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## Species of *Coccidia* (Apicomplexa: Eimeriidae) in Shrews from Alaska, U.S.A., and Northeastern Siberia, Russia, with Description of Two New Species

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# SPECIES OF COCCIDIA (APICOMPLEXA: EIMERIIDAE) IN SHREWS FROM ALASKA, U.S.A., AND NORTHEASTERN SIBERIA, RUSSIA, WITH DESCRIPTION OF TWO NEW SPECIES

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**ABSTRACT:** Fecal samples (n = 636) from 10 species of shrews collected in Alaska (n = 540) and northeastern Siberia (n = 96) were examined for the presence of coccidia (Apicomplexa: Eimeriidae). Five distinct oocyst morphotypes were observed. Three types were consistent with oocysts of previously recognized coccidia species from other shrew hosts. These were *Eimeria inyoni*, *E. vagrantis*, and *Isoospora brevicauda*, originally described from the inyo shrew (*Sorex tenellus*), dusky shrew (*S. monticolus*), and northern short-tailed shrew (*Blarina brevicauda*), respectively. We found 5 new host records for *E. inyoni*, 3 for *E. vagrantis*, and 3 for *I. brevicauda*. The 2 additional oocyst morphotypes, both from the tundra shrew (*Sorex tundrensis*), are putative new species. Sporulated oocysts of *Eimeria beringiacea* n. sp. are subspheroidal,  $17.7 \times 15.6 \mu\text{m}$  ( $14\text{--}24 \times 13\text{--}20 \mu\text{m}$ ) with a length (L)/width (W) ratio of 1.1 (1.0–1.4); these lack a micropyle (M), an oocyst residuum (OR), and a polar granule (PG). Sporocysts are ellipsoidal,  $10.3 \times 6.1 \mu\text{m}$  ( $7\text{--}14 \times 4\text{--}8 \mu\text{m}$ ), with a L/W ratio of 1.7 (1.3–2.3) and have a Stieda body (SB), Substieda body (SSB), and sporocyst residuum (SR). Oocysts of *Eimeria tundraensis* n. sp. are spheroidal to subspheroidal,  $24.8 \times 23.5 \mu\text{m}$  ( $23\text{--}26 \times 22\text{--}25 \mu\text{m}$ ), with a L/W ratio of 1.1 (1.0–1.2); these lack a M and OR, but a single PG is present. Sporocysts are elongate ellipsoidal,  $15.4 \times 8.3 \mu\text{m}$  ( $13\text{--}17 \times 7\text{--}9 \mu\text{m}$ ), with a L/W ratio of 1.9 (1.4–2.1) and have a SB, SSB, and SR.

During 3 field seasons (2000–2002), 10 species of shrews (*Sorex* spp.) were collected in Alaska and northeastern Siberia as part of the Beringia Co-evolution Project (BCP). A review of the literature and revised taxonomy by Duszynski and Upton (2000) noted that only 11 species of *Eimeria* (Schneider, 1875) and *Isoospora* (Schneider, 1881) (Apicomplexa: Eimeriidae) had been reported from 15 of the extant species of *Sorex* (also see Milek and Seville, 2003). Here, we report 2 new *Eimeria* species, 11 new host records, and numerous new geographic records from 10 species of Beringian *Sorex*, including 8 that previously had not been examined as hosts for coccidia.

## MATERIALS AND METHODS

Animals were collected under the University of Alaska–Fairbanks animal protocol 99-012 and 01-016 as well as under the Idaho State University animal protocol 03-02-442. There were 2 regional field sites in northeastern Siberia which included the Omolon and Kolyma River basins. The 8 field sites in Alaska were on federal lands. These included 4 national parks; Denali, Gates of the Arctic, Wrangell-St. Elias, and Kobuk Valley, as well as 3 national preserves; Yukon-Charley Rivers, Noatak, and Bering Land Bridge; plus 1 national monument, Cape Krusenstern.

