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### Cross-Transmission Studies with *Eimeria arizonensis*-like Oocysts (Apicomplexa) in New World Rodents of the Genera *Baiomys*, *Neotoma*, *Onychomys*, *Peromyscus*, and *Reithrodontomys* (Muridae)

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## CROSS-TRANSMISSION STUDIES WITH *EIMERIA ARIZONENSIS*-LIKE OOCYSTS (APICOMPLEXA) IN NEW WORLD RODENTS OF THE GENERA *BAIOMYS*, *NEOTOMA*, *ONYCHOMYS*, *PEROMYSCUS*, AND *REITHRODONTOMYS* (MURIDAE)

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**ABSTRACT:** Cross-transmission experiments were performed using oocysts of an *Eimeria arizonensis*-like coccidian from *Peromyscus leucopus* and *Peromyscus truei*, an *E. arizonensis*-like coccidian from *Reithrodontomys fulvescens*, *Eimeria baiomysis* and *Eimeria taylora* from *Baiomys taylora*, *Eimeria albigulae* from *Neotoma albigula*, and *Eimeria onychomysis* from *Onychomys* spp., between representatives of the above host genera. The *E. arizonensis*-like coccidian from *R. fulvescens* infected *Reithrodontomys megalotis*, *Reithrodontomys montanus*, and *Peromyscus leucopus*. Oocysts of *E. arizonensis* from *P. leucopus* could be transmitted to both *P. leucopus* and *R. megalotis*. Oocysts of *E. baiomysis* and *E. taylora* infected only *B. taylora*. Oocysts of *E. arizonensis* from *P. truei* infected *P. truei* but not *Neotoma mexicana* or *Onychomys leucogaster*. Oocysts of *E. albigulae* from *N. albigula* were infective for *N. mexicana* but not for *P. truei* or *O. leucogaster*. Oocysts of *E. onychomysis* from *Onychomys* spp. infected *O. leucogaster* but not *N. mexicana* or *P. truei*. These results demonstrate that *Peromyscus* and *Reithrodontomys*, genera known to be related very closely evolutionarily, are capable of sharing *E. arizonensis*, whereas morphologically similar coccidians (*E. albigulae*, *E. baiomysis*, and *E. onychomysis*) from more distantly related hosts, are probably distinct and more stenoxenous. This also is the first report of coccidians infecting species of *Reithrodontomys*.

Levine et al. (1957) named 10 new species of *Eimeria* from 52 rodents representing 25 species in 8 genera caught on the north rim of the Grand Canyon, Arizona. Three of these, *Eimeria albigulae*, *Eimeria arizonensis*, and *Eimeria onychomysis*, along with *Eimeria baiomysis* Levine, Ivens, and Kruidenier, 1958, are similar or indistinguishable morphologically, based on the original descriptions and drawings, even though they were found in rodents of several genera (Levine et al., 1958; Kruidenier et al., 1960). These 4 taxa were given separate specific epithets in the original descriptions, presumably based on the traditional concept that rodent coccidia are highly host specific, at least within a given host genus. Since the original descriptions, published surveys and experimental studies have clouded the boundaries between these forms. For example, *E. arizonensis* is reported to produce oocysts that differ morphologically in several features (oocyst wall smooth to pitted; number of

polar bodies; size, shape, texture of oocyst residuum) dependent upon the host in which it is found (Levine et al., 1957; Levine and Ivens, 1960, 1963). In addition to morphological differences between isolates of *E. arizonensis* from different host species, there are differences also in the electromorph banding patterns between populations of *E. arizonensis* from different host species (Reduker et al., 1987; Wash et al., 1990). Originally described from *Peromyscus truei* (Shufeldt, 1885), *E. arizonensis* has been reported since not only to infect rodents of at least 4 other species of *Peromyscus* but also of *Chaetodipus* and *Dipodomys* (Levine et al., 1957; Levine and Ivens, 1960, 1963; Ford et al., 1990). To complicate matters further, most redescrptions of *E. arizonensis* differ enough to suggest there may be multiple species confused as 1. Given the morphological similarities with the other 3 species, doubt can be cast on their validity as separate species and several questions arise. First, is each form a valid, morphologically similar host-specific species? If not, do these constitute a single, highly euryxenous species? Or, finally, are some of these valid, host-specific species, whereas others represent more euryxenous forms? The collections and cross-transmission experiments described here attempt to alleviate some of the confusion due the eimerians in murid hosts.

