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Nearctic Shrews, *Sorex* spp., as Paratenic Hosts of *Soboliphyme baturini* (Nematoda: Soboliphymidae)

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ABSTRACT: Third-stage larvae (L3) of *Soboliphyme baturini* were discovered for the first time in shrews, *Sorex cinereus* and *Sorex tundrensis* from Alaska and the Nearctic. Shrews were found to be infected with L3 at Suloia Lake, south-eastern Alaska, Togiak National Wildlife Refuge, southwestern Alaska, and at the Yukon-Charley Rivers National Preserve near the Yukon-Alaska border. Larvae in shrews from Alaska were morphologically indistinguishable from those known in both insectivores and arvicoline rodents from Russia. The occurrence of *S. baturini* in Alaskan insectivores further establishes shrews as important hosts in the transmission of *S. baturini* among mustelids and other carnivores and indicates for the first time the basis for a paratenic cycle in the Nearctic.

KEY WORDS: Nematoda, *Soboliphyme baturini*, shrews, paratenic hosts, northeast Asia, Alaska.

The third-stage larvae (L3) of *Soboliphyme baturini* Petrow, 1930 (Nematoda, Soboliphymidae) have been found repeatedly in small mammals from the Palearctic. In the Russian Far East (Magadan Region; Khabarovskii Krai; southern Primorskii Krai; Sakhalin Island), the shrews *Sorex caecutiens* Laxmann, *Sorex camtschaticus* Yudin, *Sorex daphnaeodon* Thomas, *Sorex gracillimus* Thomas, *Sorex isodon* Turov, and *Sorex unguiculatus* Dobson are known as paratenic hosts of this helminth (Domnich, 1982; Karpenko, 1985; Dokuchaev, 2001, 2003, 2005). Additional reports of paratenic hosts include gray-sided voles, *Clethrionomys rufocanus* Sundevall, from the Tomsk Oblast (Karpenko et al., 1998).

Across the Holarctic, about 25 species of carnivorous mammals, including *Martes zibellina* (Linnaeus), *Martes americana* (Turton), *Mustela vison* Schreber, *Martes erminea* Linnaeus, and *Gulo gulo* (Linnaeus), are known as definitive hosts of *S. baturini*; felids and canids are rarely infected, and usually worms do not attain sexual maturity in hosts other than mustelids (Kontrimavichus, 1969). The prevalence and intensity of infection among some mustelids from territories of Siberia and the Far East of Russia are so high that epizootic outbreaks of *Soboliphyme* have been observed (Kontrimavichus, 1962). In captive sables (*M. zibellina*), intense in-

fections may be accompanied by progressive anemia, vomiting of blood, and blood in the feces (Kadenatsii [1939] in Karmanova, 1968); infections may also be fatal (Oshmarin, 1963).

The life cycle of *S. baturini* was studied by E.M. Karmanova (1968). The intermediate hosts are oligochaetes of the family Enchytraeidae, in which larvae of *S. baturini* develop from first to third stage. Karmanova established experimentally that passive transmission could occur to mustelid definitive hosts through ingestion of infected oligochaetes, and considered that this represented the primary route for infection. She further postulated an alternative route for transmission via the ingestion of infected paratenic hosts such as insectivores and rodents (Karmanova, 1968; Zarnke et al., 2004).

Karmanova's assumption recently was confirmed based on material from the Magadan region. Shrews with high-intensity infections of larval *S. baturini* (up to 50 larvae per shrew) have been commonly reported. Such observations clearly indicate that insectivores alone can provide a predictable source of L3 *S. baturini* for mustelids throughout the year (Dokuchaev, 2001).

Although infections have been documented, currently information on the distribution of larval *S. baturini* in shrew paratenic hosts is limited to the Far East of Russia (Dokuchaev, 2003). Further data on the prevalence and intensity of larval *S. baturini* in mammalian paratenic hosts are limited, and informa-

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tion from North America is absent. We report results of collections of larval *S. baturini* in naturally infected shrews from Russia and Alaska, along with morphological comparisons of the third-stage larvae. These represent new host records for *S. baturini* in the Nearctic.

