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## Review Article

# Overview of the Cestode fauna of European shrews of the genus *Sorex* with comments on the fauna in *Neomys* and *Crocidura* and an exploration of historical processes in post-glacial Europe

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### Summary

The cestode fauna in shrews of the genus *Sorex* from the European region consists of seventeen species. Twelve cestode species have broad Palearctic distributions, three belong to the Western-Asian–European faunistic complex, and only two are endemic to the European zone. Postglacial expansion into the European territory resulted in geographic colonization by sixteen species. The large number of cestode species with transpaleartic ranges, as well as paleontological data indicating a nearly complete faunal turnover for species of *Sorex* in the Pleistocene, suggests that these parasites are more ancient than the assemblage of contemporary hosts in which they now occur, and thus represent ecological relicts. We suggest that origins of the cestode fauna pre-date those of the modern fauna of its hosts, and that initial formation and radiation occurred not later than the Pliocene. In the current review, we outline testable hypotheses to explore the structure, history and development of this fauna which appears limited to species of *Sorex*.

Keywords: Cestodes; Biogeography; Colonization; Post-Glacial Europe; *Sorex*

### Introduction

The helminth fauna of Soricomorpha and Erinaceomorpha (Mammalia) is probably the most diverse in comparison with that of other groups of vertebrates belonging to this class. Consequently, the assemblage is a good subject for the study of historical biogeography and evolution and may serve to reveal generalities about faunal structure, patterns of diversity, and the distribution of parasitic worms and their hosts. Even in the Palearctic, however, the most thoroughly examined region on the planet, the depth and scope of biodiversity information for the helminth fauna of Soricomorpha and Erinaceomorpha is uneven.

Based on extensive reviews of the current literature, the number of helminth species parasitizing these mammals in the Palearctic exceeds 300. Representatives of three mammalian families (Soricidae, Talpidae and Erinaceidae) and groups of associated parasites were relatively well examined only in the European or northwestern Palearctic. In Eurasia, and particularly the eastern zone of Eurasia, cestodes among species of Erinaceidae and Talpidae have been poorly characterized, and among Soricidae only tapeworms occurring among species of *Sorex* Linnaeus have been explored in detail. Concurrently, data on trematodes and nematodes are rather scarce, and comprehensive data on helminths in shrews of the genera *Crocidura* Wagler and *Neomys* Kaup continue to be lacking. Consequently, comparable data for faunal diversity across the Palearctic are available only for cestodes distributed among species of *Sorex* (an extensive literature in Appendix I, including papers by J. G. Baer, C. Vaucher, T. Genov, A. Soltys, A. A. Spassky, E. Murai, V. V. Tkach, S. A. Karpenko & V. D. Gulyaev, and others). We focus here on diversity and distribution for the cestodes characteristic of these shrews using comparisons of the western and eastern Palearctic to reveal insights about the history of associations for hosts and parasites in the European fauna. These studies set the foundations for our understanding of the soricomorph cestode faunas, and are a necessary precursor for fine-scale phylogeographic investigations (Avise, 2000) that will be needed to explore the history of this complex fauna.

The current article addresses three interrelated issues:

(1.) Definition and comparisons of the biogeographical characteristics of the cestode fauna in species of *Sorex* from Europe and more broadly from eastern regions of the Palearctic. Our comprehensive approach will complement two relatively short overviews of the cestode fauna among some species of *Sorex* across the Holarctic (Gulyaev, 2003, 2006). The intent here is to define and understand the

relationships, connectivity and distribution for cestodes in *Sorex*.

(2.) Analysis of the structure and composition of the cestode faunas of shrews of the genera *Sorex*, *Neomys* and *Crocidura*. The intent is to examine how tapeworm species are partitioned or distributed among generic groups of Soricidae. For this purpose, only data from the European region are appropriate as there is a paucity of information on faunal diversity from other biogeographic zones.

(3.) The final issue considered in this article is the composition of the cestode fauna associated with *Sorex* and partially *Neomys* in the deglaciated region of Europe. The intent is to address the influence of historical climatological factors and landscape changes during the post-Pleistocene as determinants of diversity and distribution for the tapeworm fauna. In our opinion, the analysis and exploration of these problems will contribute to the general knowledge of the European fauna and history of its formation.

## Materials and methods

### New collections and specimens examined

The cestode specimens assembled for the current study were collected in 2000 – 2008 from different regions: Lithuania in 2000 – 2007 (174 specimens of *Sorex araneus* Linnaeus, 51 specimens of *S. minutus* Linnaeus, and 10 specimens of *Neomys fodiens* (Pennant)); Latvia in 2006 – 2007 (49 specimens of *S. araneus* and 1 specimen of *S. minutus*); Estonia in 2007 – 2008 (37 specimens of *S. araneus*); Bulgaria in 2007 (19 specimens of *S. araneus* and 2 specimens of *S. minutus*, 42 specimens of *Crocidura leucodon* (Hermann), 4 specimens of *C. suaveolens* (Pallas), and 2 specimens of *N. fodiens*); and Karelia, Russia in 2003 (15 specimens of *S. araneus*). In total, 406 specimens representing species of 3 genera of Soricidae were examined by the method of total helminthological dissection. Prior to morphological analysis, helminths were preserved in 70 % ethyl alcohol.

Temporary and permanent preparations were made for detailed morphological studies. Cestodes were stained in aqueous carmine or haematoxylin following Erlich, differentiated in 70 % alcohol with HCl, dehydrated in ethanol series, cleared in clove oil and mounted in Canada balsam. To highlight the shape of rostellar hooks and armature for the cirrus, temporary preparations were made in Berlese's medium. Representative voucher specimens from these new surveys were deposited in collections of Institute of Ecology, Vilnius University and are available under accession numbers 21 – 27, 36, 59 – 61, 81, 121 – 123, 125, 135, 300, 336 – 339, 341, 348, 349, 353 – 362, 371, 396, 399 – 418. Results of these survey collections are summarized in Table 1.

A comprehensive summary is presented for the cestode fauna associated with species of *Sorex* based on an extensive review of survey and taxonomic data in the published literature (Appendix I) and new data for host occurrence and geographic distributions (Table 1). These data for

parasite taxonomy, host association and geographic range are explored, and become the basis for interpretations about the historical foundations of the fauna. Host taxonomy throughout the text and tables is consistent with Hutterer (2005).

## Results

### *Species composition of the cestode fauna of European Sorex shrews and its relations with the fauna of the Asian zone of the Palearctic*

The true composition of the European cestode fauna associated with Soricomorpha is difficult to reveal. Vaucher (1971, 1982) demonstrated that shrews belonging to various genera (*Sorex*, *Neomys*, *Crocidura*) have specific parasites, a pattern confirmed by relatively extensive survey and inventory summarized in the published literature (Appendix I). Several studies, however, indicate hosts that are not typical for particular species of cestodes and include records that are in apparently error. Therefore, we will first provide an overview of the composition of cestode fauna specific to *Sorex* in the European zone (Table 1), and then discuss reports and records of parasites in these shrews that we consider to be specific in other genera of Soricidae.

There are 17 cestode species that are specific to *Sorex* shrews in the European zone (Table 1). Among these, *Monocercus arionis* (Siebold, 1850) Villot, 1882 and *Hepatocestus hepaticus* (Baer, 1932) Bona, 1994 belong to the family Dilepididae, whereas all others are among the Hymenolepididae. In addition to Europe, 15 of these cestode species are widespread in Western and Eastern Siberia or also occur in the Japanese islands (e.g., *Lineolepis scutigera* (Dujardin, 1845) Karpenko, 1985, *Neoskrjabinolepis schaldybini* Spassky, 1947, *N. singularis* (Cholodkowski, 1912) Spassky, 1954, *Skrjabinacanthus jacutensis* Spassky et Morosov, 1959, *Staphylocystis furcata* (Stieda, 1862) Spassky, 1950 and *Urocystis prolifer* Villot, 1880). Additionally, description of new cestode species of the genus *Neoskrjabinolepis* Spassky in the Asian zone (Kornienko et al., 2006, 2007, 2008a) creates the need for clarification of the distribution of *N. schaldybini* and *N. singularis*.

