Journal of Helminthology

www.cambridge.org/jhl

Cestode diversity in shrews from islands in the Sea of Japan and the Sea of Okhotsk

S.A. Kornienko[1] and N.E. Dokuchaev[2]

[1]Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Frunze Str. 11, Novosibirsk 630091, Russia and [2]Institute of Biological Problems of the North, Far East Branch of the Russian Academy of Sciences, Portovaya Str. 18, Magadan 685000, Russia

Research Paper

Cite this article: Kornienko SA and Dokuchaev NE (2024). Cestode diversity in shrews from islands in the Sea of Japan and the Sea of Okhotsk. *Journal of Helminthology*, **98**, e46, 1–10
https://doi.org/10.1017/S0022149X24000324.

Received: 29 January 2024
Revised: 02 April 2024
Accepted: 08 May 2024

Keywords:
islands fauna; Eulipotyphla; richness; tapeworms

Corresponding author:
S.A. Kornienko;
Email: swetlanak66@mail.ru

Abstract

A comparative analysis of taxonomic diversity on shrew cestodes among four islands in the Sea of Japan and the Sea of Okhotsk (Sakhalin, Kunashir, Hokkaido, and Moneron) was performed. Cestode species shared among the islands were identified and their host specificity was investigated. On Sakhalin Island, 33 species of the families Hymenolepididae, Dilepididae and Mesocestoididae were recorded in four shrew species (*Sorex caecutiens*, *S. gracillimus*, *S. minutissimus* and *S. unguiculatus*). In *S. caecutiens*, *S. gracillimus*, and *S. unguiculatus* on Kunashir Island, 22 species of the same families were found and, on Hokkaido Island, 23 species of the families Hymenolepididae and Dilepididae were recorded. On Moneron Island, three species of cestodes were registered in *S. tundrensis*. The Sakhalin–Hokkaido–Kunashir complex of shrew cestodes includes eastern-Palearctic, trans-Palearctic and endemic species. High endemism (~22%) of shrew tapeworms in the Sakhalin–Kunashir–Hokkaido Islands was noted as compared to continental territories. The different numbers of cestode species in *S. unguiculatus* (31), *S. caecutiens* (29), *S. gracillimus* (19) and *S. minutissimus* (1) were found. It was concluded that the cestodes species diversity of shrews of Sakhalin–Kunashir–Hokkaido depended primarily on the history of island formation, their modern physical and geographical features, the abundance of definitive and intermediate cestodes hosts and, to a lesser extent, on the size and remoteness of the islands from the mainland and the diversity of host species.

Introduction

Two large islands, Sakhalin and Hokkaido, are washed by the waters of the Sea of Okhotsk and the Sea of Japan; Kunashir Island of the Kuril Chain are in the waters of the Sea of Okhotsk and the Pacific Ocean. Moneron Island is located in the Sea of Japan (Figure 1). The uniqueness of these islands is due to their extreme longitudinal geographical position, the diverse topography, differences in climatic conditions, the presence of warm and cold sea currents, and geological history. The islands' repeated connections to and separations from the mainland have been documented (Velizhanin, 1976; Millien-Parra & Jaeger, 1999; Pietsch *et al.*, 2003; Bogatov *et al.*, 2006). These factors determine the species diversity and geographic distribution of helminths of small mammals in this region.

Nine shrew species of the genus *Sorex* have been recorded in the south of the Russian Far East: *Sorex caecutiens* Laxmann, 1788, *S. daphaenodon* Thomas, 1907, *S. gracillimus* Thomas, 1907, *S. isodon* Turov, 1924, *S. minutissimus* Zimmermann, 1780, *S. mirabilis* Ognev, 1937, *S. roboratus* Hollister, 1913, S. *tundrensis* Merriam, 1900 and *S. unguiculatus* Dobson, 1890. Six of them inhabit Sakhalin Island: *S. caecutiens*, *S. daphaenodon*, *S. gracillimus*, *S. isodon*, *S. minutissimus* and *S. unguiculatus*) (Ochotina, 1977). On Kunashir and on the Japanese island Hokkaido, there are four species of shrews (*S. caecutiens*, *S. gracillimus*, *S. minutissimus*, and *S. unguiculatus*) (Grigoryev & Bashilov, 1988; Kostenko *et al.*, 2004; Ohdachi *et al.*, 2015). On the small Moneron Island, only *S. tundrensis* is found (Ochotina, 1976; Kostenko & Nesterenko, 2006).

Parasitologically, shrews of Northeast Asia, in particular Eastern Siberia and the Far East, have been studied quite well (Odnokurtsev & Karpenko, 1993; Melnikova *et al.*, 2003, 2005; Karpenko, 2004; Kornienko *et al.*, 2008a, b, 2014, 2018; Kornienko & Dokuchaev, 2023); the same is not true about the shrews of the islands of the Sea of Okhotsk and the Sea of Japan. Data about shrew cestodes from Sakhalin, Kunashir and Hokkaido were sampled at the end of the last century and at the beginning of the current century. These were either faunal summaries of cestodes (Sato *et al.*, 1988; Sawada & Koyasu, 1991, 1995; Sawada & Asakawa, 1992; Sawada & Kaneno, 1992; Sawada & Kobayashi, 1993; Karpenko, 1997; Sawada, 1999) or descriptions of new species (Sawada & Harada, 1990; Sawada & Koyasu, 1991; Karpenko, 1999; Lykova *et al.*, 2005, 2006; Zubova *et al.*, 2008a, b; Kornienko *et al.*, 2008a, 2023). This resulted in the assumption of high species diversity of shrew cestodes on these islands. The main objective of those studies was to inventory the available collections from the previously mentioned islands and to update the information in view of the modern concepts in taxonomy of the cestode families

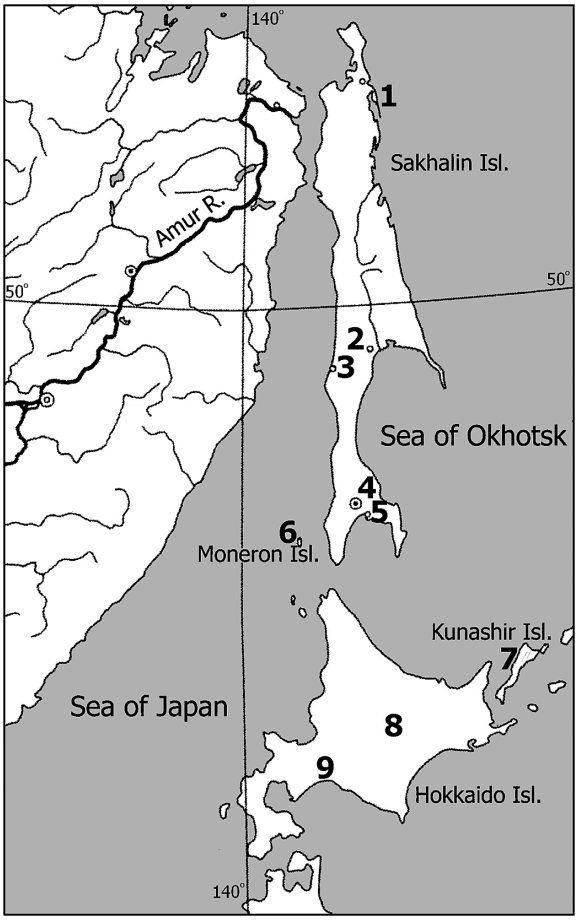

Figure 1. Sampling sites of shrew cestodes on islands Sakhalin, Hokkaido, Kunashir, and Moneron: 1: Cape Lebedinyi, 2: Poronaysky Nature Reserve, 3: Shakhtersk, 4: Sokol Biological Station, 5: Korsakov, 6: Moneron Island, 7: Kunashir Island, 8: Meto, 9: Tomakomai.

Hymenolepididae and Dilepididae (Gulyaev et al., 2007; Kornienko *et al.*, 2006, 2007, 2008a, 2016, 2019, 2023; Binkienė *et al.*, 2015; Neov *et al.*, 2019, 2021). Other interesting questions are associated with the comparison of the cestode fauna of mainland and islands, the dependence of the cestode fauna on the host-species diversity and abundance, as well as the role of the size of the islands and their remoteness from the continent for the parasite diversity.