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TABLE I. Wild-caught murid rodents from which oocysts of various *Eimeria* species were isolated to use in cross-transmission experiments.

Hosts	Collection		Eimerian isolated	Primary isolate number
	Locality	Date		
<i>Reithrodontomys fulvescens laceyi</i>	Hood Co., Texas	April 1988	<i>Eimeria arizonensis</i> -like	1
<i>Baiomys taylori taylori</i>	Dallas Co., Texas	January 1990	<i>Eimeria taylori</i>	2
<i>B. t. taylori</i>	Dallas Co., Texas	March 1988	<i>Eimeria baiomysis</i>	3
<i>B. t. taylori</i>	Dallas Co., Texas	January 1990	<i>E. baiomysis</i>	4
<i>B. t. taylori</i>	Johnson Co., Texas	November 1987	<i>E. baiomysis</i>	5
<i>Peromyscus leucopus leucopus</i>	Dallas Co., Texas	April 1988	<i>E. arizonensis</i> -like	6
<i>Peromyscus truei truei</i>	Sandoval Co., New Mexico	August 1984	<i>E. arizonensis</i> -like	7
<i>Neotoma albigula albigula</i>	Socorro Co., New Mexico	May 1982	<i>Eimeria albigulae</i>	8
<i>Onychomys arenicola</i> (2)*	Hidalgo Co., New Mexico	July 1981	<i>Eimeria onychomysis</i>	9*
<i>Onychomys leucogaster</i> (3)*	Motley Co., New Mexico	May 1980	<i>E. onychomysis</i>	9*
<i>Onychomys torridus</i> (3)*	Hidalgo Co., New Mexico	May 1983	<i>E. onychomysis</i>	9*

\* Oocysts from all 8 animals and 3 host species combined as 1 isolate.

## MATERIALS AND METHODS

### Natural hosts and primary parasite isolates

Feces and intestinal contents were collected from wild-caught hosts of 5 genera representing 6 species (Table I). Feces from hosts were placed in separate petri dishes in a thin layer of 2.5% (w/v) aqueous potassium dichromate ( $K_2Cr_2O_7$ ) and kept at ambient temperature (ca. 21–23°C) for 6–10 days to allow oocysts that were present to sporulate. Eimerians isolated from these naturally infected hosts were used either directly as inocula in cross-transmission experiments or were inoculated into conspecific or congeneric animals to increase oocyst numbers. The resulting pools of oocysts were designated as 15 isolates (1, 1A, 1B, 2, 3, 4, 5, 6, 6A, 7, 7A, 8, 8A, 9, 9A) (Table II). These oocyst isolates/fecal suspensions were stored in refrigerators (4–6°C) until they were used in experimental infections. The presumed identity of each isolate, the host from which it was isolated, the recipient host species to which it was transferred experimentally, the age and number of oocysts used as inoculum, and the consequence of each experimental inoculation are given in Table II.

### Secondary parasite isolates

Isolate 1A was collected from the feces of 2 adult *Reithrodontomys montanus griseus* Bailey, 1905, infected with isolate 1. Isolate 1B was derived from the passage of isolate 1A through *Reithrodontomys megalotis* (Baird, 1858). Isolate 6A came from laboratory-reared *Peromyscus leucopus* (Rafinesque, 1818) inoculated with isolate 6. Isolate 7A was collected from the feces of 5 laboratory-reared *P. truei* inoculated with isolate 7. Isolate 8A was collected from an adult, wild-caught *Neotoma mexicana* Baird, 1855, inoculated with isolate 8; prior to inoculation the rodent was maintained in the laboratory for several months and was coccidia-free. Isolate 9A came from the feces of 2 coccidia-free *Onychomys leucogaster* (Wied, 1841), maintained in the laboratory, that were inoculated with isolate 9. Note (Table I) that isolate 9 came from the combined feces of 8 specimens of *Onychomys* representing 3 species. This was done because all 8 original hosts each had only a very few sporulated oocysts of *E. onychomysis*.