Considering biogeography, 3 cestode species can be attributed to the West-Asian – European faunal complex (*H. hepaticus*, *Ecrinolepis tripartita* (Žarnowski, 1955) Gulyaev, 1991 and *Neoskrjabinolepis merkushevae* Kornienko et Binkienė, 2008) (Table 1). Besides Europe, *E. tripartita* was found in Western Asia (the Caucasus) whereas the other species occur in Europe and Western Siberia. Two species of hymenolepidid cestodes, *Vigisolepis spinulosa* (Cholodkovsky, 1906) Mathevossian, 1945, which represents a monotypic genus, and *Soricinia soricis* (Baer, 1928) Spassky et Spasskaya, 1954, are apparently European endemics. The latter has been repeatedly recorded in such regions of Asia, as the Altai (Kornienko & Gulyaev, 1997), Barguzin depression, Transbaikalia (El'tyshev, 1975), and Central Asia (Tokobaev, 1976). According to V. D. Gulyaev (Pers. Comm., Unpubl. Obs.), however, re-examination of the type specimen for *S. soricis* showed that those cestodes

Table 1. Specific cestodes of European *Sorex* and their distributions in the Palearctic

Cestode species	Host species	Geographic localities: published records, and new collections*
<i>Hepatocestus hepaticus</i> (Baer, 1932) Bona 1994	<i>Sorex alpinus</i> , <i>S. araneus</i> , <i>S.caecutiens</i> , <i>S. minutus</i> .	<b>Europe:</b> Belarus (9, 51, 76); Belgium (93); Czechoslovakia (26, 63, 64); Estonia*: Finland (27), France (93); Germany (93); Hungary (52); Lithuania (13); Moldova (2, 83, 86); Norway (93); Poland (40, 79, 98); Romania (77); Russia - Karelia (56), Archangel'skaya oblast' (59); Slovakia (26); Sweden (93); Switzerland. (11, 88, 93). <b>Asia:</b> Russia - Tyumenskaya oblast' (30), Northern Baraba (60), Novosibirskaya oblast' (36), Altai (37).
<i>Monocercus arionis</i> (Siebold, 1850) Villot, 1882 Syns.: <i>Taenia crassiscolex</i> Linstow, 1890; <i>Monoplydium soricinum</i> Cholodkowsky, 1906; <i>Amoebotaenia subterranea</i> Cholodkowsky, 1906.	<i>Sorex alpinus</i> , <i>S. araneus</i> , <i>S.caecutiens</i> , <i>S. isodon</i> , <i>S. roboratus</i> , <i>S. minutus</i> .	<b>Europe:</b> Austria (93), Belarus (34); Belgium (93), Bulgaria (21, 22); Czechoslovakia (52, 55, 63 – 66); Denmark (93); Estonia*, Finland (28, 29); France (33); Germany (93); Latvia*: Lithuania (13, 99); Moldova (2, 83, 84); Netherlands (93); Norway (93); Poland (61, 68, 79, 80); Romania (89); Russia - Karelia (3 – 6), Archangel'skaya oblast', Sankt Petersburg (92), Samarskaya oblast' (39), Komi (97); Slovakia (54, 87), Spain (43), Switzerland (10, 11); United Kingdom (75, 93). <b>Asia:</b> Central Caucasus (31); Russia - Northern Baraba (60), Tiumenskaya oblast' (30), Altai (36, 42, 44, 72), Magadanskaya oblast' (57), Yakutia (58).
<i>Ditestolepis diaphana</i> (Cholodkowsky 1906) Solty, 1952 Syn.: <i>Smilurilepis spasskii</i> Sadovskaya, 1965; <i>Spasskylepis ovaluteri</i> Schaldybin, 1964 sensu Vaucher, 1971.	<i>Sorex alpinus</i> , <i>S. araneus</i> , <i>S.caecutiens</i> , <i>S. caucasicus</i> , <i>S. isodon</i> , <i>S. minutissimus</i> , <i>S. minutus</i> , <i>S. raddei</i> , <i>S. tundrensis</i> , <i>S. volnuchini</i> .	<b>Europe:</b> Belarus (9, 51, 76); Belgium (93); Bulgaria (21, 22); Czechoslovakia (52, 63, 64); Denmark (93); Estonia*, Finland (27, 29), France (33); Germany (93); Hungary (41); Latvia*: Lithuania (13, 99); Netherlands (93); Norway (93); Pyrenean Mountains (67); Poland (40, 68, 79, 80, 98); Romania (77); Russia - Archangel'skaya oblast' (59), Karelia (3, 5 – 8), St. Petersburg (92), Komi (97), Novgorodskaya oblast' (15), Mordovia (74), Samarskaya oblast' (39); Slovakia (54); Spain (43); Sweden (93); Switzerland (10, 11, 93); Ukraine (95); United Kingdom (93). <b>Asia:</b> Central Caucasus (30, 31); Russia - Tyumenskaya oblast' (30), Northern Baraba (60), Altai (37, 42, 72), Zabaykalya (20), Magadanskaya oblast' (19, 57), Chukotka (18), Kunashir island (47); Central Asia (91); Japan. (72, 96).
<i>Ecrinolepis tripartita</i> (Żarnowski, 1955) Gulyaev, 1991	<i>Sorex araneus</i> , <i>S. caecutiens</i> , <i>S. caucasicus</i> , <i>S. minutus</i> , <i>S. raddei</i> , <i>S. volnuchini</i> .	<b>Europe:</b> Belarus (9); Estonia*; Bulgaria (22); Czechoslovakia (27); Finland (27, 29); Latvia*: Lithuania (13); Poland (40, 68, 98); Norway (93); Russia - Karelia (3, 5 – 9), Archangel'skaya oblast' (59); Sweden (93); Switzerland. (93). <b>Asia:</b> Central Caucasus (31, 32).

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|---|---|--|
| <i>Lineolepis scutigera</i> (Dujardin, 1845)<br>Karpenko, 1985<br>Syn.: <i>Hymenolepis toxometra</i> Baer, 1932.                            | <i>Sorex araneus</i> , <i>S. caecutiens</i> ,<br><i>S. isodon</i> , <i>S. minutissimus</i> ,<br><i>S. minutus</i> , <i>S. tundrensis</i> ,<br><i>S. unguiculatus</i> .<br><br><i>Neoskriabinolepis merkushovae</i><br>Komienko et Binkienė, 2008  | <b>Europe:</b> Belarus (51); Bulgaria (21, 22); Czechoslovakia (55, 62 – 64, 66); Denmark (93); Estonia*, Finland (27, 29); France (33); Germany (93); Latvia*; Lithuania (13, 99); Moldova (1, 83); Netherlands (78); Norway (93); Poland (40, 61, 98); Pirenean mountains (67); Russia - Archangel'skaya oblast' (59), Karelia (3, 5, 7, 8, 56), Saint Petersburg (92); Slovakia (54); Spain (43); Sweden (93); Switzerland (11, 93); Ukraine (95); United Kingdom (75, 93); Western Carpathians (55).<br><br><b>Asia:</b> Central Caucasus (31); Russia - Tyumenskaya oblast' (30), Altai (37, 42, 44), Zabaykalya (20), Yakutia (58), Magadanskaya oblast' (19, 57), Kamchatka (18), Chukotka (18).                                  |
|   | <i>S. araneus</i> , <i>S. minutus</i> .   | <b>Europe:</b> Belarus (43); Latvia*, Russia (Karelia)*, Lithuania. (43).<br><b>Asia:</b> Altai (43).  |
|   | <i>Sorex araneus</i> , <i>S. caecutiens</i> ,<br><i>S. minutus</i> , <i>S. roboratus</i> .  | <b>Europe:</b> Belarus (51, 76); Bulgaria (21, 22); Czechoslovakia (25, 64); Denmark (93); Estonia*, Finland (27, 29); France (33, 93); Germany (93); Latvia*; Lithuania (13, 99); Moldova (1, 2, 83); Netherlands (93); Norway (93); Poland (61, 68, 93); Pyrenean mountain (67), Romania (77, 90); Russia - Karelia (5 – 8), Komi (97), Mordovia (74), Samarskaya oblast' (39); Slovakia (25, 53, 87); Spain (43); Sweden (93); Switzerland (93); United Kingdom (75, 93); Western Carpathians (55).<br><br><b>Asia:</b> Russia - Altai (44, 45, 46), Zabaykalya (20), Yakutia (58), Magadanskaya oblast' (19), Chukotka (18), Kamchatka (18); Japan (69, 70, 96).   |
|   | <i>Sorex alpinus</i> , <i>S. araneus</i> ,<br><i>S. caecutiens</i> , <i>S. caucasicus</i> ,<br><i>S. gracillimus</i> , <i>S. hosonoi</i> ,<br><i>S. isodon</i> , <i>S. minutus</i> ,<br><i>S. raddei</i> , <i>S. roboratus</i> ,<br><i>S. sadonis</i> , <i>S. shinto</i> ,<br><i>S. tundrensis</i> , <i>S. unguiculatus</i> ,<br><i>S. volnuchini</i> . | <b>Europe:</b> Belarus (9, 51); Belgium (93); Czechoslovakia (25, 62-64, 66, 93); Denmark (93); Estonia*, Finland (27-29, 93); France (93); Germany (93); Hungary (41); Latvia*, Lithuania (13, 99); Netherlands (93); Norway (93); Poland (40, 61, 68, 79, 80, 93), Netherlands (78); Russia - Karelia (3, 6), Archangel'skaya oblast' (59), Novgorodskaya oblast' (16); Saint Petersburg (17, 92), Kalininskaya oblast' (94); Slovakia (54, 93); Sweden (93); Switzerland (93); United Kingdom (75, 93).<br><br><b>Asia:</b> Central Caucasus (31); Central Asia (91); Russia - Tyumenskaya oblast' (30), Northern Baraba (60), Altai (37, 42, 44 – 46), Magadanskaya oblast' (57), Chukotka (18), Kamchatka (18); Japan (69, 71, 96). |
|   | <i>Sorex araneus</i> , <i>S. caecutiens</i> ,<br><i>S. isodon</i> , <i>S. minutus</i> .   | <b>Europe:</b> Belgium (93); Czechoslovakia (65, 66); Finland (27-29); France (93); Latvia*, Lithuania*, Netherlands (93); Norway (93); Poland (93) Russia - Karelia*, Archangel'skaya oblast' (59), Mordovia (73), Samarskaya oblast' (39).<br><b>Asia:</b> Russia - Northern Baraba (60), Altai (38, 42, 44), Khabarovskiy kray (50), Primorskiy kray (50), Magadanskaya oblast' (57), Kamchatka (18), Kunashir island (47).   |
| <i>Pseudobotrialepis mathewossianae</i><br>Schaldybin, 1957<br>Syn.: <i>Hymenolepis globosoides</i> sensu<br>Vaucher, 1971 nec Soltys, 1954 |   |  |

