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## GEOGRAPHIC AND HOST RANGE OF THE NEMATODE *SOBOLIPHYPME BATURINI* ACROSS BERINGIA

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**ABSTRACT:** The nematode *Soboliphyme baturini* Petrov, 1930, was found to represent a single species with a relatively broad geographic range across Beringia and northwestern North America on the basis of the assessment of molecular sequence data for adult and juvenile parasites. Refuted are hypotheses suggesting that several cryptic species could be partitioned either among an array of mustelid definitive hosts or across the vast region that links North America and Eurasia. Host specificity for this species is examined on the basis of a comprehensive list for definitive hosts, derived from new field surveys and existing literature for *S. baturini*. Only 5 mustelids (*Gulo gulo*, *Martes americana*, *M. caurina*, *M. zibellina*, and *Neovison vison*) appear to have significant roles in the life history, persistence, and transmission of this nematode. *Soboliphyme baturini* readily switches among *M. americana*, *M. caurina*, *Mustela erminea*, or *N. vison* at any particular locality throughout its geographic range in North America, although *Martes* spp. could represent the source for nematodes in a broader array of mustelids. Molecular analyses (243 base pairs of mitochondrial gene nicotinamide dehydrogenase [ND4]) suggest that hypotheses for host specificity across an array of mustelid definitive hosts are not supported. The life cycle of *S. baturini* is explored through a review of diet literature for 2 marten species, *M. americana* and *M. caurina*, and other mustelids across the Holarctic. Shrews (Soricomorpha: Soricidae) comprise >8% of prey for these species of *Martes*, suggesting their putative role as paratenic hosts. Juvenile nematodes found in the diaphragms of soricids are genetically identical to adult *S. baturini* found in the stomachs of mustelids at the same locations in both Asia and North America, corroborating a role in transmission for species of *Sorex*.

Establishing the roles for each participant in a parasite's life cycle is essential to interpreting ecology, epidemiology, distribution, and phylogeographic history. Hosts that are components of the life cycle can be defined as definitive (parasite achieves sexual maturity), intermediate (parasite develops, but does not reach sexual maturity), and paratenic (parasite undergoes no development stages, but might be transported from one trophic level to another) (Roberts and Janovy, 2005). Hosts can also be defined as incidental, when the parasite fails to reach sexual maturity. In this case, the host is unnecessary to the parasite life cycle and, therefore, could be insignificant to a parasite's evolutionary past. On the other hand, definitive hosts can have long-term coevolutionary relationships with their parasites, or the host/parasite relationship could be acquired through host switching (e.g., Brooks and McLennan, 1993; Hoberg, 2005). Recent relationships from host switching could be the result of ecological fitting (resource tracking), in which the parasite is tracking a resource in the host rather than the host itself (Kethley and Johnston, 1975; Janzen, 1985; Brooks et al., 2006).

Significant movements of species caused by the dynamic geologic events of the Pleistocene might have brought together new sets of potential hosts and increased the incidence of host colonization (Hoberg and Brooks, 2007). Hence, determinants of host associations and their relationship to host specificity can be a complex phenomenon (Brooks et al., 2006). Molecular perspectives have proved key to revealing such complexity, especially in dynamic ecological situations such as those that existed in high latitudes over the past 2 million yr (Cook et al., 2005).

Evolutionary roles for a spectrum of potential and actual hosts, however, might be unclear for nematode parasites when there is difficulty in distinguishing minute morphological dif-

ferences between species (cryptic species) or when trying to link together adult and juvenile forms. Juveniles are often difficult to identify to species because of undeveloped morphological characters essential to diagnosis (e.g., Jenkins et al., 2005). In these cases, molecular identification is necessary when trying to match juveniles in intermediate and paratenic hosts with adult nematodes in definitive hosts (McKeand, 1998).

*Soboliphyme baturini* Petrov, 1930, is a stomach-dwelling nematode and member of the monotypic Soboliphymatidae, Dioctophymidae (Karmanova, 1986). A complex life cycle characterizes *S. baturini*, with adult nematodes maturing in the stomach of the definitive host and females then releasing eggs that are shed in feces and deposited in the soil. In the leaf litter, the eggs are consumed by the intermediate host, enchytraeid oligochaetes, where they hatch, and the resulting juveniles develop to the infective third juvenile stage (J<sub>3</sub>) and are later transmitted to mammals (Karmanova, 1986). Soricomorphs and rodents feed on these oligochaetes and could serve as paratenic hosts by bridging the trophic gap between mustelid and oligochaete, or the definitive host might consume enchytraeids directly and become infected by the nematode (Karpenko, 1985; Karpenko et al., 1998, 2007). Adult *S. baturini* can survive in the definitive host for up to 20 mo; therefore, annual cohorts could overlap, leaving the hosts constantly infected (Karmanova, 1986).

Over 50 mammal species and subspecies are recognized hosts for *S. baturini* (Appendix); however, Kontrimavichus (1985) suggested that not all of these are necessary to the life cycle. For example, felids and canids are incidental hosts, meaning the juveniles can survive in the host but fail to reach sexual maturity (Karmanova, 1986). More specifically, *S. baturini* is most commonly found in sable (*Martes zibellina* (Linnaeus)), American marten (*Martes americana* (Turton)), and Pacific marten (*Martes caurina* (Merriam)) and less frequently in ermine (*Mustela erminea* Linnaeus), wolverine (*Gulo gulo* (Linnaeus)), and mink (*Neovison vison* (Schreber)) (Petrov, 1930; Price, 1930; Shimakura and Odajima, 1934; Bezdek, 1942; Morgan, 1943; Schmidt and Kinsella, 1965; Swartz, 1968; Kontrimavichus, 1985; Karmanova, 1986; Sato et al., 1999; Rusin et al., 2003; Zarnke et al., 2004).

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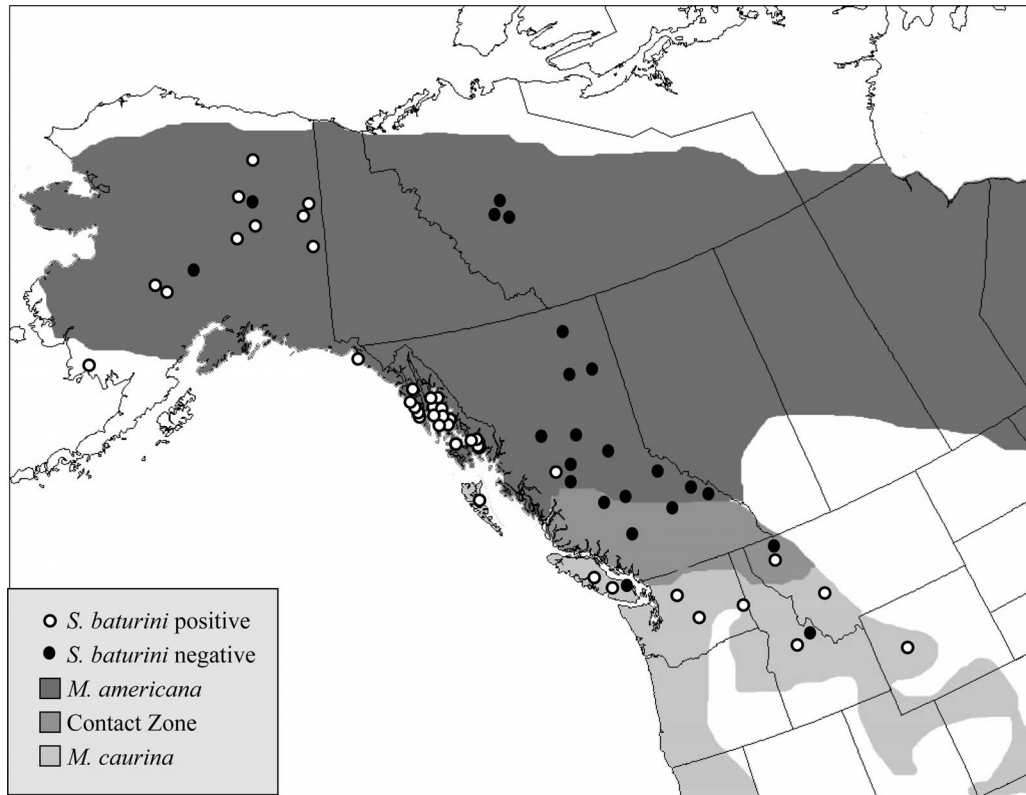


FIGURE 1. The geographic distributions of *M. caurina* and *M. americana* (modified from Hall, 1981) are overlapped with historic localities and survey results from this study for *S. baturini*. Admiralty and Kuiu Islands are the only islands known to support *M. caurina* in southeast Alaska. White dots represent occurrences of *S. baturini*. Black dots refer to necropsies of mustelids that were negative for *S. baturini*.