Shrews were caught using pitfall and museum special snap traps and their feces collected and preserved in 2.5% (w/v) aqueous potassium dichromate ( $\text{K}_2\text{Cr}_2\text{O}_7$ ) solution. Oocysts were isolated, measured, and photographed as described by Duszynski and Wilber (1997). In accordance with the guidelines suggested by Bandoni and Duszynski (1988), we submitted photomicrographs for both new eimerians to the U. S. National Parasite Collection (USPNC) in Beltsville, Maryland. Skin, skull, skeleton, and tissues of the symbiotype host of both new eimerid species are preserved in the Mammal Division of the University of Alaska Museum (UAM), Fairbanks, Alaska. All measurements are in  $\mu\text{m}$  (mean values and [ranges]), unless stated otherwise, and abbreviations follow those of Wilber et al. (1998): length (L), width (W), micropyle (M), oocyst residuum (OR), polar granule (PG), Stieda body (SB), sub-Stieda body (SSB), para-Stieda body (PSB), sporocyst residuum (SR), and refractile body (RB), but we use SZ for sporozoites.

Since each of the 3 previously described coccidia species were known from 1 or more *Sorex* species, we provide only the taxonomic summary and any discrepancies from, or changes to, the original mensural de-

scription. Host species and common names are those used by Wilson and Reeder (2005) in their updated version of *Mammal Species of the World*.

## RESULTS

We collected 636 fecal specimens from 10 different *Sorex* species in Alaska (n = 540) and Siberia (n = 96). There were 6 species in Alaska: *Sorex cinereus* Kerr, 1792, cinereus shrew; *Sorex hoyi* Baird, 1857, American pygmy shrew; *Sorex monticolus* Merriam, 1890, dusky shrew; *Sorex tundrensis* Merriam, 1900, tundra shrew; *Sorex ugunak* Anderson and Rand, 1945, barren-ground shrew; and *Sorex yukonicus* Dokuchaev, 1997, Alaskan tiny shrew; and 5 species in Siberia: *Sorex caecutiens* Laxmann, 1788, Laxmann's shrew; *Sorex daphaenodon* Thomas, 1907, Siberian large-toothed shrew; *Sorex gracillimus* Thomas, 1907, slender shrew; *Sorex isodon* Turov, 1924, taiga shrew; and *S. tundrensis*, the only species collected on both continents.

Five distinct oocyst morphotypes were recovered. Three types were consistent with oocysts of previously recognized coccidia species from shrews: *Eimeria inyoni*, *Eimeria vagrantis*, and *Isoospora brevicauda*, originally described from the inyo shrew (*Sorex tenellus*), dusky shrew (*S. monticolus*), and northern short-tailed shrew (*Blarina brevicauda*), respectively (Hertel and Duszynski, 1987a, 1987b). These same coccidia were identified from infected shrews from Alaska and Siberia: *E. inyoni* from *S. caecutiens*, *S. cinereus*, *S. hoyi*, *S. isodon*, *S. monticolus*, *S. tundrensis*, and *S. ugunak*; *E. vagrantis* from *S. caecutiens*, *S. isodon*, and *S. tundrensis*; and *I. brevicauda* from *S. cinereus*, *S. hoyi*, *S. monticolus*, and *S. caecutiens*. The 2 additional oocyst morphotypes are putative new species.

## DESCRIPTIONS

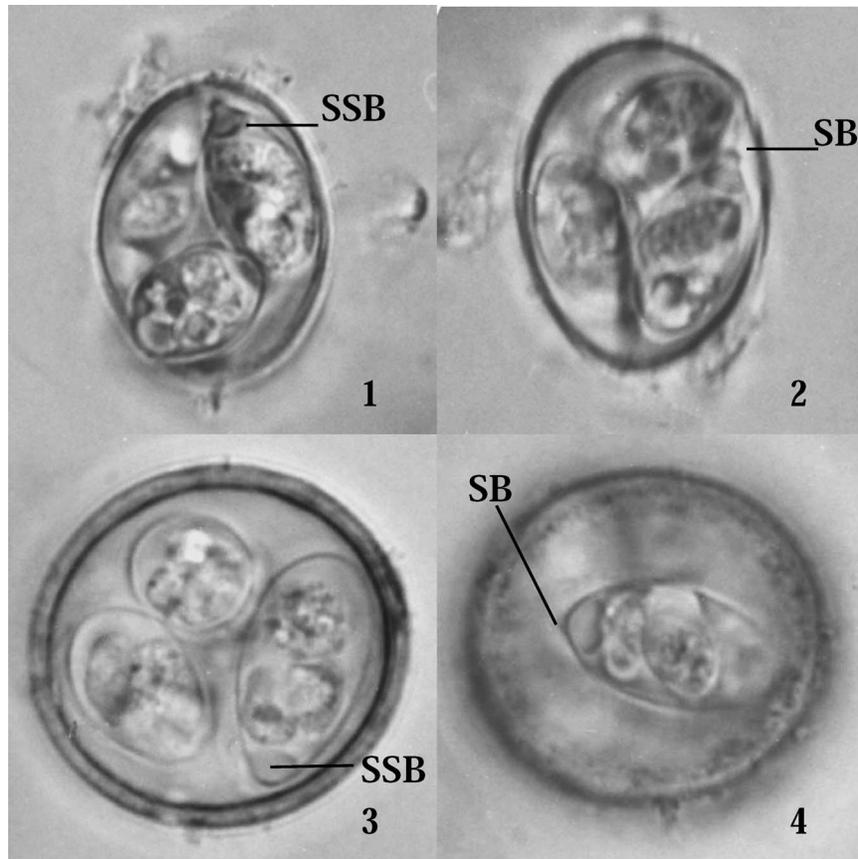
### *Eimeria beringiacea* n. sp.