### Morphologic comparisons

Measurements were made on oocysts and sporocysts of *E. arizonensis*, *E. arizonensis*-like oocysts, and *E. baiomysis* using an ocular micrometer. All measurements, representing the mean of 30 under a 100× oil lens, are in micrometers ( $\mu\text{m}$ ) followed by the ranges in parentheses. For *E. arizonensis* isolated from *P. leucopus*, the 30 measurements were taken from 10 oocysts from isolate 6 and 20 were taken from isolate 6A. For *E. arizonensis*-like oocysts, 10 oocysts measured were from isolate 1 and 20 were from isolate 1A. For *E. baiomysis*, 10 oocysts were measured from isolates 3, 4, and 5 each. For *E. albigulae* and *E. onychomysis*, the oocysts in these isolates generally conformed to those described by Levine et al. (1957).

### Experimental inoculations

All animals were housed in plastic cages with presterilized wood shavings and given water and commercial rodent mash ad libitum. They were exposed to 12-hr light/dark cycles in rooms maintained ca. 20–23°C. Prior to inoculation, oocysts of an isolate were washed 2–3× in tap water, counted with a hemacytometer, and then inoculated per os by stomach tube into experimental hosts. Feces from inoculated hosts were collected in 2 ways. For isolates 1 through 6A, recipient hosts were maintained in plastic cages. On the appropriate days postinoculation (dpi), each animal was picked up, which resulted in its defecating, and these pellets then were examined for oocysts. For isolates 7 through 9A, recipient hosts were placed in wire mesh hanging cages and all feces for each host were collected every 24 hr and examined for oocysts for 20 dpi.

Fecal pellets were examined for the presence of oocysts using sucrose flotation (specific gravity 1.30) followed by microscopic examination using Nomarski interference-contrast optics. Oocysts were allowed to sporulate in petri dishes in a thin layer of feces/dichromate (see above) and reexamined microscopically 6–10 days later to confirm identification of each coccidian.

Laboratory-reared ICR outbred *Mus musculus* Linnaeus, 1758, were purchased from Harlan Sprague-Dawley (Indianapolis, Indiana) and were 2–4 mo old

TABLE II. Experimental protocol for inoculation of *Eimeria* specimens into various rodents.

Isolate number	<i>Eimeria</i> sp.	Donor host*	Recipient*		Age of oocysts (days)	Inoculation dose (number of oocysts)	Days post-inoculation examined	Oocysts present (+) or absent (-)
			Species	Number				
1	<i>E. arizonensis</i>	<i>Reithrodontomys fulvescens</i>	<i>R. montanus</i> a	2	330	10,000	1-20	+
								Days 4-14
1A	<i>E. arizonensis</i>	<i>Reithrodontomys montanus</i> a	<i>R. megalotis</i> b	2	300	2,000	5	+, +
			<i>P. leucopus</i> †	2	300	2,000	5	+, +
			<i>Mus musculus</i>	2	300	2,000	5	-, -
1B	<i>E. arizonensis</i>	<i>Reithrodontomys megalotis</i> b	<i>P. leucopus</i>	1	168	2,000	5	+
			<i>B. taylori</i>	1	168	2,000	5, 7, 9	-
2	<i>E. taylori</i>	<i>Baiomys taylori</i>	<i>P. leucopus</i> †	2	27	2,000	5, 8	-
			<i>R. megalotis</i>	1	27	2,000	5, 8	-
			<i>P. leucopus</i> ‡	1	167	500	5, 7, 9	-, -, -
			<i>B. taylori</i> §	1	167	500	5, 7	-, +
3	<i>E. baiomysis</i>	<i>B. taylori</i>	<i>P. leucopus</i>	1	725	1,500	5, 8	-
			<i>R. megalotis</i>	1	725	1,500	5	-
4	<i>E. baiomysis</i>	<i>B. taylori</i>	<i>P. leucopus</i>	1	13	2,000	5, 8	-
5	<i>E. baiomysis</i>	<i>B. taylori</i>	<i>P. leucopus</i> ‡	1	978	2,000	5, 7, 9	-, -, -
			<i>B. taylori</i> §	1	978	2,000	5, 7	+, +
6	<i>E. arizonensis</i>	<i>Peromyscus leucopus</i>	<i>P. leucopus</i> c	1	461	400	5, 6	-, +
6A	<i>E. arizonensis</i>	<i>P. leucopus</i> c	<i>P. leucopus</i>	2	461	400	5, 6	+, +, +
			<i>B. taylori</i>	1	111	2,000	5, 7, 9	-, -, -
			<i>R. montanus</i>	1	111	2,000	5, 7	+, +
7	<i>E. arizonensis</i>	<i>Peromyscus truei</i>	<i>P. truei</i> d	5	<180	3,000	1-20	All +
								Days 4-16
7A	<i>E. arizonensis</i>	<i>P. truei</i>	<i>N. mexicana</i> e	1	<180	3,000	1-20	-
			<i>O. leucogaster</i> f	2	<180	3,000	1-20	-, -
8	<i>E. albigulae</i>	<i>Neotoma albigula</i>	<i>N. mexicana</i> e	1	<180	3,000	1-20	+
								Days 3-15
8A	<i>E. albigulae</i>	<i>Neotoma mexicana</i>	<i>O. leucogaster</i> f	2	<180	3,000	1-20	-, -
			<i>P. truei</i> d	5	<180	3,000	1-20	All -
9	<i>E. onychomysis</i>	<i>Onychomys</i> spp.	<i>O. leucogaster</i> f	2	<180	3,000	1-20	+, +
								Days 2-11
9A	<i>E. onychomysis</i>	<i>Onychomys leucogaster</i>	<i>N. mexicana</i> e	1	<180	3,000	1-20	-
			<i>P. truei</i> d	5	<180	3,000	1-20	All -

