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EIMERIA SPECIES (APICOMPLEXA: EIMERIIDAE) INFECTING PEROMYSCUS RODENTS IN THE SOUTHWESTERN UNITED STATES AND NORTHERN MEXICO WITH DESCRIPTION OF A NEW SPECIES

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ABSTRACT: Of 198 deermice (*Peromyscus* spp.) collected from various localities in the southwestern United States and northern Mexico, 106 (54%) had eimerian oocysts in their feces when examined. These included 50 of 106 (47%) *Peromyscus truei*, 34 of 54 (63%) *Peromyscus maniculatus*, 4 of 17 (24%) *Peromyscus leucopus*, and 18 of 21 (86%) *Peromyscus eremicus*. The following *Eimeria* were identified from infected mice: *Eimeria arizonensis* and *Eimeria langebarteli* from *P. truei*; *E. arizonensis*, *Eimeria peromysci*, and *Eimeria delicata* from *P. maniculatus*; *E. arizonensis* and *Eimeria lachrymalis* n. sp. from *P. eremicus*; and *E. langebarteli* from *P. leucopus*. Of the 106 *Peromyscus* found positive for *Eimeria*, 97 (91.5%) harbored only a single eimerian species at the time of examination. Sporulated oocysts of *E. lachrymalis* n. sp. were ellipsoid, $27-35 \times 17-21$ ($30.8 \pm 1.7 \times 19.1-0.9$) μm , possessed a smooth wall and one polar granule, but lacked a micropyle and an oocyst residuum. Sporocysts were teardrop-shaped, $9-13 \times 6-10$ ($10.9 \pm 0.9 \times 7.9 \pm 0.5$) μm , and had a Stieda body and sporocyst residuum, but no substieda body. Prepatent periods in experimental infections were 3-6 days after inoculation (DAI) for *E. arizonensis* (hosts: *P. eremicus*, *P. maniculatus*, *P. truei*); 4-5 DAI for *E. peromysci* (host: *P. maniculatus*); 6-9 DAI for *E. langebarteli* (hosts: *P. truei*, *P. leucopus*); and 8-10 DAI for *E. lachrymalis* (host: *P. eremicus*). Patency in these infections lasted 6-11 days for *E. arizonensis*, 5-10 days for *E. peromysci*, 14-40+ days for *E. langebarteli*, and 19-50+ days for *E. lachrymalis*. *Eimeria lachrymalis* appears to produce occult infections in *P. eremicus* that can be reactivated upon inoculation of the host with *E. arizonensis*.

From 1979 to 1983, the deermice *Peromyscus truei*, *Peromyscus maniculatus*, *Peromyscus leucopus*, and *Peromyscus eremicus* were collected from various localities in Sonora and Baja California, Mexico, southern California, Arizona, and New Mexico, and examined for the presence of coccidian oocysts in their feces. Five *Eimeria* spp. were found infecting these hosts, 4 of which have been previously described, and 1 that is described here as new. We also include data on prepatent and patent periods for 4 *Eimeria* spp. infecting *Peromyscus* hosts. Because detailed information on oocyst structure and/or photomicrographs are lacking for previously described *Peromyscus* eimerians, redescrptions and photomicrographs of the oocysts are also provided.

MATERIALS AND METHODS

Hosts were live-trapped and either taken to the laboratory for later inoculation experiments or killed within a few hours after capture. When killed, the abdominal cavity was opened, the colon and cecum were

removed and slit lengthwise, and these were placed, with their contents, into vials of 2.5% aqueous (w/v) $\text{K}_2\text{Cr}_2\text{O}_7$. Samples were processed for oocysts in the laboratory by separating fecal contents from intestinal tissue, filtering, incubating at room temperature (RT, 22-23 C), and examining by coverslip flotation as described by Duszynski et al. (1982). Oocysts were measured with an ocular micrometer and photographed with Panatomic-X 35 mm film with a Zeiss Universal Photomicroscope equipped with Neofluor and Nomarski-interference $100\times$ objective lenses. All measurements are given in μm with means ± 1 SD following the ranges. *Eimeria* spp. with morphologically similar oocysts were examined statistically using Multivariate Analysis of Variance (MANOVA) along with Duncan's Multiple Range Test from the Statistical Analysis Systems (SAS) package on the University of New Mexico IBM 360 computer.