(Figs. 1, 2, 5)

**Sporulated oocyst:** Oocyst shape (n = 136): subspheroidal; number of walls: 2; wall thickness: ~0.8; outer wall smooth, lacking any striations or stippling. Inner wall barely discernible; L  $\times$  W:  $17.7 \times 15.6$  ( $14\text{--}24 \times 13\text{--}20$ ); L/W ratio: 1.1 (1.0–1.4); M, OR, PG: all absent. Oocyst is small in size, with no distinctive features.

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FIGURES 1–4. Photomicrographs of sporulated oocysts of 2 new *Eimeria* spp. from shrews from Alaska and Russia. Scale bar = 10  $\mu$ m for all figures. (1, 2) *Eimeria beringiacea* found in *S. tundrensis* from Alaska's Bering Land Bridge National Preserve. (3, 4) *Eimeria tundraensis* found in *S. tundrensis* from Alaska's Yukon-Charley Rivers National Preserve. SB, Stieda body, SSB, sub-Stieda body.

**Sporocyst and sporozoites:** Sporocyst ( $n = 136$ ) ellipsoidal, pointed at 1 end;  $L \times W$ :  $10.3 \times 6.1$  ( $7-14 \times 4-8$ );  $L/W$  ratio: 1.7 (1.3–2.3); SB is nipple-like with height = to width; SSB is equal in height to SB, but 2–3 $\times$  wider, giving the SB/SSB complex a nipple/areola-like appearance; PSB: absent; SR: present; SR: homogeneous membrane-bound sphere; SZ: highly granular, comma-shaped without distinct RBs. SB/SSB complex resembles a nipple/areola-like structure.

#### Taxonomic summary

**Type host:** *Sorex tundrensis* Merriam, 1900, tundra shrew, female.

**Collected:** S. O. MacDonald, A. N. Lazutkin, A. J. Lynch, S. Runck, 25 July 2001.

**Other hosts:** *S. caecutiens*; *S. cinereus*; *S. daphaenodon*; *S. monticolus*; *S. ugyunak*.

**Prevalence:** 3/74 (4%) *S. caecutiens*; 2/254 (<1%) *S. cinereus*; 2/7 (40%) *S. daphaenodon*; 2/132 (2%) *S. monticolus*; 3/80 (4%) *S. tundrensis*; 2/21 (10%) *S. ugyunak*.

**Type locality:** North America: Alaska, Yukon-Charley Rivers National Preserve, Charlie River Quad, 12.5 km ENE of Kathul Mountain ( $65^{\circ}22.475'N$ ,  $142^{\circ}0.901'W$ ).

**Geographic distribution:** North America: Alaska; Asia: Siberia, Omolon River Basin.

**Sporulation:** Unknown.

**Prepatent and patent periods:** Unknown.

**Site of infection:** Unknown. Oocysts recovered from feces and intestinal contents.

**Material deposited:** Photosyntypes of sporulated oocysts from the symbiotype host are deposited in the USNPC (No. 100355). Skin, skull, skeleton, and tissues of the symbiotype host are preserved in the Mammal Division of the UAM (No. 57101 [AF52094]).