In North America, *S. baturini* is thought to be limited largely to the Pacific coast, with an eastward range extension to the southern Rocky Mountains. The southern range of this nematode coincides with the distribution of *M. caurina*, but intensive surveys need to be completed from southern and central British Columbia southward to northern New Mexico and northern California to adequately define this distribution. Further north, the nematode's distribution also includes the extreme western range of *M. americana* in southeast Alaska along the coast and in interior Alaska (Fig. 1). Occurrence of this nematode in *M. americana* apparently reflects 2 episodes of host switching (Koehler, 2006) in the Holocene, when *M. americana* expanded its range westward into both interior and coastal Alaska (Small et al., 2003).

*Soboliphyme baturini* is a prime candidate for studies that use molecular techniques to address the role of paratenic hosts in transmission and in exploring associations with definitive hosts. Worldwide host surveys over the past 76 yr resulted in recognition of a variety of potential definitive, intermediate, and paratenic hosts; yet, the roles that each of these host species played in the evolution of this nematode remain unclear (Fig. 2; Appendix). Additionally, the specifics of the life cycle of *S. baturini* have yet to be completely deduced, including the role of shrews as paratenic hosts and designation of the potential host species as either definitive or incidental.

In this study, the distribution of *S. baturini* was assessed with the use of new and historical data. Additionally, the following questions are explored. First, does *S. baturini* represent a single

widespread species, or is there evidence for cryptic species partitioned across 5 mustelid hosts (i.e., *M. americana*, *M. caurina*, *M. zibellina*, *M. erminea*, and *N. vison*)? Second, are soricomorphs paratenic hosts of *S. baturini*? These hypotheses are the foundation for assessing the life history and distribution of *S. baturini*.

## METHODS AND MATERIALS

In conjunction with the Beringian Coevolution Project (Hoberg et al., 2003; Cook et al., 2005), adult and juvenile *S. baturini* were obtained from 21 geographic sites across eastern Siberia and the Pacific Northwest (Table I). Adult nematodes from North American localities were acquired through necropsies of 756 salvaged mustelid carcasses from commercial trappers, including 460 *M. americana*, 124 *M. caurina*, 59 *Martes pennanti* (Erxleben), 70 *M. erminea*, 40 *N. vison*, 2 *Taxidea taxus* (Schreber), and 1 *G. gulo* (Table I). Of this total, 286 carcasses from interior British Columbia ( $n = 231$ ), central Northwest Territories ( $n = 45$ ), and Montana and Idaho ( $n = 10$ ) (Table I) were studied to refine the eastern boundary of this nematode. Additional adult and juvenile specimens were obtained through collaborative efforts with other scientists (Appendix). Unpublished records from the U.S. National Parasite Collection (USNPC; USDA, Beltsville, Maryland) and from the University of Alaska Museum (AF; Fairbanks, Alaska) were also included. Specimens of adult *S. baturini* in stomachs of mustelids or J<sub>3</sub> of presumptive *S. baturini* in diaphragms of soricids were preserved in 70 or 95% ethanol and stored at  $-20^{\circ}\text{C}$  before analysis. Each specimen was subsampled, with the midsection of the body being reserved for molecular sequencing, and the head and tail of individual adults or J<sub>3</sub> were archived as physical vouchers deposited in the Museum of Southwestern Biology (University of New Mexico, Albuquerque, New Mexico) (Table II).

Total genomic DNA was extracted from the midsections of individual

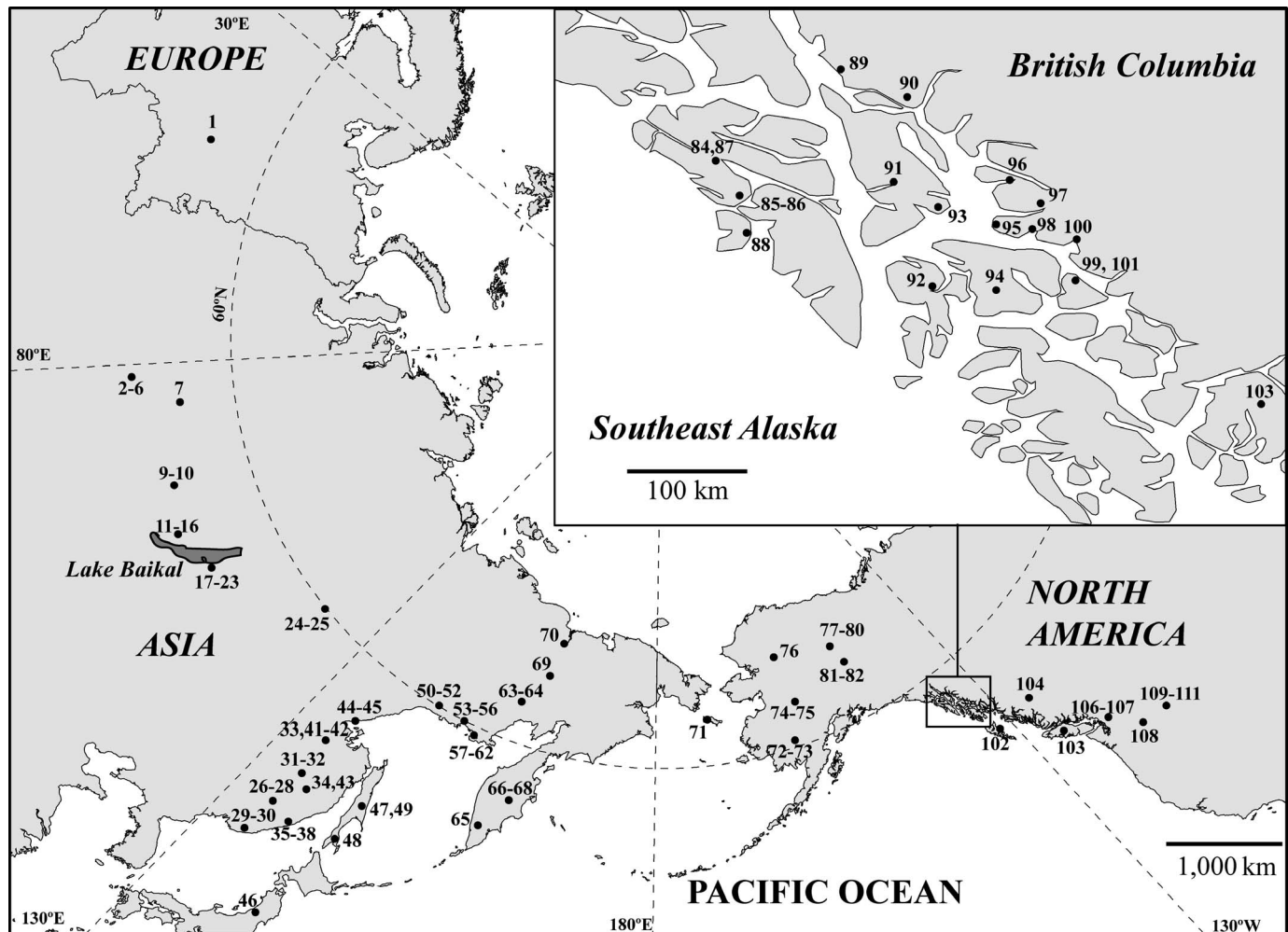


FIGURE 2. The distribution of *S. baturini* is based on published records and museum specimens and is centered on Beringia. Inset shows detail of localities in southeast Alaska. Numbers correspond to locality IDs in the Appendix.

worms with a commercial kit (AquaPure Genomic DNA Isolation Kit, Bio-Rad Laboratories, Hercules, California). A multilocus approach was employed to explore the potential for cryptic diversity in *S. baturini*. We assessed variation of 2 mitochondrial genes, nicotinamide dehydrogenase (ND4) and cytochrome oxidase I (COI). Phylogenetic species criteria (Adams, 1998; Brooks and McLennan, 2002; Nadler, 2002) were adopted in exploring whether *S. baturini* represents a single species among mustelids.

A 293-base pair (bp) region of the mitochondrial gene, COI (primers SoboCO1F 5'GCTCAGCTTCGGACAGTTTC3' and SoboCO1R 5'TCATGCAAATGAACATCTAGGG3'; Tran [2003]) was used to test for reciprocal monophyly including 3 representatives of *S. baturini* from major geographic localities within its range (Table III). Outgroups were *Soboliphyme abei* (Asakawa et al., 1988) in *Sorex unguiculatus* Dobson from Japan and *Soboliphyme jamesoni* Read, 1952, in *Sorex tundrensis* Merriam from Yakutsk, Russia. An additional outgroup includes *Trichinella britovii* Pozio, La Rosa, Murrell, and Lichtenfels, 1992; *T. nativa* Britov and Boev, 1972; and *T. murelli* Pozio and LaRosa, 2000.