\* Names followed by same letter indicate the same animals.

† Same animals. Inoculated first with isolate 1B and then reinoculated 28 days later with isolate 2.

‡ Same animal. Inoculated with both isolates simultaneously.

§ Same animal. Inoculated with both isolates simultaneously.

at the times of inoculation. *Peromyscus leucopus* were all F<sub>2</sub> generation and part of a captive breeding colony at Kansas State University. Feces from the cages of these animals have been checked periodically over the last 2 yr and no coccidian oocyst has ever been seen. The *P. truei* recipients were all F<sub>1</sub> generation, laboratory-reared mice derived from the parents from which isolate 7 was obtained. These mice had been checked numerous times before inoculation to assure they were coccidia-free.

To obtain large numbers of isolate 1, 2 adult *R. montanus griseus* were collected from Dallas County, Texas. Feces of both animals were checked daily for 14 days prior to inoculation with oocysts of isolate 1. Following inoculation of these 2 mice, feces were checked daily for unsporulated oocysts to determine prepatent and patent periods. Other specimens of *Reithrodontomys* used for inoculations were adults collected from Osborne and Pottawatomie counties, Kansas. These mice were placed in individual cages and their feces examined for oocysts at 1, 4, and 11 days postcapture. Inoculations using Kansas mice were at 11 days postcapture.

*Baiomys taylori* (Thomas, 1887) were F<sub>1</sub> generation offspring from animals collected from Dallas County, Texas. Mice were 5-10 mo old when used as recipient hosts. Each was placed in a separate cage, and feces were examined daily for 1 wk to assure the absence of extraneous infection prior to its inoculation.

Uninfected control animals could not be used for all inoculation experiments because of the difficulty in obtaining some animals. However, pairs of uninfected *P. leucopus*, housed separately from experimental hosts, were used as controls for experimental inoculations with isolates 1A, 1B, 2 (167 days), 5, 6, and 6A. An individually housed *R. megalotis* collected in Kansas also was used as a control during inoculation of isolate 1A. One *B. taylori*, a littermate of the other pygmy mouse used, served as control for inoculations with isolates 2 (167 days) and 5. For controls, feces were examined, as above, on the same day(s) that experimentally infected hosts were examined.

Voucher specimens of rodents are deposited in either the Arkansas State University Museum of Zoology, the Texas Tech University Museum, or in the University of New Mexico Museum of Southwestern Biology.

TABLE III. Measurements of oocyst features of *Eimeria* species collected from *Peromyscus leucopus*, species of *Reithrodontomys*, and *Baiomys taylori*.\*