The purpose of the present study is to analyze the data about the species diversity of cestodes parasitizing shrews on the islands in the Sea of Okhotsk and the Sea of Japan (Sakhalin, Kunashir, Hokkaido and Moneron). We present a comparative analysis of the taxonomic composition of shrew cestodes across the islands and the mainland. This allows us to identify cestode species shared among islands (or mainland) or endemic to certain islands as well as to study the effects of the size and remoteness of the islands and the diversity of hosts on the cestode diversity.

Materials and Methods

We carried out a helminthological study on shrews in the summer of 2005–2007 on the islands Sakhalin, Kunashir, Moneron, and Hokkaido (Figure 1).

On Sakhalin, shrews were analyzed in a northern part of the island (Cape Lebediniy, N 53°09′, E 143°13′), a central part of the island (Poronaysky Nature Reserve, N 49°13′ E 143°06′, and Shakhtersk town N 49°09′, E 142°06′) as well as in the southern part of the island (Sokol Biological Station [SBS], N 47°14′, E 142°46′, and environs of the towns Korsakov N 46°46’, E 143°00’ and Yuzhno-Sakhalinsk, N 47°01′, E 142°43′). We examined for cestodes 316 individuals of five species: *S. unguiculatus*, *S. gracillimus*, *S. caecutiens*, *S. minutissimus*, and *S. daphaenodon.*

On Kunashir Island, the materials were collected at cordons of the Kuril Nature Reserve (Rudniy N 44°22′, E 146°00′, Andreyevskiy N 43°53′, E 145°37′, Filatovskiy, N 44°11′, E 146°01′, and Ozerniy, N 43°52′, E 145°28′) in June–July 2006. We examined 119 individuals of three species for cestodes: *S. unguiculatus*, *S. gracillimus*, and *S. caecutiens.*

On Moneron Island (N 46°16′, E 141°14′) in 2005, only two individuals of *S. tundrensis* were captured and examined.

On Hokkaido Island, the specimens were collected in August 2005 in a central part (Meto: N 43°23′, E 143°20′) and a southwestern part (Tomakomai: N 42°37′, E 141°45′). We examined for cestodes 69 shrews: *S. unguiculatus*, *S. caecutiens*, and *S. gracillimus.*

Data on the number of shrew individuals studied are given in Table 1.

In addition, we reexamined the collection of cestodes from shrews sampled in 1989 by S.V. Karpenko in the Kuril Nature Reserve (Kunashir Island) in the vicinity of Golovnino Village (N 43°44′, E 145°31′) (Karpenko, 1997).

To compare species composition of cestodes among shrew species, we used the Jaccard Similarity Coefficient (Cj) (Magurran, 1988): $Cj = j/(a + b - j)$, where a is the number of species in the first set being compared, b is the number of species in the second compared set, and j is the number of species common between the two sets.

Results

In the shrews inhabiting islands Sakhalin, Kunashir, Hokkaido and Moneron, 36 species of cestodes were recorded. They belonged to three families Hymenolepididae Perrier, 1897, Dilepididae Fuhrmann, 1907, and Mesocestoididae Perrier, 1897. Among the studied islands, differences were found in both species diversity and number of taxa. Shrews from Sakhalin were parasitized by 33 cestode species, whereas those from Kunashir had 22, and those from Hokkaido were hosts to 23 species (Table 2). In two *S. tundrensis* individuals caught on Moneron Island, only three species of cestodes were detected (*M. baicalensis*, *N. nadtochijae*, and *S. furcata*). The species *Dilepis undula* and *Mesocestoides* sp. were registered as being in larval stages only. *D. undula* larvae were found in the intestine. *D. undula* is a parasite of birds, and shrews are considered as its abortive host. Larval forms of *Mesocestoides* sp. (parasitic as adults in intestines of carnivore mammals and birds of prey) occurred in the body cavity of shrews.

Our inventory of the shrew cestode collection from Sakhalin revealed 33 species of 19 genera of tapeworms (Zubova et al., 2008a) (Table 2). *Spalania crassisaccata* (=*Ecrinolepis crassisaccata*) was incorrectly identified earlier as *S. collaris* Karpenko, 1984 (=*Ecrinolepis collaris*), a species parasitizing shrews in Siberia and the Russian Far East (Karpenko, 1984, 2004; Odnokurtsev & Karpenko, 1993; Melnikova et al., 2003, 2005; Kornienko et al., 2014, 2018; Kornienko & Dokuchaev, 2023). On the studied islands, it had been replaced by the morphologically similar *S. crassisaccata.* Specimens previously identified as *Neoskrjabinolepis formosa* by Zubova et al., (2008a) were recognised by the present study as

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

Table 1. Numbers of studied shrews (*Sorex*) from islands Sakhalin, Kunashir, Hokkaido, and Moneron

Shrew species	Sakhalin			Hokkaido		Kunashir	Moneron
	North	Center	South	Center	South-West		
S. caecutiens	3	14	6	–	17	1	–
S. daphaenodon	–	1	–	–	–	–	–
S. gracillimus	–	26	15	–	11	15	–
S. minutissimus	–	–	4	–	–	–	–
S. tundrensis	–	–	–	–	–	–	2
S. unguiculatus	–	13	234	28	13	103	–
Total	3	54	259	28	41	119	2

Table 2. The occurrence of shrew cestodes in the south of the Far East of Russia and on islands Sakhalin, Kunashir, and Hokkaido

Cestode species	South of Far East of Russia	Sakhalin			Hokkaido				Kunashir
		North	Center	South	North	Center	Southwest	East	
Family Dilepididae Fuhrmann, 1907									
Dilepis undula (Schrank, 1788) Weinland, 1858, larva	–	–	–	+	–	–	–	–	–
Monocercus baicalensis (Eltyshev, 1971) Gulyaev & Kornienko, 1998	+	–	+	+	**	+**	+**	**	+*
Monocercus sp.	–	–	–	–	**	–	–	**	–
Polycercus paradoxa (Rudolphi, 1802)	+	–	+	+	–	+	–	–	+*
Family Hymenolepididae Perrier, 1897									
Ditestolepis diaphana (Cholodkowsky, 1906) Soltys, 1952	+	+	+	+	–	+	+	–	+*
Diorchilepis ezoensis Lykova, Gulyaev, Melnikova & Karpenko, 2006	–	–	+	+	–	**	–	**	+
Ecrinolepis longibursata (Morosov, 1957) Gulyaev, 1991	+	–	+	–	–	–	+	**	–
E. kontrimavichusi Melnikova, Lykova & Gulyaev, 2004	+	–	–	–	–	–	–	–	–
E. ezoensis (Sawada et Koyasu, 1995) Gulyaev, Zubova, Dokuchaev & Ohdachi, 2009	–	–	–	–	–	–	+**	–	–
E. macrospina (Karpenko, 1986) Gulyaev, 1991	+	+	+	+	–	–	–	–	–
E. orientales Melnikova, Lykova & Gulyaev, 2005	+	–	–	–	–	–	–	–	–
Lineolepis parva Rausch et Kuns, 1950	+	–	+	+	**	+**	+**	–	+*
L. skrjabini Spassky & Morosov, 1959	+	+	+	+	–	**	–	–	–
Lineolepis sp.	–	–	–	+	–	–	–	–	+*
Mathevolepis petrotschenkoi Spassky, 1948	+	–	–	–	–	–	–	–	–
M. junlanae Melnikova, Lykova & Gulyaev, 2005	+	–	–	–	–	–	–	–	–
M. skrjabini (Sadovskaja, 1965) Gulyaev & Karpenko, 1998	+	+	+	+	–	+	+	**	+
M. larbicus Karpenko, 1982	+	–	+	+	–	–	–	–	–
Neoskrjabinolepis corticirrosa Kornienko, Gulyaev & Melnikova, 2007	+	–	–	–	–	–	–	–	–
N. kedrovensis Kornienko, Gulyaev & Melnikova, 2007	+	–	+	+	**	+	+	–	–
N. kunashiriensis Kornienko & Gulyaev, 2011	–	–	+	+	**	+**	**	–	+*
N. longicirrosa Kornienko, Gulyaev & Melnikova, 2006	+	–	–	–	–	–	–	–	–
N. nadtochijae Kornienko, Gulyaev & Melnikova, 2006	+	–	+	+	–	+	–	–	+*
N. nana Kornienko & Gulyaev, 2011	–	–	+	+	–	–	–	–	+
N. nuda Kornienko, Gulyaev, Melnikova & Georgiev, 2008	–	–	+	+	**	+**	**	–	+*
N. paradoxa Kornienko, Makarikova & Dokuchaev, 2023	–	–	+	+	–	–	–	–	–