The ND4 gene was used to further resolve the intraspecific phylogenies as suggested by Blouin (2002). A 243-bp region of ND4 was amplified from 8 worms (Table II) by polymerase chain reaction (PCR) with primers SoboND4F 5'GGGAGGGCCACTTACCTTAT3' and SoboND4R 5'GCCACAAACTTCTTCACGTCT3'. Primers for ND4 were designed with the use of Primer3 (Rozen and Skaletsky, 2000) on the basis of an alignment of published *Xiphinema americanum* Cobb, 1913 (GenBank NC005928), and *Trichinella spiralis* (Owen, 1835) (GenBank NC002681) ND4 genes.

Total reaction volumes were 25  $\mu$ l consisting of 14.25  $\mu$ l of H<sub>2</sub>O; 1  $\mu$ l of 10  $\mu$ M primer each; 1  $\mu$ l of DNA template ( $\sim$ 5 ng/ $\mu$ l); 2.5  $\mu$ l each of 25 mM MgCl<sub>2</sub>, 10 mM dNTPs, and 10 $\times$  PCR Buffer II; and 0.25  $\mu$ l of Taq (5 units/ $\mu$ l, AmpliTaq<sup>®</sup>, Applied Biosystems, Foster City, California). PCRs were run on PTC-200 thermocyclers (MJ Research, Waltham, Massachusetts) with the following parameters: initial denaturation at 94 C for 60 sec, subsequent denaturations for 30 sec, annealing at 67 C for 15 sec, and extension of 72 C for 30 sec, repeated for an additional 34 cycles, followed with a final extension of 72 C for 10 min. Product was visualized via electrophoresis on a 0.8% agarose gel and cleaned with 30% polyethylene glycol (PEG) and QiaQuick<sup>®</sup> cleanup kit (Qiagen Inc., Germantown, Maryland). BigDye<sup>®</sup> Terminator v.3.1 (Applied Biosystems) was used for cycle sequencing reactions. Excess dyes and primer were removed with Sephadex<sup>®</sup> G-50 spin columns or sodium acetate ethanol wash (Applied Biosystems). Forward and reverse strands were sequenced with an ABI PRISM<sup>®</sup> 3100 Genetic Analyzer.

Ambiguous sites were resolved with Sequencher<sup>®</sup> 4.6 (Genecodes, Ann Arbor, Michigan). Alignments were made with ClustalW (Chenna et al., 2003). All sequences were identical in length and no insertions or deletions were necessary. Mitochondrial sequences were translated to amino acids and examined for stop codons to check against pseudogenes. Sequences were deposited in GenBank, and physical vouchers were deposited in the Museum of Southwestern Biology (Table II). In total, 8 adult and J<sub>3</sub> nematodes were sequenced from 6 mustelids and 2 soricids to examine the amount of sequence divergence among putative specimens of *S. baturini* (Table II).



TABLE I. Locality data for mustelids that were examined for *S. baturini* throughout northwest North America. Prevalences and mean intensities of *S. baturini* from each locality are indicated.

Scientific name	n	Mean			Locality	State/Province	Latitude	Longitude
		Prevalence	intensity	Range				
<i>Gulo gulo</i>	1	0	0	0	Yukon Flats	Alaska	66.15	-147.55
<i>Martes americana</i>	10	0	0	0	100-Mile House	British Columbia, Canada	51.71	-121.55
<i>M. americana</i>	10	0	0	0	Enderby	British Columbia, Canada	50.68	-119.05
<i>M. americana</i>	22	4.5	1	1	Francois Lake	British Columbia, Canada	53.98	-126.43
<i>M. americana</i>	57	0	0	0	Kootenai National Park	British Columbia, Canada	50.47	-115.67
<i>M. americana</i>	14	78.6	14.7	1-38 ± 12.2	Kuiu Island	Alaska	56.72	-133.92
<i>M. americana</i>	75	85.3	20.7	1-200 ± 29.8	Kupreanof Island	Alaska	56.79	-133.50
<i>M. americana</i>	17	94.1	27.3	10-53 ± 15.2	Mitkof Island	Alaska	56.68	-132.92
<i>M. americana</i>	45	0	0	0	Norman Wells	Northwest Territories, Canada	65.23	-127.00
<i>M. americana</i>	5	0	0	0	Prince George	British Columbia, Canada	54.44	-123.39
<i>M. americana</i>	9	22.2	5.5	2-9 ± 4.9	Revillagigedo Island	Alaska	55.77	-131.60
<i>M. americana</i>	10	0	0	0	Smithers	British Columbia, Canada	54.75	-126.65
<i>M. americana</i>	133	53.4	12	1-80 ± 15.9	Thomas Bay	Alaska	57.02	-132.85
<i>M. americana</i>	41	2.4	1	1	Yukon Flats	Alaska	66.15	-147.55
<i>M. caurina</i>	56	87.5	21.9	3-97 ± 16.9	Admiralty Island	Alaska	57.20	-134.29
<i>M. caurina</i>	5	0	0	0	Idaho	Idaho	44.96	-113.64
<i>M. caurina</i>	3	0	0	0	Montana	Montana	48.20	-114.30
<i>M. caurina</i>	58	1.7	1	1	Vancouver Island	British Columbia, Canada	49.17	-123.93
<i>M. pennanti</i>	59	0	0	0	Central BC	British Columbia, Canada	52.00	-123.67
<i>Mustela erminea</i>	10	0	0	0	100-Mile House	British Columbia, Canada	51.71	-121.55
<i>M. erminea</i>	2	50	1	1	Admiralty Island	Alaska	57.20	-134.29
<i>M. erminea</i>	10	0	0	0	Fort Nelson	British Columbia, Canada	58.83	-123.75
<i>M. erminea</i>	10	0	0	0	Kupreanof Island	Alaska	56.79	-133.50
<i>M. erminea</i>	11	0	0	0	Mitkof Island	Alaska	56.68	-132.92
<i>M. erminea</i>	1	0	0	0	Queen Charlotte Islands	British Columbia, Canada	53.25	-132.00
<i>M. erminea</i>	7	0	0	0	Smithers	British Columbia, Canada	54.75	-126.65
<i>M. erminea</i>	5	0	0	0	Thomas Bay	Alaska	57.02	-132.85
<i>M. erminea</i>	7	0	0	0	Vancouver Island	British Columbia, Canada	49.17	-123.93
<i>Neovison vison</i>	1	0	0	0	100-Mile House	British Columbia, Canada	51.71	-121.55
<i>N. vison</i>	5	0	0	0	Enderby	British Columbia, Canada	50.68	-119.05
<i>N. vison</i>	5	0	0	0	Francois Lake	British Columbia, Canada	53.98	-126.43
<i>N. vison</i>	1	0	0	0	Kupreanof Island	Alaska	56.79	-133.50
<i>N. vison</i>	1	100	1	1	Mitkof Island	Alaska	56.68	-132.92
<i>N. vison</i>	2	0	0	0	Montana	Montana	48.20	-114.30
<i>N. vison</i>	7	0	0	0	Prince George	British Columbia, Canada	54.44	-123.39
<i>N. vison</i>	1	0	0	0	Smithers	British Columbia, Canada	54.75	-126.65
<i>N. vison</i>	2	0	0	0	Vancouver Island	British Columbia, Canada	49.17	-123.93
<i>Taxidea taxus</i>	2	0	0	0	Washington	Washington	47.00	-120.00

TABLE II. Specimens of *S. baturini* used in constructing the haplotype network for ND4 sequences. Specimens were obtained through the Beringian Coevolution Project or other collaborators throughout the Beringian region. Museum of Southwestern Biology and GenBank accession numbers, host species, host status (definitive or paratenic), and locality data are included.