<i>Skryabinacanthus jacutensis</i> Spassky et Morosov, 1959 Syn.: <i>Pseudoparadilepis ankeli</i> Brendow, 1969	<i>Sorex araneus</i> , <i>S. gracilimus</i> , <i>S. isodon</i> , <i>S. minutissimus</i> , <i>S. minutus</i>	<b>Europe:</b> France (33, 93); Germany (14); Russia - Archangel'skaya oblast' (59); Switzerland (93). <b>Asia:</b> Russia - Altai (42, 44, 72), Yakutia (85); Japan (69, 70, 96).
<i>Soricinita infirma</i> (Żarnowsky, 1955) Vaucher, 1994 Syn.: <i>Ditestolepis secunda</i> Schaldybin, 1964.	<i>Sorex alpinus</i> , <i>S. araneus</i> , <i>S. caecutiens</i> , <i>S. isodon</i> , <i>S. minutus</i> , <i>S. roboratus</i> .	<b>Europe:</b> Belarus (9, 51); Bulgaria (21, 22); Czechoslovakia (66); Finland (27-29); France (93); Germany (93); Lithuania (13, 90); Poland (98); Pyrenees Mountains (67); Russia - Karelia (6), Komi (97), Mordovia (74); Slovakia (53); Spain (43); Switzerland (93); Western Carpathians (55). <b>Asia:</b> Central Caucasus (31); Central Asia (91); Russia - Altai (42, 44), Zabaykalya (20), Yakutia (58), Khabarovskiy kray (50), Primorskiy kray (50), Chukotka (18), Kamchatka (18).
<i>Soricina soricis</i> (Baer, 1928) Spassky et Spasskaya, 1954	<i>Sorex alpinus</i> ; <i>S. araneus</i> , <i>S. minutus</i> .	<b>Europe:</b> Belarus (34, 51), Czechoslovakia (25); Moldova (1, 2); Russia-Samarskaya oblast' (39); Slovakia (54); Switzerland (10).
<i>Spasskylepis ovaluteri</i> Shaldybin, 1964 Syn.: <i>S. phoedorovi</i> Karpenko, 1983.	<i>Sorex araneus</i> , <i>S. caecutiens</i> , <i>S. caucasica</i> , <i>S. isodon</i> , <i>S. minutus</i> , <i>S. raddei</i> , <i>S. roboratus</i> , <i>S. volnuchini</i> .	<b>Europe:</b> Belarus (9, 51); Estonia*; Latvia*; Lithuania (13); Russia - Karelia (7, 8), Komi (97), Mordovia (74). <b>Asia:</b> Central Caucasus (31, 32), Russia - Altai (24, 35), Magadanskaya oblast (19), Primorskiy kray, (48, 50), Chukotka (18), Kamchatka (18); Northern Mongolia (24).
<i>Staphylomys furcata</i> (Stieda, 1862) Spassky, 1950	<i>Sorex alpinus</i> , <i>S. araneus</i> , <i>S. caecutiens</i> , <i>S. isodon</i> , <i>S. minutus</i> , <i>S. roboratus</i> , <i>S. unguiculatus</i> .	<b>Europe:</b> Austria (93); Belarus (9, 51, 76); Belgium (93); Bulgaria (21); Czechoslovakia (63 - 65); Estonia*, Finland (27 - 29); France (33); Germany (93); Latvia*; Lithuania (13, 104); Moldova (1, 2, 83); Netherlands (93); Norway (93), Poland (40, 61, 79, 80, 98); Romania (77, 90); Russia - Archangel'skaya oblast' (59), Karelia (3, 5 - 8), Komi (97), Mordovia (74), Samarskaya oblast' (39); Slovakia (54); Spain (43); Sweden (93); Switzerland (10, 93); United Kingdom (93); Western Carpathians (55, 96). <b>Asia:</b> Central Caucasus (31), Kyrgyzstan (91), Tadzhikistan (81); Russia - Tyumenskaya oblast' (30), Altai (23, 37, 42), Khabarovskiy kray (50), Primorskiy kray, (50), Kamchatka (18), Kunashir island (47); Japan (69, 70, 96).
<i>Staphylomystoides stefanskii</i> (Żarnowski, 1954) Vaucher, 1994	<i>Sorex araneus</i> , <i>S. caecutiens</i> , <i>S. daphnaeodon</i> , <i>S. minutissimus</i> , <i>S. minutus</i> , <i>S. roboratus</i> .	<b>Europe:</b> Belarus*; Estonia*, Finland (93); France (33); Latvia*; Lithuania (13); Moldova (83); Poland (98); Russia - Karelia (7), Mordovia (74); Spain (43); Switzerland (93); Western Carpathians (55). <b>Asia:</b> Central Caucasus (31); Russia - Altai (42, 44), Habarovskiy kray (50), Primorskiy kray (50), Yakutia (58).

- Urocytis prolifer* Villot, 1880  
Syns.: *Hymenolepis curiosa* Stammer, 1955, *Pseudodiorchis multispinosa* Żarnowski, 1955, *Pseudodiorchis kampinosi* Rybicka, 1958, *Echinoproboscilepis kedrovensis* Sadovskaja, 1965, *Coronacanthus parvithamata* Sawada et Harada, 1990. *Vigisolepis spinulosa* (Cholodkovsky, 1906) Mathevossian, 1945  
Syn. V. *barbosolex* Spassky, 1949

*Sorex araneus*, *S.caecutiens*, *S.gracilimus*, *S.isodon*, *S.minutus*, *S.roboratus*, *S.sadonis*, *S.shinto*, *S.unguiculatus*.  
**Europe:** Bulgaria (21, 22), Finland (27, 29); France (33, 93); Germany (93); Latvia\*, Lithuania (13, 104); Moldova (1, 2, 83); Netherlands (93); Poland (40, 68, 98); Romania (77, 90); Russia - Karelia (5, 6, 56), St. Petersburg (15), Komi (97); Pyrenean mountains (67); Switzerland (12, 93); United Kingdom (75).  
**Asia:** Central Caucasus (31), Russia - Altai (42, 44), Magadanskaya oblast (57), Primorskiy kray, (50), Kamchatka (18), Kunashir island (47); (Japan 69, 70, 96).

*S.alpinus*, *S.araneus*, *S.caecutiens*, *S.minutus*.

**Europe:** Austria (93); Belarus (9, 34); Belgium (93); Bulgaria (21, 22); Czechoslovakia (25, 62-64, 66), Denmark (93); Estonia\*: Finland (27, 28), France (93); Germany (93); Latvia\*: Lithuania (13, 104); Moldova (1, 2, 83); Netherlands (93); Norway (93), Poland (40, 61, 68, 79, 80); Romania (77); Russia - Arhangelskaya oblast' (59), Karelia (6, 56), Komi (97), Ivanovskaya oblast' (82), Novgorodskaya oblast' (15), St. Petersburg (92), Kaliminskaya oblast' (94), Mordovia (74), Samarskaya oblast' (39); Slovakia (54); Switzerland (11, 93); United Kingdom (75); Western Carpathians (55).

\* New records based on recent collections in Lithuania, Latvia, Estonia, and Karelia during the current study.

◆ Distribution documented here is transpalearctic as indicated by the literature. However, recent description of new species of this genus from Eastern Siberia suggest that the actual range for these previously recognized taxa may be limited to Europe and Western Siberia (for details see Kornienko et al. 2008).