**Etymology:** Beringia is the geographic name of the vast area between

the Kolyma River in the Russian Far East and the Mackenzie River in the Northwest Territories of Canada. The nomen triviale is derived from the geographical area where the 6 host species were collected and *-acea* (L), pertaining to.

#### Remarks

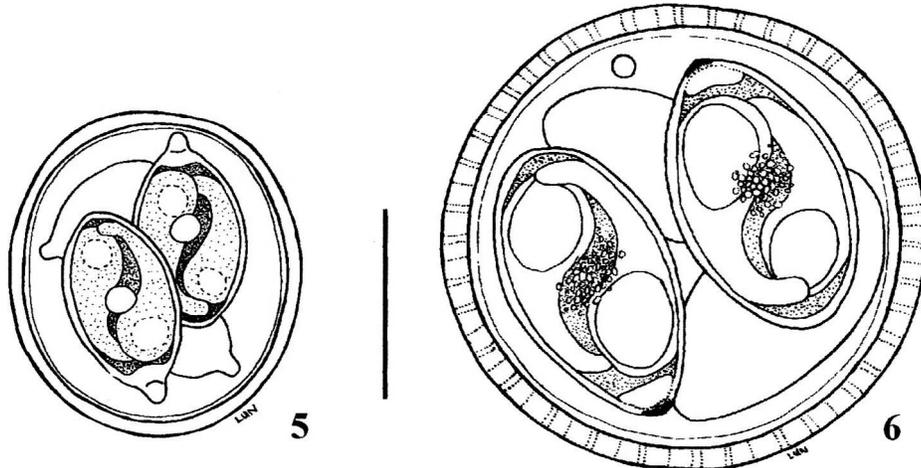
Sporulated oocysts of this new species resemble those of 2 *Eimeria* spp. first identified by Hertel and Duszynski (1987a), i.e., *E. inyo* from the inyo shrew (*S. tenellus*) and *E. brevicauda* from *B. brevicauda*. *Eimeria beringiacea* differs from them by having slightly smaller oocysts ( $18 \times 16$ ) than either *E. inyo* ( $22 \times 19$ ) or *E. brevicauda* ( $20 \times 20$ ). The most telling difference is *E. beringiacea*'s nipple/areola-like SB/SSB, which *E. inyo* and *E. brevicauda* both lack. The SB/SSB resembles that seen in *E. vagrantis*, but *E. beringiacea* oocysts are much smaller in size ( $18 \times 16$  versus  $27 \times 22$ ). *Eimeria beringiacea*, although similar in size to *Eimeria chagasi* Yakimoff and Gousseff, 1935, differs because *E. chagasi* lacks a SB and SSB.

#### *Eimeria tundraensis* n. sp.

(Figs. 3, 4, 6)

**Sporulated oocyst:** Oocyst ( $n = 50$ ) spheroidal to subspheroidal; number of walls, 2; wall thickness  $\sim 1.5$ . Outer wall striated, yellow,  $\frac{3}{4}$  of total thickness; inner wall smooth, colorless;  $L \times W$ :  $24.8 \times 23.5$  ( $23-26 \times 22-25$ );  $L/W$  ratio: 1.1 (1.0–1.2). M and OR: both absent; PG: present, single sphere,  $\sim 1$ . Oocyst with thick outer wall.

**Sporocyst and sporozoites:** Sporocyst ( $n = 50$ ) elongate, ellipsoidal;  $L \times W$ :  $15.4 \times 8.3$  ( $13-17 \times 7-9$ );  $L/W$  ratio: 1.9 (1.4–2.1). SB present; small, flat, refractile, 4 $\times$  wider than high. SSB present; large, non-refractile and trapezoid in shape with rounded corners. PSB: absent. SR: present as non-membrane bound clump of loosely associated re-



FIGURES 5, 6. Composite line drawings of sporulated oocysts of *E. beringiacea* (5) and *E. tundraensis* (6). Scale bar = 10  $\mu$ m, both figures.

fractile globules. SZ: comma-shaped with large RB at 1 end; SZs relatively small compared to space within sporocyst. Sporocyst elongate, ellipsoid, with small refractile SB and large non-refractile SSB.

#### Taxonomic summary

*Type host:* *Sorex tundrensis* Merriam, 1900, tundra shrew, subadult.  
*Collected:* S. O. MacDonald, A. N. Lazutkin, A. J. Lynch, S. Runck, 25 July 2001.