Specimen	GenBank	Host species	Host style	Country	Locality	Latitude	Longitude
NK 135687	EF457895	<i>Martes americana</i>	Definitive	U.S.	Kupreanof Island	56.73	-133.57
NK 128108	EF457893	<i>M. americana</i>	Definitive	U.S.	Fairbanks, Alaska	65.18	-146.58
NK 122046	EF457892	<i>M. caurina</i>	Definitive	U.S.	Admiralty Island	57.28	-134.03
NK 159571	EF457891	<i>M. zibellina</i>	Definitive	Russia	Kamchatka	56.00	160.00
NK 122064	EF457890	<i>Mustela erminea</i>	Definitive	U.S.	Admiralty Island	57.44	-133.84
NK 122289	EF457896	<i>Neovison vison</i>	Definitive	U.S.	Mitkof Island	56.68	-132.92
NK 159582	EF457894	<i>Sorex cinereus</i>	Paratenic	U.S.	Eagle, Alaska	63.83	-142.16
NK 159576	EF457889	<i>S. unguiculatus</i>	Paratenic	Russia	Lazovski	43.28	134.05

TABLE III. Specimens of *Soboliphyme* used in constructing the MrBayes tree for COI sequences. Specimens were obtained through the Beringian Coevolution Project or other collaborators throughout the Beringian region. Museum of Southwestern Biology and GenBank accession numbers, host species, and locality data are included.

Specimen	GenBank	Species	Host species	Country	Locality	Latitude	Longitude
NK 135687	EF519531	<i>Soboliphyme baturini</i>	<i>Martes americana</i>	U.S.	Kupreanof Island	56.73	-133.57
NK 128108	EF519532	<i>S. baturini</i>	<i>M. americana</i>	U.S.	Fairbanks, Alaska	65.18	-146.58
NK 159571	EF519530	<i>S. baturini</i>	<i>M. zibellina</i>	Russia	Kamchatka	56.00	160.00
NK 139168	EF519533	<i>S. jamesoni</i>	<i>Sorex tundrensis</i>	Russia	Yakutsk	62.02	129.61
NK 139584	EF519534	<i>S. jamesoni</i>	<i>S. roboratus</i>	Russia	Yakutsk	62.07	128.94
NK 159581	EF519535	<i>S. abei</i>	<i>S. unguiculatus</i>	Japan	Hokkaido	43.05	141.35
NA	DQ007892	<i>Trichinella britovi</i>	NA	NA	NA	NA	NA
NA	DQ007894	<i>T. murrelli</i>	NA	NA	NA	NA	NA
NA	AB252966	<i>T. nativa</i>	NA	NA	NA	NA	NA

Maximum parsimony (MP) optimality criteria was used for phylogenetic reconstruction by PAUP\* (Swofford, 2002), considering all characters as unordered with 4 possible states (A, C, G, T); uninformative characters were excluded from the MP analysis. A branch and bound search was performed with COI sequences. Node support was evaluated with nonparametric bootstrap methodology and the use of 5,000 replicates for MP (Felsenstein, 1985). The Markov chain Monte Carlo (MCMC) sampling procedure was performed by the program MrBayes (Ronquist and Huelsenbeck, 2003) to estimate the posterior probability of phylogenetic trees. The program was executed twice with 5,000,000 generations run, 4 heated chains, and 45,000 trees saved. The median joining algorithm (Bandelt et al., 1999) in the program Network v4.1.1.2 (Fluxus Engineering, Suffolk, U.K.) was used to create a haplotype network for the 8 sequences of the ND4 gene (Table II).

## RESULTS

### Host surveys

Examination of historical accounts of *S. baturini*, along with data from the current study (Appendix), indicate that *S. baturini* is found predominantly in *M. americana*, *M. caurina*, and *M. zibellina*. Of 756 mustelids necropsied, 204 (27%) were infected and 3,674 specimens of *S. baturini* were recovered (Fig. 1; Table I). No *S. baturini* were found in *G. gulo* (n = 1), *M. pennanti* (n = 59), or *T. taxus* (n = 2). Only 1 *M. erminea* (n = 70) and 1 *N. vison* (n = 40) were infected, both in southeast Alaska. The highest prevalence of *S. baturini* in *M. americana* was from southeast Alaska. Of those hosts surveyed near the eastern boundary of the known range for *S. baturini*, only 1 worm was found (Francois Lake, interior British Columbia, n = 114) and none was found in the Northwest Territories (n = 45). *Martes caurina* had the highest prevalence of infection on Admiralty Island (88%) and *M. americana* had highest prevalences on Kuiu (79%), Kupreanof (85%), and Mitkof islands (94%).

### Assessment of distribution from current and historical data

Records of occurrence of *S. baturini* in North America, including those from this study, were mapped over the current distribution of the principle hosts, *M. americana* and *M. caurina* (Fig. 1). Two equivocal historical records of *S. baturini* occurred farther east in North America. A specimen of *S. baturini* reported from Madison, Wisconsin (Morgan, 1943), is unsubstantiated because the author does not refer to any specific locality. This specimen was identified at the USNPC by B. Chit-

wood in 1933, where the practice used at that time often referred geographic records to the city or laboratory, rather than to the actual geographic origin of the specimen. Another account of *S. baturini* was recovered in a single wolverine (*G. gulo*) from the province of Quebec, Canada (Bezdek, 1942). Because wolverines are long-distance dispersers (Hornocker and Hash, 1981) and infections of *S. baturini* can persist for 20 mo (Karmanova, 1986), this record might have been a chance dispersal event. Alternatively, that specimen could have been sent to a laboratory in Quebec from a western locality. If these 2 records are discounted, then the eastern limit of viable *S. baturini* populations would be the Rocky Mountains. We suggest this to be the case on the basis of the ease of detection of this large stomach-dwelling nematode combined with a series of published assessments of diets of mustelids in North America. In addition, extensive parasitological surveys of mustelids and other potential carnivore hosts east of the Rocky Mountains have not detected this parasite (Erickson, 1946; Meyer and Chitwood, 1951; Dick and Leonard, 1979; Jennings and Threlfall, 1982; Poole et al., 1983).

The Old World distribution of *S. baturini* appears limited to the region east of the Ural Mountains. Accounts of *S. baturini* west of the Urals may be attributed to human translocations of *M. zibellina* from the Baikal region after their earlier extirpation (Monakhov, 2001).

### Molecular identification of nematodes

Molecular analysis does not refute the hypothesis that *S. baturini* is a single widespread species. Sequences of COI from 3 putative adult *S. baturini* representing populations from disparate geographic localities in the Nearctic and Palearctic exhibited minimal variation, and MP analyses unequivocally demonstrated reciprocal monophyly relative to the presumptive sister species *S. abei* and *S. jamesoni* (Fig. 3). After initial assessment of this locus aimed at species-level identification, our focus shifted from COI to ND4 on the basis of expectations of greater variability and information content to explore variation in worms from different hosts at particular sites.

Sequences at the ND4 locus could not be reliably aligned between *S. baturini* and respective outgroups. Minimal diversity was demonstrated in sequences of ND4 for 6 adults and 2 J<sub>3</sub> larvae. Nematodes found in different mustelid hosts collected from similar geographic locations had identical sequences for

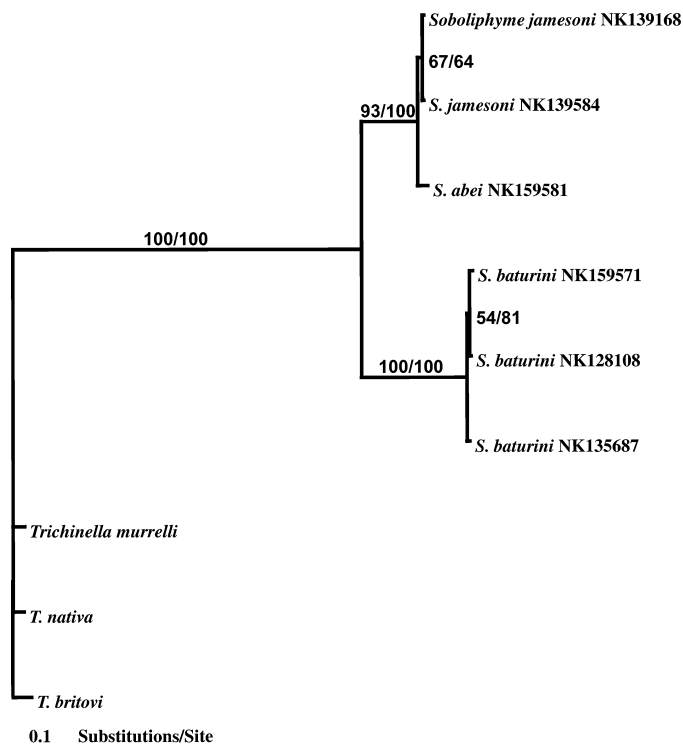


FIGURE 3. Reciprocal monophyly is established for *S. baturini* with a majority consensus tree for maximum parsimony. A maximum parsimony tree was generated with an exhaustive search from 293 bp of the COI mtDNA gene sequences of *S. baturini*, *S. abei*, *S. jamesoni*, and *Trichinella* sp. MrBayes tree topology has both Bayesian and MP nodal supports listed (Bayesian/MP). Trees were rooted with *Trichinella* sp. Major and minor subdivisions are illustrated.

central southeast Alaska (*M. americana*, *N. vison*) and Admiralty Island (*M. caurina*, *M. erminea*), respectively (Fig. 4). Sequences of specimens from putative *S. baturini* in soricids from Russia and Alaska also were identical or differed minimally when compared with worms inhabiting mustelids from the same geographic regions (Fig. 4). For example, nematode sequences from *M. zibellina* and *S. unguiculatus* Dobson were identical and differed by only 2 bp between *M. americana* and *S. cinereus* Kerr collected from 2 localities separated by 300 km in interior Alaska. This is evidence that shrews are paratenic hosts and that at any particular locality these worms are infecting a variety of hosts. Additionally, diet of New World marten and Old World sable (Table IV) indicated that shrews are consumed frequently.