(*Continued*)

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

Table 2. (*Continued*)

Cestode species	South of Far East of Russia	Sakhalin			Hokkaido				Kunashir
		North	Center	South	North	Center	Southwest	East	
Novobrachylepis morosovi (Karpenko, 1993) Özdikmen, 2010	+	–	+	+	–	+	+	**	+*
N. triovaria (Karpenko, 1990) Özdikmen, 2010	+	–	–	–	–	–	–	–	–
N. sorextscherskii (Morosov, 1957) Özdikmen, 2010	+	–	+	+	–	–	–	–	–
Pseudobothrialepis mathevossianae Schaldybin, 1957	+	–	–	+	–	+	–	–	+*
Skrjabinacanthus diplocoronathus Spassky, Morosov, 1959	+	–	+	+	**	+**	+**	**	+*
S. jakutensis Spassky & Morosov, 1959	–	–	–	–	**	–	–	–	–
Soricinia bargusinica Eltyschev, 1975	+	–	+	+	–	–	–	–	+
S. infirma (Zarnowsky, 1955) Czaplinski & Vaucher, 1994	+	–	–	–	–	–	–	–	–
S. quarta (Karpenko, 1983) Karpenko, 1999	+	–	+	+	–	+	–	**	+*
S. sawadai Zubova, Gulyaev & Kornienko, 2010	–	–	+	+	–	–	–	–	–
Spalania collaris (Karpenko, 1984) Karpenko, 1998	+	–	–	–	–	–	–	–	–
S. crassisaccata (Sawada et Asakawa, 1992) Karpenko, 1998	–	–	+	+	**	+	–	–	+*
Spasskylepis ovaluteri Schaldybin, 1964	+	–	–	–	–	–	–	–	–
S. tiunovi Melnikova, Lykova & Karpenko, 2005	+	–	–	+	–	–	–	–	–
Staphylocystis amurensis Karpenko, 1984	+	–	–	–	–	–	–	–	–
S. furcata (Stieda, 1862) Spassky, 1950	+	–	+	+	**	+**	+**	–	+*
S. sibirica (Morosov, 1957) Spassky & Andrejko, 1970	+	–	+	+	–	–	–	–	+
Staphylocystis sp.	–	–	+	+	**	+**	+	–	+*
Staphylocystoides spasskii (Karpenko, 1984)	+	–	+	+	–	–	–	–	–
S. stefanskii Zarnowsky, 1954	+	–	–	–	–	–	–	–	–
Urocystis prolifer Villot, 1880	+	–	+	+	**	+**	**	**	+*
Family Mesocestoididae Perrier, 1897									
Mesocestoides sp., larva	+	–	–	+	–	–	–	–	*
The number of species	**35**	**4**	**28**	**32**	**12**	**19**	**14**	**9**	**22**
	35		**33**			**23**			**22**

*Shrew cestodes of Kunashir Island from Karpenko's collection (1997).
**Species of shrew cestodes from Hokkaido Island that have been found by Japanese authors (Sato et al., 1988; Sawada & Koyasu, 1991, 1995; Sawada & Asakawa, 1992; Sawada & Kaneno, 1992).

belonging to *N. kedrovensis*. The cestode genus that had the greatest number of species on Sakhalin was *Neoskrjabinolepis* (six species). The genera *Lineolepis*, *Soricinia*, and *Staphylocystis* were represented by three species each, and the genera *Ecrinolepis*, *Mathevolepis*, *Novobrachylepis*, and *Spalania* by two species each. The remaining genera were represented by one species each. Specimens of *Staphylocystis* and *Lineolepis* differed from the known species of these genera and were recognised as new species.

In the north of the Sakhalin Island, only three *S. caecutiens* individuals were caught, in which four species of cestodes were found (Table 2). In the southern and central parts of the island, 32 and 28 species of cestodes were found, respectively, and some differences in species composition were noted. These differences most likely were due to sample sizes from different parts of the island (259 specimens in the south and 54 specimens in the central part of the island). In the south of the island, *E. longibursata* was not found. Given that *E. longibursata* was recorded on central Sakhalin and Hokkaido, it can be supposed that this species might be present on southern Sakhalin, too.

Previously, we had found 18 species of cestodes of 14 genera in shrews in Hokkaido (Zubova et al., 2008b). The cestode genus having the greatest number of taxa on Hokkaido was *Neoskrjabinolepis* (four species) (Table 2). The genera *Ecrinolepis*, *Lineolepis*, *Skrjabinacanthus*, and *Staphylocystis* proved to be represented by two taxa each, whereas *Mathevolepis*, *Novobrachylepis*, and *Soricinia* were registered by one species each. Representatives of the genera *Spasskylepis* and *Staphylocystoides* were not found in Hokkaido. The analysis of some previous articles (Sato et al., 1988; Sawada & Koyasu, 1991, 1995; Sawada & Asakawa, 1992; Sawada & Kaneno, 1992; Sawada & Kobayashi, 1993) containing clear-cut photographs of cestodes allowed the expansion of the list of cestode species parasitizing shrews in Hokkaido to 23 taxa (Table 2). The number of cestode species on southwestern Hokkaido was almost 25% less than on central Hokkaido (14 and 19 species, respectively) (Table 2). The data published by Japanese parasitologists (Sato et al., 1988; Sawada & Koyasu, 1991; Sawada & Asakawa, 1992; Sawada & Kaneno, 1992) enabled us to estimate the species diversity of cestodes in

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

the north and east of the island, where 12 and 9 species, respectively, were recorded (Table 2).

Shrews of Kunashir were parasitized by 22 cestode species of 14 genera (Table 2). The collection contained larvae of *Mesocestoides* sp., which had not been mentioned before (Karpenko, 1997; Kornienko et al., 2008b). The most diverse cestode genera on Kunashir were *Neoskrjabinolepis* and *Staphylocystis* (four and three species, respectively). Most of cestode genera (*Lineolepis*, *Mathevolepis*, *Monocercus*, *Novobrachylepis*, and *Spalania*) were represented by one taxon (Table 2). Cestodes of the genera *Ecrinolepis*, *Spasskylepis*, and *Staphylocystoides* were not found on the island.

Of the 36 species of the cestode complex of shrews from Sakhalin–Hokkaido–Kunashir, fewer than half (15) of 13 genera were shared by all three islands (Table 2). On Sakhalin, the number of cestode species (33) was one-third greater than that on Kunashir and Hokkaido (22 and 23, respectively); this was due to the finding on Sakhalin of such mainland species as *E. macrospina*, *M. larbicus*, *N. sorextscherskii*, *S. tiunovi*, and *S. spasskii.* All the species parasitizing shrews of Kunashir were also registered on Sakhalin and amounted to 67% of the species diversity of Sakhalin. Between Hokkaido and Sakhalin, there were 20 common species (56%). Although the same number of cestode species had been recorded in Hokkaido and Kunashir shrews, only 17 species (61%) were shared between them.

A comparative analysis of species composition of shrew cestodes between the mainland (Primorsky Krai and Khabarovsk Krai) and the islands showed that 48 species of cestodes of 19 genera were registered on island and mainland; of them, one third (35%) were ubiquitous here (Karpenko, 1997; Melnikova et al., 2003, 2005; Kornienko et al., 2008b; Zubova et al., 2008a, b). Despite similar numbers of cestode species recorded in shrews on the mainland and on Sakhalin Island (35 and 33 species, respectively), these regions differed appreciably in taxonomic composition: fewer than half (23 taxa) were common between the mainland and Sakhalin (Table 2). Jaccard similarity coefficients for species complexes of shrew cestodes on the considered territories (Sakhalin versus mainland 0.51, Sakhalin vs. Hokkaido 0.56, Sakhalin vs. Kunashir 0.67, and Kunashir vs. Hokkaido 0.61) indicated comparable levels of similarity between the mainland and islands Sakhalin, Hokkaido, and Kunashir.