MATERIALS AND METHODS

Specimens of insectivores were examined from multiple localities in Alaska between 1994 and 2001. Twenty seven specimens of *Sorex cinereus* Kerr were caught between 8 and 12 July 1994 from the area of Suloia Lake, southeast Alaska, USA (57°25'11"N; 135°43'12"W). In August 2001, 302 shrews from the Togiak National Wildlife Refuge, southwest Alaska (59°18'4"N, 161°6'50"W; 59°18'25"N, 161°4'27"W), previously preserved in ethanol and in the museum collections of University of Alaska Museum (Fairbanks, Alaska), were necropsied and examined for parasites; shrews were collected in 1996 by K. N. Peirce and J. V. Peirce. Additional specimens of *S. cinereus* and *Sorex tundrensis* Merriam were collected and examined from the Yukon-Charley Rivers National Preserve, Alaska, near the border of the Yukon Territory, Canada (65°18'29"N; 142°02'08"W).

Larvae were preserved in 70% ethanol or 10% formalin. Representative specimens from the area of Suloia Lake have been deposited in the Institute of Animal Systematics and Ecology of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia. The others have been deposited in Institute of Biological Problems of the North Far Eastern Branch of the Russian Academy of Sciences, Magadan, Russia.

RESULTS

Soboliphyme baturini was found to represent a common nematode parasite in insectivores from Alaska, and third-stage larvae were found for the first time in shrews, *S. cinereus* and *S. tundrensis*, from the Nearctic. Among 27 *S. cinereus* at Suloia Lake, 11 of 12 overwintered shrews were infected by L3 of *S. baturini*; intensity of infection ranged from 4 to 10. In contrast, 15 young of the year shrews were not infected. Prevalence of infection was 40.7% for all shrews and 91.7% for overwintered shrews only.

In August 2001, at the University of Alaska Museum, inspection of 302 shrews from Togiak National Wildlife Refuge showed that 24 *S. cinereus* and one *S. tundrensis* were infected by larvae of this nematode. Prevalence of infection was 8.3%, and intensity ranged from 1 to 6 (mean = 1.9 ± 0.32). In the summer of 2001, *S. baturini* larvae also were found in the same shrew species (data not available) from the Yukon-Charley Rivers National Preserve.

Morphology of L3

Ovoid capsules, which measured approximately $2.4\text{--}3.6 \times 3.5\text{--}4.7$ mm and were located on the abdominal side of the diaphragm, each contained single L3 of *S. baturini*. This is the first report of *S. baturini* in Nearctic shrews; thus, we present a comparative morphological analysis of the Palearctic and Nearctic forms based on comparisons of L3 in *S. cinereus* from the area of Suloia Lake (Table 1; Figs. 1–4).

The L3 of *S. baturini* have a well-developed cup-shaped oral sucker and dense, coiled body. Dorsally, the cuticle of the sucker has clear longitudinal striations. The cuticle of the body has well-marked longitudinal and transverse striations. The hypodermis is marked by a rectangular pattern. The oral sucker is oval and slightly subterminal to the ventral side. On the border of the oral capsule are three pairs of cone-shaped papillae. The nerve ring is located near the base of the oral capsule. Seven cervical glands are disposed as in adult specimens of *S. baturini* (see Karmanova, 1968). The genital primordium is tubular and elongate. Sexual dimorphism is apparent in the L3, and the caudal bursa of the male is discernible.

Male (Fig. 1): Body length = 3.7–5.9 mm (Table 1); maximum width, 0.32–0.35 mm, attained near mid-level of intestine. Oral sucker = 0.50–0.55 mm length \times 0.48–0.55 mm width. Esophagus = 0.90–1.35 mm long; esophageal glands begin to branch out at 0.030–0.035 mm from orifice of oral sucker. Caudal region of body is slightly flattened dorso-ventrally. Bursa, rudimentary, is just beginning to form.

Female (Fig. 2): Body length = 3.2–5.7 mm; maximum body width, 0.22–0.25 mm, attained near mid-level of intestine. Oral sucker = 0.40–0.50 mm length \times 0.38–0.55 mm width. Esophagus = 0.90–1.25 mm long; esophageal glands begin to branch out at 0.030–0.035 mm from orifice of oral sucker. Caudal extremity is pointed.

Comparisons of larvae

The nematodes from different specimens of *S. cinereus* varied greatly in esophageal length (overall range was about 0.40 mm) and especially in body length (range was 2.2 and 2.5 mm for males and females, respectively). There was little variability in the dimensions of the remaining organs. Smaller larvae of *S. baturini* from one shrew had food remains, potentially blood or host tissue, in the esophagus and intestine (Fig. 3). Among larger larvae

Table 1. Comparative data for third-stage larvae of *Soboliphyme baturini* in oligochaetes, shrews, and voles from the Palearctic and in shrews from the Nearctic (Alaska); all measurements are in millimeters.