Prepatent and patent periods were determined for the *Eimeria* spp. through laboratory inoculation experiments. Before inoculation, *Peromyscus* spp. were suspended in wire cages over pans of $\text{K}_2\text{Cr}_2\text{O}_7$, so their feces could be collected and examined several times for oocysts. If negative, hosts were ether-anesthetized and inoculated by gavage with sporulated oocysts of the appropriate *Eimeria* spp. isolated from field samples. Infected mice were kept in hanging cages and given food and water ad lib. Feces were collected daily at about the same hour and examined for the presence of unsporulated oocysts. Once patency started, fecal suspensions containing oocysts were homogenized, strained through 40-, and 60-mesh wire screens, and placed in a closed glass container at RT through which

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forced air was bubbled gently to agitate and aerate the oocysts.

RESULTS

Peromyscus and *Eimeria* spp., along with collection localities, are presented in Table I.

Eimeria peromysci

(Figs. 1, 2)

Description: As given by Levine et al. (1957).

Host: *Peromyscus maniculatus rufinus* (Merriam).

Locality: See Table I.

Prevalence: In 3 of 34 (9%) infected *P. maniculatus*.

Site of infection: Unknown, oocysts recovered from intestinal contents.

Prepatent period: Four to 5 DAI in *P. maniculatus* (experimental).

Patent period: Five to 10 days in *P. maniculatus* (experimental).

Comments: This species was originally described from *P. truei* in Arizona.

Eimeria arizonensis

(Figs. 3–6, 16)

Eimeria arizonensis Levine, Ivens, and Kruidenier, 1957, oocysts were found in the feces of infected *P. eremicus*, *P. maniculatus*, and *P. truei*. These oocysts were similar in size and general characteristics to the original description and drawings of *E. arizonensis* but a few differences did exist. Data presented here will be a redescription of *E. arizonensis* from *P. truei* and *P. maniculatus*, and a description from a new host, *P. eremicus*. Oocysts from these 3 hosts are qualitatively similar but do vary slightly in sporocyst length and width (Table II). Levine and Ivens (1960, 1963) also recognized slight morphological differences in *E. arizonensis* oocysts from *P. truei*, *P. maniculatus*, and *P. leucopus*, but did not consider them sufficient to warrant elevation of each form to specific status. Because no cross-transmission experiments were done with *E. arizonensis* from *Peromyscus* spp., we also consider the various morphological forms to represent a single species that exhibits slight morphological variation in oocysts isolated from different hosts.

Description: Oocysts subspheroid (common) to slightly ellipsoid; wall 0.8–2.4 (1.5 ± 0.2) consists of 2 layers: outer varies from smooth (rare) to rough (common), inner is smooth, micropyle absent; 1 (common) to 4 (rare) round to ellipsoid polar bodies present; oocyst residuum varies from a few clustered globules to a single homogenous globule (2.4–7.9); sporulated oocysts ($n = 477$) $17\text{--}30 \times 15\text{--}26$ ($23.6 \pm 2.5 \times 20.8 \pm 1.8$) with L:W ratio 1.00–1.44 (1.13 ± 0.07); sporocysts ($n = 477$) lemon-shaped, $8\text{--}16 \times 6\text{--}10$ ($12.1 \pm 1.4 \times 7.7 \pm 0.8$) with L:W ratio 1.04–2.13 (1.56 ± 0.16); Stieda body prominent (1.6×2.4); sporocyst residuum consisting of several granules, dispersed, often in a row between sporozoites; sporozoites apparently arranged head to tail with 1 obvious refractile body (3.2×6.4); oocyst:sporocyst L:L ratio 1.47–2.85 (1.97 ± 0.26); oocyst:sporocyst W:W ratio 2.16–3.72 (2.70 ± 0.25).

