neoskrjabinolepis* occurring in Kamchatka, only two were found, *N. nadtochijae* and *N. longicirrosa*; and only *S. quarta* was identified in the genus *Soricinia*. Cestodes of the genera *Staphylocystoides* and *Soricinia*, as well as species of *P. mathevossianae*, *S. ovaluteri*, and *U. prolifer* were not found in *S. daphaenodon*. Only representatives of the genus *Lineolepis* were registered in the endemic shrew species (*S. camtschaticus* and *S. leucogaster*). In the first host species were found *L. parva* and *L. skrjabini*, and in the second host *L. pribilofensis* only (Table 2).

3.2. Prevalence of Infection of Shrew Cestodes of Kamchatka Peninsula and Paramushir Island

Analysis of the prevalence of cestode infection found that about 70% of all shrew species in Kamchatka and 95% on Paramushir Island were infected with tapeworms (Table 3). The shrews *S. caecutiens* and *S. isodon* in Kamchatka were approximately equally infected (P = 72.5 ± 5.4% and 76.9 ± 6.7%, respectively) (Table 3). The highest rate of infection of shrews was registered in the south of Kamchatka; in its central and eastern parts, the infestation of animals was significantly lower, although sample sizes were also correspondingly lower in these areas (Table 3). *S. caecutiens* and *S. isodon* in the south of the peninsula were infected equally often (P = 87.8 ± 5.1% and 77.4 ± 7.5%, respectively). About 60% of infected *S. caecutiens* occurred in the central part of Kamchatka and only a quarter (3 out of 12 animals) in the eastern areas. In the central and eastern regions of the peninsula, only a few specimens of *S. isodon* (5 and 3, respectively) were collected;

however, most of them (3 and 3, respectively) were infected with cestodes. Almost all *S. daphaenodon* (9 out of 10) collected in the vicinity of Esso village (central Kamchatka) and in the vicinities of Yelizovo and Pinachevo villages (the south of the peninsula) were infected with cestodes. *S. camtschaticus* were infected much less frequently (2 out of 7). *S. isodon* on Paramushir Island exhibited higher prevalence of infection with cestodes than in Kamchatka. *S. caecutiens* on Paramushir Island was not numerous in 2007; however, cestodes were found in all eight specimens.

Table 3. The prevalence of shrews cestodes in Kamchatka and Paramushir (prevalence of infection and its standard error P ± SE, %); *—the small number of shrew specimens (the number of shrews with cestodes).

Shrew Species	Kamchatka				Paramushir
	Centre (Esso)	South (Yelizovo/Pinachevo)	East (Uzon)	Total	
S. caecutiens	62.5 ± 12.1	87.8 ± 5.1	25 ± 12.5	72.5 ± 5.4	8 (8) *
S. camtschaticus *	-	3 (1)	4 (1)	7 (2)	-
S. daphaenodon *	6 (5)	4 (4)	-	10 (9)	-
S. isodon	5 (3)	77.4 ± 7.5	3 (3) *	76.9 ± 6.7	94.2 ± 2.8
S. leucogaster *	-	-	-	-	1 (1) *

Of particular interest is the comparison of the structure of the cestode community of shrews in Kamchatka and Paramushir Island (Table 4). Cestode prevalence in Kamchatka ranged from approximately 1–50%, with *E. collaris*, *N. longicirrosa,* and *L. skrjabini* as the most prevalent species. On Paramushir, *S. ovaluteri* and *N. longicirrosa* were the most prevalent species at 46.1–47.4%, respectively, followed by *L. pribilofensis* and *L. parva* (P = 43.6 ± 5.6% and 37.2 ± 5.5%, respectively). In Kamchatka, *E. collaris* dominated, while it was absent on the island. Representatives of the genera *Neoskrjabinolepis*, *Lineolepis*, *Monocercus*, and *Spasskylepis* were the most abundant taxa in both regions. In Kamchatka and Paramushir different species of these taxa have higher prevalence. For example, the species *L. skrjabini*, which was often recorded in Kamchatka, was not recorded in Paramushir Island, where two other representatives of the *Lineolepis* genus, *L. parva* and *L. pribilofensis*, were among the most common species. In addition, the most common species of cestodes in Paramushir shrews were *N. longicirrosa*, *N. nadtochijae*, *S. ovaluteri,* and *Monocercus* sp. (Table 4), which were much less common in Kamchatka. For example, *N. nadtochijae*, *L. pribilofensis,* and *Monocercus* sp. were rare in Kamchatka (P = 5.4 ± 2.1%; 2.7 ± 1.5%; 0.9 ± 0.9%, respectively). At the same time, the some cestodes species demonstrated a lower prevalence both in Paramushir and Kamchatka. The species *S. sibirica*, *N. kedrovensis*, *P. mathevossianae,* and *D. undula* turned out to be equally rare in all the studied sites.