DISCUSSION

Sampling

Identifying the role of putative hosts in a parasite’s life cycle (e.g., definitive, intermediate, or paratenic) is essential to understanding the evolutionary history and assessing the significance of processes such as ecological fitting in host/parasite dynamics. Wide taxon and geographic sampling is required to first document the range of a parasite, identify species limits, and characterize the role of component hosts. Here, we establish species identity, describe the geographic range, and identify the

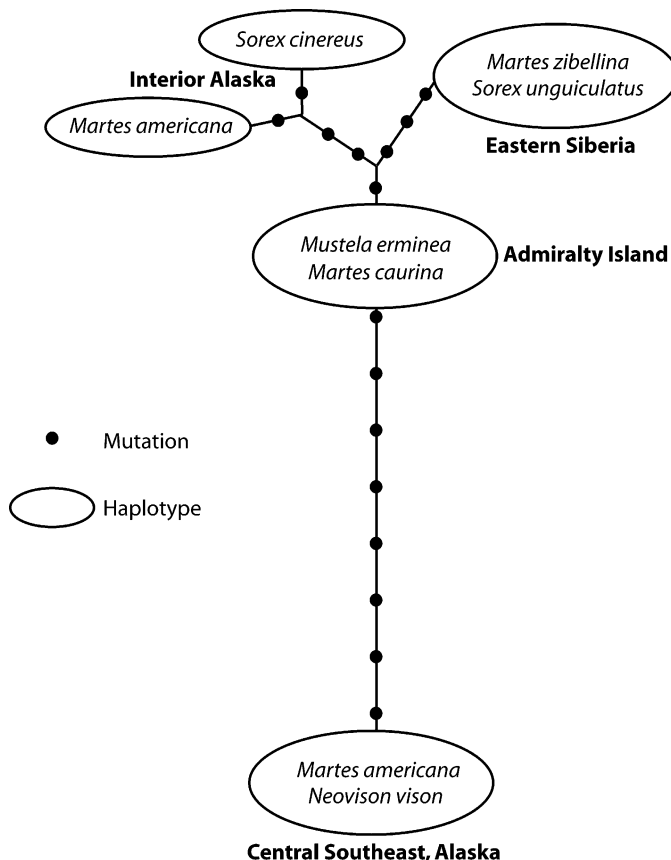


FIGURE 4. Network of *S. baturini* haplotypes (243 bp of the ND4 gene) constructed by the median joining method. Juvenile *S. baturini* (soricid hosts) are similar to adult *S. baturini* (mustelid hosts). Nematodes of *Neovison vison* and *M. erminea* are identical to nematodes in *M. caurina* and *M. americana*. Dots represent mutational changes. Ovals indicate haplotypes.

paratenic and definitive host associations of the Holarctic nematode, *S. baturini*.

Genetic diversity and species

Minimal genetic diversity was observed in putative populations of *S. baturini* (Fig. 3; Table III). Application of phylogenetic criteria (e.g., Adams, 1998; Brooks and McLennan, 2002; Nadler, 2002) establishes *S. baturini* as a single species. Cryptic species and species complexes have been reported and predicted among assemblages of Beringian helminths, including nematodes and cestodes (Hoberg et al., 1999; Haukisalmi, 2001, 2004) as a consequence of the complex history of faunal expansion and geographic colonization and isolation in this region. Among a diversity of parasitic helminths, minimal variation in morphological characters contrasts with “hidden molecular diversity,” a general phenomenon for helminths in Beringia and elsewhere (Hoberg et al., 2003; Haukisalmi et al., 2004; Cook et al., 2005). *Soboliphyme baturini* might be an exception to this generality (Koehler, 2006). Molecular comparisons did not detect substantial genetic variation among nematodes from different hosts, a finding consistent with the hypothesis that *S. baturini* represents a single species across its wide geographic range that spans Beringia (Koehler, 2006).

Low genetic diversity, multiple hosts, and relatively widespread geographic distribution suggest a shallow temporal association for *S. baturini* and mustelids that could be compatible with a history of geological and host colonization. Molecular characterization of *S. baturini* occurring in *G. gulo* and *M. pennanti* is still needed.

### Geographic range and life cycle

The distribution of *S. baturini* in marten from 3 major localities throughout Alaska was mapped (Zarnke et al., 2004; Fig. 1) on the basis of the following prevalences: northern (19%, n = 2,166), southwestern (30%, n = 1,058), and southeastern (47%, n = 3,028). Our expanded survey of marten and other mustelid hosts demonstrated high prevalences in southeast Alaska (64% n = 334). Only 1 worm was found east of the Coast Range (Table I; Fig. 1), suggesting that the distribution of *S. baturini* is restricted primarily to the Pacific Northwest.

The absence of *S. baturini* in central and eastern North America can be attributed to the distribution of intermediate hosts required for transmission. Experimental evidence found that only oligochaetes from the Enchytraeidae were suitable hosts for development of *S. baturini* (Karmanova, 1963). Enchytraeids are found on every continent, with greatest abundance in moist temperate regions (O'Connor, 1967). Karmanova (1986) concluded that the distribution of *S. baturini* was dependant on geography and meteorological conditions and potentially limited by availability of suitable enchytraeids. She found *S. baturini* most common in floodplains of major rivers in eastern Asia where enchytraeids thrive in areas of humid forest litter. During periods of drought, enchytraeids survive near water sources but perish during periods of extended flooding. Kaufmann et al. (2002) showed that enchytraeids colonize soils within 40 yr of deglaciation, so their distribution would be limited by rates of geographic expansion as glaciers retreat. Consequently, the temperate rainforest climate of southeast Alaska and associated refugial habitats appear to have been ideal for the persistence of *S. baturini* during full glacial advances of the Late Pleistocene (Koehler, 2006). Future identification of specific enchytraeids capable of hosting *S. baturini*, and then careful documentation of the distributions of these hosts, could substantially broaden our understanding of the geographic limits of this nematode.

Among the vast array of definitive hosts examined (Appendix), only a few are thought to be important to the life cycle of *S. baturini*. Reviews by Kontrimavichus (1985) and Karmanova (1986) concluded that marten and sable were the principle definitive hosts. In North America, coastal Alaska and British Columbia have a high prevalence of *S. baturini* in both *M. caurina* and *M. americana* (59%, n = 362), whereas other mustelids (i.e., *N. vison* [25%, n = 4] and *M. erminea* [3%, n = 36]) had lower prevalence, although sample size is low for both. If *N. vison* and *M. erminea* were essential to the life cycle of *S. baturini*, one might expect higher prevalence and the parasite should be common in those hosts when marten are not in sympatry.

Kontrimavichus (1962) examined 707 mustelids from the Khabarovsk region of the Russian Far East, including 281 *N. vison* (91% infected), 196 *M. sibirica* Pallas (39% infected), and 196 *M. zibellina* (70% infected). The author noted that *N.*

*vison* might be more susceptible to infection because of close association with water. Larger samples of *N. vison* are needed in North America to effectively understand the role of this host in the Pacific Northwest.