Hosts: *Peromyscus eremicus eremicus* (Baird), *Peromyscus truei truei* (Shufeldt), *P. maniculatus rufinus* (Merriam).

Locality: See Table I.

Prevalence: In 8 of 18 (45%) infected *P. eremicus*, 25 of 34 (75%) infected *P. maniculatus*, and 18 of 50 (36%) infected *P. truei*.

Site of infection: Unknown, oocysts recovered from intestinal contents.

Prepatent period: Four to 6 DAI in *P. eremicus*, 3 to 4 DAI in *P. maniculatus*, 3 to 4 DAI in *P. truei* (all experimental).

Patent period: Six to 11 days in *P. eremicus*, 9 to 11 days in *P. maniculatus*, 9 to 11 days in *P. truei* (all experimental).

Eimeria langebarteli

(Figs. 7–10, 17)

Description: Oocysts ellipsoid with 1 obvious, smooth wall, 0.8–1.2 (0.9 ± 0.2), lacking a micropyle; 1 to 2 polar granules, dumbbell-shaped (common) to ellipsoid or irregular (rare); no oocyst residuum; sporulated oocysts ($n = 215$) $16\text{--}26 \times 11\text{--}17$ ($21.0 \pm 2.6 \times 13.4 \pm 1.3$) with L:W ratio 1.34–1.83 (1.57 ± 0.11); sporocysts ($n = 215$) ellipsoid, $7\text{--}12 \times 4\text{--}7$ ($9.8 \pm 0.9 \times 5.5 \pm 0.6$) with L:W ratio 1.41–2.31 (1.79 ± 0.18); sporocyst wall thin and delicate, Stieda body often appearing unattached due to the thinness of wall; Stieda body small (0.8×1.4); ‘knob-like’ in shape, substieda body absent; sporocyst residuum varies from small, homogenous globule, to 1 or 2 tight clusters of small granules, to tiny granules dispersed in sporocyst; sporocyst residuum often obscured by sporozoites; sporozoite cytoplasm ‘grainy,’ with an obvious posterior refractile body (2.4×3.2); oocyst:sporocyst L:L ratio 1.76–2.55 (2.16 ± 0.21); oocyst:sporocyst W:W ratio 1.88–3.18 (2.46 ± 0.23).

Hosts: *Peromyscus leucopus tornillo* Mearns, and *P. truei truei* (Shufeldt).

Locality: See Table I.

Prevalence: In 4 of 4 (100%) infected *P. leucopus*, and 19 of 50 (38%) infected *P. truei*.

Site of infection: Unknown, oocysts recovered from intestinal contents.

Prepatent period: Six to 9 DAI in *P. leucopus*, 6 to 9 DAI in *P. truei* (both experimental).

Patent period: Nineteen to 40+ days in *P. leucopus*, 14 to 40+ days in *P. truei* (both experimental).

Comments: This species was originally described from *Peromyscus boylii* from Chihuahua, Mexico (Ivens et al., 1959). Although oocysts collected from *P. leucopus* were slightly smaller than those collected from *P. truei* ($P \leq 0.05$, Duncan’s Multiple Range Test), oocysts from both hosts overlapped in measurements and were identical in qualitative traits. For these reasons, and because no cross-transmission experiments were performed, we consider the 2 forms to represent a single species.

Eimeria delicata

(Figs. 11, 12)

Description: As given by Levine and Ivens (1960).

Host: *Peromyscus maniculatus*.

Locality: See Table I.

Prevalence: In 2 of 34 (6%) infected *P. maniculatus*.

TABLE I. *Eimeria* spp. recovered from 5 *Peromyscus* spp. in this study and as reported in the literature.

