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Eimerians from Different Karyotypes of the Japanese Wood Mouse (Apodemus spp.), with Descriptions of Two New Species and a Redescription of Eimeria montgomeryae Lewis and Ball, 1983

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EIMERIANS FROM DIFFERENT KARYOTYPES OF THE JAPANESE WOOD MOUSE (APODEMUS SPP.), WITH DESCRIPTIONS OF TWO NEW SPECIES AND A REDESIGNATION OF EIMERIA MONTGOMERYAE LEWIS AND BALL, 1983

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ABSTRACT: Examination of 131 wood mice (Apodemus spp.) representing 2 species and 6 subspecies collected from the Japanese islands of Hokkaido, Honshu, Kyushu, and Tsushima showed that 70 mice (53%) had coccidian oocysts in their feces. These included 21 of 42 (50%) Apodemus argenteus argenteus; 7 of 14 (50%) Apodemus argenteus hokkaidi; 2 of 3 (67%) Apodemus argenteus sagax; 3 of 9 (33%) Apodemus speciosus ainu; 36 of 61 (59%) Apodemus speciosus speciosus; and 1 of 2 (50%) Apodemus speciosus tusimaensis. Four distinct coccidians were identified: Eimeria argenteus n. sp. from A. a. argenteus, A. a. hokkaidi, A. a. sagax, and A. s. speciosus; Eimeria inuyamensis n. sp. from A. a. argenteus, A. s. speciosus, and A. s. tusimaensis; Eimeria montgomeryae Lewis and Ball, 1983, from A. a. argenteus, A. a. hokkaidi, A. a. sagax, A. s. ainu, and A. s. speciosus; and Eimeria uptoni Lewis and Ball, 1983, from A. a. argenteus, A. a. hokkaidi, and A. s. speciosus.

Standard karyotypes were prepared from selected specimens of each host subspecies. All 3 subspecies of A. argenteus and A. s. tusimaensis have a 2n = 46; A. s. ainu, from Hokkaido, has a 2n = 48; and A. s. speciosus has at least 2 chromosomal races, 1 on northern (2n = 48) and 1 on southern (2n = 46) Honshu. Both chromosomal races of A. s. speciosus, as well as the other subspecies of Apodemus examined, shared their coccidian parasites freely.

As part of a long-term study at the University of New Mexico, we are using parasite burdens and other host measurements (e.g., pelage, skeleton, chromosomes, enzymes, etc.) as tools to better understand the genetic relatedness of many groups of small mammals throughout North America, Mexico, and other parts of the world and to investigate the degree of correlation between host variability and parasite host-specificity. During the summer of 1981, we collected small mammals from throughout Japan in a study to look at zoogeographic distribution patterns of Asian insectivores and their possible genetic relationship to their North American counterparts. In addition to moles and shrews, we also collected 131 Apodemus Kaup, 1829, representing 2 species and 6 subspecies. Since the genetics of Japanese wood mice had been well studied (Tsuchiya and Yosida, 1971; Tsuchiya et al., 1973; Tsuchiya, 1974) and since these hosts had not been examined for coccidia in Japan, it was of interest to look at this host–parasite system as a potential model to study the subtleties of coccidian host-specificity in rodents.

MATERIALS AND METHODS

All hosts were live-trapped and killed in the field. The intestinal tract was removed and feces from the

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width (≈2.5); sporocyst residuum a compact mass of granules enfolded by sporozoites. Our oocysts were 271 days old when measured.