☒ Vaucher (1971) has reduced *Spastylepis ovaliferi* as a synonym of *Diestolepis diaephana* and some authors probably refer to this species under that name. The validity of *S. ovaliferi* was restored by Gulyaev et al. (2004).

**Authors:** 1 - Andreiko 1969; 2 - Andreiko 1973; 3 - Anikanova, Boyko 2003; 4 - Anikanova, Yeshko 2001; 5 - Anikanova et al. 2002; 7 - Anikanova et al. 2005a; 8 - Anikanova et al. 2005b; 9 - Arzamasov et al. 1969; 10 - Baer 1928; 11 - Baer 1932; 12 - Baer, Santa 1960; 13 - Binkinen 2006; 14 - Brendo 1969; 15 - Cholodkovsky 1912; 17 - Cholodkovsky 1913; 18 - Dokuchaev et al. 2003; 19 - Domnich 1985; 20 - Elyshev 1975; 21 - Genov 1984; 22 - Genov 1984; 22 - Genov Georgiev 1998; 23 - Gulyaev Kornienko 1998; 24 - Gulyaev et al. 2004; 25 - Hanzelová Rýšavý 1996; 26 - Hanzelová Rýšavý 1999; 27 - Haukisalmi. Henttonen 1994; 29 - Haukisalmi. Henttonen 1998; 30 - Hritanko, Gashev 2005; 31 - Irzhavskiy, Gulyaev 2002; 32 - Irzhavskiy, Gulyaev 2003; 33 - Jourdane 1971; 34 - Karasev 1972; 35 - Karpenko 1996; 37 - Karpenko 1998; 38 - Karpenko, Gulyaev 1990; 39 - Kirillova, Kirillov 2007; 40 - Kisieliewska 1961; 41 - Kobulei 1953; 42 - Kornienko, Gulyaev 1997; 45 - Kornienko, Gulyaev 2005; 46 - Kornienko et al. 2006; 47 - Kornienko et al. 2008b; 48 - Lykova 2005; 49 - Mas-Coma, Gallego 1977; 50 - Melnikova 2005; 51 - Merkusheva, Bobkova 1981; 52 - Meszaros, Murai 1983; 53 - Meszaros et al. 1981-1982; 54 - Mituch 1968; 55 - Murai, Meszaros, 1984; 56 - Novikov 1992; 57 - Novikov 1995; 58 - Odnokurcev, Karpenko 1993; 59 - Okulova et al. 2003; 60 - Panov, Karpenko, 2004; 61 - Pojmanska, 1957; 62 - Prokopčík 1956; 63 - Prokopčík 1958, 64 - Prokopčík 1959; 65 - Prokopčík, Grosehaft 1961; 66 - Prokopčík et al. 1974; 67 - Ribas et al. 1988; 70 - Sawada et al. 1992; 72 - Sawada et al. 1995; 73 Schaldbin 1957; 74 - Schaldbin 1964; 75 - Sharpe 1964; 76 - Shimakov 2001; 77 - Skolka et al. 2004; 78 - Smit 1974; 79 - Solty's 1952; 80 - Solty's 1954; 81 - Sosnina 1961; 82 - Spassky 1949; 83 - Spassky, Andreiko 1970; 84 - Spassky, Andreiko 1971; 85 - Spassky, Morosov 1959; 86 - Spassky et al. 1969; 87 - Štefančíkova et al. 1994; 88 - Swiderski et al. 2000; 89 - Terzea 1970; 90 - Tkach 1993; 91 - Tokobaev 1976; 92 - Vasilyev 1949; 93 - Vaucher 1971; 94 - Vikitrov et al. 1964; 95 - Vysotskaya 1997; 96 - Yushkov, 1995; 98 - Žarnowski 1955; 99 - Žasinyé 2001.

attributed to this species from Asia belong to the species *S. infirma* (Žarnowski, 1955) Vaucher, 1994.

Consequently, this summary indicates that the cestode fauna of European *Sorex* is similar to that of Western Asia, but its species richness is much lower. For example, 28 species are widespread in Western Siberia, three of them are endemic in this territory, and ten species are widespread in both Western and Eastern Siberia. The cestode fauna of East Siberia is even more diverse; besides Transpalearctic and Transsiberian species it contains no less than 16 endemic species. Therefore, according to the present data, the Eastern Siberian fauna of *Sorex* cestodes contains 2.5 times more species than the European fauna. Data on *Sorex* cestodes (Kornienko *et al.*, 2008b) of Kunashir, a comparatively small island (1.5 thousand km<sup>2</sup>), between the Sea of Okhotsk and western North Pacific, reflect the biodiversity of this region. There have been 20 species of *Sorex* cestodes found on the island, i.e., more than in the entire region of Europe. Five of the species (*Ditestolepis diaphana* (Cholodkowsky, 1906) Soltyš, 1952, *U. prolifer*, *S. furcata*, *Pseudobothrialepis mathevossiana* Schaldybin, 1957, and *S. jacutensis*) are transpalearctic, eight of them are endemics of islands in the Pacific Ocean (Sakhalin, Kurils, Hokkaido) and the remaining ones belong to the faunal complex of the East Palearctic. Distinctive features of the Asian Palearctic cestode fauna, in contrast to Europe, are the presence of three endemic genera of Hymenolepididae (*Brachylepis* Karpenko & Gulyaev, 1999, *Mathevolepis* Spassky, 1948, and *Diorchilepis* Lykova, Gulyaev, Melnikova & Karpenko, 2006) and a substantially greater number of species in the genera *Ecrinolepis* Spassky and Karpenko, 1983 and *Neoskrjabinolepis* Spassky, 1947. The geographical and historical reasons for the similarity of the cestode fauna of *Sorex* in Western Asia and Europe as well as low diversity of the latter will be discussed further.

#### Cestode faunas of *Sorex*, *Neomys* and *Crocidura*

Cestodes of various Soricidae are specific to their hosts. Specificity is normally (only with a few exceptions) expressed at the level of host genus but not subfamily. Both *Sorex* and *Neomys* belong to the subfamily Soricinae, and parasites in hosts of the latter genus belong to 6 genera and 15 species of Hymenolepididae (Table 2); among these, there are no parasites specific to *Sorex* (Table 2). Specific parasites of European *Crocidura* include 12 species of hymenolepidids belonging to 3 (or 4) genera (Table 2). According to data available in literature, 11 of the species specific to *Neomys* and *Crocidura* were also discovered in shrews of the genus *Sorex* (Table 2). Additionally, 7 species of cestodes specific to *Sorex* were reported in *Neomys*, whereas 4 were found in *Crocidura* (Table 3).

Overall, the cestode fauna of various genera of Soricidae have some degree of similarity. This apparent similarity, however, is misleading and influenced both by patterns of specificity and potential errors in identification. In the case of *Sorex*, an extremely large number of apparently non-specific cestodes were reported in articles by Mituch

(1968) from Slovakia and by Prokopič (1956, 1958, 1959, 1972) from Czechoslovakia, i.e., from the Carpathian region. All of these records are problematic, and are considered to be in error or in need of direct confirmation. The re-examination of Mituch's collection revealed that there were no cestode slides. Worms along with specimen-tags indicating identification were kept in glass-tubes filled with formalin. The re-examination of these cestode specimens, carried out when preservation conditions permitted, showed that the earlier species identifications were incorrect. According to Dr. F. Moravec, the Curator of the Institute of Parasitology of the Academy of Sciences of the Czech Republic, cestode slides from Prokopič's collection were in poor condition and unfit for the re-examination. Results of the examination of Mituch's collection will be published as a separate article following the current review. It is apparent, however, that records and identifications of cestodes in Soricidae from the Carpathian Mountains require confirmation.

#### Cestode fauna of *Sorex* in the postglacial zone of Europe

The composition of the cestode fauna of *Sorex* in the deglaciated zone of Europe was reviewed. These included studies from Lithuania (Žasitytė, 2001; Binkienė, 2006), Finland (Haukisalmi, 1989; Haukisalmi & Henttonen, 1994, 1998), Karelia, Russia (Anikanova & Yeshko, 2001; Anikanova & Boyko, 2003; Anikanova *et al.*, 2002, 2005a, 2005b; Novikov 1992), Archangelsk Oblast (Okulova *et al.*, 2003), and the Komi Republic, Russia (Yushkov, 1995). In addition, we used data from new collections (as reported herein) from Lithuania, Latvia, Estonia, and the North of the European zone of Russia (the Vologodskaya Oblast and Karelia).