We performed a comparative analysis of the distribution of cestodes among three species of shrews (*S. caecutiens, S. gracillimus*, and *S. unguiculatus*) among the previously mentioned islands and found considerable differences. Insignificant sampling of the remaining shrew species made it impossible to include them in the analysis (Table 1). On the studied islands, the largest numbers of cestode species were recorded in *S. unguiculatus* (32) and *S. caecutiens* (29). In *S. gracillimus*, 19 cestode taxa were found. *S. unguiculatus* had the highest species diversity of cestodes on all islands (Table 3).

On Sakhalin, *S. unguiculatus* and *S. caecutiens* were infected by similar numbers of cestode species (30 and 26, respectively). Only

Table 3. Distribution of cestodes among shrew species (*Sorex*) on islands Sakhalin, Kunashir and Hokkaido (*Sc*: *Sorex caecutiens*; *Sg*: *S. gracillimus*; *Sm*: *S. minutissimus*; *Su*: *S. unguiculatus*)

	Sakhalin				Hokkaido			Kunashir		
Cestode species	Sc	Sg	Sm	Su	Sc	Sg	Su	Sc	Sg	Su
D. undula (larva)	–	–	–	+	–	–	–	–	–	–
D. diaphana	+	+	–	+	+	–	+	–	–	+
D. ezoensis	+	+	–	+	–	**	–	–	+*	+*
E. longibursata	+	–	–	–	–	**	+	–	–	–
E. ezoensis	–	–	–	–	+**	–	–	–	–	–
E. macrospina	+	+	–	+	–	–	–	–	–	–
L. parva	+	–	–	+	+	–	+**	–	–	+*
L. skrjabini	+	–	–	+	–	–	**	–	–	–
Lineolepis sp.	+	–	–	+	–	–	–	–	+	+
M. skrjabini	+	+	–	+	–	–	+**	–	+	+
M. larbicus	+	–	–	+	–	–	–	–	–	–
Mesocestoides sp. (larva)	–	–	–	+	–	–	–	–	–	*
M. baicalensis	+	+	–	+	–	–	+**	–	+	+
Monocercus sp.	–	–	–	–	–	–	**	–	–	–
N. kedrovensis	+	–	–	+	+**	–	+**	–	–	–
N. kunashiriensis	+	+	–	+	**	**	+**		+*	+*
N. nadtochijae	+	–	–	+	–	–	+	+	+*	+*
N. nana	–	+	–	–	–	–	–	–	+	–
N. nuda	+	+	–	+	**	**	+**	–	+*	+*
N. paradoxa	+	–	–	+	–	–	–	–	–	–
N. morosovi	+	+	–	+	+	–	+**	+	*	+*

(*Continued*)

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

Table 3. (*Continued*)

Cestode species	Sakhalin				Hokkaido			Kunashir		
	Sc	Sg	Sm	Su	Sc	Sg	Su	Sc	Sg	Su
N. sorextscherskii	+	–	–	–	–	–	–	–	–	–
P. paradoxa	–	–	–	+	–	–	+	–	–	+
P. mathevossianae	–	+	–	+	–	–	+	–	–	+*
S. diplocoronathus	+	+	+	+	+**	+**	+**	–	+	+*
S. jakutensis	–	–	–	–	–	**	–	–	–	–
S. bargusinica	+	–	–	+	–	–	–	–	–	+
S. quarta	+	+	–	+	–	–	+**	–	+	+*
S. sawadai	+	–	–	+	–	–	–	–	–	–
S. crassisaccata	+	+	–	+	–	–	+**	–	–	+*
S. tiunovi	–	+	–	+	–	–	–	–	–	–
S. furcata	+	+	–	+	+	–	+**	–	–	+*
S. sibirica	+	–	–	+	–	–	–	–	–	+
Staphylocystis sp.	–	–	–	+	+	–	+**	–	–	+
S. spasskii	+	–	–	+	–	–	–	–	–	–
U. prolifer	+	+	–	+	–	**	+**	–	*	+*
The number of species	**26**	**17**	**1**	**30**	**10**	**7**	**20**	**2**	**12**	**20**

*Shrew cestodes of Kunashir Island from Karpenko's collection (1997).
**Species of shrew cestodes from Hokkaido Island that have been found by Japanese authors (Sato et al., 1988; Sawada & Koyasu, 1991, 1995; Sawada & Asakawa, 1992; Sawada & Kaneno, 1992).

17 species were found in *S. gracillimus*. Fewer than half of the species of cestodes (13 species) used as definitive host all three species of soricids (Table 3). *S. unguiculatus* on Hokkaido and Kunashir were parasitized by the largest number (20) of cestode species. On Hokkaido in *S. caecutiens* and *S. gracillimus*, 10 and seven cestode species, respectively, were found. On Kunashir Island, *S. gracillimus* was a definitive host for 12 species, whereas *S. caecutiens* had only two (Table 3).

Most species of cestodes parasitized all three species of shrews, whereas a few cestodes species were found only in a single shrew species. *N. nana* was found only in *S. gracillimus* and the larval stages of *D. undula* and *Mesocestoides* sp. were detected only in *S. unguiculatus* (Table 3). On Hokkaido, only cestodes *N. kunashiriensis*, *N. nuda*, and *S. diplocoronathus* parasitized all three shrew species; one half of the species of cestodes was detected in *S. unguiculatus* alone. Cestodes *D. ezoensis* and *S. jakutensis* were found only in *S. gracillimus*, and the endemic *E. ezoensis* occurred only in *S. caecutiens* (Table 3). On Kunashir, only *N. nadtochijae* and *N. morosovi* were shared by all species of shrews and nine out of 20 cestode species were found in *S. unguiculatus* alone (Table 3).

Discussion

Data on species diversity of shrew cestodes on Sakhalin Island had remained very scarce until the beginning of this century. At the time, there was only one publication (Sawada & Kobayashi, 1993) on cestodes of soricid mammals of Sakhalin; that paper showed only three species of cestodes: *Ditestolepis longicirrosa* Sawada & Harada, 1990, *Neoskrjabinolepis singularis* (Cholodkovsky, 1912) Spassky, 1954 and *Soricinia japonica* Sawada & Koyasu, 1991. Our analysis of the drawings and descriptions of cestodes from that publication allowed us to clarify their taxonomic position. The photographs of *D. longicirrosa* presented by Sawada and Kobayashi (1993) as well as in the original description of the species (Sawada & Harada, 1990) actually match *Ecrinolepis longibursata*.

At the time of publication by Sawada and Kobayashi (1993), there was a longstanding discussion about the existence within the genus *Neoskrjabinolepis* of one or two species having a trans-Palearctic range (i.e., *N. singularis* and *N. schaldybini* Spassky, 1947 [Kornienko et al., 2023]). Later, we proved the validity of both species, and a further 15 species have been described within the genus (Kornienko et al., 2006, 2023). Additionally, it has been reported that *N. singularis* does not occur east of Transbaikalia (Kornienko et al., 2023). Photos of rostellar hooks of *N. singularis* and their size reported by Sawada and Kobayashi (1993) correspond to *N. kedrovensis*.

The original description of *Soricinia japonica* by Sawada & Koyasu (1991) was based on fragments of strobila of two species of the tribe Ditestolepidini, including a species with serial metamerism and a species with gradual metamerism; this led to an incorrect species diagnosis and to and assumption that this was a new species. Two photographs of the general view of the cestode presented by Sawada & Koyasu (1991) clearly illustrated the difference in the structure of the strobila. The left photo there showed a cestode with a gradual strobilar maturation corresponding to *Novobrachylepis morosovi*, and the right photo presented a strobila with serial maturation corresponding to *Mathevolepis skrjabini*. Therefore, Sawada and Kobayashi (1993) recorded four species of cestodes on Sakhalin: *E. longibursata*, *M. skrjabini*, *N. kedrovensis*, and *N. morosovi*. Later, several new cestode species have been described from Sakhalin shrews belonging to genera *Soricinia*, *Spasskylepis*, and *Neoskrjabinolepis*: *S. sawadai*, *S. tiunovi*, *N. nana*, and *N. paradoxa* (Lykova et al., 2005; Zubova et al., 2010; Kornienko & Gulyaev, 2011; Kornienko et al., 2023).