Despite the greater species diversity of shrew cestodes in Kamchatka compared to Paramushir Island (22 and 14, respectively), Paramushir Island had a higher prevalence of infection than the peninsula. For example, the prevalence of such species as *L. parva*, *L. pribilofensis*, *N. longicirrosa*, *N. nadtochijae*, *Monocercus* sp., and *S. ovaluteri* were several times higher on Paramushir than in Kamchatka (Table 4).

In particular, comparison of the diversity and prevalence of cestodes of *S. isodon* on Paramushir Island and Kamchatka found that insular *S. isodon* demonstrated not only a greater number of cestode species (13 and 11, respectively), but also a higher prevalence (Table 4). Two species, *N. longicirrosa* and *L. parva*, were common dominant species in Kamchatka and Paramushir. However, *M. baicalensis*, which is dominant in *S. isodon* in Kamchatka, was not as common on Paramushir, and *L. skrjabini* was not recorded on the island at all.

Table 4. Cestode infections of *S. caecutiens* and *S. isodon* in Kamchatka and Paramushir (P ± SE, %), *—cestodes found in *S. isodon* in Kamchatka, **—cestodes found in *S. caecutiens* on Paramushir.

Cestode Species	Kamchatka					Paramushir
	S. caecutiens			*S. isodon*	Total	*S. isodon*
	Uzon	Esso	Yelizovo/Pinachevo	Yelizovo/Pinachevo		
D. undula	-	-	2.9 ± 2.8	16 ± 7.3	5.4 ± 2.1	6.4 ± 2.8
E. collaris	25 ± 12.5	50 ± 12.5 *	37.1 ± 8.2	8 ± 5.4	28.6 ± 4.3	-
L. parva	-	6.3 ± 6.1	5.7 ± 3.9	28 ± 8.9	12.5 ± 3.1	37.2 ± 5.5
L. pribilofensis	-	6.3 ± 6.1 *	-	-	2.7 ± 1.5	43.6 ± 5.6 **
L. skrjabini	-	6.3 ± 6.1 *	22.9 ± 7.1	23 ± 9.4	18.8 ± 3.7	-
M. baicalensis	-	6.3 ± 6.1 *	5.7 ± 3.9	32 ± 9.3	14.3 ± 3.3	15.4 ± 4.1 **
Monocercus sp.	-	-	-	-	0.9 ± 0.9 *	32.1 ± 5.3
N. corticirrosa	25 ± 12.5	12.5 ± 8.3	14.3 ± 5.9	-	8.9 ± 2.7	-
N. kedrovensis	-	12.5 ± 8.3	2.9 ± 2.8	-	3.6 ± 1.8	2.6 ± 1.8 **
N. longicirrosa	-	6.3 ± 6.1 *	31.4 ± 7.8	24 ± 8.5	19.6 ± 3.8	47.4 ± 5.7 **
N. nadtochijae	-	-	14.3 ± 5.9	4 ± 3.9	5.4 ± 2.1	30.8 ± 5.2 **
P. mathevossianae	-	12.5 ± 8.3 *	-	-	2.7 ± 1.5	2.6 ± 1.8
S. bargusinica	-	6.3 ± 6.1	2.9 ± 2.8	-	1.8 ± 1.3	-
S. infirma	-	18.8 ± 9.8	11.4 ± 5.4	-	6.3 ± 2.3	-
S. quarta	-	6.3 ± 6.1 *	20 ± 6.8	12 ± 6.5	10.7 ± 2.9	17.9 ± 4.3 **
S. ovaluteri	16.7 ± 10.8 *	18.8 ± 9.8 *	14.3 ± 5.9	-	10.7 ± 2.9	46.1 ± 5.6 **
S. sibirica	-	-	2.9 ± 2.8	-	0.9 ± 0.9	2.6 ± 1.8 **
Staphylocystis sp.	-	12.5 ± 8.3	2.9 ± 2.8	-	6.3 ± 2.3	-
S. spasskii	-	6.3 ± 6.1	-	-	0.9 ± 0.9	14.1 ± 3.9 **
U. prolifer	-	-	5.7 ± 3.9	4 ± 3.9	2.7 ± 1.5	-