A compilation of these data suggests that sixteen out of seventeen European cestode species are characteristic of this region (Table 1). Only one species of hymenolepidid, *Soricinia soricis*, is known in the areas that were not affected by glaciation. In Northern Europe, *Skrjabinacanthus jacutensis* was defined as a rare parasite that was found only once in the Archangelsk Oblast (Okulova *et al.*, 2003). This species, however, commonly occurs in Western Europe (Brendow, 1969; Jourdane, 1971; Vaucher, 1971) and in Northern Asia (Yakutia, Magadanskaya Oblast, and Kamchatka) (Karpenko & Gulyaev, 1990; Novikov, 1995; Dokuchaev *et al.*, 2003; Melnikova, 2005). Thus, the degree of similarity between the fauna of *Sorex* cestodes in the postglacial part of Europe and its Southern territories is very high (over 95 percent).

The putative history and distribution for cestodes in *Neomys* from Northern Europe contrasts with that demonstrated for *Sorex*. As it was already noted, in the South of the continent, the cestode fauna of *Neomys* is distinguished by a relatively high diversity and specificity being represented by 15 species in 6 genera (Table 2). In the regions of postglacial Europe (Lithuania, Karelia, and the Komi Republic) where these shrews were examined, only one species of specific parasite, *Neomylepis magnirostellata* (Baer, 1931) Tkach, 1998, was discovered in Lithuania

Table 2. Genera and Species of Cestodes found in European species of *Neomys*, *Crocidura* and *Suncus*.  
Those species also reported as occurring in *Sorex* are indicated

**Cestodes in *Neomys*:**

***Coronacanthus*** Spassky: *C. integra* (Hamann, 1891)\*, *C. magnihamatus* Vasileva, Tkach et Genov, 2005, *C. omissa* (Baer et Joyeux, 1943) and *C. vassilevi* Genov, 1980.

***Cryptocotylepis*** Skryabin et Matevosyan: *C. globosoides* (Soltys, 1954)\* (also Western Siberia);

***Insectivorolepis*** Žarnowski: *I. globosa* (Baer, 1931)\*;

***Neomylepis*** Tkach: *N. magnirostellata* (Baer, 1931)\*;

***Triodontolepis*** Yamaguti: *T. bifurca* (Hamann, 1891)\* (also Central Caucasus), *T. boyanensis* Vasileva, Tkach et Genov, 2005, *T. hamanni* (Mražek, 1891)\*, *T. ryšavyi* Prokopich, 1972, *T. skrjabini* Spassky et Andrejko, 1968\*, *T. šumavensis* (Prokopič, 1957) and *T. torrentis* Murai, 1987;

***Vaucherilepis*** Tkach, Vasileva et Genov: *V. trichophorus* Tkach, Vasileva et Genov, 2003.

**Refs:** **Europe** – Andreiko, 1969, 1973; Arzamasov *et al.*, 1969; Baer, 1931, 1932; Genov, 1980, 1984; Genov & Georgiev, 1998; Hanzelová and Ryšavý, 1996; Mas-Coma, 1977a; Merkusheva & Bobkova, 1981; Mituch, 1968; Murai, 1987; Murai & Meszaros, 1984; Prokopič, 1956, 1957, 1958, 1959; Prokopič & Groschaft, 1961; Ribas *et al.*, 2003a; Schaldybin, 1964; Soltys, 1954; Spassky & Andreiko, 1970; Štefančíková *et al.*, 1994; Tkach, 1991, 1998; Tkach & Swiderski, 1996; Vasileva *et al.*, 2005; Vaucher 1971.

**Asia** - Gulyaev & Kornienko, 1999; Irzhavskii & Gulyaev, 2002; Kornienko, 2001; Panov & Karpenko, 2004; Sawada & Kobayashi, 1993

**Cestodes in *Crocidura*:**

***Hilmylepis*** Skryabin et Matevosyan: *H. prokopici* Genov, 1970 and *H. raillieti* (Joyeux et Baer, 1950);

***Pseudhydymenolepis*** Joyeux et Baer: *P. graeca* Vaucher, 1984 and *P. redonica* Joyeux et Baer, 1935;

***Staphylocystis*** Villot: *S. biliarius* Villot, 1877, *S. brusatae* (Vaucher, 1971) (also in Central Asia), *S. loossi* (Hilmy, 1936), *S. pistillum* (Dujardin, 1845)\*, *S. scalaris* (Dujardin, 1845)\*, *S. tiara* (Dujardin, 1845)\* (also in Central Asia and Caucasus), and *S. uncinata* (Stieda, 1862) (also in Western Siberia);

***Vampirolepis*** Spassky: *Vampirolepis khalili* (Hilmy, 1936)\* (requires confirmation).

**Refs:** **Europe** - Arzamasov *et al.*, 1969; Baer, 1928, 1932; Bellocq *et al.*, 2007; Chiriac & Barbu, 1962; Chiriac & Hamar, 1966; Fuentes *et al.*, 2005; Genov, 1970, 1984; Genov & Georgiev, 1998; Hanzelová & Ryšavý, 1996; Joyeux & Baer, 1936; Mas-Coma & Jourdane, 1977; Mas-Coma, 1977b; Mas-Coma *et al.*, 1984; Mituch, 1968; Murai & Meszaros, 1984; Quentin *et al.*, 1971; Prokopič, 1959, 1972; Ribas *et al.*, 2003; Shimalov, 2007; Skolka *et al.*, 2004; Torres *et al.*, 2003; Vasileva *et al.*, 2005; Vaucher, 1971, 1984.

**Asia** – Irzhavskii & Gulyaev, 2002; Ishigenova & Ivanova, 2005; Karpenko, 2001; Sosnina, 1961; Tokobaev, 1976; Velikanov, 2003

**Cestodes in *Suncus Ehrenberg*:**

***Staphylocystis*:** *S. banyulsensis* (Mas-Coma, Fons, Galan-Puchades et Valero, 1986), *S. cerberensis* (Mas-Coma, Fons, Galan-Puchades et Valero, 1986), *S. Claudevauchereri* (Mas-Coma, Fons, Galan-Puchades et Valero, 1984).

\*Also found in *Sorex*- References for cestodes of *Neomys*: (Andreiko, 1973; Genov, 1984; Hanzelová & Ryšavý, 1996; Haukisalmi, 1989; Haukisalmi & Henttonen, 1994; Jourdane, 1971; Meszaros & Murai, 1983; Mituch, 1968; Prokopič, 1956, 1958, 1959, 1972; Shimalov, 2001; Spassky & Andreiko, 1970; Štefančíková *et al.*, 1994). References for cestodes of *Crocidura*: (Baer, 1928, 1932; Hanzelová and Ryšavý, 1996; Karasev, 1972; Merkusheva & Bobkova, 1981; Mituch, 1968; Pojmanska, 1957; Prokopič, 1956, 1958, 1959; Shimalov, 2001; Vasiljev, 1949).

(our data). In Karelia, Anikanova *et al.* (2002) discovered single specimens of *Monocercus arionis* and *Neoskrjabinolepis schaldybini*, both parasites typical in *Sorex*, in each of 2 *N. fodiens* examined. Yushkov (1995), however, did not find any cestodes in five animals examined in the Komi Republic. It can be assumed that one factor explaining the depauperate cestode fauna in *Neomys* from the postglacial part of Europe is the low abundance of potential hosts. In the regions located south from the deglaciated area, however, which support a great abundance of water shrews, diversity of the cestode fauna remains limited.

Having examined 288 specimens of *N. fodiens* and 71 of *N. anomalus* collected from Belovezha (Eastern Poland), Soltys (1954) found only three cestode species (*Cryptocotylepis globosoides* (Soltys, 1954) Karpenko et Gulyaev, 1990, *N. magnirostellata* and *Triodontolepis bifurca* (Hamann, 1891) Yamaguti, 1959). These observations suggest that a relatively high diversity fauna for cestodes in *Neomys* is limited inclusively from southern Europe up to the Carpathian Mountains.

The depauperate cestode fauna in the Northern part of the area is also typical for *Crocidura*. The study of these

shrews in Central Poland found no cestode species which are specific to that host genus. In 6 out of the 25 specimens of *Crocidura leucodon*, Žarnowski (1955) found *S. furcata*, a common parasite of *Sorex*. Meanwhile, Pojmanska (1957) did not find any cestodes in 6 specimens of *C. leucodon* from the Poznan region. The observed differences in the composition of cestode faunas in *Sorex* and those characteristic of *Neomys* and *Crocidura* in the postglacial territory of Europe (relative species richness) can be explained by differences in the colonization history, as explored in detail in subsequent sections.

of high quality (e.g., Hoberg *et al.*, 2009). Nonetheless, mistakes occurring in the literature must be corrected. Therefore, we are convinced that all cases of parasites discovered in apparently atypical hosts must be accompanied by detailed descriptions, and the worms themselves must be archived in museum collections as vouchers for further examination and as evidence of the record.

In a general sense, however, infection of atypical hosts with cestodes that otherwise demonstrate specificity cannot be ruled out (e.g., Bondarenko & Kontrimavichus, 2006).