Parameter	Oocyst source		
	<i>Baiomys taylori</i>	<i>Peromyscus leucopus</i>	<i>Reithrodontomys</i> spp.
Oocyst size	24.3 × 20.0 (20–30 × 17–24)	24.3 × 19.8 (21–27 × 17–22)	24.1 × 20.2 (20–30 × 17–26)
Oocyst SI†	1.2 (1.1–1.3)	1.2 (1.1–1.4)	1.2 (1.1–1.5)
Oocyst residuum (OR) diameter	7.0 (6–9)	8.3 (7–10)	8.2 (4–12)
Number OR globules	1–10	1–50	1–30
Oocyst outer walls	Light–moderate pitting	Smooth–moderate pitting	Smooth–moderate pitting
Polar granule‡	2.0 (1–3)	2.1 (2–3)	2.3 (2–3)
Sporocyst size	11.9 × 8.2 (10–14 × 7–9)	11.4 × 7.8 (11–13 × 7–9)	11.4 × 7.9 (10–14 × 7–9)
Sporocyst SI†	1.45 (1.3–1.6)	1.5 (1.3–1.6)	1.5 (1.3–1.55)
Stieda body size (height × width)	1.6 × 2.8 (1–2 × 2–4)	1.6 × 2.4 (1–2 × 2–3)	1.5 × 2.6 (1–2 × 2–3)
Sporozoite size§	15.8 × 3.4 (14–18 × 3–4)	14.0 × 3.2 (11–17 × 3–4)	14.6 × 3.2 (13–18 × 3–3.4)
Refractile body size	5.5 × 3.0 (5–6 × 2.8–3.2)	6.3 × 3.2 (5–8 × 2–4)	5.9 × 3.1 (5–7 × 3–4)

\* Measurements are means in micrometers (n = 30) with ranges in parentheses.

† SI, shape index (length/width).

‡ Long axis measurement.

§ Size in situ.

## RESULTS

Oocysts we isolated from hosts of 5 genera, *Baiomys*, *Neotoma*, *Onychomys*, *Peromyscus*, and *Reithrodontomys*, were morphologically similar to those of *E. arizonensis*, described originally from species of *Peromyscus*. Detailed structural comparisons were made among 3 of our isolates from 3 closely related hosts (Table III), and photomicrographs of isolates from each genus can be compared in Figures 1–15.

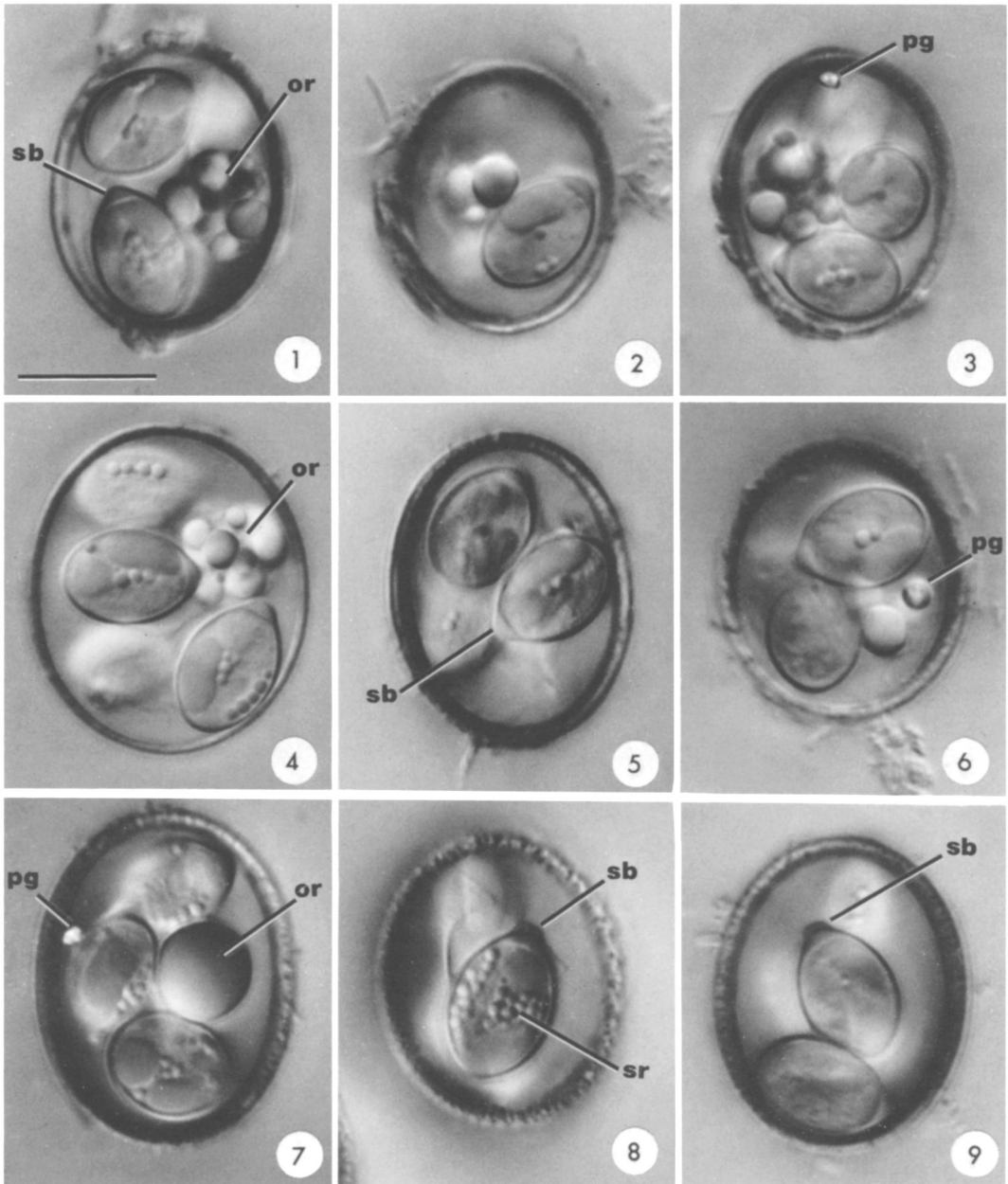
Sporocysts were lemon-shaped, with globular oocyst residua (either homogeneous or fragmented), and usually 1 (but up to 4) polar granule(s) was present. Stieda bodies were prominent, sub- and parastieda bodies absent, and sporozoites each possessed a large, posterior refractile body, but no anterior body. The only notable difference was that the Stieda body associated with sporocysts of *E. baiomysis* was more flattened than those on sporocysts from specimens of *Peromyscus*, *Neotoma*, or *Reithrodontomys* (cf. Figs. 1, 4, 10 vs. 9).