*Other hosts:* None reported to date.

*Prevalence:* 2/80 (3%).

*Type locality:* North America: Alaska, Yukon-Charley Rivers National Preserve, Charlie River Quad, 12.5 km ENE of Kathul Mountain (65°22.475'N, 142°0.901'W).

*Geographic distribution:* North America: Alaska, Yukon-Charley Rivers National Preserve.

*Sporulation:* Unknown.

*Prepatent and patent periods:* Unknown.

*Site of infection:* Unknown. Oocysts recovered from feces and intestinal contents.

*Material deposited:* Photosyntypes of sporulated oocysts from the symbiotype host are deposited in the USNPC (No. 100356). Skin, skull, skeleton, and tissues of the symbiotype host are preserved in the Mammal Division of the UAM (No. 57100 [AF52093]).

*Etymology:* Tundra refers to a treeless mountain habitat dominated by dwarf shrubs, grasses and sedges, and mosses and lichens. The nomen triviale is derived from this habitat type, where the host shrew is found, and *-ensis* (L), belonging to that locality.

#### Remarks

Including *E. tundraensis*, there are 9 described *Eimeria* spp. in shrews that have a SSB. The oocysts and sporocysts of *E. tundraensis* (25  $\times$  24 and 15  $\times$  8) are larger than those of *E. brevicauda* (20  $\times$  20 and 11  $\times$  8), *E. cryptotis* (16  $\times$  15 and 11  $\times$  7), *E. whitakeri* (17  $\times$  16 and 11  $\times$  8), *E. neomyi* (18  $\times$  16 and 12  $\times$  8), *E. longirostris* (17  $\times$  17 and 11  $\times$  6), and *E. beringiae* (18  $\times$  16 and 10  $\times$  6). *Eimeria inyoni* has oocysts and sporocysts that are more similar in size (22  $\times$  19 and 12  $\times$  7) to those of *E. tundraensis*, yet *E. inyoni* lacks the thick double-walled oocyst that is characteristic of *E. tundraensis*. The oocysts and sporocysts of *E. fumeus* (28  $\times$  22 and 15  $\times$  9) and *E. vagrantis* (27  $\times$  22 and 16  $\times$  9) are as large or larger than those of *E. tundraensis*. The main distinguishing factor between the sporocysts of *E. fumeus* and *E. tundraensis* is the PSB, which the former has and the latter doesn't. *Eimeria tundraensis* sporocysts can be set apart from those of *E. vagrantis* by the flat, wide SB and trapezoidal SSB that characterizes it. In contrast, the sporocysts of *E. vagrantis* have a characteristic nipple-like SB/SSB.

## TAXONOMIC SUMMARIES AND REMARKS

### *Eimeria inyoni* Hertel and Duszynski, 1987b

#### Taxonomic summary

*Synonym:* *Eimeria palustris* Hertel and Duszynski, 1987a, nomen preec; non *Eimeria palustris* Barnard, Ernst and Stevens, 1971.

*Type host:* *Sorex tenellus* Merriam, 1895, inyo shrew.

*Other hosts:* *S. cinereus* (this study); *Sorex fumeus* Miller, 1895, smoky shrew; *Sorex haydeni* Baird, 1858, prairie shrew; *Sorex longirostris* Bachman, 1837, southeastern shrew; *S. monticolus* (this study; previously thought to be *S. vagrans*, see Duszynski and Upton [2000]); *Sorex ornatus* Merriam, 1895, ornate shrew; *Sorex pacificus* Coues, 1877, Pacific shrew; *Sorex palustris* Richardson, 1828, American water shrew; *Sorex trowbridgii* Baird, 1857, Trowbridge's shrew; *S. caecutiens* (this study); *S. hoyi* (this study); *S. isodon* (this study); *S. tundrensis* (this study); *S. ugyunak* (this study).

*Prevalence* (this study): 5/74 (7%) *S. caecutiens*; 50/254 (20%) *S. cinereus*; 11/44 (25%) *S. hoyi*; 1/12 (8%) *S. isodon*; 27/132 (20%) *S. monticolus*; 6/80 (8%) *S. tundrensis*; 7/21 (33%) *S. ugyunak*.

*Type locality:* North America: New Mexico, Santa Fe County, 8 km N, 12.9 km E, Santa Fe.