Analysis of the cestode infection of *S. caecutiens* in Kamchatka revealed the same cestode species richness in the south and central regions of the peninsula (16 and 15, respectively), but their prevalence differed significantly (Table 4). In all the studied localities of Kamchatka, *E. collaris* dominated. At the same time, the cestode *N. longicirrosa* dominated along with *E. collaris* in the south. The species *L. skrjabini*, *S. ovaliteri*, *N. nadtochijae*, *N. corticirrosa,* and *S. infirma* were the next most common species. Other species were classified as rare or very rare. In the central regions of the peninsula, most than half of the species (8 out of 15) were quite rare, and six species were fairly common (*N. corticirrosa*, *N. kedrovensis*, *S. infirma*, *S. ovaliteri*, *P. mathevossianae,* and *Staphylocystis* sp.).

4. Discussion

The first data on shrew cestodes in Kamchatka were presented by S.V. Karpenko [5]. In 1982, he examined 197 specimens of six shrew species (*S. caecutiens*, *S. daphaenodon*, *S. isodon*, *S. cinereus* (=*S. camtschaticus*), *Sorex* sp., and *Neomys fodiens* Pennant 1771) collected in the neighborhood of Azhabachye Lake on the east coast of the peninsula (Figure 1). There are doubts concerning correct identification of these shrew species. For instance, the Eurasian water shrew *N. fodiens* does not inhabit Kamchatka. Moreover, about one-third of the collected shrews were not identified to species. In total, S.V. Karpenko found 10 cestode species in shrews: *Ditestolepis diaphana* (Cholodkowsky, 1906) Soltys, 1952;

E. collaris; *L. skrjabini*; *Molluscotaenia baicalensis* (Eltyshev, 1971); *Neoskrjabinolepis singularis* (Cholodkowsky, 1912) Spassky, 1954; *P. mathevossianae*; *S. bargusinica*; *S. quarta*; *S. soricis* (Baer, 1925) Spassky, 1954; and *S. furcata* [5].

During the revision of S.V. Karpenko's collection, erroneous identifications of cestodes were found, and species not included in his list were added. Thus, the specimens identified as *D. diaphana* actually belonged to the morphologically close species *S. ovaluteri*. In our material, *D. diaphana* was not recorded in shrews in either Kamchatka or Paramushir. Therefore, the report of *D. diaphana* in Kamchatka should be considered erroneous. *Soricinia soricis* and *Staphylocystis furcata* are also misidentified species. The cestode *S. soricis* is parasitic only in European shrews [19], and the specimens identified by S.V. Karpenko as *S. soricis* were in fact *S. infirma*. The cestode *Staphylocystis furcata* was redefined as *Staphylocystis sibirica*. In addition, the collection contained several specimens of cestodes that we had assigned to the genus *Staphylocystis*, whose species identity could not be determined due to their poor condition (a strong degree of strobila maceration and the absence of scolex and rostellar apparatus).