<i>Peromyscus</i> spp.	Locality	No. hosts infected/ examined (%)	<i>Eimeria</i> spp. identified	
			This study (no. hosts infected)	Previous studies (ref.)
<i>boylii</i>	Mexico: Cuauhtemoc, Chihuahua	2/4 (50)	—	<i>langebarteli</i> (Ivens et al., 1959)
<i>eremicus</i>	Mexico: Baja California Norte; Valle de Trinidad	4/4 (100)	<i>arizonensis</i> (3) <i>lachrymalis</i> (1)	<i>eremici</i> (Levine et al., 1957)
	Baja California Norte; Rancho Santa Catarina	0/1 (0)	—	
	Baja California Norte; Sierra San Pedro Martir	1/1 (100)	<i>arizonensis</i> (1)	
	Baja California Norte; Mission de San Borgas	1/1 (100)	<i>arizonensis</i> (1)	
	Sonora; Algodones	1/1 (100)	<i>arizonensis</i> (1)	
	USA: New Mexico; Socorro Co., Ladrone Mt.	11/13 (85)	<i>arizonensis</i> (1) <i>lachrymalis</i> (9)* both of above (1)	
	Total	18/21 (86)	<i>arizonensis</i> (7) <i>lachrymalis</i> (10) both of above (1)	
<i>leucopus</i>	USA: New Mexico; Socorro Co., Ladrone Mt.	4/17 (24)	<i>langebarteli</i> (4)*	<i>leucopi</i> (von Zellen, 1961) <i>arizonensis</i> (Levine and Ivens, 1960) <i>roudabushi</i> (Levine and Ivens, 1960) <i>carolinensis</i> (von Zellen, 1959)
<i>maniculatus</i>	Mexico: Baja California Norte; Sierra San Pedro Martir	6/7 (86)	<i>arizonensis</i> (2) unspor. (4)†	<i>arizonensis</i> (Levine and Ivens, 1963) <i>siniffi</i> (Levine and Ivens, 1960) <i>delicata</i> (Levine and Ivens, 1960)
	Baja California Norte; E. San Telmo	3/5 (60)	<i>arizonensis</i> (2) unspor. (1)†	
	Baja California Norte; Sierra Juarez	5/8 (63)	<i>arizonensis</i> (5)	
	USA: California; San Diego Co., Cleveland National Forest	3/4 (75)	<i>arizonensis</i> (2) unspor. (1)†	
	California; Riverside Co., Black Mt.	7/10 (70)	<i>arizonensis</i> (5)* <i>delicata</i> (1) both of above (1)	
	California; San Bernardino Co., San Bernardino Mts.	9/16 (56)	<i>arizonensis</i> (6) <i>peromysci</i> (2)* both of above (1)	
	California; Los Angeles Co., Angeles National Forest	1/4 (25)	<i>arizonensis</i> (1)	
	Total	34/54 (63)	<i>arizonensis</i> (23) <i>peromysci</i> (2) <i>delicata</i> (1) <i>arizonensis</i> + <i>peromysci</i> (1) <i>arizonensis</i> + <i>delicata</i> (1) unspor. (6)†	
<i>truei</i>	Mexico: Baja California Norte; Sierra Juarez	26/31 (84)	<i>arizonensis</i> (6) <i>langebarteli</i> (7) both of above (3) unspor. (10)†	<i>arizonensis</i> (Levine et al., 1957) <i>peromysci</i> (Levine et al., 1957)
	Baja California Norte; Valle de Trinidad	0/1 (0)	—	
	Baja California Norte; Sierra San Pedro Martir	6/6 (100)	<i>arizonensis</i> (1) <i>langebarteli</i> (5)	
	USA: Arizona; Cochise Co., Chiricahua Mts.	2/2 (100)	<i>langebarteli</i> (2)	
	California; Los Angeles Co., Angeles National Forest	10/21 (48)	<i>arizonensis</i> (3) <i>langebarteli</i> (2) both of above (2) unspor. (3)†	

TABLE I. *Continued.*

<i>Peromyscus</i> spp.	Locality	No. hosts infected/ examined (%)	<i>Eimeria</i> spp. identified	
			This study (no. hosts infected)	Previous studies (ref.)
	California; Riverside Co., Black Mts.	3/4 (75)	<i>arizonensis</i> (1) <i>langebarteli</i> (0) both of above (1) unspor. (1)†	
	California; San Diego Co., Cleveland National Forest	0/1 (0)	—	
	California; San Bernardino Co., San Bernardino Mts.	1/2 (50)	unspor. (1)†	
	New Mexico; Socorro Co., Ladrones Mt.	2/38 (5)	<i>arizonensis</i> (1) unspor. (1)†	
	Total	50/106 (47)	<i>arizonensis</i> (12) <i>langebarteli</i> (16) both of above (6) unspor. (16)†	
Totals		106/198 (53)	5	9

* Samples used in inoculation experiments.