*Geographic distribution:* North America: Ontario, Manitoba, Alaska, Arizona, California, Colorado, Florida, Massachusetts, Minnesota, New Mexico, Oregon, Pennsylvania, Vermont, Virginia, and Washington; Asia: Siberia (this study), Kolyma and Omolon River Basins.

*Sporulation:* Unknown.

#### Remarks

The morphology of *E. inyoni* oocysts ( $n = 289$ ) from shrews in Alaska is similar to that provided by Hertel and Duszynski (1987a) for the same species collected and described in New Mexico, except that the oocysts and sporocysts measured in the original description were larger than those we measured (21.6  $\times$  19.3 and 11.9  $\times$  7.4 versus 17.9  $\times$  16.6 and 10.3  $\times$  5.9, respectively). Other key structural features, including multiple PBs in the oocyst and the presence of a SSB in the sporocyst, were the same. The only difference was that we observed 2 oocyst walls, while Hertel and Duszynski (1987a) and Milek and Seville (2003) both reported 1. Duszynski (2002) suggested that reports of oocysts having a single wall often are in error (based on numerous EM studies) and should be overlooked when comparing older descriptions. The recovery of *E. inyoni* from the American pygmy, tundra, and barren-ground shrews in Alaska, as well as the recovery from taiga and Laxmann's shrews in Siberia, are new host and geographic records for this parasite. A line drawing and photomicrographs of sporulated oocysts of *E. inyoni* are published (Hertel and Duszynski, 1987a; Duszynski and Upton, 2000) and photosyntypes are in the USNPC No. 86350.

***Eimeria vagrantis* Hertel and Duszynski, 1987a****Taxonomic summary**

*Synonym:* None.

*Type host:* *Sorex monticolus* Merriam, 1890, dusky shrew (previously thought to be *S. vagrans*).

*Other hosts:* *Sorex fumeus*; *S. trowbridgii*; *S. caecutiens* (this study); *S. isodon* (this study); *S. tundrensis* (this study).

*Prevalence* (this study): 6/74 (8%) *S. caecutiens*; 1/12 (8%) *S. isodon*; 1/80 (1%) *S. tundrensis*.

*Type locality:* North America: New Mexico, Otero County, 8.8 km NE Cloudcroft.

*Geographic distribution:* North America: Alaska, Arizona, New Mexico, Oregon, Vermont, and Washington; Asia: Siberia (this study), Omolon and Kolyma River Basin.

*Sporulation:* Exogenous. Oocysts sporulated in 7–10 days in 2.5% aqueous (w/v)  $K_2Cr_2O_7$  solution at  $\sim 23$  C (Hertel and Duszynski, 1987a).

**Remarks**

Sporulated oocysts/sporocysts of *E. vagrantis* from the dusky shrew in New Mexico (Hertel and Duszynski, 1987a) are similar in size to those from *S. tundrensis* in Alaska ( $n = 57$ ) and from *S. caecutiens* and *S. isodon* in Siberia ( $26.6 \times 21.8$  and  $15.9 \times 9.0$  versus  $27.5 \times 22.3$  and  $15.9 \times 8.4$ , respectively). Hertel and Duszynski (1987a) reported small, multiple PGs, while we failed to observe any PGs in our specimens. In *E. vagrantis*, the sporocysts are tightly packed together inside their oocyst, so it is possible that we simply couldn't visualize the very small multiple PGs seen by Hertel and Duszynski (1987a). The recovery of *E. vagrantis* from the tundra, taiga, and Laxmann's shrews establishes new host and geographic records for this parasite. A line drawing and photomicrographs of sporulated oocysts of *E. vagrantis* are published (Hertel and Duszynski, 1987a; Duszynski and Upton, 2000) and photosyntypes are in the USNPC No. 86354.

***Isospora brevicauda* Hertel and Duszynski, 1987a****Taxonomic summary**

*Synonym:* None.

*Type host:* *Blarina brevicauda* (Say, 1823), Northern short-tailed shrew.

*Other hosts:* *Sorex monticolus*; *S. caecutiens* (this study); *S. cinereus* (this study); *S. hoyi* (this study).

*Prevalence* (this study): 4/74 (5%) *S. caecutiens*; 2/254 (<1%) *S. cinereus*; 1/44 (2%) *S. hoyi*; 4/132 (3%) *S. monticolus*.