Sporadic cases of *S. baturini* in *G. gulo* have been reported from Montana (Price, 1930), Quebec (Bezdek, 1942), and interior Alaska (USNPC 033728). Rausch (1959) examined 108 *G. gulo* from throughout northern and interior Alaska and reported no *S. baturini*. When found in *G. gulo*, specimens have been mature adults. The Holarctic distribution (Wilson and Reeder, 2005) and large dispersal capabilities for wolverines (Hornocker and Hash, 1981) suggest they may have been crucial to the dissemination and maintenance of *S. baturini* throughout its geographic range. Another mustelid, *M. pennanti*, has been recorded as a host to *S. baturini* in Montana (USNPC 067206) and in southeast Alaska (AF 24441). The absence of *S. baturini* in 59 *M. pennanti* collected from throughout British Columbia and 162 *M. pennanti* from Manitoba (Dick and Leonard, 1979) reinforces the conclusion that *M. pennanti* is an uncommon host for *S. baturini*. Populations of *M. pennanti* in Washington, Oregon, and Montana should be screened for *S. baturini*. The appearance of *S. baturini* in *M. pennanti* could be the result of ecological fitting (Janzen, 1985; Brooks et al., 2006), where parasites track a resource provided by the host, rather than as a manifestation of the host specificity. Ecological fitting could be applied to other hosts (e.g., *N. vison* and *M. erminea*) as well because deep coevolutionary, or even cophylogeographic relationships, have not been demonstrated (Koehler, 2006). A temporally shallow association is consistent with minimal genetic diversity relative to hosts and geography.

When the situation arises, *S. baturini* can infect other species because resources required to complete its life cycle are available. In addition to the potential role of refugia (e.g., coastal and Beringia) in the evolution of this nematode (Fleming and Cook, 2002; Cook et al., 2006), resources available to *S. baturini* in marten apparently are optimal along the coast and in interior Alaska. Zarnke et al. (2004) arrived at a similar conclusion, suggesting that some environmental condition in southeast Alaska favors the survival and transmission of *S. baturini*.

Absence of *S. baturini* from European marten (*Martes martes* (Linnaeus) or *Martes foina* (Erxleben)) could result from constraints of historical biogeography (*S. baturini* never occurred in Europe), diet (paratenic or intermediate hosts), or features of the hosts related to this nematode's ability to track resources available only in *M. americana*, *M. caurina*, and *M. zibellina*. For comparison with another nematode, *M. martes* and *M. foina* are hosts to *Skrjabingylus petrowi* Bageanov, 1936. This nematode of the frontal sinuses does not occur naturally in *M. zibellina* or North American marten (Kontrimavichus, 1985; Kontrimavichus et al., 1985; Koubek et al., 2004). As with *S. baturini*, soricids have been implicated as paratenic hosts for species of *Skrjabingylus* (Gamble and Riewe, 1982). Hence, diet does not appear to be a limiting factor in the contrasting distributions of these 2 nematodes because soricids are eaten by *M. foina* and *M. martes* (Clevenger, 1994; Helldin, 1999).

*Soboliphyme baturini* might fail to achieve sexual maturity in *M. erminea*. Schmidt and Kinsella (1965) reported juvenile *S. baturini* in *M. erminea* collected near Juneau, Alaska. *Mus-tela erminea* from our study were infected only by juvenile *S. baturini*. Additional specimens of this nematode recovered from



TABLE IV. Summary of diet analyses of *Martes* spp. used to determine whether shrews are important to the diet of *Martes* spp. Studies are from a range of localities throughout the Palearctic and Nearctic distribution of *Martes* spp. Studies examined stomach contents unless otherwise noted. The amount of vegetation and soil debris in the diet is also reported.

Locality	Species	n	Shrew prevalence (%)	Debris	Source
Algonquin Park, Ontario, Canada	<i>Martes americana</i>	118	13.0	Debris	Francis and Stephenson, 1972
Ontario, Canada	<i>M. americana</i>	392	13.0	No mention	Thompson and Colgan, 1987
Western Newfoundland, Canada	<i>M. americana</i>	56	10.7	No mention	Bateman, 1968
Newfoundland, Canada	<i>M. americana</i>	704	9.9	No mention	Gosse and Hearn, 2005
Glacier National Park, Montana	<i>M. americana</i>	1,758	7.6	No mention	Weckwerth and Hawley, 1962
Northern British Columbia, Canada	<i>M. americana</i>	127	7.5	No mention	Quick, 1955
Maine	<i>M. americana</i>	412	7.0	No mention	Soutiere, 1979
Sequoia National Forest, California	<i>M. caurina</i>	150 scat	6.7	Woody debris 23%, rock 2%	Zielinski and Duncan, 2004
Alberta and British Columbia, Canada	<i>M. americana</i>	112	3.5	Moss 1%	Cowan and Mackay, 1950
Southeast Manitoba, Canada	<i>M. americana</i>	107	1.9	Vegetation 12%	Raine, 1987
South-central Alaska	<i>M. americana</i>	467	1.7	Inorganic matter ignored	Buskirk and MacDon-ald, 1984
Northwest Territories, Canada	<i>M. americana</i>	172	1.2	58% debris	Douglass et al., 1983
Selway Bitterroot Wilderness, Montana	<i>M. americana</i>	129	1.0	No mention	Koehler and Hornocker, 1977
Grand Teton National Park, Wyoming	<i>M. americana</i>	528	0.7	Mentions specific berries only	Murie, 1961
Interior Alaska	<i>M. americana</i>	466	0	No mention	Lensink et al., 1955
Northwestern Montana	<i>M. americana</i>	64	0	Lichen and grass	Marshall, 1946
Colorado	<i>M. caurina</i>	32	45.0	17% vegetation	Gordon, 1986
Yosemite National Park, California	<i>M. caurina</i>	40	8.0	Debris and vegetation 63%	Hargis and McCullough, 1984
Northeast Oregon	<i>M. caurina</i>	1,014	6.4	5% wood, lichen, grass	Bull, 2000
Tahoe National Forest, California	<i>M. caurina</i>	300 scat	2.2	Vegetation 8%	Zielinski et al., 1983
Vancouver Island, British Columbia, Canada	<i>M. caurina</i>	701	1.6	45% conifer needles, moss, fern fronds	Nagorsen et al., 1989
Queen Charlotte Islands, British Columbia, Canada	<i>M. caurina</i>	97	0	74% vegetation	Nagorsen et al., 1991
Scotland	<i>M. martes</i>	174	0	Debris	Putman, 2000
Shantar Islands, Russia	<i>M. zibellina</i>	152	2.0	No mention	Dulkeit, 1929
Northern China	<i>M. zibellina</i>	221	0	No mention	Buskirk et al., 1996
Magadan region, Kava River, Russia	<i>M. zibellina</i>	30	10.0	Seeds 50%, berry 3%	Ivanov, 1985
Magadan region, Kava River, Russia	<i>M. zibellina</i>	14	46.1	Seeds 23%, berry 14%	Ivanov, 1985
Magadan region, Bolshoi Anyui River, Russia	<i>M. zibellina</i>	79	2.5	Seeds 25%	Ivanov, 1985
Magadan region, Chelomdzha River, Russia	<i>M. zibellina</i>	30	6.7	Seeds 63%, berries 3–10%, fruits 60%	Ivanov, 1985
Magadanski preserve, Russia	<i>M. zibellina</i>	1,552	3.9	Seeds 16%, berries and fruits 25%	Devyatkin and Ivanov, 1995

*M. erminea* are needed to fully explore this contention. Scarcity of *S. baturini* in *M. erminea* might also be attributed to the relatively large size of the nematode, a factor that might inhibit its occurrence in the stomach of smaller mustelids. Constraints of host and parasite body size are reviewed in Poulin (1998). Therefore, ermine could be considered an incidental host and subsequently might not be significant in shaping the evolution-ary past of *S. baturini*.

#### Paratenic hosts, diet, and transmission

Experimental infections by ingestion found that only oligochaetes from the Enchytraeidae were suitable intermediate hosts for *S. baturini* (Karmanova, 1963). Whether the definitive host directly consumes the infected enchytraeid or is first eaten by a paratenic host has been debated (Domnich, 1982; Karpenko, 1985; Kontrimavichus, 1985; Karmanova, 1986; Karpenko et

al., 1998, 2007; Dokuchaev, 2003; Zarnke et al., 2004). Domnich (1982) proposed that shrews serve as paratenic hosts on the basis of morphological similarities between adult *S. baturini* in mustelids and encysted juvenile nematodes in the diaphragms of shrews. Dokuchaev (2001, 2003) concluded that the high prevalence of juvenile *S. baturini* (up to 50) in soricids was a sufficient year-round source for the maintenance of infection in mustelids.

Molecular evidence revealed that J<sub>3</sub> nematodes in shrews were identical to definitively identified adult *S. baturini* in mustelids (Fig. 4) from the same localities, thus lending support to the hypothesis that a paratenic relationship exists. Recovery of mature *S. baturini* from a mustelid that was fed juvenile nematodes from infected shrews would unequivocally demonstrate a role in transmission for species of *Sorex* and perhaps other soricomorphs.