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

Until now, only two papers have been published presenting information about helminth fauna of soricid mammals on Kunashir (Karpenko, 1997; Kornienko et al., 2008b). *N. singularis* and *L. scutigera* are among the 11 species of cestodes found by Karpenko (1997) (Table 2, indicated with an asterisk). *N. kunashiriensis*, *N. nadtochijae*, and *N. nuda* have erroneously been reported under the name *N. singularis*. The cestodes earlier labelled as *L. scutigera* were identified by us as *L. parva*. Besides, we found a species of *Staphylocystis*, which is identical to a cestode from shrews of Sakhalin, which further studies may find to represent a new species.

In shrews from Hokkaido Island, 18 cestode species have been detected (11 of them described as new taxa). These are *Choanotaenia* sp. Sawada & Koyasu, 1991, *Coronacanthus parvihamatus* Sawada & Koyasu, 1990, *Ditestolepis cyclocephala* Sawada & Koyasu, 1991, *D. longicirrosa* Sawada & Harada, 1990, *D. ezoensis* Sawada & Koyasu, 1991, *D. crassisaccata* Sawada & Asakawa, 1992, *Hymenolepis magnirostellata* Sawada & Kaneno, 1992; *Insectivorolepis macracetabulosa* Sawada & Koyasu, 1991, *Sinuterilepis ezoensis* Sawada & Koyasu, 1995, *Soricinia japonica* Sawada & Koyasu, 1991, *Vampirolepis* sp. Sawada & Asakawa, 1992 (Sato et al., 1988; Sawada & Koyasu, 1991, 1995; Sawada & Asakawa, 1992; Sawada & Kaneno, 1992; Sawada, 1999). As a consequence, a belief has emerged about the high species diversity and high endemism of shrew cestodes on Hokkaido Island. Descriptions of some of these species have been superficial, with many inaccuracies, and have been accompanied by schematic drawings of segments or blurry photographs. Some of these articles are brief faunistic summaries of discovered cestodes, without reporting their morphological features. Several species were misidentified and reported by the same species name. Nonetheless, descriptions and photographs of several species presented by the above authors allowed to clarify the taxonomic position of several species. The cestode *Ditestolepis longicirrosa* described by Sawada and Harada (1990) matches the species *Ecrinolepis longibursata*. The species *Coronacanthus parvihamatus* described by Sawada and Koyasu (1990), is actually *U. prolifer*. In the next year, Sawada and Koyasu (1991) described several further new species: *Ditestolepis ezoensis*, *Insectivorolepis macracetabulosa*, and *Soricinia japonica*. Later, *D. ezoensis* was found in shrews of Sakhalin, redescribed and transferred to the genus *Diorchilepis* erected for it (Lykova et al., 2006). *I. macracetabulosa* has been recognised as a synonym of *Soricinia quarta* (Zubova et al., 2010).

Sawada and Koyasu (1991) found a cestode of the genus *Choanotaenia* at the juvenile stage of development. The absence of morphological characteristics (except for the number and size of rostellar hooks and other features) did not permit to identify this cestode. Currently, the cestode species from soricid hosts originally designated as *Choanotaenia* spp. are considered members of the genus *Monocercus* Villot, 1882 (Melnikova & Gulyaev, 2004).

Sawada and Kaneno (1992) provided a description and photographs of a new species, *Hymenolepis magnirostellata*, with the shape of the scolex and extended unarmed rostellum matching the genus *Staphylocystis*. Most likely, its rostellar hooks were lost because of maceration of the strobila. The quality of the description does not allow determining taxonomic position of this cestode.

Sawada and Asakawa (1992) described another new species, *Ditestolepis crassisaccata*, which has later been transferred to the genus *Spalania* Karpenko, 1998, and redescribed as *S. crassisaccata* (Sawada & Asakawa, 1992) Karpenko, 1998 (Karpenko, 1998; Karpenko & Chechulin, 2000).

Sawada and Asakawa (1992) reported a juvenile specimen of *Vampirolepis* Spassky, 1954 as *Vampirolepis* sp. Vaucher (1992) revised the genus *Vampirolepis*, all hymenolepidid cestodes parasitizing bats and having armed rostellar apparatus have been transferred to it. Cestodes from soricids with similar structure of the rostellar apparatus and rostellar hooks were placed in the genus *Staphylocystis* (Spassky, 1954; Czaplinski & Vaucher, 1994). Therefore, the cestodes *Vampirolepis* sp. and *H. magnirostellata* found in shrews of Hokkaido belong to the genus *Staphylocystis*. Because their species identification remains questionable, we designated shrew cestodes from Hokkaido as *Staphylocystis* sp. (Tables 2 and 3). *Sinuterilepis ezoensis*, described by Sawada and Koyasu (1995), has been transferred to the genus *Ecrinolepis* as *Ecrinolepis ezoensis* (Gulyaev et al., 2009).

In three shrew species from Hokkaido, Sato et al. (1988) registered 10 species of cestodes, including three species of *Neoskrjabinolepis*: *N. schaldybini*, *N. singularis*, and *Neoskrjabinolepis* sp. Their drawings of the rostellar hooks match *N. kedrovensis*, *N. kunashiriensis*, and *N. nuda*. Other recorded species were *L. skrjabini*, *S. furcata*, *S. diplocoronathus*, *S. jakutensis*, *U. prolifer* [Syn. *Pseudodiorchis prolifer* (Villot, 1880) Kisielewska, 1960], *L. scutigera* (Dujardin, 1845) [Syn. *Staphylocystis toxometra* (Baer, 1932) Yamaguti, 1959], and *M. baicalensis* [Syn. *Molluscotaenia baicalensis* (Eltyshev, 1975)]. As mentioned, *L. scutigera* does not parasitize shrews of the Pacific Islands; consequently, we believe that those authors found *L. parva*.

The analysis of the previously mentioned papers and the examination of the collection of shrew cestodes from Sakhalin, Kunashir, and Hokkaido enabled us to improve the list of shrew cestodes in the study area. This group now includes 36 species.

According to the theory of island biogeography, the number of species on islands is smaller than on the continent and depends on many factors. These are the size of islands, their remoteness from the mainland, biotopic conditions of species, species diversity and abundance of hosts, type of helminth life cycle, etc. (MacArthur & Wilson, 1967; Mas-Coma & Feliu, 1984; Miquel et al., 1996; Goüy de Bellocq et al., 2003; Bugmyrin, 2014). The results of a comparative analysis of the cestode diversity of shrews from the mainland and the Sakhalin – Kunashir – Hokkaido island complex are contradictory and do not provide an unambiguous answer.

Although there are fewer species of shrews (6) on Sakhalin than on the mainland (9), they are parasitized by almost the same number of cestode species (35 and 33, respectively). This can most likely be explained by the short distance between Sakhalin and the mainland, the similarity of their current physical-geographical state, similar feeding spectrum, broad host specificity of cestodes and the history of the island's formation.

According to the theory of island biogeography, the number of species on an island is proportional to its size and distance from the mainland. The diversity of shrew cestodes on Hokkaido is one third less (23 species) than on Sakhalin, given their relatively similar area. This is probably due to the remoteness of Hokkaido from the mainland as well as the history of the island's formation. During the Pleistocene, the islands were repeatedly separated from the mainland. It is known that the last separation of Sakhalin from Hokkaido occurred approximately 12,000 years ago, and the last separation of Sakhalin from mainland was 7000 years ago (Velizhanin, 1976). This resulted into a relatively brief isolation, both among the islands and between those islands and the mainland, which allowed some cestode species to penetrate from the mainland to Sakhalin. Kunashir Island has c. 50 times smaller size than Sakhalin and Hokkaido. However, almost the same number of cestode species (22 species) as in Hokkaido was detected. Probably,

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

the similarity of habitats on Hokkaido and Kunashir and their recent separation (75,000 years ago) formed the basis of the species richness of cestodes.