Characters	*Oligochaetes Palearctic	†Insectivores Palearctic	‡Insectivores Palearctic (24 males; 18 females)	§Arvicolinae Palearctic (5 males)	Sorex spp. Alaska (present study) (8 males; 6 females)
Capsule dimensions (L × W)	no data	1.5 × 2.0	3–4 × 5–6	no capsules	2.4–3.6 × 3.5–4.7
Body (L)	1.521–2.220	4.41 3.76–4.20	3.12–3.20 3.15–3.45	3.10–3.50 no data	3.7–5.9 3.2–5.7
Body (W)	0.181	0.37 0.33	0.225–0.234 0.24–0.26	0.34–0.38 no data	0.32–0.35 0.22–0.25
Oral sucker (L × W)	0.164 × 0.208	0.51 × 0.57 0.33–0.39 × 0.52–0.54	0.33–0.36 × 0.37–0.39 0.30–0.32 × 0.37–0.39	0.50–0.55 × 0.60–0.64 no data	0.48–0.55 × 0.50–0.55 0.38–0.55 × 0.40–0.50
Esophagus (L)	0.592	1.53 1.20	0.75–0.92	1.5–1.6 no data	0.90–1.35 0.90–1.25
Genital primordium (L)**	no data	no data	no data	2.0–2.1	1.845–2.083
Genital primordium (W)**	no data	no data	no data	0.09–0.10	0.036–0.060
Bursa dimensions**	no data	0.16 × 0.19	no data	0.025–0.030 × 0.11–0.12	0.059 × 0.060

* Karmanova (1968).

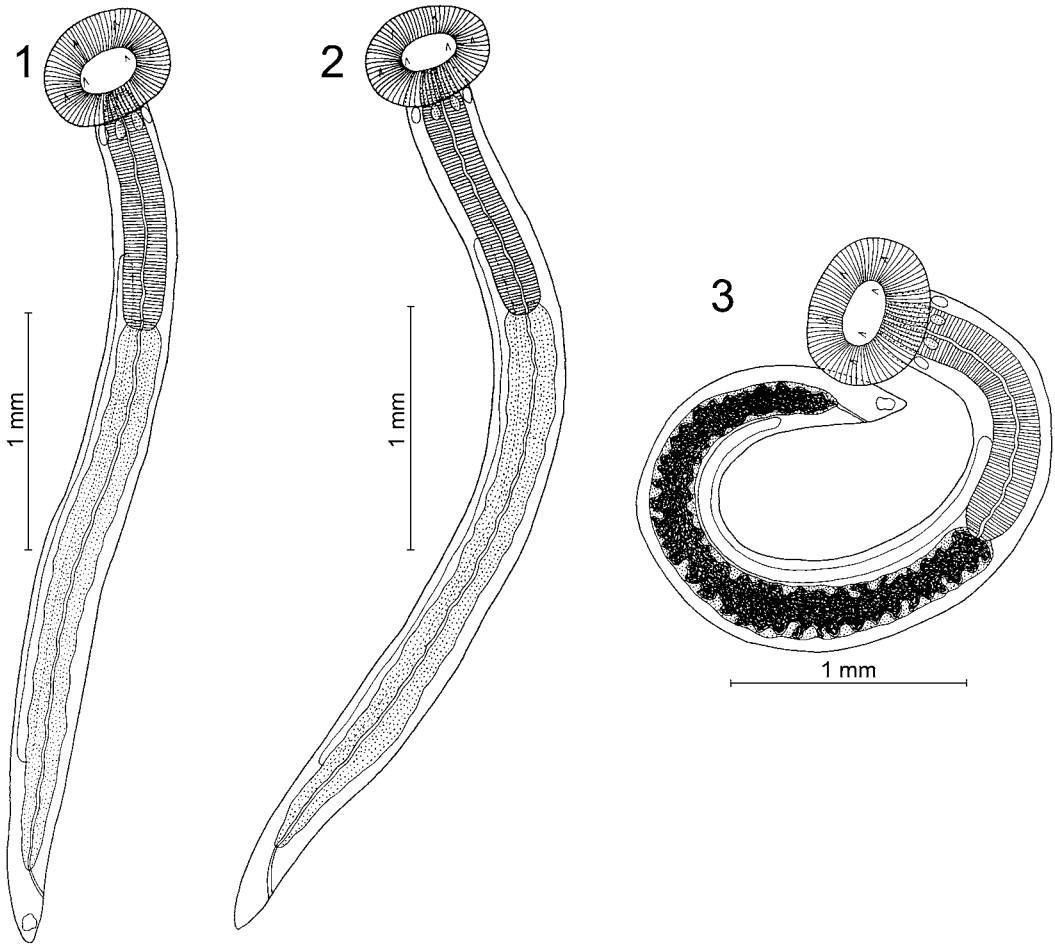
† Donnich (1982).