According to S.V. Karpenko [5], each of the genera *Neoskrjabinolepis* and *Lineolepis* contained only one species (*N. singularis* and *L. skrjabini*, respectively). However, in his collection, along with the species *L. skrjabini*, we also found a North American species, *L. parva*. *N. singularis* was not actually in Karpenko's collection. This species parasitizing shrews in the western part of the Palearctic has not been recorded east of Baikal Lake [8,10]. We found, instead of *N. singularis,* the complex of four species of *Neoskrjabinolepis*, *N. corticirrosa*, *N. kedrovensis*, *N. longicirrosa*, and *N. nadtochijae*, in the collections of S.V. Karpenko. In addition, the systematic position of the species *Molluscotaenia baicalensis* has been clarified. After the transfer of the genus *Molluscotaenia* to a synonym of the genus *Monocercus* [38], all its species were transferred to the latter, and the species *M. baicalensis* was named *Monocercus baicalensis*. In addition to the species *M. baicalensis*, we found a cestode with a number of morphological features (in particular, the length and shape of rostellar hooks) differing from the already known species of the *Monocercus* genus, which gives us ground to assume that this cestode is a new species. Thus, the revision of the collection of shrew cestodes from Kamchatka allowed us not only to clarify the species list of cestodes compiled by S.V. Karpenko [5], but also to increase it from 10 to 15 tapeworm species.

Fifty species of cestodes have been recorded in shrews in the Russian Far East, which is the greatest species richness compared to other regions of the Palearctic [5,11,27,29]. In Kamchatka and Paramushir Island, to date, 22 species of tapeworms have been identified, with 15 being common to both territories. The fauna of shrew cestodes on Paramushir Island is significantly depleted in comparison with Kamchatka. One-third of species recorded in the south of Kamchatka are absent on the island (Table 1). These results have confirmed the general trends observed in the parasite fauna of most isolated populations (of the island fauna) of small mammals associated with a poorer species diversity of parasites. At the same time, there is a high infestation rate with certain species of parasites [39–46]. At the same time, the structure of the insular community is distinctly different. Despite the lower cestode species richness on Paramushir, the shrews here were reliably more often infected with cestodes, as evidenced by both high values of the overall prevalence and by infection with the particular cestode species. For instance, on Paramushir Island, there were no *E. collaris* and *L. skrjabini*, which in Kamchatka were the most prevalent species. On the other hand, the most prevalent cestode species on the island were rare in Kamchatka. The peculiarity of this cestode community is also demonstrated by the dominant position of *S. ovaluteri*, which is rare in other helminth assemblages of the Palearctic shrews [29,47,48].

One of the most important results of this study is the finding of three hymenolepidids of the genus *Lineolepis*: *L. parva*, *L. pribilofensis,* and *L. skrjabini* [6,32]. Cestode *L. pribilofensis* was the only species recorded in shrews from the Beringian Islands (the Pribilof Islands) [45,49]. The presence of the first two Nearctic species in the south of Kamchatka and on Paramushir Island indicates early Pleistocene introduction of these cestodes from North America by the forest form of the shrew, now represented by *S. camtschaticus* [50].

This fact confirms the existence of shrew cestodes with an all-Beringian range and the presence of Quaternary exchanges through the Beringian land bridge by the shrew parasites between Western and Eastern Beringia [32,51].

The multispecies genus *Neoskrjabinolepis*, represented in Kamchatka by four species and on Paramushir Island by three, deserves special interest. Two species (*N. corticorosa* and *N. longicirrosa*) are distributed throughout Northeastern Asia, while the species *N. nadtochijae* and *N. kedrovensis* were previously known only in the south of the Russian Far East and in Yakutia. This is the first record of *N. nadtochijae* in Kamchatka.

The finding of *Mesocestoides lineatus* larvae in shrews on Paramushir Island confirms the role of these insectivores in the transmission of the parasite in predatory mammals [52]. On Paramushir, this occurs primarily through the red fox (*Vulpes vulpes* L., 1758) as the definitive host.

The predominance of *S. caecutiens* in Kamchatka and *S. isodon* on Paramushir Island, as well as the high degree of infection in the animals, allows us to conclude that these two species make the main contribution to helminth communities of shrews in the region. Shrews on Paramushir Island in our study were infected with cestodes much more often than in Kamchatka, which confirms the data obtained earlier [46].

5. Conclusions

Out of the 50 species of cestodes reported from shrews in the Far East of Russia, 22 species from 12 genera in Kamchatka and 15 species from 10 genera on Paramushir Island were found. The fauna of shrew cestodes on Paramushir Island is considerably depleted in comparison with Kamchatka. Representatives of the three genera *Novobrachylepis*, *Mathevolepis*, *Ditestolepis*, commonly found as parasites of shrew communities in Yakutia, Western Siberia, and the South of the Russian Far East, are absent in Kamchatka. On the other hand, three potentially new species designated as *Lineolepis* sp., *Staphylocystis* sp., and *Monocercus* sp. have been discovered here. The distinctness of this parasite fauna may indicate the isolation of shrews over time in a Kamchatkan refugium.