### Taxonomic summary

**Diagnosis:** Pelléry (1954) described *Eimeria apodemus*, from *Apodemus sylvaticus* Linnaeus, 1758, and *Apodemus flavicollis* Melchior, 1834, in Hungary, to have asymmetrical ellipsoid oocysts that measured 24 × 20 (21–27 × 15–22) with a smooth brown outer oocyst wall and no polar bodies; the sporocysts were ellipsoid, 12 × 7, with no Stieda body. Lewis and Ball (1983) saw *E. apodemus* in the same 2 host species from the British Isles, but described the oocysts they saw to have a rough outer wall, 1–3 polar bodies, and ovoid sporocysts with a large Stieda body. Lewis and Ball (1983) also described *E. montgomeryae*, from *A. sylvaticus*, to have oocysts with a roughly-pitted outer wall, 1–3 polar bodies, and ovoid sporocysts with large Stieda bodies; oocysts of *E. montgomeryae* were 22 × 19 (18–24 × 16–23). The shape indices of the oocysts and sporocysts of the *E. apodemus* and *E. montgomeryae* measured and described by Lewis and Ball (1983) are identical, as are their line drawings. We are convinced (1) that Pelléry (1954) could not have missed such key oocyst characters as a rough oocyst wall, polar bodies, and Stieda body in his description of *E. apodemus* and, therefore, (2) that the *E. apodemus* and *E. montgomeryae* described by Lewis and Ball (1983) represent a single species with a very broad range of oocyst sizes; this is not unusual in rodent coccidia (see Duszynski, 1971). In looking at the oocysts from Japanese *Apodemus* spp. it was clear that we had a form that was identical to *E. montgomeryae* except that the sporocysts of our form had a distinct substieda body (Figs. 1–4) that was always approximately the same width as the Stieda body (this is an important distinction, see below). In the paper by Lewis and Ball (1983), their figure 3h is a photomicrograph of a sporocyst of *E. montgomeryae*; it shows a distinct substieda body (the same width as the Stieda body) which they omitted in their description and in their line drawing of *E. montgomeryae*. We have included this key character in our redescription (above).

**Hosts and localities:** See Table I.

**Site of infection:** Unknown. Oocysts recovered from feces.

**Prevalence:** Found in 8 of 21 (38%) infected *Apodemus argenteus* argenteus, 2 of 7 (29%) infected *Apodemus argenteus* hokkaidi, 1 of 2 (50%) infected *Apodemus argenteus* sagax, 2 of 3 (67%) infected *Apodemus speciosus* ainu, and 21 of 36 (58%) infected *Apodemus speciosus* speciosus.