Isolate 1, from *Reithrodontomys fulvescens* J. A. Allen, 1894, was transmissible to *R. megalotis*, *R. montanus griseus*, and *P. leucopus* but not to *M. musculus* or *B. taylori*. Isolate 3, *E. baiomysis*, readily infected *B. taylori* but not *P. leucopus* or *R. megalotis*. McAllister and Upton (1988) reported a morphologically dissimilar

coccidian, *Eimeria taylori* McAllister and Upton, 1988, to infect *P. leucopus* as well as *B. taylori*. However, it too was not infective for *P. leucopus* or *R. megalotis*. Isolate 6, *E. arizonensis* from *P. leucopus*, was infective for 2 *P. leucopus* and for 1 *R. megalotis* but not for *B. taylori*. Isolate 7, *E. arizonensis* from *P. truei*, was infective for *P. truei* but not for *N. mexicana* or *O. leucogaster*. Isolate 8, *E. albigulae* from *Neotoma albigula* Hartley, 1894, was infective for *N. mexicana* but not for *O. leucogaster* or *P. truei*. Isolate 9, *E. onychomys* combined from 8 specimens representing 3 species of *Onychomys*, was infective for *O. leucogaster* but not for *N. mexicana* or *P. truei*.

## DISCUSSION

Dogma dictates that eimerians are highly host specific, being limited naturally to a narrow range of host species, usually congeners or, less frequently, only to conspecifics (Marquardt, 1973; Joyner, 1982). However, during the last 2 decades, there have been both cross-transmission studies (Todd and Hammond, 1968a, 1968b; de Vos, 1970; Mayberry and Marquardt, 1973; Mayberry et al., 1982) and observations from wild-caught rodents (Vance and Duszynski, 1985; Hill and Duszynski, 1986; McAllister and Upton, 1988; Ford et al., 1990) that suggest some