Finding two Nearctic species *L. parva* and *L. pribilofensis* in shrews in Kamchatka and Paramushir Island testifies to the possibility of Quaternary exchanges between the shrew parasites of the Western and Eastern Beringia.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Mammal Collection of the Institute of Biological Problems of the North FEB RAS (IBPN, Magadan, Russia) with field number labels NED No/Year (N.E. Dokuchaev) and VDG No/Year (V.D. Gulyaev), Mammal Collection of the Institute of Systematics and Ecology

of Animals (ISEA SB RAS, Novosibirsk, Russia) with field number labels SVK No/Year (S.V. Karpenko).
RUSSIA, Kamchatka Peninsula, the vicinities of the settlement Esso:
Sorex caecutiens (NED42/2002, 52/2002, 53/2002, 54/2002, 57/2002, 60/2002, 65/2002, 66/2002, 71/2002, 76/2002, 77/2002, 79/2002, 81/2002, 87/2002, 88/2002, 93/2002),
Sorex daphaenodon (NED49/2002, 51/2002, 61/2002, 62/2002, 63/2002, 64/2002).
Sorex isodon (NED50/2002, 58/2002, 78/2002, 80/2002, 82/2002).
RUSSIA, Kamchatka Peninsula, the vicinities of the settlement Yelizovo:
Sorex caecutiens (VDG7/2002, 8/2002, 10/2002, 12/2002, 13/2002, 16/2002, 17/2002, 18/2002, 19/2002, 20/2002, 23/2002, 24/2002, 25/2002).
Sorex daphaenodon (VDG2/2002).
Sorex isodon (VDG1/2002, 3/2002, 4/2002, 5/2002, 6/2002, 9/2002, 11/2002, 14/2002, 15/2002, 21/2002, 22/2002).
RUSSIA, Kamchatka Peninsula, the vicinities of the settlement Pinachevo:
Sorex caecutiens (NED180/2007, 183/2007, 184/2007, 199/2007, 202/2007, 203/2007, 209/2007, 219/2007, 221/2007, 222/2007, 223/2007, 224/2007, 232/2007, 234/2007, 235/2007, 236/2007, 237/2007, 242/2007, 247/2007, 248/2007, 249/2007, 261/2007, 263/2007).
Sorex camtschaticus (NED182/2007, 233/2007, 264/2007).
Sorex daphaenodon (NED181/2007, 201/2007, 220/2007, 260/2007).
Sorex isodon (NED185/2007, 186/2007, 197/2007, 198/2007, 205/2007, 206/2007, 226/2007, 227/2007, 238/2007, 239/2007, 240/2007, 252/2007, 253/2007, 254/2007, 255/2007).
RUSSIA, Kamchatka Peninsula, caldera Uzon:
Sorex caecutiens (NED27/2009, 28/2009, 29/2009, 30/2009, 33/2009, 34/2009, 35/2009, 37/2009, 38/2009, 39/2009, 40/2009, 42/2009).
Sorex camtschaticus (NED24/2009, 25/2009, 26/2009, 41/2009).
Sorex isodon (NED31/2009, 32/2009, 36/2009).
RUSSIA, Kamchatka Peninsula, Azhabachye Lake:
Sorex caecutiens (SVK 1/1982, 2/1982, 4/1982, 7/1982, 8/1982, 10/1982, 14/1982, 17/1982, 33/1982, 36/1982, 59/1982, 64/1982, 81/1982, 118/1982, 120/1982, 125/1982, 177/1982, 185/1982, 187/1982, 208/1982, 212/1982, 214/1982, 216/1982, 230/1982, 240/1982, 250/1982, 259/1982, 270/1982, 272/1982, 278/1982, 281/1982, 288/1982, 304/1982, 356/1982, 405/1982, 408/1982, 415/1982, 418/1982, 430/1982, 454/1982).
Sorex isodon (SVK 3/1982, 5/1982, 6/1982, 15/1982, 22/1982, 56/1982, 97/1982, 101/1982, 158/1982, 211/1982, 232/1982, 237/1982, 248/1982, 255/1982, 284/1982, 305/1982, 341/1982, 342/1982, 345/1982, 347/1982, 397/1982, 400/1982, 445/1982)
Sorex daphaenodon (SVK 252/1982, 302/1982, 393/1982, 395/1982).
Sorex camtschaticus (SVK 25/1982, 27/1982, 425/1982, 450/1982, 451/1982).
Sorex sp. (SVK 11/1982, 12/1982, 13/1982, 24/1982, 18/1982, 19/1982, 20/1982, 21/1982, 23/1982, 24/1982, 65/1982, 69/1982, 70/1982, 75/1982, 105/1982, 119/1982, 126/1982, 127/1982, 135/1982, 141/1982, 155/1982, 165/1982, 171/1982, 179/1982, 234/1982, 235/1982, 247/1982, 258/1982, 289/1982, 290/1982, 325/1982, 350/1982, 351/1982, 353/1982, 370/1982, 374/1982, 394/1982, 412/1982, 413/1982, 432/1982, 435/1982, 436/1982).
RUSSIA, Paramushir Island:
Sorex caecutiens (NED 132/2007, 138/2007, 139/2007, 140/2007, 141/2007, 149/2007, 150/2007, 152/2007).
Sorex isodon (NED7/2007, 8/2007, 9/2007, 10/2007, 11/2007, 12/2007, 13/2007, 14/2007, 15/2007, 17/2007, 18/2007, 19/2007, 31/2007, 32/2007, 33/2007, 34/2007, 35/2007, 36/2007, 37/2007, 38/2007, 40/2007, 41/2007, 53/2007, 54/2007, 55/2007, 56/2007, 57/2007, 58/2007, 59/2007, 60/2007, 67/2007, 68/2007, 69/2007, 72/2007, 73/2007, 74/2007, 75/2007, 76/2007, 77/2007, 78/2007, 85/2007, 86/2007, 87/2007, 102/2007, 103/2007, 104/2007, 105/2007, 106/2007, 107/2007, 108/2007, 109/2007, 110/2007, 111/2007, 112/2007, 126/2007, 127/2007, 128/2007, 129/2007, 133/2007, 134/2007, 135/2007, 136/2007, 137/2007, 151/2007, 153/2007, 154/2007).
Sorex leucogaster (NED148/2007).