† Coccidia not identifiable because of unsporulated oocysts.

Site of infection: Unknown, oocysts recovered from intestinal contents.

Comments: No inoculation experiments were performed with this species.

***Eimeria lachrymalis* n. sp.**
(Figs. 13–15)

Description: Oocysts ellipsoid with 1 obvious, smooth wall, $0.8\text{--}1.6$ (1.5 ± 0.2), lacking a micropyle; 1 (common) to 2 (rare) polar granules, round to ellipsoid in shape, no oocyst residuum; sporulated oocysts ($n = 85$) $27\text{--}35 \times 17\text{--}21$ ($30.8 \pm 1.7 \times 19.1 \pm 0.9$) with L:W ratio $1.4\text{--}1.8$ (1.6 ± 0.1); sporocysts ($n = 85$) ovoid, tapered at one end (teardrop-shaped), thin walled, $9\text{--}13 \times 6\text{--}10$ ($10.9 \pm 0.9 \times 7.9 \pm 0.5$) with L:W ratio $1.00\text{--}1.65$ (1.39 ± 0.13); Stieda body small and 'cap-like' (0.5×1.6), substieda body absent; sporocyst residuum globular mass, round to ellipsoid, often equal in size to area covered by both sporozoites, somewhat obscured by sporozoites; sporozoites with 'grainy' cytoplasm, with an obvious posterior refractile body (3.2×6.4); oocyst:sporocyst L:L ratio $2.50\text{--}3.38$ (2.80 ± 0.13); oocyst:sporocyst W:W ratio $2.01\text{--}2.86$ (2.44 ± 0.16).

Taxonomic summary

Diagnosis: This species most closely resembles *E. langebarteli*, but differs by being larger, having teardrop-shaped rather than ellipsoid sporocysts, and possessing a distinctly different sporocyst residuum.

Host: *Peromyscus eremicus eremicus* (Baird), cactus mouse, Museum of Southwestern Biology, Division of Mammals, MSB 40235 (F) J. Bandoli #76, 26 May 1979; MSB 48663 (M), 48664 (F), 48671 (F), 48672 (M), 48673 (F), 48674 (M), D. W. Reduker #599–600, 603–606, 20–21 March 1982; MSB 48676 (M), 48677 (F), D. W. Reduker #613–614, 1 May 1982; experimental animals #10, 13, D. W. Reduker, coll., 28 May 1982.

Locality: Mexico: Baja California Norte and Sonora. USA: New Mexico; Socorro Co.; Ladrones Mt.

Prevalence: In 11 of 18 (61%) infected *P. eremicus*.

Site of infection: Unknown, oocysts recovered from intestinal contents.

Prepatent period: Eight to 10 DAI in *P. eremicus* (experimental).

Patent period: Nineteen to 50+ days in *P. eremicus* (experimental).

Etymology: The specific name is derived from the teardrop-shaped sporocysts of this species.

Prepatent and patent periods

Prepatent and patent periods for *E. arizonensis* and *E. peromysci* were discrete and predictable following

TABLE II. *Comparison of E. arizonensis oocysts from 3 Peromyscus host species for 9 quantitative characters. Presented are average values for each trait (μm). Underscored character means indicates no significant differences between those samples (Duncan's Multiple Range Test, α = 0.05).*

Character	Host:	<i>E. arizonensis</i>		
		<i>P. eremicus</i> (n = 106)	<i>P. truei</i> (n = 188)	<i>P. maniculatus</i> (n = 184)
Oocyst length		24.25	23.31	23.60
Oocyst width		20.96	20.63	20.95
Sporocyst length		10.93	11.72	13.06
Sporocyst width		7.53	7.47	8.13
Oocyst L:W ratio		1.16	1.13	1.13
Sporocyst L:W ratio		1.45	1.58	1.61
Oocyst:sporocyst L:L		2.23	2.00	1.80
Oocyst:sporocyst W:W		2.79	2.78	2.58
Oocyst wall width		1.54	1.50	1.37