We have not found a direct connection between helminth species diversity and host species' diversity and host abundance. The cestodes of shrews are characterised by broad host specificity. The same cestode species can be found in different species of *Sorex* (e.g., *S. diplocoronathus* has been found in all shrew species on the islands), although individual cestode species may parasitize only one host species (e.g., *N. nana* has been found in *S. gracillimus* only). This is most likely due to the similar food spectrum of different species of shrews. The absence of certain invertebrates (intermediate hosts of cestodes) needed for the realization of the cestode life cycle may lead to the extinction of a number of cestode species on the islands.

The highest number of cestode species on the studied islands was recorded for *S. unguiculatus*. Species richness of cestodes in *S. unguiculatus* on Hokkaido and Kunashir is one-third less than this on Sakhalin. In *S. caecutiens* from Hokkaido Island, almost three times fewer species of cestodes were registered as compared to Sakhalin (10 and 26, respectively). The lowest number of cestode species on all studied islands was recorded in *S. gracillimus*. *S. unguiculatus* was dominant in the shrew community on the studied islands (Voronov et al., 1969; Nesterenko, 1999; Loktionova et al., 2016; Nesterenko et al., 2016). As a rule, the dominant position of a certain shrew species in the community of various shrews ensures its leading role in the maintenance of cestode infection in shrew communities (Kornienko et al., 2014; Kornienko & Dokuchaev, 2023).

On the other hand, we found almost the same number of cestode species in *S. unguiculatus* and *S. caecutiens* (30 and 26 species, respectively) on Sakhalin, although the sample size of the two shrew species differed by several times. A similar situation was found for *S. unguiculatus* in Hokkaido and Kunashir. At the same time, it is undeniable that the chance of finding more cestode species increases with increasing host abundance. Species richness of shrew cestodes on the islands could increase if host specimens consisted of at least 40–50 individuals (Poulin, 1998). The species *E. longibursata*, recorded on the mainland, Sakhalin and Hokkaido, was not found on Kunashir. It is possible that this species also parasitized shrews of Kunashir, and its absence may be explained either by small sample size or by rarity of this cestode species on Kunashir.

It should be noted that, despite the same number of cestode species on the mainland, Sakhalin, Hokkaido and Kunashir, the taxonomic composition of the cestode community varied (Cj=0.51–0.67) (i.e., the cestode genera were represented by different species on the mainland and the different islands).

In the "Sakhalin–Kunashir–Hokkaido" complex of shrew cestodes, mostly eastern Palearctic (16) species were found. Trans-Palearctic taxa are represented by six species (*D. diaphana*, *P. mathevossianae*, *S. diplocoronathus*, *S. furcata*, *S. quarta*, and *U. prolifer*). According to recent data, *D. diaphana*, which used to be considered a single species, is actually a species complex (Kornienko et al., 2019). Therefore, to determine the species identity of *D. diaphana sensu lato* found on the islands, additional investigations are necessary. Furthermore, according to Spassky and Andrejko (1970), the name *S. furcata* harbors several morphologically and ecologically similar species. This notion has been confirmed by our discovery (on islands Sakhalin, Kunashir, and Hokkaido) of cestodes assigned to the genus *Staphylocystis* but having characteristics different from those of *S. furcata*. Additional research is needed to determine taxonomic status of the found cestodes.

It has been demonstrated that the biota of Sakhalin and Kuril Islands (Kunashir) features low endemism (Bogatov et al., 2003, 2006; Pietsch et al., 2003). For example, in the micromammal fauna of Sakhalin, the proportion of endemics is no more than 14%, whereas in the theriofauna of Japan as a whole (including Honshu and other islands), there are ~40% of endemic forms of mammals (Millien-Parra & Jaeger, 1999). Among shrew cestodes of Sakhalin, only two species (*N. paradoxa*, and *S. sawadai*) of 33 (6%) are endemic, whereas the cestode fauna of Hokkaido contains one endemic species (*E. ezoensis*). On Kunashir Island, there are no endemic species of shrew cestodes. Our comparison indicates that approximately 22% (8 of 36 species) of cestodes (*D. ezoensis*, *E. ezoensis*, *N. kunashiriensis*, *N. nana*, *N. nuda*, *N. paradoxa*, *S. crassisaccata*, and *S. sawadai*) occur only on the Sakhalin–Kunashir–Hokkaido Island complex and hence are island endemics. For three species of the genera *Staphylocystis*, *Lineolepis* and *Monocercus*, it is needed to further clarify their taxonomic status, which may result in recognizing them as endemics of this island complex.

The presence of trans- and eastern-Palearctic species in the studied faunal complex and the absence of island autochthons among shrews point to repeated and unidirectional incursion of shrews into the islands (primarily on Sakhalin Island) in the Quaternary. According to the "rule of six" (Dokuchaev, 2005), the return migration of shrews was prevented by complete saturation of their communities on the mainland. Multiple invasions from the mainland to the islands at different time points, the complex dynamic structure of the shrew community on the islands depending on their physiographic conditions, the abundance of definitive hosts and the presence of intermediate hosts of cestodes have ultimately caused the high diversity and endemism of shrew cestodes on the studied islands.

Acknowledgements. We thank V.D. Gulyaev, Yu.A. Melnikova, T.A. Makarikova, and A.A. Makarikov for help with the fieldwork in Sakhalin Oblast. We are also very grateful to S.D. Ohdachi for organization of N.E. Dokuchaev's field work in Hokkaido. The study was supported by Federal Fundamental Scientific Research Programs (No. 1021051703269-9-1.6.12 and 123032000021-4). The English language was corrected and certified by shevchuk-editing.com.

Financial support. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Competing interest. The authors declare no conflict of interest.

Ethical standards. The authors carefully reviewed the ethical standards of the journal and hereby certify that the procedures used with the investigated species comply fully with those standards. The authors assert that all procedures and methods contributing to this work and used in the current study comply with the ethical standards of the relevant national and institutional guides with laws of the Russian Federation and were approved by the ethics committee of the ISEA, Novosibirsk, Russia.

References

Binkienė, R, Kornienko, SA and Tkach, VV (2015) *Soricinia genovi* n. sp. from *Neomys fodiens* in Bulgaria, with redescription of *Soricinia globosa* (Baer, 1931) (Cyclophyllidea: Hymenolepididae). *Parasitology Research* **114**, 209–218. DOI: 10.1007/s00436-014-4180-6

Bogatov, VV, Pietsch, TW, Zhuravlev, YuN, Storozhenko, SY, Lelej, AS, Barkalov, VY, Kholin, SK and Prozorova, LA (2003) Origin patterns of the terrestrial and freshwater biota of the Kuril archipelago. *The Bulletin of the North-East Scientific Center of FEB RAS* **3**, 9–18. [In Russian.]

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

Bogatov, VV, **Pietsch, TW**, **Storozhenko, SY**, **Barkalov, VY**, **Lelej, AS**, **Kholin, SK**, **Krestov, PV**, **Kostenko, VA**, **Makarchenko, EA**, **Prozorova, LA and Shedko, SV** (2006) Origin patterns of the terrestrial and freshwater biota of the Sakhalin Island. *The Bulletin of the North-East Scientific Center of FEB RAS* **2**, 32–47. [In Russian.]

Bugmyrin, S (2014) *Calodium* (*Capillaria*) *hepaticum* (Nematoda, Capillariidae) in insular small rodent populations. *Principy Ekologii* **4**, 18–30. [In Russian.]

Czaplinski, B and Vaucher, C (1994) Family Hymenolepididae Ariola, 1899. In Khalil, LF, Jones, A and Bray, RA (eds), *Keys to the cestode parasites of vertebrates*. Wallingford, UK: CAB International. pp. 595–663.

Dokuchaev, NE (2005) "Rule of six" for the forming of multispecies communities in shrews *Sorex*. In Proceedings of the Ninth International Mammalogical Congress *(IMC 9):* Roles of Mammalogy on Coexistence of Wild Mammals and Human. Sapporo, Hokkaido University, 69–70.

Goüy de Bellocq, J, **Sarà, M**, **Casanova, JC**, **Feliu, C and Morand, S** (2003). A comparison of the structure of helminth communities in the woodmouse, *Apodemus sylvaticus*, on islands of the western Mediterranean and continental Europe. *Parasitology Research* **90**, 64–70. DOI 10.1007/s00436-002-0806-1

Grigoryev, EM and Bashilov, SV (1988) On the distribution of the Siberian Shrew (*Sorex minutissimus* Zimm., 1780) in the Kunashir Island. The Bulletin of Moscow Society of Naturalists. Biological Series **93**, 71–73. [In Russian.]