### Table I. Eimeria spp. found in and diploid numbers of Apodemus spp. collected in Japan.

<table>
<thead>
<tr>
<th>Apodemus spp.</th>
<th>Collection locality</th>
<th>No. hosts examined (%)</th>
<th>Eimeria spp. identified from hosts</th>
<th>No. hosts karyotype typed</th>
<th>Diploid chromosome no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>argenteus argenteus</td>
<td>Honshu, Aichi, Inuyama City, near Jyakko Temple</td>
<td>6/15 (40)</td>
<td>argenteus, inuyamensis, uptoni, sp.*</td>
<td>4</td>
<td>46</td>
</tr>
<tr>
<td>argenteus argenteus</td>
<td>Honshu, Nagano 2.4 km E of Hakamurara</td>
<td>14/22 (64)</td>
<td>argenteus, inuyamensis, montgomeryae, uptoni, sp.*</td>
<td>5</td>
<td>46</td>
</tr>
<tr>
<td>argenteus argenteus</td>
<td>Honshu, Yamagata Pref., 3.5 km N of Zao-Onsen Mt. Lodge</td>
<td>1/4 (25)</td>
<td>montgomeryae</td>
<td>1</td>
<td>46</td>
</tr>
<tr>
<td>argenteus argenteus</td>
<td>Kyushu, Oita Pref., mole farm near Ogieko</td>
<td>0/1</td>
<td></td>
<td>1</td>
<td>46</td>
</tr>
<tr>
<td>a. hokkaidi</td>
<td>Hokkaido, Univ. of Hokkaido Experimental Research Station</td>
<td>7/14 (50)</td>
<td>argenteus, montgomeryae, uptoni, sp.*</td>
<td>2</td>
<td>46</td>
</tr>
<tr>
<td>a. sagax</td>
<td>Tsushima Island, Nagasaki Pref., Mine</td>
<td>2/3 (67)</td>
<td>argenteus, montgomeryae, sp.*</td>
<td>2</td>
<td>46</td>
</tr>
<tr>
<td>s. speciosus</td>
<td>Honshu, Aichi, Inuyama City, near Jyakko Temple</td>
<td>10/23 (43)</td>
<td>argenteus, montgomeryae, uptoni, sp.*</td>
<td>2</td>
<td>46</td>
</tr>
<tr>
<td>s. speciosus</td>
<td>Honshu, Nagano 2.4 km E of Hakamurara</td>
<td>4/7 (57)</td>
<td>argenteus, montgomeryae, uptoni, sp.*</td>
<td>1</td>
<td>48</td>
</tr>
<tr>
<td>s. speciosus</td>
<td>Honshu, Niigata Pref., Shinhji T., Shinhji Country Club</td>
<td>10/12 (83)</td>
<td>inuyamensis, montgomeryae, sp.*</td>
<td>3</td>
<td>48</td>
</tr>
<tr>
<td>s. speciosus</td>
<td>Honshu, Yamagata Pref., 3.5 km N of Zao-Onsen Mt. Lodge</td>
<td>5/11 (45)</td>
<td>argenteus, montgomeryae, uptoni, sp.*</td>
<td>1</td>
<td>48</td>
</tr>
<tr>
<td>s. speciosus</td>
<td>Kyushu, Oita Pref., mole farm near Ogieko</td>
<td>7/8 (88)</td>
<td>argenteus, inuyamensis, montgomeryae, uptoni, sp.*</td>
<td>4</td>
<td>46</td>
</tr>
<tr>
<td>s. speciosus</td>
<td>Tsushima Island, Nagasaki Pref., Mine</td>
<td>1/2 (50)</td>
<td>inuyamensis</td>
<td>1</td>
<td>46</td>
</tr>
<tr>
<td>6</td>
<td>7</td>
<td>70/131 (53)</td>
<td>4</td>
<td>29</td>
<td>2</td>
</tr>
</tbody>
</table>

* Oocysts were unsporulated/deteriorated.

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**Eimeria argenteus n. sp.**

(Figs. 5–7, 11)

**Description:** Oocyst subspheroid, wall ≈1.5 consisting of 2 layers: outer layer golden, pitted (Fig. 7) ≈1/3 of total thickness; micropyle and oocyst residuum absent; 1–2 polar bodies present; sporulated oocysts (n = 87) 22.5 × 19.3 (18–29 × 16–24) with L/W ratio 1.18 (1.00–1.50); sporocysts (n = 92) ovoid, 12.7 × 7.3 (11–14 × 6–9) with L/W ratio 1.74 (1.51–1.99); Stieda and substieda body present with substieda body at least 2 times wider than Stieda body (Figs. 5, 6); sporocyst residuum 1 large spheroid globule ≈4.4; sporozoites with 2 refractile bodies. Oocysts were 340 days old when measured.
Taxonomic summary

**Diagnosis:** This species most closely resembles *E. montgomeryae*, but differs in that the sporocysts have substieda bodies that are always 2 times wider than their associated Stieda body and the sporocysts have a residuum that is a single, homogeneous body rather than a compact group of granules.

**Type host:** *Apodemus argenteus argenteus* Temminck, 1845, Japanese wood mouse, Museum of Southwestern Biology, Division of Mammals, MSB 45248 (female), S. B. George #715, 23 May 1981.

**Type locality:** Honshu, Aichi, Inuyama City, near Jyakkoin Temple.

**Other hosts and localities:** See Table I.

**Site of infection:** Unknown. Oocysts recovered from feces.

**Prevalence:** Found in 8 of 21 (38%) infected *A. a. argenteus*, 3 of 7 (43%) infected *A. a. hokkaidi*, 1 of 2 (50%) infected *A. a. sagax*, and 5 of 36 (14%) infected *A. s. speciosus*.