FIGURES 1-6. 1. *Eimeria peromysci* from *Peromyscus maniculatus*. 2. *E. peromysci*; note oocyst residuum (arrow). Nomarski interference. 3. *E. arizonensis* from *P. truei*. 4. *E. arizonensis* from *P. truei*; note oocyst residuum (*). Nomarski interference. 5. *E. arizonensis* from *P. eremicus*. 6. *E. arizonensis* from *P. maniculatus*. 2,500 $\times$.

FIGURES 7-14. 7. *Eimeria langebarteli* from *P. truei*; note sporocyst residuum (arrow). 8. *E. langebarteli* from *P. truei*. Nomarski interference. 9. *E. langebarteli* from *P. leucopus*. 10. *E. langebarteli* from *P. leucopus*. Nomarski interference. 11. *E. delicata* from *P. maniculatus*. 12. *E. delicata*. Nomarski interference. 13. *E. lachrymalis* n. sp. from *P. eremicus*; note sporocyst residuum (arrow). 14. *E. lachrymalis* n. sp.; note nucleus (arrow). Nomarski interference. 2,435 $\times$.

FIGURES 15–17. Line drawings of eimerian oocysts from *Peromyscus* spp. 15. *Eimeria lachrymalis* n. sp. from *Peromyscus eremicus*. 16. *E. arizonensis*. Composite drawing made from oocysts recovered from *P. eremicus*, *P. maniculatus*, and *P. truei*. 17. *E. langebarteli* from *P. leucopus* and *P. truei*. Bar = 5 μ m.

inoculation of hosts with sporulated oocysts. Prepatent and patent periods of *E. langebarteli* and *E. lachrymalis* were less predictable. Furthermore, small numbers of unsporulated oocysts were observed in the feces of experimentally inoculated individuals from all 3 host species for more than 40–50 days after the initiation of patency (see above). Fecal examinations ceased at this time, so the exact length of patent periods for these *Eimeria* were not established.

Peculiarities were seen in the temporal appearance of *E. lachrymalis* oocysts in the feces of *P. eremicus*. Initially, 7 uninfected *P. eremicus* were inoculated with field isolates of *E. lachrymalis*, prepatent and patent periods were recorded, and hosts were returned to individual cages after oocyst yield slowed or ceased. On

3 subsequent occasions (2 and 5 mo apart), the same mice were inoculated with sporulated *E. arizonensis* oocysts isolated from *P. eremicus*. Before inoculation, the mice were examined for the presence of oocysts in their feces and found to be negative. Unsporulated oocysts of *E. arizonensis* appeared in the feces of experimentally infected *P. eremicus* between 4 and 6 DAI as expected. Additionally, low numbers of unsporulated *E. lachrymalis* oocysts were found in the feces of several individual mice during the course of infection. In the first inoculation experiment, 2 of 4 *P. eremicus* shed unsporulated *E. lachrymalis* oocysts after inoculation with *E. arizonensis* (1 to 11 DAI), during the second experiment, 3 of 7 shed unsporulated *E. lachrymalis* oocysts (3 to 8 DAI), and during the third

experiment, 3 of 3 shed unsporulated *E. lachrymalis* oocysts (8+ DAI). Although present in the feces, unsporulated *E. lachrymalis* oocysts never occurred in large numbers.

DISCUSSION

The genus *Peromyscus* is a diverse assemblage of rodents containing approximately 59 distinct species (Hall, 1981). Despite their widespread North American distribution, ecological diversity (Baker, 1968), relative ease in trapping and in laboratory maintenance, little attention has been given them in surveys for Coccidia. The literature reports only 5 *Peromyscus* spp. (8.5%) examined for *Eimeria*, from which 9 *Eimeria* have been described (Table I). Given the relatively high natural infection rate of *Peromyscus* populations with *Eimeria* (e.g., 54%, this study; 17–72%, von Zellen, 1961), the potential for discovery of additional *Eimeria* spp. as more *Peromyscus* spp. are examined appears substantial.