Gulyaev, VD, **Kornienko, SA and Dokuchaev, NE** (2007) The cestodes of the genus *Staphylocystoides* Yamaguti, 1959 (Cestoda, Hymenolepididae) in shrews of Beringia. *The Bulletin of the North-East Scientific Center of FEB RAS* **4**: 75–84. [In Russian.]

Gulyaev, VD, **Zubova, OA**, **Dokuchaev, NE and Ohdachi, SD** (2009) Revised description of *Ecrinolepis ezoensis* (Sawada et Koyasu, 1995) comb. n. (Cestoda, Cyclophyllidea, Ditestolepidini) in shrews from Hokkaido, Japan. *The Bulletin of the North-East Scientific Center of FEB RAS* **4**: 54–57. [In Russian.]

Karpenko, SV (1984) The new species of hymenolepidids (Cestoda) from the shrews of Transbaikalye. In Cherepanov AI (Ed.), *Chlenistonogie I gel'minty*. Novosibirsk, Nauka, pp. 107–117. [In Russian.]

Karpenko, SV (1997) Helminths of shrews on Kunashir Island. In Fedorov KF (Ed.), *Parasites and diseases caused by them in Siberia*. Novosibirsk, Publishing house of the Siberian Branch of the Russian Academy of Agricultural Sciences, 53–54. [In Russian.]

Karpenko, SV (1998) Helminths of shrews from sub mountain region of Western Altai. In Volkov FA and Marchenko VA (eds), *Parasites in natural complexes and disturbed situations*. Novosibirsk, Publishing house of the Siberian Branch of the Russian Academy of Agricultural Sciences, 69–71. [In Russian.]

Karpenko, SV (1999) Cestodes of the genus *Soricinia* (Cyclophyllidea, Hymenolepidini) from Holarctic region shrews. *Zoologicheskiy Zhurnal* **78**, 922–928. [In Russian.]

Karpenko, SV (2004) Helminths of shrews of the Khabarovsk Kray. *Natural resources of the Khabarovsk Kray: problems of science and education*. Khabarovsk, 80–86. [In Russian.]

Karpenko, SV and Chechulin, AI (2000) Redescription of *Spalania crassisaccata* (Cestoda, Cyclophyllidae, Hymenolepididae) from shrews of Kunashir Island. *Zoologicheskiy Zhurnal* **79**, 1147–1154. [In Russian.]

Kornienko, SA and Dokuchaev, NE (2023) Cestode diversity of shrews on the Kamchatka Peninsula and Paramushir Island. *Diversity* **15**, 99. DOI:10.3390/d15010099

Kornienko, SA and Gulyaev, VD (2011) New cestodes of the genus *Neoskrjabinolepis* (Cestoda, Hymenolepididae) from shrews of the Far East. *Zoologicheskiy Zhurnal* **90**, 1296–1303. [In Russian.]

Kornienko, SA, **Binkienė, R and Tkach, VV** (2016) Revision of the genus *Soricinia* Spassky & Spasskaja, 1954 (Cestoda: Cyclophyllidea: Hymenolepididae) with redescriptions of three species, an amended generic diagnosis and an identification key to species. *Systematic Parasitology* **93**, 451–465. DOI: 10.1007/s11230-016-9639-7

Kornienko, SA, **Dokuchaev, NE and Odnokurtsev, VA** (2018) Shrew' cestodes of the Central and Southern Yakutia. *Zoologicheskiy Zhurnal* **97**, 1110–1120. [In Russian.] DOI: 10.1134/S0044513418090076

Kornienko, SA, **Gulyaev, VD and Melnikova, YA** (2006) On the morphology and systematics of cestodes of the genus *Neoskrjabinolepis* Spassky, 1947 (Cyclophyllidea, Hymenolepididae). *Zoologicheskiy Zhurnal* **85**, 134–145. [In Russian.]

Kornienko, SA, **Gulyaev, VD and Melnikova, YA** (2007) New species of cestodes of the genus *Neoskrjabinolepis* Spassky, 1947 (Cyclophyllidea, Hymenolepididae) from shrews of Russia. *Zoologicheskiy Zhurnal* **86**, 259–269. [In Russian.]

Kornienko, SA, **Makarikov, A and Dokuchaev, NE** (2014) Cestodes of small mammals in Bolshoy Shantar island (sea of Okhotsk western part). *Bulletin of the North-East Scientific Center*, FE Branch RAS **2**, 65–69. [In Russian.]

Kornienko, SA, **Makarikova, TA and Dokuchaev, NE** (2023) *Neoskrjabinolepis paradoxa* n. sp. from shrews on Sakhalin Island, Russia, with an amended diagnosis of *Neoskrjabinolepis* Spassky, 1947 (Cestoda: Cyclophyllidea: Hymenolepididae), a key and a review on geographical distribution of the species. *Journal of Helminthology* **97** DOI: 10.1017/S0022149X23000524

Kornienko, SA, **Binkienė, R**, **Dokuchaev, NE and Tkach, VV** (2019) Molecular phylogeny and systematics of cestodes with rudimentary rostellum (Cestoda: Hymenolepididae) from Holarctic Sorex shews (Eulipotyphla: Soricidae). *Zoological Journal of the Linnean Society* **187**, 965–986. DOI:10.1093/zoolinnean/zlz061

Kornienko, SA, **Gulyaev, VD**, **Melnikova, YA and Georgiev, BB** (2008a) *Neoskrjabinolepis nuda* n. sp. from shrews in Sakhalin Island, Russia, with a taxonomic review of *Neoskrjabinolepis* Spassky, 1947 (Cyclophyllidea, Hymenolepididae). *Systematic Parasitology* **70**, 147–158.

Kornienko, SA, **Zubova, OA**, **Gulyaev, VD and Dokuchaev, NE** (2008b) Cestodes of shrews from Kunashir Island. In Galaktionov KV and Dobrovolskij AA (eds), *Parasitology in XXI century – problems, methods, solutions*. St. Petersburg, Lema, 265–268 [In Russian.]

Kostenko, VA and Nesterenko, VA (2006) Mammals (Mammalia) of the Moneron Island. pp. 306–313. In Storozhenko, SYu (Ed) *The Flora and fauna of Moneron Island (Materials of International Sakhalin Island Project)* Vladivostok, Dalnauka. [In Russian.]

Kostenko, VA, **Nesterenko, VA and Trukhin, AM** (2004) Mammals of the Kuril Archipelago. Vladivostok, Dalnauka, 186 p. [In Russian.]

Loktionova, EYu, **Nesterenko, VA and Burkovsky, OA** (2016) Dominance structure in taxocaenoses of Northern Sakhalin shrews. *The Bulletin of the North-East Scientific Center of FEB RAS* **2**, 93–99. [In Russian.]

Lykova, KA, **Gulyaev, VD**, **Melnikova, YA. and Karpenko, SV** (2006) *Diorchilepis*, a new genus of cestodes (Cyclophyllidea, Hymenolepididae, Ditestolepidini) and redescription of *Diorchilepis ezoensis* comb. n. from shrews of Sakhalin Island and the Kuril Islands. *Zoologicheskiy Zhurnal* **85**, 1506–1510. [In Russian.]

Lykova, KA, **Melnikova, YA and Karpenko, SV** (2005) *Spasskylepis tiunovi* sp. n. (Cyclophyllidea, Hymenolepididae) – a new cestode species from shrews of the Far East. *Parasitologiya* **39**, 285–292. [In Russian.]

MacArthur, RH and Wilson, EO (1967) *The Theory of Island Biogeography*. Princeton: Princeton Univ. Press. 293 p.

Magurran, AE (1988) *Ecological Diversity and Its Measurements*. Princeton: Princeton University Press. 179p.

Mas-Coma, S and Feliu, C (1984) Helminthofauna from small mammals (insectivores and rodents) on the Pityusic islands. In Kuhbier J, Alcover JA and Guerau d'Arellano C (eds), *Biogeography and ecology of the Pityusic Islands*. Junk, Barcelona, pp. 469–525.