‡ Karpenko (1985).

§ Karpenko et al. (1998).

|| Males in numerator and females in denominator.

** Data are for males only.



Figures 1–3. Larval *Soboliphyme baturini* from Suloia Lake, southeastern Alaska, U.S.A. **1.** Male L3 from an overwintered female specimen of *Sorex cinereus*. **2.** Female L3 from an overwintered female specimen of *Sorex cinereus*. **3.** Male L3 with food particles, presumably host tissue or blood, retained in the intestinal tract, from an overwintered male of *S. cinereus*.

from another shrew, the esophagus and intestine were empty (Figs. 1, 2). We assume that in the first case, the larvae were younger and had encapsulated more recently. The presence of food remains in the esophagus and intestine of smaller larvae, which presumably have recently completed migration across the intestinal wall, may be compatible with this conclusion.

DISCUSSION

The nematode larvae in *S. camtschaticus* from the Palearctic and those in *S. cinereus* from the Nearctic were morphologically similar and did not differ significantly in size. Also, larvae of *S. baturini* in *S. daphaenodon* that were caught in Khabarovskii

Krai and in *C. rufocanus* from the Tomsk Oblast did not show any essential differences (Table 1). Third-stage larvae from all mammalian hosts are in general agreement with those originally described by Karmnova (1968).

The morphological similarity for these L3 of *S. baturini*, irrespective of host and geographic origin, may further suggest, consistent with the current taxonomy, that there is only a single species with a widespread distribution in mustelid hosts from the Nearctic and Palearctic. This hypothesis and the relationship of Nearctic and Palearctic populations of *S. baturini* remain to be evaluated in detail based on phylogeographic analyses of mitochondrial DNA (A. Koehler et al., unpublished data).

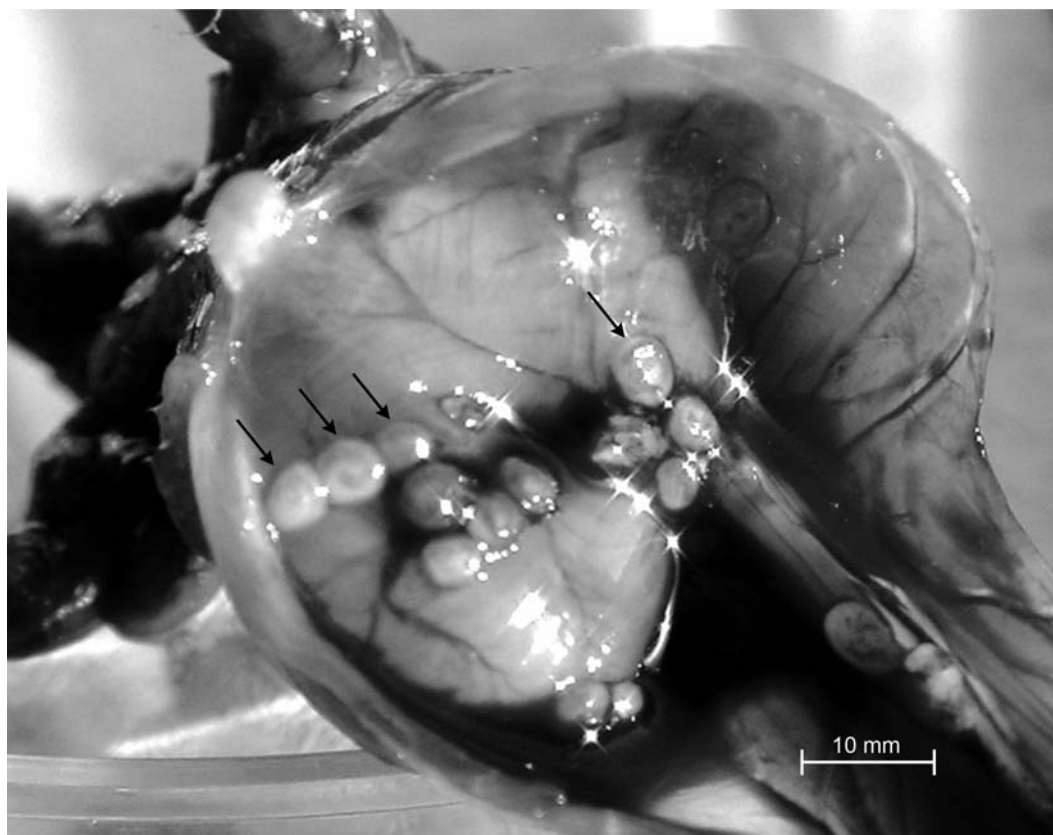


Figure 4. Larvae of *Soboliphyme baturini* encapsulated on the diaphragm of a shrew paratenic host; positions of some L3's are indicated by arrows.