**Etymology:** The specific name is derived from the specific part of the scientific name of the host.

**Eimeria inuyamensis** n. sp.  
(Figs. 8, 9, 12)

**Description**

Oocyst elongate-ellipsoid, wall ≤ 1.0 consisting of 2 layers, outer layer slightly sculptured = 1/3 of total thickness; microple and oocyst residuum absent; 1-2 polar bodies present; sporulated oocysts (n = 14) 25.6 × 16.2 (22-29 × 14-18) with L:W ratio 1.59 (1.50-1.75); sporocysts (n = 14) ovoid 11.3 × 7.4 (10-14 × 6-8) with L:W ratio 1.55 (1.32-1.88); Stieda body present; substieda body absent; sporocyst residuum a large granular mass; sporozoites with at least 1 refractile body present at posterior end. Oocysts were 360 days old when measured.

Taxonomic summary

**Diagnosis:** Musaev and Veisov (1963) described *Eimeria divichinica*, from *A. sylvaticus* in the USSR, to have smooth-walled oocysts 24 × 19 (16-32 × 10-26), without polar bodies, and usually with ellipsoid sporocysts 11 × 7 (7-13 × 5-11) or spheroid sporocysts 8 (8-11), but in either case without a Stieda body. Lewis and Ball (1983) described oocysts which they called *E. divichinica* from *A. sylvaticus* and *A. flavicollis* in the British Isles. These oocysts, with the same general shape of *E. divichinica*, were 25 × 18 (22-28 × 15-20) with 1-3 polar bodies and with ovoid sporocysts, 15 × 9 (13-15 × 8-10), that had definite Stieda bodies. We believe that Lewis and Ball (1983) relied too much on the similarity of shape of these 2 forms and not enough on more definitive characters such as size and the presence or absence of Stieda and polar bodies. *Eimeria inuyamensis* most closely resembles *Eimeria divichinica* sensu Lewis and Ball (1983) which we believe they should have, but did not, name as new. The only difference between their description and ours is that we saw a slightly sculptured outer oocyst wall whereas the oocysts they saw had smooth outer walls. The difference may be attributed to the age and storage medium (2% H₂SO₄) of our oocysts (see Discussion).

**Type host:** *Apodemus sylvaticus* Linnaeus, 1758 (from Lewis and Ball, 1983).

**Type locality:** See Lewis and Ball (1983).

**Other hosts and localities:** See Lewis and Ball (1983) and Table I.

**Site of infection:** Unknown. Oocysts recovered from feces.

**Prevalence:** Found in 4 of 21 (19%) infected *A. a. argenteus*, 2 of 36 (6%) infected *A. s. speciosus* and 1 of 1 *Apodemus speciosus* tusimaensis.

**Etymology:** The specific name is derived from the locality where the first infected host was collected in our study.

**Eimeria uptoni** Lewis and Ball, 1983

**Description**

Oocyst subspheroid, with wall < 1; microple and oocyst residuum absent; polar body present; sporulated oocysts (n = 5) 13.9 × 11.4 (9-16 × 8-14) with L:W ratio 1.22 (1.11-1.31); sporocysts (n = 5) ovoid, 7.6 × 4.7 (5-10 × 3-6) with L:W ratio 1.61 (1.50-1.70); Stieda body present; substieda body absent; sporocyst residuum a compact mass. Oocysts were 354 days old when measured.

**Taxonomic summary**

**Diagnosis:** This species was described by Lewis and Ball (1983) and our observations agree with theirs.

**Hosts and localities:** See Table I.

**Prevalence:** Found in 4 of 21 (19%) infected *A. a. argenteus*, 2 of 7 (29%) infected *A. a. hokkaidi* and 11 of 36 (31%) infected *A. s. speciosus*.