Melnikova, YA and Gulyaev, VD (2004) A new cestode species – *Monocercus dokuchaevi* sp. nov. (Cyclophyllidea: Dilepididae) from shrews in Northeastern Asia. *Parazitologiya* **78**, 68–73. [In Russian.]

Melnikova, YA, **Gulyaev, VD and Dokuchaev, NE** (2003) The structure of community of cestodes of shrews of West Beringia and the Far East. In Alekseev AN (Ed.), *Problems of modern parasitology*. St. Petersburg, Lema, 18–20. [In Russian.]

Melnikova, YA, **Gulyaev, VD and Dokuchaev, NE** (2005) Cestoda of insectivorous mammals of Russian Far East. In *Scientific investigations of nature in Lazovsky Reserve*. Vladivostok, Russkiy Ostrov, 82–90. [In Russian.]

Millien-Parra, V and Jaeger, JJ (1999) Island biogeography of the Japanese terrestrial mammal assemblages: an example of a relict fauna. *Journal of Biogeography* **26**, 959–972. DOI: 10.1046/j.1365-2699.1999.00346.x

Miquel, J, **Fons, R**, **Feliu, C**, **Marchand, B**, **Torres, J and Clara, JP** (1996) Helminthes parasites des rongeurs Muridés des îles d'Hyères (Var, France): aspects écologiques. Vie Milieu 46, pp. 219–223.

https://doi.org/10.1017/S0022149X24000324 Published online by Cambridge University Press

Neov, B, **Vasileva, GP**, **Radoslavov, G**, **Hristov, P**, **Littlewood, DTJ and Georgiev, BB** (2019) Phylogeny of hymenolepidid cestodes (Cestoda: Cyclophyllidea) from mammalian hosts based on partial 28S rDNA, with focus on parasites from shrews. *Parasitology Research* **118**, 73–88. DOI: 10.1007/s00436-018-6117-y

Neov, B, **Vasileva, GP**, **Radoslavov, G**, **Hristov, P**, **Littlewood, DTJ and Georgiev, BB** (2021) Phylogeny of hymenolepidids (Cestoda: Cyclophyllidea) from mammals: Sequences of 18S rDNA and COI genes confirm major clades revealed by the 28S rDNA analyses. *Journal of Helminthology* **95**(**E23**). DOI: 10.1017/S0022149X21000110

Nesterenko, VA (1999) Insectivores of the south Far East and their communities. Vladivostok, Dalnauka. 173p. [In Russian.]

Nesterenko, VA, **Loktionova, EYu and Burkovsky, OA** (2016) Dinamics of shrew taxocene structure in southern of Sakhalin. *Contemporary Problems of Ecology* **3**, 333–342. [In Russian.] DOI: 10.15372/SEJ20160305

Ochotina, MV (1976) New form of shrew (Insectivora) from Moneron Island. *Zoologicheskiy Zhurnal* **55**, 590–595. [In Russian.]

Ochotina, MV (1977) Shrews (Insectivora, Soricidae) from Sakhalin Island. *Zoologicheskiy Zhurnal* **56**, 243–249. [In Russian.]

Odnokurtsev, VA and Karpenko, SV (1993) Structure of the helminth fauna of shrews in Yakutia. In *Fauna, ecology and practical significance of phyto- and zooparasitic organisms*. Kishinev, Shtiintsa, pp. 65–76. [In Russian.]

Ohdachi, SD, **Ishibashi, Y**, **Iwasa, MA**, **Fukui, D and Saitoh, T** (eds). (2015) *The Wild Mammals of Japan*. Second edition. Kyoto: Shoukadoh Book Sellers. 511 p.

Pietsch, TW, **Bogatov, VV**, **Amaoka, K**, **Zhuravlev, YN**, **Barkalov, VY**, **Gage, S**, **Takahashi, H**, **Lele, AS**, **Storozhenko, SY and Minakawa, N** (2003) Biodiversity and biogeography of the islands of the Kuril Archipelago. *Journal of Biogeography* **30**, 1297–1310. DOI: 10.1046/j.1365-2699.2003.00956.x

Poulin, R (1998) Comparison of three estimators of species richness in parasite component communities. *Journal of Parasitology* **84**, 485–490.

Sato, H, **Kamiya, H and Ohbayashi, M** (1988) Hymenolepidid and dilepidid cestodes with armed rostellum in shrews, *Sorex* spp. from Hokkaido, Japan. *Japanese Journal of Veterinary Research* **36**, 119–131.

Sawada, I (1999) A Checklist of Cestode species from Asian Insectivora. *Journal of Industrial Economics* **13**, 109–123.

Sawada, I and Asakawa, M (1992) Helminth fauna of shrews on Teuri To, Rishiri To and Rebun To in Hokkaido, Japan. *Bulletin of Nara Sangyo University* **8**, 165–170.

Sawada, I and Harada, M (1990) Cestodes of field micromammalians (Insectivora) from central Honshu, Japan. *Zoological Science* **7**, 469–475.

Sawada, I and Kaneno, S (1992) *Hymenolepis magnirostellata* sp. n. (Cestoda: Hymenolepididae) with records of the known Cestodes from the shrews of Hokkaido. *Japanese Journal of Parasitology* **41**, 283–286.

Sawada, I and Kobayashi, S (1993) Cestode Parasites of Shrews in South Saghalien. *Proceedings of the Japanese Society of Systematic Zoology* **49**, 1–5.

Sawada, I and Koyasu, K (1990) Further studies on Cestodes from Japanese shrews. *Bulletin of Nara Sangyo University* **6**, 187–202.

Sawada, I and Koyasu, K (1991) Cestodes of some Micromammalians (Insectivora) from Hokkaido, Japan. *Japanese Journal of Parasitology* **40**, 567–575.

Sawada, I and Koyasu, K (1995) Helminth *Sinuterilepis ezoensis* sp. nov. (Cestoda: Hymenolepididae) parasitic on *Sorex caecutiens saevus* from Hokkaido, Japan. *Bulletin of the Biogeographical Society of Japan* **50**, 15–17.

Spassky, AA (1954) Classification of hymenolepidids of mammals. *Trudy Gel'mintologicheskoi Laboratorii* **7**, 120–167. [In Russian.]

Spassky, AA and Andrejko, OF (1970) Cestodes of insectivora of Moldavia. *Parazity Zhivotnykh i Rastenii* **5**, 44–59. [In Russian.]

Vaucher, K (1992) Revision of the genus *Vampirolepis* Spasskij, 1954 (Cestoda: Hymenolepididae). *Memórias do Instituto Oswaldo Cruz* **81**(**1**), 299–304. DOI: 10.1590/S0074-02761992000500056

Velizhanin, AG (1976) Time of isolation of the North Pacific mainland islands. *Proceedings of the USSR Academy of Sciences* **231**(**1**), 205–207. [In Russian.]

Voronov, GA, **Zagorodskih, EE and Perminov, LE** (1969) Shrews *Sorex* of Northern Sakhalin. *Scientific Notes of the Perm State Pedagogical Institute. Perm* **79**, 65–74. [In Russian.]

Zubova, OA, **Gulyaev, VD and Kornienko, SA** (2010) *Soricinia sawadai* sp. n. (Cyclophyllidea: Hymenolepididae), a new cestode species from the shrews of Sakhalin Island. *Parasitologiya* **44**, 232–239. [In Russian.]

Zubova, OA, **Kornienko, SA**, **Gulyaev, VD and Dokuchaev, NE** (2008a) Cestodes of the shrews of the Sakhalin Island. In Galaktionov KV and Dobrovolskij AA (eds), *Parasitology in XXI century – problems, methods, solutions*. St. Petersburg: Lema, 265–268. [In Russian.]

Zubova, OA, **Kornienko, SA**, **Gulyaev, VD and Dokuchaev, NE** (2008b) Cestodes of the shrews of the Hokkaido (Japan). In Movsessian, SO, Be′er, SA, Zinovieva SV, Pelgunov, AN and Spiridonov, SE (eds), *Biodiversity and ecology of parasites of terrestrial and water cenoses*. Moscow, Publishing house of the Russian Agricultural Academy, 135–138. [In Russian.]