*Type locality:* North America: Ohio.

*Geographic distribution:* North America: Alaska, Ohio, and Wyoming; Asia: Siberia (this study), Omolon River Basin.

*Sporulation:* Exogenous. Oocysts sporulated in 7–10 days in 2.5% aqueous (w/v)  $K_2Cr_2O_7$  solution at  $\sim 23$  C (Hertel and Duszynski, 1987a).

**Remarks**

Hertel and Duszynski (1987a) and Duszynski and Upton (2000) suggested that coccidia of soricomorphs (formally insectivores, see Wilson and Reeder, 2005) generally do not cross host genus boundaries, yet Milek and Seville (2003) reported *I. brevicauda*, a coccidium originally described from *B. brevicauda*, in *S. monticolus*. The oocysts and sporocysts in the original description (Hertel and Duszynski, 1987a) were smaller than those we measured in *S. caecutiens* ( $n = 34$ ;  $16.5 \times 16.2$  and  $11.6 \times 7.6$  versus  $19.4 \times 17.4$  and  $13.2 \times 8.8$ , respectively), but the difference may be attributed to host differences, time collected during patency (see Duszynski, 1971), or other factors. Milek and Seville (2003) reported oocysts of an intermediate size ( $17.5 \times 16.7$ ). The recovery of *I. brevicauda* from *S. cinereus*, *S. hoyi*, and *S. caecutiens* represents new host and geographic records. A line drawing and photomicrographs of sporulated oocysts of *I. brevicauda* are published (Hertel and Duszynski, 1987a; Duszynski and Upton, 2000) and photosyntypes are in the USNPC No. 86356.

**DISCUSSION**

This study compares the coccidia of shrew species separated by a geographic barrier, the Bering Strait. Because shrews are known to have distinct within-habitat species diversity and richness, they have the potential to lend insight into the study of competitive interactions and co-existence in small mammals (Findley and Yates, 1991). For example, within a single broad habitat, e.g., a forest community, and different zones within that community, e.g., mixed conifer, red fir, oak woodlands, etc., each are dominated by a single, different species of *Sorex*, with co-existing species rather rare (Williams, 1991).

Recently, Fumagalli et al. (1999) suggested that there are 2 distinct monophyletic groups within the genus *Sorex*. One group, subgenus *Sorex*, has a primarily Palearctic distribution except for *S. tundrensis*, which is Holarctic. The other subgenus, *Otiosorex*, is primarily Nearctic in distribution. Before the present study, only 3 *Sorex* species (subgenus *Sorex*) from Asia, *Sorex araneus* L., 1758, *Sorex arcticus* Kerr, 1792, and *Sorex minutus* L., 1766, had been sampled for coccidia and 2 eimerians, *E. chagasi* Yakimoff and Gousseff, 1935 and *E. dissimilis* Yakimoff and Gousseff, 1935, were described (Duszynski and Upton, 2000). The remaining known species of coccidia ( $n = 9$ ) had only had been reported from North American shrews (subgenus *Otiosorex*). Our a priori hypothesis was that shrews of the subgenera *Sorex* and *Otiosorex* would be infected with different coccidia. We anticipated that *E. chagasi* and *E. dissimilis* would be recovered from Siberian shrews, while Alaskan shrews would have coccidia similar to other *Otiosorex* shrews, assuming host/parasite phylogenies would mirror one another, e.g., pocket gophers and their lice, (see Desmastes and Hafner, 1993). Our results, however, did not support this hypothesis. *Eimeria chagasi* and *E. dissimilis* were not found in any Russian samples. Instead, 4 of 5 coccidia species reported in this paper were found on both continents. *Eimeria beringiacea* was only found in *S. tundrensis* from Alaska. Interestingly, *S. tundrensis* is Holarctic. It is likely that, had our sample size of *S. tundrensis* from Russia been larger, we might also have found *E. beringiacea*.