Juvenile *S. baturini* found in the diaphragms of shrews should not be confused with adults representing 8 other species of *Soboliphyme* known to reach sexual maturity in the stomachs of soricomorphs (*S. abei*, Asakawa et al., 1988; *S. ataahai* Ganzoring et al., 2002; *S. caucassica* Matsaberidze, 1965; *S. hirudiniformis* Kirshenblat, 1964; *S. jamesoni* Read, 1952; *S. occidentalis* Ribas and Casanova, 2004; *S. soricis* Baylis and King, 1932; *S. uotrichi* Machida and Uchida, 1982). Karpenko et al. (2007) reported finding juvenile *S. baturini* in species of *Sorex* from Asia and for the first time from North America. Juvenile *S. baturini* have also been reported in *Myodes rufocanus* (Sundevall) (Karpenko et al., 1998), but their identity has not been confirmed with molecular genetic assessment.

Existing literature on diets of *M. americana* and *M. caurina* indicates that these mustelids eat shrews (Table IV). Of the 27 papers examined on marten diet, 81% reported shrews in the diet. Shrews composed 8.8% of the diet on average, with a range of 0.7% to 46%. Gordon (1986) reported that 45% of the diet in a population of Colorado marten consisted of shrews. She hypothesized that marten consumed shrews during severe winters when the typical prey base was unavailable. An alternative hypothesis regarding mustelid infections of *S. baturini* would be the ingestion of oligochaetes, either accidentally with debris on food items or by direct consumption. About 50% of the diet literature examined mentioned plant or soil debris in the host digestive tracts (Table IV); thus, the exact mechanism for infection could involve multiple pathways.

Molecular evidence now links the juveniles of *S. baturini* in shrews with mature *S. baturini* in definitive mustelid hosts at the same geographic locations. Shrew consumption by marten also has been thoroughly documented. What remains unresolved is the extent to which marten hosts become infected with *S. baturini* as a result of consuming infected shrews. Soricomorphs are distributed throughout a variety of habitats (Nagorsen et al., 1996) and are frequently sympatric with mustelids. The abundance of shrews, and prevalence of infection for *S. baturini* in potential paratenic hosts, might serve as key determinants of the distribution of this nematode among mustelids across high-latitude environments. In turn, the use of parasitic juvenile and egg stages greatly increases the availability and scope of material to phylogeneticists and population geneticists, who often lack sufficient samples from remote or politically inaccessible localities (e.g., Jenkins et al., 2005).

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APPENDIX. Summary of reported carnivore, rodent, and soricomorph hosts of *S. baturini* from throughout its Holarctic distribution. Role in the life cycle is indicated for both definitive and paratenic hosts. Host ID numbers correspond to the specimens in Figure 2. Locality data, including specific locality, country, and approximate latitude and longitude, are also included. Data from unpublished collections: AF = University of Alaska Museum; AK = Alaska; BC = British Columbia; Is. = Island; NWR = National Wildlife Refuge; USNPC = U.S. National Parasite Collection; WA = Washington.

Host	Common name	Role	ID	Locality	Country	Author/Data source	Latitude	Longitude
<i>Alopex lagopus</i>	Arctic fox	D	71	St. Lawrence Is., AK	U.S.	Rausch et al., 1990	63.70	-171.70
<i>Felis catus</i>	Domestic cat	D	66	Kamchatka	Russia	Petrov, 1930	56.00	160.00
<i>Gulo gulo</i>	Wolverine	D	80	Brooks Range, AK	U.S.	Swanson, USNPC 084031.00	68.00	-147.00
<i>G. gulo</i>	Wolverine	D	20	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
<i>G. gulo</i>	Wolverine	D	111	Montana	U.S.	Price, 1930	46.58	-112.03
<i>G. gulo</i>	Wolverine	D	112	Quebec	Canada	Bezdek, 1942	54.00	-72.00
<i>G. gulo</i>	Wolverine	D	17	Russia, Baikal	Russia	Kontrimavichus, 1985	53.00	107.67
<i>Lutra lutra</i>	European otter	D	2	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
<i>Martes americana</i>	American marten	D	77	Chena River, Fairbanks	U.S.	Swartz, 1968; this study	64.83	-147.70
<i>M. americana</i>	American marten	D	84	Chichagof Is., AK	U.S.	This study	57.87	-135.77
<i>M. americana</i>	American marten	D	98	Farragut Bay, AK	U.S.	This study	57.12	-133.23
<i>M. americana</i>	American marten	D	104	Francois Lake, BC	Canada	This study	53.98	-126.43
<i>M. americana</i>	American marten	D	94	Kupreanof Is., AK	U.S.	This study	56.78	-133.48
<i>M. americana</i>	American marten	D	74	McGrath, AK	U.S.	This study	63.13	-156.52
<i>M. americana</i>	American marten	D	101	Mitkof Is., AK	U.S.	This study; Bezdek, 1942	56.58	-132.80
<i>M. americana</i>	American marten	D	76	Northern Alaska	U.S.	Zarnke et al., 2004	70.00	-151.50
<i>M. americana</i>	American marten	D	97	Port Houghton, AK	U.S.	This study	57.32	-133.33
<i>M. americana</i>	American marten	D	95	Pt. Highland, AK	U.S.	This study	57.15	-133.45
<i>M. americana</i>	American marten	D	103	Revillagigedo Is., AK	U.S.	This study	55.65	-131.50
<i>M. americana</i>	American marten	D	87	Southeastern Alaska	U.S.	Zarnke et al., 2004	57.80	-135.70
<i>M. americana</i>	American marten	D	75	Southwestern Alaska	U.S.	Zarnke et al., 2004	62.96	-155.60
<i>M. americana</i>	American marten	D	100	Thomas Bay, AK	U.S.	This study	57.02	-132.85
<i>M. americana</i>	American marten	D	96	Windham Bay, AK	U.S.	This study	57.57	-133.45
<i>M. americana</i>	American marten	D	106	Wisconsin, Madison	U.S.	Morgan, USNPC 044742.00	48.45	-121.10
<i>M. americana</i>	American marten	D	79	Yukon Flats, AK	U.S.	This study	66.15	-147.55
<i>M. americana</i>	American marten	D	88	Kruzof Is., AK	U.S.	AF 19914	57.13	-135.55
<i>M. americana</i>	American marten	D	91	Admiralty Is., AK	U.S.	This study	57.53	-134.25
<i>M. caurina</i>	American marten	D	109	Idaho	U.S.	Marshall, USNPC 043903.02	45.00	-115.00
<i>M. caurina</i>	American marten	D	92	Kuiu Is., AK	U.S.	This study	56.53	-134.05
<i>M. caurina</i>	American marten	D	102	Queen Charlotte Islands, BC	Canada	This study	53.25	-132.00
<i>M. caurina</i>	American marten	D	105	Vancouver Island, BC	Canada	This study	49.67	-125.83
<i>M. caurina</i>	American marten	D	107	Washington (North Cascades)	U.S.	Hoberg et al., 1990	47.00	-120.00
<i>M. caurina</i>	American marten	D	108	Pullman, WA	U.S.	Gorham, USNPC 047327.00	46.72	-117.17
<i>M. flavigula</i>	Yellow-throated marten	D	43	Khabarovskii krai	Russia	Kontrimavichus, 1985	48.01	136.81
<i>M. flavigula</i>	Yellow-throated marten	D	26	Primorskii krai	Russia	Kontrimavichus, 1985	46.00	134.00
<i>M. melampus</i>	Japanese marten	D	46	Akita, Aomori	Japan	Sato et al., 1999	39.75	140.08
<i>M. pennanti</i>	Fisher	D	110	Montana, Flathead	U.S.	Worley, USNPC 067206.00	47.88	-114.12
<i>M. pennanti</i>	Fisher	D	89	Juneau, AK	U.S.	AF 24441	58.58	-134.83
<i>M. zibellina</i>	Sable	D	3	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
<i>M. zibellina</i>	Sable	D	11	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
<i>M. zibellina</i>	Sable	D	67	Kamchatka	Russia	Kontrimavichus, 1985	56.00	160.00
<i>M. zibellina</i>	Sable	D	41	Khabarovskii krai	Russia	Kontrimavichus, 1985	51.20	136.74
<i>M. zibellina</i>	Sable	D	10	Tuva	Russia	Kontrimavichus, 1985	53.00	96.00
<i>M. zibellina</i>	Sable	D	53	Chelomdza River, Magadan	Russia	Domnich and Obushenkov, 1983	60.27	147.61
<i>M. z. kamtschadatica</i>	Sable	D	68	Kamchatka	Russia	Kontrimavichus, 1985	56.00	160.00

APPENDIX. Continued.