**Site of infection:** Unknown. Oocysts recovered from feces.

**DISCUSSION**

*Apodemus* spp. are ubiquitous in Europe and Asia, occupying a similar niche there as *Peromyscus* spp. do in North America. The genetics...

of Apodemus spp. has been well studied in Japan. Tsuchiya and Yosida (1971), Tsuchiya et al. (1973), and Tsuchiya (1974) found that the Japanese wood mouse, A. speciosus, has 2 chromosomal races which differ by a Robertsonian conversion. One race (2n = 46) is located in southern Japan, while the other race (2n = 48) is located in northern Japan. These 2 groups contact one another along a line extending from Toyama to Hamamatsu on the main island of Honshu in central Japan. Some mice in the areas of contact have been found which have a chromosome number of 2n = 47 (Tsuchiya and Yosida, 1971). The chromosomal races cannot be distinguished by their morphological characteristics, nor is there a discernible difference be-
between them in several biochemical and immunological characters (Tsuchiya et al., 1973; Tsuchiya, 1974). In addition, 3 subspecies of *A. argenteus* occur sympatrically with the subspecies of *A. speciosus* throughout Japan.

All of the known coccidians from *Apodemus* spp. have been described from Europe and the USSR from *Apodemus agrarius, A. flaviollis*, and/or *A. sylvaticus*. The exact number of valid coccidians is debatable as Levine and Ivens (pers. comm.) list 26 species (eimerians, isosporans), while Lewis and Ball (1983) prefer to synonymize at least 7 of those names from *A. flaviollis* and *A. sylvaticus*. Regardless of the exact number of coccidians described from this host genus, Japanese wood mice had not been examined for Coccidia prior to our study. Thus, it seemed of interest to determine the extent to which variation, if any, might occur between coccidians of the 2 chromosomal races of *A. speciosus* and/or between *A. speciosus* and *A. argenteus* from Japan.

Although 4 different species of *Eimeria* were found infecting Japanese *Apodemus*, specificity for any race or species of host was conspicuously lacking. This is notable in that *A. speciosus* and *A. argenteus* do not appear to be particularly closely related. A recent electrophoretic study of these hosts conducted in our laboratory shows that they are highly divergent genetically and their broad sympatric occurrence throughout Japan suggests that they have diverged sufficiently to avoid serious competition. Yet all 6 subspecies and both chromosomal races were found infected with from 1 to 4 species of *Eimeria* and appeared equally susceptible to each.

A variety of possible explanations for this observation exists. Our results are consistent with a growing body of evidence that *Eimeria* infecting most hosts may only be specific at higher taxonomic levels such as the genus and more generalized at the level of the host species/subspecies. From our studies on the genetics of the hosts we examine, we are beginning to see that coccidians which show the former pattern (i.e., specificity at the genus level) are found in hosts characterized by high levels of karyotypic variability and polymorphism. We are just beginning to look at hosts (e.g., moles) that are karyotypically conservative. It should prove informative if their coccidians are tied to the species level of the host. If so, these patterns may be indicative of a general underlying process that will certainly deserve further investigation.

We are beginning to see a consistent pattern emerge in the host–parasite relationship that exists among surface dwelling rodents and their eimerian and isosporan parasites. In previous studies on jumping mice (Duszynski et al., 1982), kangaroo rats (Stout and Duszynski, 1983), woodrats (Reduker and Duszynski, 1985), deer mice (Reduker et al., 1985), and voles (Vance and Duszynski, 1985), a very high percentage of infected hosts in all surveys (100%, 85%, 90%, 92%, 91%, respectively) had only 1 coccidian species when examined (i.e., it appears that only 1 parasite will infect a given host at any one time). In this study, 56 of 70 (80%) infected *Apodemus* spp. harbored only 1 coccidian when examined. There appears to be some component of the host–parasite relationship that makes this 1 host–1 coccidian association so dominant in naturally occurring host communities, especially when many host species are known to serve as good hosts for 3, 4, or more coccidians. As we examine other host groups it will be of interest to learn if this pattern remains consistent. If it does, isolation of the causal mechanism could have significant implications for treatment of coccidiosis.

Finally, we must point out that all oocysts were collected and stored in 2% aqueous (v/v) H2SO4. This medium, unlike 2% aqueous (w/v) K2Cr2O7, seems to be especially harsh on the integrity of oocyst structure and leads to lower sporulation rates than one would expect of this normally resistant coccidian structure.

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LITERATURE CITED