The distribution of *S. baturini* in insectivores appears to be extensive across Alaska (from the southeast to subarctic latitudes, including the Yukon-Charley Rivers National Preserve) and likely coincides to some degree with the distribution of this parasite in mustelid definitive hosts in this region and elsewhere in North America (e.g., Hoberg et al., 1990; Zarnke et al., 2004). Martens are considered to be the most important host for these nematodes (Kontrimavichus, 1969), but apparently there are additional and currently unidentified environmental factors that serve as determinants of distribution (Zarnke et al., 2004). Food habits of primary mustelid hosts may be characterized as opportunistic, although arvicoline rodents are considered to be dominant through the annual cycle based primarily on scat analysis (e.g., Strickland et al., 1990). Insectivores, including species of *Sorex*, have been identified as prey for martens in Alaska but appear to be a minor component of the diet, most often represented during

the winter (Buskirk and MacDonald, 1984; Clark et al., 1987). Our studies may establish the basis for recognizing shrews as important paratenic hosts involved in transmission of *S. baturini*.

The migration of *S. baturini* larvae in the paratenic host appears to be a complicated process. Larvae must first pass through the intestinal wall and then through host tissues to the site of localization near the diaphragm (Fig. 4). Such a pattern is consistent with the occurrence of blood or host tissue in the intestinal tract of the encapsulated helminth. Residues of presumed host tissue retained in the intestine or esophagus are only seen in relatively small specimens. This also suggests that, over time, larval parasites may deplete such resources during growth, and in our opinion, the larger larvae of *S. baturini* with empty intestines represent infections of longer duration.

The third-stage larvae of *S. baturini* exhibit considerable growth in mammalian paratenic hosts, but they remain encapsulated and do not develop to

maturity in the gastrointestinal system (Table 1). It is interesting in this regard that insectivores serve as definitive hosts for at least 8 species of *Soboliphyme* that occur as adult parasites in shrews (*Soboliphyme abei* Asakawa, Kamiya, and Ohbayashi, 1988; *Soboliphyme atahai* Ganzorig, Batsiakhan, Oku, and Kamiya, 2003; *Soboliphyme jamesoni* Read, 1952; *Soboliphyme soricis* Baylis and King, 1932) or moles (*Soboliphyme hirudiniformis* Kirshchenblatt, 1946; *Soboliphyme caucasica* Mazaberidse, 1965; *Soboliphyme urotrichi* Machida and Uchida, 1982; and *Soboliphyme occidentalis* Ribas and Casanova, 2004) primarily from the Palearctic (Karmanova, 1968; Ganzorig et al., 2003; Ribas and Casanova, 2006). *Soboliphyme baturini* remains the only species known in carnivores that circulates through shrew paratenic hosts and may be the only species with a Holarctic distribution; apparently reports of *S. jamesoni* in the Palearctic require confirmation (Ganzorig et al., 2003). The phylogeny for species of *Soboliphyme* is unresolved, and thus the relationships for faunas in mustelids and insectivores remain to be explored (Ganzorig et al., 2003).

Data from the current study further emphasize the importance of insectivores as paratenic hosts for *S. baturini* and suggest that shrews may be more prominent in the diets of martens than previously recognized. Insectivores, and to a lesser degree arvicoline rodents such as *Clethrionomys* spp., may serve a critical role in active transmission of *S. baturini* to mustelids and other carnivorous definitive hosts via predator-prey interactions. The mode of passive transmission to mustelids, canines, and other definitive hosts by ingestion of plants with infected oligochaetes may represent an incidental route for infection.

ACKNOWLEDGMENTS

We are grateful to J. A. Cook, Curator of Mammals, Museum of Southwest Biology, University of New Mexico, for access to specimens and opportunities to conduct field studies. We thank the University of Alaska Museum for access to specimens of shrews. The USDA, Forest Service in part supported field and laboratory studies by N. Dokuchaev in Alaska. We appreciate comments provided by A. Koehler on the distribution of *Soboliphyme* and food habits in martens. This work was also supported by the Russian Fund for Fundamental Research grant 05-04-49010. This paper is a contribution of the Beringian Coevolution Project, funded in part by grants from the National Science Foundation (0196095, 0415668) to J. A. Cook and E. P. Hoberg.

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