Table 3. Records for Genera and Species of Cestodes considered specific in European *Sorex* which are also reported as occurring in species of *Crocidura* and *Neomys*; listing published reports and authors

#### *Sorex* Cestodes in *Neomys*

*Ditestolepis diaphana* (Genov & Georgiev, 1998; Schaldybin, 1964; Mituch, 1968; Panov & Karpenko, 2004)

*Hepatoceastus hepaticus* (Andreiko, 1973)

*Monocercus arionis* (Andreiko, 1973; Anikanova *et al.*, 2002; Baer, 1928; Genov & Georgiev, 1998; Kisielewska, 1961; Mituch, 1968; Murai & Meszaros, 1984; Panov & Karpenko, 2004; Soltys, 1954; Štefančíková *et al.*, 1994; Schaldybin, 1964)

*Neomylepis magnirostellata* (Baer, 1932; Genov, 1984)

*Neoskrjabinolepis singularis* (Andreiko, 1973; Prokopič, 1959; Mituch, 1968; Hanzelová & Ryšavý, 1996; Panov & Karpenko, 2004)

*Neoskrjabinolepis schaldybini* (Schaldybin, 1964).

*Pseudobotriolepis mathevossianae* (Panov & Karpenko, 2004)

*Soricinia soricis* (Andreiko, 1973; Spassky et Andreiko, 1970; Mituch, 1968; Hanzelová & Ryšavý, 1996)

*Staphylocystis furcata* (Prokopič, 1959; Mituch, 1968; Hanzelová & Ryšavý, 1996; Soltys, 1954)

*Urocystis prolifer* (Genov, 1984)

*Vigisolepis spinulosa* (Spassky & Andreiko, 1970; Andreiko, 1973; Hanzelová & Ryšavý, 1996; Mituch, 1968)

#### *Sorex* Cestodes in *Crocidura*

*Ditestolepis diaphana*, (Genov & Georgiev, 1998; Prokopič, 1956, 1958, 1959; Andreiko, 1973; Baer, 1928; Kobulei, 1953)

*Monocercus arionis* (Genov & Georgiev, 1998; Prokopič, 1956, 1958, 1959; Andreiko, 1973; Baer, 1928)

*Neoskrjabinolepis singularis* (Prokopič, 1956, 1958, 1959; Hanzelová & Ryšavý, 1996; Kobulei, 1953; Tokobaev, 1976)

*Staphylocystis furcata* (Mituch, 1968; Hanzelová & Ryšavý, 1996; Prokopič, 1958, 1959; Žarnowski, 1955; Tokobaev, 1976)

## Discussion

### Host specificity and defining cestode faunal diversity

Interpretations of faunal diversity are strongly dependent on factors, particularly specificity, that control the distribution of different species or species groups of tapeworms relative to an array of potential and recognized hosts. This point emphasizes the importance of accurate identification tied to archival specimens (vouchers) that document the results of comprehensive survey and inventory (e.g., Brooks & Hoberg, 2000; Hoberg *et al.*, 2009). In this light, the problematic nature of apparently erroneous records for non-specific cestodes in *Sorex* from the Carpathians and an absence of suitable vouchers documenting the fauna becomes of greater importance. Revision of separate helminth groups based on the re-examination of the original collections is complicated and further confounded by the lack of representative vouchers

Such host-switching or colonization as an ecological and microevolutionary process may be the basis or precursor for subsequent diversification through “hostal radiation” (Kontrimavichus, 1985; see also Hoberg & Brooks, 2008). Conceptually, this view of colonization processes is compatible with ecological fitting where parasites track plesiomorphic resources of hosts rather than particular taxa or host species in ecological and evolutionary time (Brooks *et al.*, 2006; Hoberg & Brooks, 2008; Agosta & Klemens, 2008). These phenomena may occur among the parasites of Soricidae, and represent more general determinants for diversity and structure among complex host-parasite assemblages. The cestode fauna of shrews contains a spectacular example of host switching by *Staphylocystis furcata*, a common and wide-spread *Sorex* parasite. The other eight known species of this genus are typical cestodes of Crocidurinae with five species parasitizing *Crocidura* and three among species of *Suncus* Ehrenberg.

### *Exploring and developing an historical context for the European fauna*

Europe is an historical concept. Geographically it is a huge peninsula which encompasses a region on the western edge of Eurasia. Ecologically, the major part of Europe belongs to the Siberian-European ecozone. Certain peculiarities, however, such as its isolation from overland regions in the South by the Mediterranean and inland seas, its specific climate greatly influenced by the Atlantic Ocean, and by cyclical or episodic processes associated with Pleistocene glaciations have undoubtedly affected its biota and contributed to its relative distinctiveness. Processes that took place during the last glaciation and the subsequent re-colonization through post-glacial expansion for floras and faunas are of major significance. Paleontological and historical biogeographical evaluations along with more recent genetic data and phylogeographic studies have revealed much about the structure of the fauna and responses to stadial and interstadial environments (Hewitt, 1999, 2004; Lister, 2004; Avise, 2000). Two points are pertinent: (1) Western Europe is the only region that has been relatively well studied based on the most informative genetic methods. In Eastern Europe as well as in the Asian part of the Palearctic just a few investigations of this kind have been conducted, which makes detailed phylogeographic analyses difficult to carry out. (2) Although the data presently available are scarce, they show that colonization of Northern Europe by shrews proceeded both from the South and the East.

The history and directionality for geographic colonization has been established relative to studies on both soricomorphs and arvicoline rodents. Mitochondrial DNA studies on widespread species of small mammals, including *Sorex araneus* and *S. minutes* (Bilton *et al.*, 1998) suggest that colonization may have occurred from glacial refugia in central Europe - western Asia. In a karyological study of *Sorex araneus*, Polyakov *et al.* (2001) established that the colonization stream for *S. araneus* extended from east to west eventually reaching the middle of Scandinavia. Data exploring the phylogeographic history for the arvicoline *Microtus agrestis* L., revealed temporal and spatial congruence with this history of post-Pleistocene expansion (Jaarola & Searle, 2002). They demonstrated that the contact zone for Eastern and Southern populations of *M. agrestis* in Scandinavia is located nearly in the same place as that for *S. araneus*; to the East of the Baltic Sea, that is in the territory of Lithuania. These data were later confirmed by Baltrūnaitė *et al.* (2006), who showed that the contact zone for populations of *M. agrestis* covers the territory of Belarus. This postulated scenario for postglacial colonization in Europe, however, is not universal across all taxa that have been evaluated.

Investigation of the cytochrome-b gene in the vole *Microtus arvalis* Pallas showed a different picture for phylogeography and distribution for this species in Europe (Haynes *et al.*, 2003). It allows us to assume that during the postglacial period, expansion even of closely related spe-

cies proceeded from different refugia, and probably, over disparate time frames. The same data raise some doubts about the validity of the popular opinion that the present-day European biota survived on Southern peninsulas, mostly in the Balkans and Iberia. Jaarola and Searle (2004) revealed that the cyt-b gene of *M. agrestis* from the region of the Mediterranean Sea differs from that of Northern populations within the range evaluated by the authors as an indicator of interspecies divergence. Differences in cyt-b genes show that the continental region of Europe could not have been inhabited from Mediterranean refugia.

The only parasitic species for which genetic structure has been examined comparatively well in Southern Europe (Nieberding *et al.*, 2008) is the nematode *Heligmosomoides polygyrus* (Dujardin, 1845). These studies demonstrated allopatric and genetically discrete lineages which reflected geography; nematode lineages in *Apodemus*, however, were not differentiated according to host species. Nieberding *et al.* (2008) showed that geographic differentiation is connected with three major Southern European refugia, reflecting a history in the Quaternary. These studies were also consistent in identifying a role for eastern refugia in the geographic colonization of northern Europe at the termination of the Pleistocene.

Unfortunately, there have been few phylogeographical investigations of cestodes conducted, and none exploring relationships for faunas in soricomorphs. Specimens now being assembled through survey and inventory can contribute to eventual phylogeographic analyses, and would be expected to clarify many aspects of the formation of the present-day European fauna. An example is seen in the studies of *Andrya arctica* Rausch, 1952 (= *Paranoplocephala arctica* (Rausch, 1952) sensu Haukisalmi *et al.* (2001) carried out by Wickström *et al.* (2001, 2003) which provide a clear picture for the history of colonization by collared lemmings of the genus *Dicrostonyx* Gloger across Beringia. Further, complex patterns for geographic colonization and host associations linking the Palearctic and Nearctic have been revealed by helminths in arvicoline rodents and mustelids (e.g., Cook *et al.*, 2005; Waltari *et al.*, 2007; Zarlenga *et al.*, 2006; Koehler *et al.*, 2009).