Of the 106 mice found positive for *Eimeria* in this study, only 9 (8.5%) had 2 *Eimeria* spp. simultaneously as indicated by oocysts in the feces. The majority were infected with a single eimerian at the time of examination. Even within a single *Peromyscus* population where more than 1 *Eimeria* sp. is present, the incidence of multispecies infection remains low (0–33%) (Table I). This is unexpected given the long patencies of *E. langebarteli* and *E. lachrymalis*. Similar patterns have been observed in previous surveys of peromyscine coccidia. For example, of 87 individual *Peromyscus* hosts examined between 1957 and 1963 (references, Table I), 5 individuals (5.7%) were reported to harbor more than 1 *Eimeria* sp. at the time of examination [1 *P. truei* infected with *E. peromysci* and *E. arizonensis* (Levine et al., 1957); 4 *P. leucopus* infected with *E. carolinensis* and *E. leucopi* (von Zellen, 1961)]. Three of 87 (3%) were found to harbor an eimerian and *Tyzzeria peromysci* (Levine and Ivens, 1960). These low multispecies infection rates are comparable to those obtained by Stout and Duszynski (1983) in their survey of *Dipodomys* coccidia and to those of Vance and Duszynski (1985) in their survey of coccidia from *Microtus* spp. Mechanisms responsible for the predominance of single species infections in *Peromyscus* and other hosts are currently unknown. Whether this phenomenon is under genetic or ecologic control (e.g., Doran, 1953) is a subject for future investigation.

Originally described from Arizona *P. truei*, *E. arizonensis* (or a very similar taxon) was later

described from *P. maniculatus* and *P. leucopus* from Illinois (Levine and Ivens, 1960, 1963). Oocysts described from *Peromyscus* in this study are very similar to the original description except for the following: (1) the oocyst wall is composed of at least 2 layers, an inner smooth one and an outer rough one, (2) the texture of the outer wall varies from smooth (rare) to rough (common), and (3) no “membrane lining the oocyst” (Levine et al., 1957) was observed. This ‘membrane’ mentioned in the original description was never shown in a diagram or photograph of the oocysts, and although Levine and Ivens (1960) crushed oocysts from *P. maniculatus* and *P. leucopus*, 2 oocyst walls were never observed. Our experience with this eimerian is that crushing oocysts does not always separate the walls. Only rarely are the 2 walls distinctly visible. Variation in outer wall texture has been shown to be typical of intraspecific variation in certain *Eimeria* (e.g., Christensen and Porter, 1939) and may be the case for this taxon as well.

Oocysts of *E. arizonensis* are very similar in morphology to those described and illustrated for *Eimeria baiomysis* Levine, Ivens, and Kruidenier, 1958. This eimerian was originally described from a single *Baiomys taylori*, a cricetine rodent considered a close relative of *Peromyscus* (Hooper and Musser, 1964; Yates et al., 1979). In the original description of *E. baiomysis*, Levine et al. (1958) state that the oocyst of this eimerian “differs from . . . *E. arizonensis* in having a rough, pitted wall.” In a subsequent survey, Levine and Ivens (1960) acknowledged the ‘moderately pitted’ nature of the wall in some *E. arizonensis* from *P. maniculatus* and *P. leucopus*. Thus, the descriptions and illustrations of these 2 species appear synonymous. The validity of *E. baiomysis* as a species distinct from *E. arizonensis* should be examined more closely.