Host	Common name	Role	ID	Locality	Country	Author/Data source	Latitude	Longitude
<i>M. z. princeps</i>	Sable	D	18	Trans Baikal region	Russia	Kontrimavichus, 1985	53.00	107.67
<i>M. z. sahalinensis</i>	Sable	D	49	Sakhalin Is.	Russia	Shimakura and Odajima, 1934	51.00	143.00
<i>Meles meles</i>	European badger	D	4	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
<i>Mustela altaica</i>	Mountain weasel	D	21	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
<i>M. altaica</i>	Mountain weasel	D	12	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
<i>M. erminea kaneyi</i>	Baikal ermine	D	13	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
<i>M. erminea</i>	Ermine	D	93	Admiralty Island, AK	U.S.	Koehler, unpubl. data	57.44	-133.84
<i>M. erminea</i>	Ermine	D	69	Omolon R., Chukotka	Russia	Domnich and Obushenkov, 1983	65.23	160.55
<i>M. erminea</i>	Ermine	D	90	Juneau, AK	U.S.	Schmidt and Kinsella, 1965	58.40	-134.50
<i>M. erminea</i>	Ermine	D	8	Tuva	Russia	Kontrimavichus, 1985	51.50	95.00
<i>M. erminea</i>	Ermine	D	24	Yakutia	Russia	Kontrimavichus, 1985	60.00	121.00
<i>M. erminea</i>	Ermine	D	70	Lower Kolyma River, Yakutia	Russia	Gubanov, 1964	68.54	160.82
<i>M. eversmanni</i>	Steppe polecat	D	22	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
<i>M. e. michnoi</i>	Baikal steppe polecat	D	14	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
<i>M. lutreola</i>	European mink	D	1	Chuvashia	Russia	Kontrimavichus, 1985	55.50	47.00
<i>M. nivalis</i>	Least weasel	D	39	Khabarovskii krai	Russia	Kontrimavichus, 1985	49.31	136.53
<i>M. sibirica</i>	Siberian weasel	D	5	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
<i>M. sibirica</i>	Siberian weasel	D	23	Buryatia, east of Lake Baikal	Russia	Kontrimavichus, 1985	53.00	109.00
<i>M. sibirica</i>	Siberian weasel	D	15	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
<i>M. sibirica</i>	Siberian weasel	D	40	Khabarovskii krai	Russia	Kontrimavichus, 1985	49.31	136.53
<i>M. sibirica</i>	Siberian weasel	D	27	Primorskii krai	Russia	Kontrimavichus, 1985	46.00	134.00
<i>M. sibirica</i>	Siberian weasel	D	35	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
<i>M. sibirica</i>	Siberian weasel	D	9	Tuva	Russia	Kontrimavichus, 1985	51.50	95.00
<i>Neovison vison</i>	American mink	D	6	Altai	Russia	Kontrimavichus, 1985	52.50	83.00
<i>N. vison</i>	American mink	D	78	Chena River, Fairbanks	U.S.	Swartz, 1968	64.83	-147.70
<i>N. vison</i>	American mink	D	42	Khabarovskii krai	Russia	Kontrimavichus, 1985	51.20	136.74
<i>N. vison</i>	American mink	D	99	Mitkof Is., AK	U.S.	This study	56.68	-132.92
<i>N. vison</i>	American mink	D	28	Primorskii krai	Russia	Kontrimavichus, 1985	46.00	134.00
<i>N. vison</i>	American mink	D	36	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
<i>N. vison</i>	American mink	D	25	Yakutia	Russia	Kontrimavichus, 1985	60.00	121.00
<i>N. vison</i>	American mink	D	54	Chelomdza River, Magadan	Russia	Domnich and Obushenkov, 1983	60.27	147.61
<i>Nyctereutes procyonoides</i>	Raccoon dog	D	31	Khabarovskii krai	Russia	Kontrimavichus, 1985	48.80	135.45
<i>Prionailurus bengalensis euphilurus</i>	Leopard cat	D	37	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
<i>Vulpes vulpes</i>	Red fox	D	32	Khabarovskii krai	Russia	Kontrimavichus, 1985	48.80	135.45
<i>V. vulpes</i>	Red fox	D	38	Sikhote-Alin' Preserve	Russia	Kontrimavichus, 1985	45.20	136.50
<i>V. vulpes</i>	Red fox	D	19	Trans Baikal region	Russia	Kontrimavichus, 1985	53.00	107.67
<i>V. v. beringiana</i>	Red fox	D	65	Kamchatka Cape of Lopatka	Russia	Petrov, 1930	50.86	156.68
<i>V. v. daurica</i>	Daurian fox	D	16	Irkutsk and Buryatia	Russia	Kontrimavichus, 1985	52.30	104.25
<i>Myodes rufocanus</i>	Gray red-backed vole	P	7	Tomskaya Oblast	Russia	Karpenko et al., 1998	56.46	84.96
<i>Sorex caecutiens</i>	Laxmann's shrew	P	58	Magadan (Snow Valley)	Russia	Domnich, 1982; this study	59.73	150.87
<i>S. caecutiens</i>	Laxmann's shrew	P	50	Okhotsk village	Russia	This study	59.37	143.35
<i>S. caecutiens</i>	Laxmann's shrew	P	55	Talon village	Russia	This study	59.75	148.65
<i>S. caecutiens</i>	Laxmann's shrew	P	63	Buyunda River, Magadan	Russia	This study	62.43	153.34
<i>S. caecutiens</i>	Laxmann's shrew	P	44	Bol'shoi Shantar Is.	Russia	This study	54.87	137.49
<i>S. caecutiens</i>	Laxmann's shrew	P	30	Lazovski Nature Preserve	Russia	This study	43.26	134.24
<i>S. camtschaticus</i>	Kamchatka shrew	P	59	Magadan (Snow Valley)	Russia	Dokuchaev, 2003	59.73	150.87
<i>S. cinereus</i>	Cinereus shrew	P	81	Alaska	U.S.	This study	65.44	-142.44

## APPENDIX. Continued.

Host	Common name	Role	ID	Locality	Country	Author/Data source	Latitude	Longitude
<i>S. cinereus</i>	Cinereus shrew	P	85	Chichagof Is., AK	U.S.	Karpenko et al., 2007	57.41	-135.71
<i>S. cinereus</i>	Cinereus shrew	P	72	Togiak NWR	U.S.	Karpenko et al., 2007	59.05	-160.37
<i>S. cinereus</i>	Cinereus shrew	P	82	Yukon-Charley Rivers N P	U.S.	Karpenko et al., 2007	63.83	-142.16
<i>S. daphaenodon</i>	Siberian large-toothed shrew	P	33	Khabarovskii krai	Russia	Karpenko, 1985	51.67	135.74
<i>S. daphaenodon</i>	Siberian large-toothed shrew	P	60	Magadan (Snow Valley)	Russia	Dominch, 1982	59.73	150.87
<i>S. gracillimus</i>	Slender shrew	P	61	Magadan (Snow Valley)	Russia	Dokuchaev, 2003	59.73	150.87
<i>S. gracillimus</i>	Slender shrew	P	51	Okhotsk village	Russia	This study	59.37	143.35
<i>S. isodon</i>	Taiga shrew	P	52	Okhotsk village	Russia	This study	59.37	143.35
<i>S. isodon</i>	Taiga shrew	P	57	Magadan	Russia	Dominch, 1982	59.63	150.83
<i>S. isodon</i>	Taiga shrew	P	62	Magadan (Snow Valley)	Russia	This study	59.73	150.87
<i>S. isodon</i>	Taiga shrew	P	56	Talon village	Russia	This study	59.75	148.65
<i>S. isodon</i>	Taiga shrew	P	64	Buyunda R., Magadan	Russia	This study	62.43	153.34
<i>S. isodon</i>	Taiga shrew	P	45	Bol'shoy Shantar Is.	Russia	This study	54.87	137.49
<i>S. tundrensis</i>	Tundra shrew	P	73	Togiak NWR	U.S.	This study	59.05	-160.37
<i>S. tundrensis</i>	Tundra shrew	P	83	Yukon-Charley Rivers National Preserve	U.S.	Karpenko et al., 2007	63.83	-142.16
<i>S. unguiculatus</i>	Long-clawed shrew	P	29	Lazovski Nature Preserve	Russia	This study	43.28	134.05
<i>S. unguiculatus</i>	Long-clawed shrew	P	34	Khabarovskii krai	Russia	This study	48.14	136.35
<i>S. unguiculatus</i>	Long-clawed shrew	P	47	Sakhalin Is.	Russia	Dokuchaev, 2003	50.84	142.65
<i>S. unguiculatus</i>	Long-clawed shrew	P	48	Sakhalin Is.	Russia	This study	47.24	142.77