Pleistocene level events, and particularly patterns of geographic colonization in the Quaternary have served to influence the structure of the fauna. These events in shallow evolutionary time, however, are not the sole influence on diversity and distribution of assemblages of hosts and parasites in the region. The contemporary fauna has considerably deeper origins, which may be explored through an extensive historical record for soricomorphs in the Palearctic. Again, indicated here, is the importance of historical backbones that establish the conditions that often serve as determinants or contribute to the structure of contemporary faunas (e.g., Hobert & Brooks, 2008, 2010). Information on the evolution and palaeontology of shrews, which in Europe has been studied more thoroughly than in any other part of the world can provide a certain basis for the current discussion.

The first Soricidae are known in Europe from the Early

Oligocene. Soricids attained considerable diversity during the Late Oligocene and Early Miocene, when they completely replaced the earlier Heterosoricidae. Extinction of heterosoricid shrews can be attributed to climate change, and a shift to colder and drier conditions. In Europe by the Middle Pliocene, Soricidae was represented by 17 genera and 32 species belonging to seven tribes (Rzebik-Kowalska, 1998). Soricidae included Soricinae with the tribes Anourosoricini and Blarinellini, several species of which are currently known in South-Eastern Asia, the tribe Blarinini, currently found only in North America, and the extinct Eurasian tribe Beremendiini. Representatives of the first two tribes became extinct in Europe during the Early Pleistocene and the tribe Beremendiini vanished during the Middle Pleistocene (Rzebik-Kowalska, 1998).

The most ancient *Sorex* were discovered in North America in deposits of Early Miocene age (Harris, 1998). Although well-dated discoveries of these shrews in Europe belong to the Late Miocene, some hypotheses claim that this area was inhabited by *Sorex* during the Middle and even the Early Miocene (Rzebik-Kowalska, 1998). In the Pliocene *Sorex*, just like all Soricidae were abundant and widely distributed. Faunal turnover is apparent, and the last occurrences of such species as *S. bavaricus* Terzea in Romania (Terzea, 1970), *S. casimiri* Rzebik-Kowalska in Poland (Rzebik-Kowalska, 1991), and *S. subminutus* Sulimski in France (Clot *et al.*, 1976) date back to the Late Pliocene. During the Pleistocene many species of *Sorex* became extinct. According to Rzebik-Kowalska (1998), this period witnessed extinction of no less than fourteen species of the genus in Europe, the latest discoveries of these species dating from the Early as well as Middle and Late Pleistocene.

Among Recent European *Sorex* species, *S. minutus* Linnaeus has the most ancient origin, extending to the Early Pliocene (Rzebik-Kowalska, 1991, confirmed by several authors). Meanwhile, for other living species of the genus occurrences do not extend deeper than the Pleistocene: *Sorex araneus* Linnaeus, *S. cuniculus* Laxmann and *S. minutissimus* Zimmermann since the Early Pleistocene, *S. alpinus* Schinz since the Middle Pleistocene, and *S. coronatus* Millet and *S. granarius* Miller since the Late Pleistocene. According to Rzebik-Kowalska (1998) the origin of other known species is quite recent.

Species occupying areas or geographic ranges of extremely different size and apparently, of heterogenous origin, form the basis of the modern European *Sorex* fauna. Four species occupy relatively small geographic areas; i.e. *S. alpinus*, *S. coronatus*, *S. granarius* and *S. samniticus* Altobello are European endemics. The present-day distributions of *S. araneus* and *S. minutus* cover Europe and Western Siberia up to Lake Baikal. The latter species, however, is known in Japan as a fossil (Storch *et al.*, 1998). In contrast, *S. caecutiens*, *S. isodon* and *S. minutissimus* are known across the extent of the Palearctic region. It should be noted that only the very Northern regions of Europe are inhabited by *S. isodon* and *S. minutissimus*, and their expansion appears similar to that of the vole, *Myodes rutilus* (Pallas).

This observation, suggests that contemporary populations of these species colonized the postglacial territory of Europe from the East, although fossils of *S. minutissimus* are known from Central and Southern Europe from the Early and Middle Pleistocene, while those of *S. isodon* are not recorded in Europe (Rzebik-Kowalska, 1998).

In Asia, fossil shrews have been poorly studied relative to the European fauna. Central and East Asia, as a cradle of various European taxa which appeared as immigrants during the Pliocene and Pleistocene, are considered as an extremely important region for the evolution of shrews (Storch *et al.*, 1998). Faunal changes which have been documented in the paleontological record appear to reflect climatic trends during transitions across the boundaries of Miocene-Pliocene and Pliocene-Pleistocene. Patterns are consistent with increasing diversity through the Pliocene, followed by declines through the Quaternary and are indicative of processes which took place in Europe (Storch *et al.*, 1998). Diversity was reflected also in habitat structure, for example, southern regions of Western Siberia were dominated by steppe landscapes both during the Pliocene (Zazhygin & Zykin, 1984; Zykin *et al.*, 1989, 1995) and the Pleistocene (Storch *et al.*, 1998). This implies a more restricted variety of habitats suitable for shrews, as compared with more diverse environments in Central Europe, which were forested at that time, and had a more complex topography. These patterns and processes are reflected not only by mammalian faunas, but also by faunas of land and fresh-water mollusks and by sedimentary conditions. An extended history for shrews in the Palearctic and one associated with episodes of faunal turnover indicates complex drivers for diversity of the helminth fauna associated with these mammals.

#### *Historical relationships for shrews and tapeworms*

Considering the cestode fauna of European *Sorex*, we can conclude that it is quite ancient and possibly older than the contemporary host fauna in which it now circulates, and thus represents an assemblage of ecological relicts (Hoberg & Brooks, 2008). This assumption appears supported by the composition and distribution of the fauna where seventy percent of the recognized tapeworm species in the European zone have transpalearctic distributions and are known throughout Northern Asia. Some of the species are known even on the Japanese Islands, part of which were connected to the continent and resembled peninsulas in the Pleistocene. Sixteen percent of the species known in Europe are also widespread in Western Asia, and only two species (constituting less than twelve percent), are most likely European endemics. The hypothesis for the structure and history of the cestode fauna of *Sorex* in the deglaciated regions of Europe as ecological relicts requires evaluation based on a context provided by host and parasite phylogenies (e.g., Hoberg & Brooks, 2008).

The history for the *Sorex*-fauna serves to explain some aspects of cestode diversity and host associations. Although the soricomorph fauna is ancient, during the Pleistocene European *Sorex* underwent nearly a complete

faunal turnover (all species, except *S. minutus* were replaced). The assemblage of contemporary species clearly have different origins and geographic sources reflecting a history for episodic geographic expansion and isolation. The cestode fauna is ecologically conservative as reflected in the predominance of species that exhibit transpalearctic and Western Asian distributions.

Conservatism in conjunction with faunal turnover for hosts suggests that the contemporary assemblage of cestode species originated prior to the radiation for the majority of contemporary host species. This pattern is compatible with lineage persistence for parasites which is driven by host colonization (a shift to a new host group or species) followed by extinction of an assemblage of ancestral hosts (Hoberg, 2005; Hoberg & Brooks, 2008). Such a hypothesis can only be examined in the context of robust phylogenies for both host and parasite groups, and is currently beyond the capacity of this study or research program, given that considerable knowledge about diversity for this fauna remains to be revealed through survey and inventory. Further, radiation driven by host and geographic colonization also must be explored in the context of phylogeny. For example, similar to the dynamics demonstrated for species of tapeworms in the genus *Taenia* Linnaeus, 1758 among carnivores, guild structure, ecological conservatism and ecological fitting may be substantial drivers or determinants of diversity for assemblages of parasites among *Sorex* and other soricomorphs (Hoberg, 2006).

Caveats aside, it is possible to assume that cestode species formed earlier than the majority of present-day host species. In the absence of paleontological data, or molecular-based divergence estimates, it is problematic to specify a well supported time-frame for diversification of the cestode fauna among species of *Sorex*. In our opinion, however, there are justifiable reasons to postulate the Pliocene as a period of appearance and expansion of Palearctic cestode species. Alternatively it is possible that initial origins and radiation are considerably deeper in time, such that the fauna in part may have been acquired from the Heterosoricidae which appeared in the Early Oligocene and became extinct in the Pliocene.

As paleontological and evolutionary markers, cestodes of *Sorex* clearly demonstrate that the drivers for diversity across provincial regions of the Palearctic differ. For example, in the European cestode fauna transpalearctic species make up two thirds of all species, whereas in Western Siberia (according to data available in literature) they make up only about half, and in Eastern Siberia approximately one third. Such data support the contention of mammalogists about the significance of Central and Eastern Asia in the evolution of Soricidae, and, naturally, of their parasites. Low diversity of the cestode fauna of European *Sorex* can be explained by its remoteness from the primary evolutionary centers, and by origins related to geographic expansion.