A likely explanation for these separate lineages having the same parasites is that the evolutionary predecessor of the 2 lineages was a host to these coccidia. This would suggest that the coccidia have been associated with these shrews for at least 11.5 million yr (the best estimate of the divergence time of *Sorex* and *Otiosorex* [Fumagalli et al., 1999]). It also implies a broad co-accommodation of hosts by the parasites (Brooks, 1979). Data by Fumagalli et al. (1999) and Demboski and Cook (2003) indicate a rapid radiation of *Sorex* species in both the New and Old World. According to "Manter's Rule," parasites evolve slower than their hosts (Manter, 1955, 1966). DNA sequence information from coccidia may shed further light on host relationships (Hnida and Duszynski, 1999a, Reduker et al., 1987). Unfortunately, however, due to the relatively small abundance of oocysts in all of our infected hosts, most of which were expended to measure and photograph for our descriptions, we were unable to isolate and sequence various regions of DNA to add to our new species descriptions. Until a time that can be accomplished, we are unable to speculate whether or not there has been insufficient time for these coccidia to speciate.

There is high species diversity of shrews in both northeastern

Asia and northwestern Alaska (Ohdachi et al., 1997; Demboski and Cook, 2003). The geographic origin (Nearctic versus Palearctic) of *Sorex* spp. shrews remains controversial. The geography and geologic events of Beringia and the formation of lineages within *Sorex* is still debated vigorously (see Fumagalli et al., 1999). As recently as 10,000–16,000 yr ago, Russia and Alaska were connected by the Bering Land Bridge (Hopkins et al., 1982). Lack of interspecific or intraspecific phylogenetic data for these coccidia prevents us from rejecting the possibility that recent mixing of hosts between continents has led to similarity in their coccidia fauna.

In general, little is known about host specificity in shrew coccidia. Studies on the coccidia in the mammalian order Rodentia by Hnida and Duszynski (1999b), Upton et al. (1992), and Wilber et al. (1998) suggest that coccidia specificity varies by host family. Wilber et al. (1998) synonymized many of the *Eimeria* species previously described from Sciuridae (squirrels). Their work was based on interpretations of species descriptions, and they suggested that many of the *Eimeria* species in Sciuridae are able to cross generic boundaries, based on previously published cross-transmission studies. Other transmission experiments by Hnida and Duszynski (1999b) and Upton et al. (1992) found that in Muridae (rats and mice), *Eimeria* may cross host species, but usually not generic boundaries; however, Milek and Seville (2003) did report soricomorph (=insectivore) coccidia crossing the genus boundary (*I. brevicauda* infecting *S. monticolus*). The present study reports that 3 more species, i.e., *S. caecutiens*, *S. cinereus*, and *S. hoyi*, are able to act as hosts of *I. brevicauda*. Host specificity in coccidia, and in this case for soricomorphs, is an area that needs additional study.

The results of this study are quantitatively similar to those of Hertel and Duszynski (1987a). They had a more diverse sampling of hosts (20 species, 2 genera versus 10 species, 1 genus), but a smaller sample size (458 versus 636); yet overall, the percentage of all hosts infected is quite similar (24% versus 22%). Only 2 shrews collected in the present study were host to multiple infections of coccidia. Both cases (1 *S. hoyi* and 1 *S. monticolus*) had co-infections of *E. inyoni* and *I. brevicauda*. The trend of low coccidia prevalence (~24%) and scarcity of multiple infections in shrews also was noted by Hertel and Duszynski (1987a). That trend is in stark contrast to that observed in moles (Talpidae). Given that moles and shrews are considered by some as sister taxa (Stanhope et al., 1998), one might expect that they would exhibit similarity in prevalence of infections with coccidia. In general, moles have very high prevalences with multiple coccidia species (see Duszynski and Upton, 2000, for summary). Factors such as the ecology, genetics, and physiology of the host that dictate why such a difference is seen in shrew versus mole coccidia infections still remain unclear years later (Duszynski, 1986; Duszynski and Upton, 2000).

To date, 23 *Sorex* species have been surveyed for coccidia (15 prior and 8 in this study), and this is less than half of all extant *Sorex* species known to date. Including the present study, 13 species of coccidia have been reported from *Sorex* species and only 78–79 coccidia species from all Soricomorpha (formerly Insectivora). The Soricomorpha has 4 families, 6 subfamilies, 13 tribes, 45 genera, and 327 extant species (Wilson and Reeder, 2005). Given this diversity of species, Duszynski and Upton's (2000) estimate that less than 6% of all the coccidia

that likely infect soricomorphs have been described to date. Stated another way, it is possible that there are still more than 1,200 species of coccidian yet to be discovered in the Soricomorpha.

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