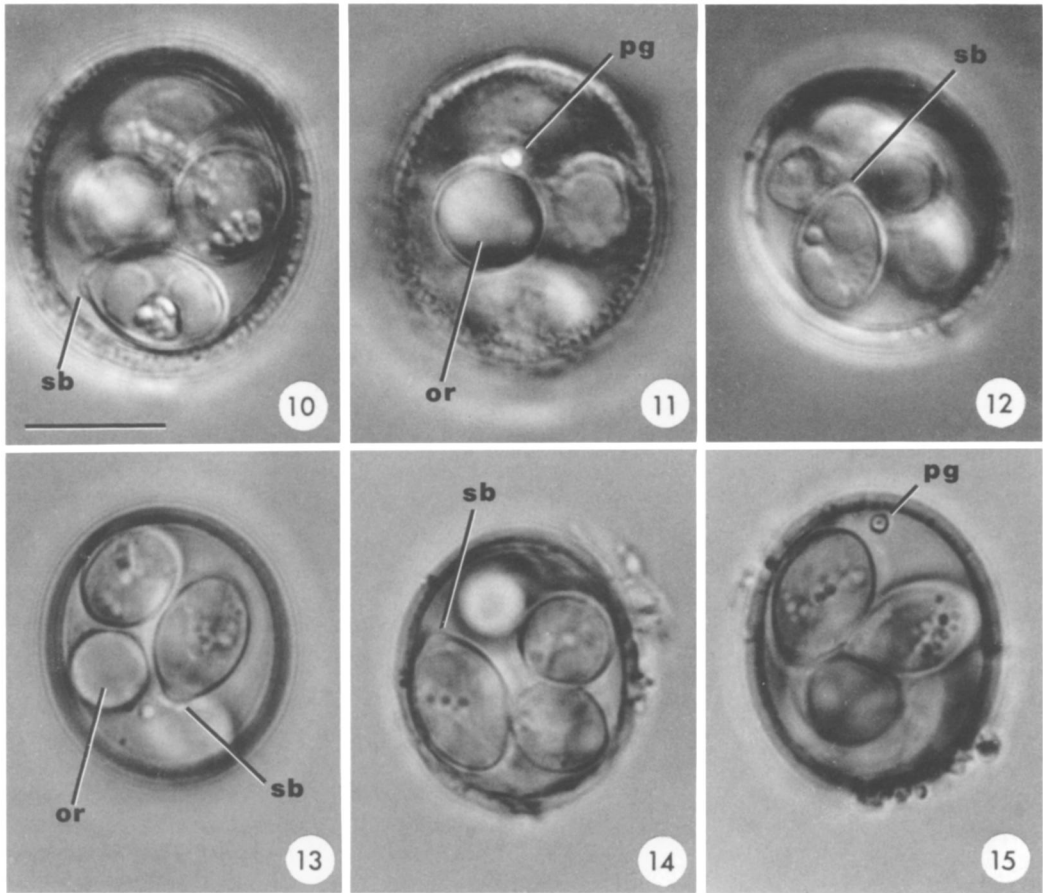


FIGURES 1-9. Nomarski-interference contrast photomicrographs of sporulated oocysts of various *Eimeria* species from rodents. 1-3. *Eimeria arizonensis* from *Peromyscus leucopus*. 4-6. *Eimeria arizonensis* from *Reithrodontomys fulvescens*. 7-9. *Eimeria baiomysis* from *Baiomys taylori*. Scale bar = 10  $\mu$ m for all figures. Abbreviations: or, oocyst residuum; pg, polar granule; sb, Stieda body; sr, sporocyst residuum.

rodent coccidians are more general in their host requirements and may be able to infect animals in several genera or even in different families.

When working with coccidians from wild animals, the problem of correctly identifying the coccidians found is compounded by the fact that

some species seem to exhibit a great deal of phenotypic plasticity in the structure of their sporulated oocysts, not only among and within host species, but also in oocysts from the same host (e.g., Parker and Duszynski, 1986; Gardner and Duszynski, 1990). A similar situation occurs in



FIGURES 10–15. Nomarski-interference contrast photomicrographs of sporulated oocysts of various *Eimeria* species from rodents. 10–12. *Eimeria albigulae* from *Neotoma albigula*. 13–15. *Eimeria onychomysis* from *Onychomys leucogaster*. Scale bar = 10  $\mu\text{m}$  for all figures. Abbreviations: or, oocyst residuum; pg, polar granule; sb, Stieda body.

1 of the most ubiquitous coccidians found in murid rodents, *E. arizonensis*. Oocysts of this form were said to be “composed of a single smooth layer, lined by a thin membrane”; they also usually had “a single large, clear, colorless residual globule, about 3.6  $\mu\text{m}$  in diameter” (Levine et al., 1957). Later, Levine and Ivens (1960) reported *E. arizonensis* from species of *Peromyscus* in Illinois. In *P. maniculatus* the oocyst wall was described as “slightly to moderately pitted” and the oocyst residuum as a “cluster of large, homogeneous granules/globules”; whereas in *P. leucopus* in Illinois, the oocysts had walls that were “sometimes smooth, but usually more or less pitted” with oocyst residua of “a single large, waxy-appearing globule about 4.” Reduker et al. (1985), surveying species of *Peromyscus* from the southwestern U.S.A. and northern