Deglaciated areas of Europe were populated by a significant component of European cestode species (over 90

percent). This is explained by the fact that the larger part of this territory was forested and provided favourable conditions for the habitation of shrews and development of their parasites. The temporal and spatial aspects of geographic colonization (both process and directionality) require further studies. Cases of finding parasites in *Sorex* that are typical of other shrew genera deserve attention as well (e.g., Tables 2 and 3). According to data available in the literature, such cases are rare, although understanding patterns of faunal diversity, for example, those linking *Sorex*, *Neomys* and *Crocidura* may ultimately reveal insights into broader ecological and historical processes for host colonization in space and time.

## Conclusions

We outline a testable hypothesis for the origins and structure of the cestode fauna associated with *Sorex* in the European zone of the Palearctic. The cestode fauna associated with shrews and with *Sorex* in particular in the Palearctic and in the European zone has been assembled as a mosaic over a considerable period of time extending into the Tertiary. Based on empirical data, considerations of geographic and host distribution, and patterns of helminth species diversity, the similarity of the fauna among species of *Sorex* in Europe and its linkages to the Asian-Palearctic region were established prior to the Pleistocene. Considerable faunal turnover for host groups and species extended over the late Pliocene and Pleistocene, but this was not apparently accompanied by extinction or extirpation (at a local level) for assemblages of cestode parasites; thus the cestode fauna may be older than the contemporary host fauna in which it occurs. This is postulated based on the broad geographic ranges now occupied by many species extending from Eurasia into the western Palearctic that are associated with the contemporary *Sorex* fauna. Actually, many cestode species are likely to have become extinct in Europe coincidental with their hosts. Many species, however, were resistant to ecological transitions of the Pleistocene, and were apparently more persistent than their arrays of host species. Thus, the contemporary fauna represents a mosaic of relatively archaic and recent parasite species in which determinants of diversity have been strongly ecological (host and geographic colonization) in contrast to coevolutionary (cospeciation). These patterns are consistent with the proposal for recognition of macroevolutionary mosaics (Hoberg & Brooks, 2008, 2010), and shows that changes in host-parasite systems are dynamic, complex and heterogenous in space and time. The level of extinction, speciation, and colonization of European shrews of the genus *Sorex* in the Pleistocene was higher than that of their cestodes. Due to their resistance and ecological potential the majority of persistent or surviving species of cestodes could easily colonize the postglacial territory of Europe and this occurred on trajectories from east to west during the Quaternary.

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Appendix I. Summary of literature documenting the helminth fauna of Soricomorpha and Erinaceomorpha from Europe and the Eastern Palearctic.  
When general studies or reviews documenting faunas in a specific region were available, earlier articles were not cited.

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### Parasites of Insectivores in the European Region-

**Austria** (Prokopič & Mahnert, 1970; Vaucher, 1971); **Belarus** (Grigor'ev, 1963; Arzamasov *et al.*, 1969; Karasev, 1972; Merkusheva & Bobkova, 1981; Shimalov, 2001; Shimalov & Shimalov, 2001); **Belgium** (Vaucher, 1971); **Bulgaria** (Genov, 1984; Michev *et al.*, 1998; Vasileva *et al.*, 2005; Tkach *et al.*, 2003); **Carpathian Mountains** (Tkach & Swiderski, 1996; Murai & Meszaros, 1984); **Czechoslovakia** (Prokopič, 1956, 1957, 1958, 1959; Prokopič & Groschaft, 1961; Vaucher, 1971); **Denmark** (Vaucher, 1971); **Elba Island** (Ribas *et al.*, 2003b); **Finland** (Vaucher, 1971; Haukisalmi 1989; Haukisalmi & Henttonen 1994); **France** (Baer, 1932; Jourdane, 1971; Vaucher, 1971; Mas-Coma *et al.*, 1984, 1986a, 1986b); **Germany** (Brendow, 1969); **Great Britain** (Lewis, 1968; Sharpe, 1964); **Greece** (Vaucher, 1984); **Hungary** (Kobulei, 1953; Meszaros & Murai, 1983; Murai, 1987); **Iberian Peninsula** (Casanova *et al.*, 1996; Feliu *et al.*, 2001; Mas-Coma, 1977a, 1977b; Mas-Coma & Gallego, 1977); **Italy** (Andreani & Valle, 1988; Milazzo *et al.*, 2002; Poglajen *et al.*, 2003); **Lithuania** (Žąsitytė, 2001; Žąsitytė & Grikiene, 2002; Binkienė, 2006); **Moldova** (Andreiko, 1973; Spassky & Andreiko, 1969, 1970, 1971; Spassky *et al.*, 1969); **Netherlands** (Vaucher, 1971; Smit, 1974); **Norway** (Vaucher, 1971); **Poland** (Soltys, 1952, 1954; Żarnowski, 1955; Pojmanska, 1957; Rybicka, 1959; Furmaga, 1959, 1961; Kisielewska, 1961; Vaucher, 1971); **Pyrenees Mountains** (Euzet & Jourdane, 1968; Ribas *et al.*, 2003a, b); **Romania** (Terzeo, 1970; Tkach 1993); **Russia: Karelia** (Anikanova & Yeshko, 2001; Anikanova & Boyko, 2003; Anikanova *et al.*, 2001, 2002, 2005a, 2005b; Novikov, 1992); **Archangel'skaya oblast'** (Okulova *et al.*, 2003); **Saint Petersburg** (Cholodkovsky, 1913; Vasilyev, 1949); **Komi** (Yushkov, 1995); **Mordovia** (Schaldybin, 1957, 1964); **Nizhegorodskaya oblast'** (Morosov, 1957b); **Novgorodskaya oblast'** (Cholodkovsky 1906, 1912); **Kalininskaya oblast'** (Petrov & Savinov, 1959; Viktorov *et al.*, 1964); **Ivanovskaya oblast'** (Spassky, 1949); **Samarskaya oblast'** (Kirillova & Kirillov, 2007); **USSR** (Petrov & Tshertkova, 1959); **Slovakia** (Mituch, 1968; Meszaros *et al.*, 1981 – 1982; Štefančíková *et al.*, 1994; Hanzelová & Ryšavý, 1996, 1999); **Spain** (Bellocq *et al.*, 2007; Fuentes *et al.*, 2005); **Sweden** (Vaucher, 1971); **Switzerland** (Baer, 1928, 1931, 1932; Vaucher, 1971; Swiderski *et al.*, 2000); **Ukraine** (Tkach, 1991, 1998; Tkach *et al.*, 2003; Vysotskaya, 1997); **Western Europe** (Vaucher, 1971, 1982; Casanova *et al.*, 2002; Ribas & Casanova, 2005); **Palearctic** (Ribas & Casanova, 2006).

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### Parasites of Insectivores in the Eastern Palearctic Region-

**Central Caucasus** (Irzhavskiy & Gulyaev, 2002, 2003; Irzhavskiy *et al.*, 2005a, 2005b; Prokopič & Matsaberidze, 1971, 1972); **Central Asia** (Sosnina, 1961; Vaucher & Tenora, 1971; Ryšavý *et al.*, 1976; Tokobaev, 1976; Tkach & Velikanov, 1990, 1991; Karpenko, 1994, 2001; Velikanov, 1997a, 1997b, 2003; Velikanov & Tkach, 1993); **Siberia** (Afanas'eva, 1993; Dokuchaev *et al.*, 2003; Domnich, 1985; Eltyshev, 1971, 1975; Fedorov, 1975; Gulyaev & Kornienko, 1998, 1999; Gulyaev *et al.*, 2004, 2007, 2009; Hritanko & Gashev, 2005; Karpenko, 1982, 1983, 1984a, 1984b, 1984c, 1990, 1993, 1996, 1998; Karpenko & Chechulin, 1990; Karpenko & Gulyaev, 1990, 1999; Kornienko, 2001; Kornienko & Gulyaev, 1997, 2005; Kornienko & Lykova, 2005; Kornienko *et al.*, 2006, 2008a, b; Lykova, 2005; Lykova *et al.*, 2006; Melnikova, 2005; Melnikova & Gulyaev, 2004; Melnikova *et al.*, 2005; Morozov, 1957a; Novikov, 1995; Odnokurcev & Karpenko, 1993; Panov & Karpenko, 2004; Sadovskaya, 1954, 1965; Sawada *et al.*, 1995; Shakhmatova & Gulyaev, 1990; Spassky & Karpenko, 1983; Spassky & Morosov, 1959; Vaucher & Tenora, 1971; Yun, 1963); **Japan** (Ohbayashi, 1973; Ohbayashi *et al.*, 1972; Sato *et al.*, 1988; Sawada 1993, 1999; Sawada & Harada, 1986, 1990, 1991, 1993, 1994; Sawada & Kaneko, 1992; Sawada & Kobayashi, 1993; Sawada & Koyasu, 1990, 1991a, 1991b, 1991c, 1991d, 1995; Sawada & Saito, 1993; Sawada *et al.*, 1992, 1993; Yokohata, 2010; Yokohata *et al.*, 1989).

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