Appendix B

The helminthological collection in the Institute of Systematics and Ecology of Animals (ISEA SB RAS, Novosibirsk, Russia), NED Number of slide/field number labels/Year (N.E. Dokuchaev), VDG Number of slide/field number labels/Year (V.D. Gulyaev), SVK Number of slide/field number labels/Year (S.V. Karpenko)

RUSSIA, Kamchatka Peninsula, the vicinities of the settlement Esso:

Sorex caecutiens (NED 2/42/2002, 1–3/53/2002, 1/54/2002, 1/57/2002, 1/66/2002, 1/71/2002, 1/76/2002, 1/81/2002, 1–2/88/2002, 1/93/2002),

Sorex daphaenodon (NED 1/51/2002, 1/61/2002, 1/62/2002, 1/63/2002, 1/64/2002).

Sorex isodon (NED 1/58/2002, 2/80/2002, 1/82/2002).

RUSSIA, Kamchatka Peninsula, the vicinities of the settlement Yelizovo:

Sorex caecutiens (VDG 1/8/2002, 1–2/10/2002, 1/13/2002, 1/16/2002, 1/17/2002, 1/19/2002, 1/20/2002, 1/23/2002, 1/24/2002, 1–2/25/2002).

Sorex daphaenodon (VDG 1/2/2002).

Sorex isodon (VDG 1/1/2002, 1–2/3/2002, 1/6/2002, 1–49/2002, 1/11/2002, 1/14/2002, 1/15/2002, 1/22/2002).