Mexico, found *E. arizonensis*-like oocysts in 41 of 102 (40%) specimens of *Peromyscus* (*Peromyscus eremicus* (Baird, 1858), *Peromyscus maniculatus* (Wagner, 1845), *P. truei*) and provided a “combined” redescription based on measurements/observations of nearly 500 sporulated oocysts. These observations lead to the conclusion that *E. arizonensis* is not exceptionally species specific and that it is a highly polymorphic form similar to *Eimeria opimi* described from South American fossorial rodents (Gardner and Duszynski, 1990). This may be true, but the possibility also exists that the variation seen in sporulated oocysts of *E. arizonensis* actually represents several isolates of 1 species or several species that are morphologically similar.

Finally, to further complicate an answer to the question, “What is the real *E. arizonensis*?” sev-

eral species of coccidia described from murid rodents are reported to have sporulated oocysts that are nearly identical to those of *E. arizonensis*; among these are *E. albigulae* from *N. albigula*, *E. baiomysis* from *B. taylori*, and *E. onychomysis* from *O. leucogaster*. Unfortunately, the descriptions of these forms are inadequate by today's standards and only line drawings exist in the original descriptions; there is no original published photograph or phototype on deposit with any accredited national museum (see Bandoni and Duszynski, 1988), so that oocysts representing the original forms seen cannot be compared directly.

In an attempt to help unravel the mystery of *E. arizonensis*, we did some initial cross-transmission studies using *E. arizonensis*-like oocysts from various hosts and passed them to other hosts. Our results must be interpreted cautiously, given the shortcomings of the experimental design. These results suggest the following: *Eimeria arizonensis*-like oocysts are capable of infecting a broad range of hosts in at least 2 genera, *Peromyscus* and *Reithrodontomys*. Although these data are in contrast to the traditional concept of species or genus specificity among the coccidia, it is not surprising given that these genera are closely related evolutionarily (Hooper and Musser, 1964; Carlton, 1980). On the other hand, oocysts of *E. albigulae*, *E. baiomysis*, and *E. onychomysis*, all structurally similar to *E. arizonensis*, appear to be separate species, at least based on the limited number of recipient animals we used and the fact that some of them had to be reinoculated with different forms/species at different times during their captivity. These results also suggest that *E. arizonensis*-like oocysts reported by Ford et al. (1990) from heteromyids of the genera *Chaetodipus* and *Dipodomys* are most likely not *E. arizonensis*. In addition, we speculate that should *E. arizonensis*-like oocysts be recovered from golden mice, *Ochrotomys nuttalli* (Harlan, 1832), they most likely will represent the same parasite species found in species of *Peromyscus* and *Reithrodontomys*. Golden mice are considered the closest living relative to *Peromyscus* species (Carlton, 1980).

Although the oocysts of *E. albigulae* (see Reduker and Duszynski, 1985: figs. 1, 2) and *E. arizonensis* from species of *Peromyscus* and *Reithrodontomys* (Figs. 1–6) are indistinguishable, our modest cross-transmission experiments suggest they are host-specific forms. Also, oocysts we isolated from *O. leucogaster* appear only

to be infective for *O. leucogaster*. We are aware, however, that other factors (e.g., unknown immune status of our recipients) may have influenced the negative results we saw, and that just because a few recipient hosts do not become infected does not necessarily mean that under natural conditions, where millions of random cross-transmission events take place between hosts that occupy similar space and time, that such successful host transfers could not occur.

Oocysts of *E. baiomysis*, although also morphologically similar to those of *E. arizonensis*, have Stieda bodies that are slightly more flattened (cf. Figs. 1–6 vs. Figs. 7–9). Our transmission experiments further suggest that the 2 are distinct species. In addition, the transmission studies between specimens of *Baiomys* and *Peromyscus* suggest that the report of *E. taylori* in *P. leucopus* was a misidentification (McAllister and Upton, 1988). It appears likely that these oocysts in *P. leucopus* were those of *Eimeria langebarteli* Ivens, Kruidenier, and Levine, 1959. Thus, even though *B. taylori* is considered a close relative of *P. leucopus*, our results are consistent with the genetic analysis by Yates et al. (1979) that suggests both genera are less closely related than are *Reithrodontomys* and *Peromyscus*.

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