RUSSIA, Kamchatka Peninsula, the vicinities of the settlement Pinachevo:

Sorex caecutiens (NED 1/180/2007, 1/183/2007, 1/184/2007, 1/199/2007, 1/202/2007, 1/203/2007, 1/219/2007, 1/221/2007, 1/222/2007, 1/223/2007, 1/224/2007, 1/232/2007, 1/234/2007, 1–7/235/2007, 1/236/2007, 1/237/2007, 1/242/2007, 1/247/2007, 1/249/2007, 1/261/2007, 1/263/2007).

Sorex camtschaticus (NED 1–5/264/2007).

Sorex daphaenodon (NED 1/181/2007, 1/201/2007, 1/260/2007).

Sorex isodon (NED 1–8/185/2007, 1–2/186/2007, 1–2/198/2007, 1/206/2007, 1–3/226/2007, 1/227/2007, 1–4238/2007, 1/240/2007, 1/253/2007, 1/254/2007, 1/255/2007).

RUSSIA, Kamchatka Peninsula, caldera Uzon:

Sorex caecutiens (NED1/27/2009, 1–3/39/2009, 1/42/2009)

Sorex camtschaticus (NED1/24/2009).

Sorex isodon (NED1/31/2009, 1/36/2009).

RUSSIA, Kamchatka Peninsula, Azhabachye Lake:

Sorex caecutiens (SVK 7/1982, 10/1982, 17/1982, 33/1982, 36/1982, 59/1982, 81/1982, 118/1982, 120/1982, 125/1982, 208/1982, 212/1982, 214/1982, 216/1982, 230/1982, 240/1982, 259/1982, 270/1982, 272/1982, 278/1982, 281/1982, 288/1982, 304/1982, 356/1982, 405/1982, 408/1982, 430/1982, 454/1982).

Sorex isodon (SVK 22/1982, 56/1982, 97/1982, 101/1982, 158/1982, 211/1982, 232/1982, 237/1982, 248/1982, 305/1982, 341/1982, 342/1982, 397/1982)

Sorex camtschaticus (SVK 25/1982, 27/1982)

Sorex daphaenodon (SVK 302/1982, 395/1982)

Sorex sp. (SVK 11/1982, 12/1982, 24/1982, 70/1982, 75/1982, 105/1982, 119/1982, 141/1982, 234/1982, 235/1982, 247/1982, 258/1982, 289/1982, 290/1982, 325/1982, 350/1982, 351/1982, 353/1982, 370/1982, 394/1982, 412/1982, 413/1982, 432/1982, 435/1982, 436/1982)

RUSSIA, Paramushir Island:

Sorex caecutiens (NED 1/132/2007, 1–4/138/2007, 1/139/2007, 1/140/2007, 1/141/2007, 1/149/2007, 1–3/150/2007, 1–2/152/2007).

Sorex isodon (NED1–6/7/2007, 1–3/8/2007, 1–3/9/2007, 1–2/10/2007, 1–3/11/2007, 1/12/2007, 1–4/13/2007, 1–3/14/2007, 1–3/15/2007, 1/17/2007, 1/18/2007, 1/19/2007, 1/31/2007, 1/32/2007, 1/33/2007, 1/34/2007, 1/35/2007, 1/36/2007, 1/37/2007, 1/38/2007, 1/40/2007, 1/41/2007, 1/53/2007, 1/54/2007, 1/55/2007, 1/56/2007, 1–14/57/2007, 1/58/2007, 2/59/2007, 1/60/2007, 1/67/2007, 1/68/2007, 1/69/2007, 1/72/2007, 1/73/2007, 1–2/74/2007, 1–4/75/2007, 1/76/2007, 1/77/2007, 1/78/2007, 1/85/2007, 1/86/2007, 1/87/2007, 1/102/2007, 1–2/103/2007, 1/104/2007, 1/105/2007, 1/106/2007, 1/107/2007, 1/108/2007, 1–3/109/2007, 1/110/2007, 1/111/2007, 1/112/2007, 1–2/126/2007, 1/127/2007, 1–2/128/2007, 1/129/2007, 1/133/2007, 1/134/2007, 1/135/2007, 1–4/136/2007, 1/137/2007, 1/151/2007, 1/153/2007, 1–3/154/2007).

Sorex leucogaster (NED 1/148/2007).

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