The morphology of a parasite and/or its development has been shown to vary according to the host species in which it develops (see Dogiel, 1966). A similar phenomenon may be responsible for the sporocyst size differences observed in *E. arizonensis* oocysts isolated from different host species and the oocyst size differences observed between *E. langebarteli* isolated from *P. truei* and *P. leucopus*. In light of classical coccidian taxonomic practices, size differences observed between *E. langebarteli* oocysts from 2 different hosts may be sufficient to warrant specific status for the 2 eimerian forms. The size differences, however, may be a manifestation of

their development in 2 distinctly different host species. Future systematic work with structurally similar eimerian taxa from different hosts should address whether the variation observed reflects interspecific genetic differences between the parasites, intraspecific geographic variation, or variation manifested through multiple host species occupation. Only through detailed cross-transmission studies can these questions be addressed with rigor. Such tests, coupled with statistical analysis of oocyst morphology, electrophoretic analysis (Jeffers and Shirley, 1982), and ultrastructural analysis should provide sufficient data bases from which improved systematic conclusions can be drawn.

Prepatent and patent period observations

The extended patencies of *E. langebarteli* and *E. lachrymalis* are unusual for eimeriid taxa, but not unique. For example, *Isospora serini* may shed oocysts in the feces of the canary host for months after reaching patency (Box, 1977). The chronic nature of oocyst yield in this species has been attributed to its utilization of macrophages as host cells for asexual development rather than shorter-lived enterocytes (Box, 1981). Perhaps an analogous situation occurs in these species infecting *Peromyscus*.

Although generally accepted that the number of asexual generations and thus patency in most species of *Eimeria* is genetically predetermined and little influenced by the host's immune response (Rose, 1982), exceptions do exist. *Eimeria mivati* in poultry, and *Eimeria zuernii* and *Eimeria bovis* in cattle, have displayed prolonged and chronic oocyst production after immunosuppressant treatment of their respective hosts (Rose, 1970; Long and Rose, 1970; Niilo, 1970). Similar results have been obtained with *Toxoplasma gondii* infections in immunosuppressed feline hosts (Dubey and Frenkel, 1974). Additionally, chronic oocyst production is characteristic of *Cryptosporidium* spp. infecting nude mice and immunocompromised humans (Heine et al., 1984; Current et al., 1983). Extended patencies in ovine *Eimeria* have been experimentally produced after hosts are given multispecific eimerian infections (Catchpole et al., 1976). These studies all suggest that in certain coccidial infections, including those produced by *Eimeria* spp., patent periods, and perhaps the number of asexual generations, may be totally dependent upon the host's immune response. Suppression of the host response through drug treatment or modification through multispecies infections may al-

low asexual developmental stages (meronts?) to persist over long periods of time (Long and Rose, 1970). Whether the long patencies observed in *E. langebarteli* and *E. lachrymalis* infecting *Peromyscus* are genetically predetermined or a result of the parasite's ability to avoid or modify the host's specific immune response is presently unknown.

Reactivation of latent *E. lachrymalis* infection after inoculation of *P. eremicus* with *E. arizonensis* is also an unusual phenomenon for *Eimeria*. Similar behavior has been noted in *Eimeria ellipsoidalis* infecting cattle. Calves previously recovered from *E. ellipsoidalis* infection inoculated with sporulated *E. bovis* oocysts will reshed *E. ellipsoidalis* oocysts at approximately 11 DAI, followed by *E. bovis* oocysts at about 19 DAI (Speer, pers. comm.). These observations suggest that *E. lachrymalis* and *E. ellipsoidalis* may have the ability to exist as cryptic asexual stages within their hosts, possibly within non-enterocytic tissues of the gut or associated organs. Infection with a second species may somehow release or modify the host's immunosuppressant ability allowing for continued development of cryptic asexual stages into functional gametocytes. Evidence for host immunity or multi-species infections influencing production and/or activation of cryptic asexual stages in the host has been found in feline toxoplasmosis and chicken coccidiosis (Dubey and Frenkel, 1974; Dubey, 1976, 1978; Long and Millard, 1976).

Reshedding of *E. lachrymalis* oocysts from chronically infected *P. eremicus* inoculated with *E. arizonensis* occurs sooner than expected given 'normal' patency for *E. lachrymalis* (1 to 8 DAI with *E. arizonensis*). This suggests that occult meronts rather than sporozoites are present because activated sporozoites would be expected to manifest a longer prepatent period (7 to 10 DAI).

Incidence of chronic and occult coccidiosis in vertebrate hosts may be more extensive than previously realized in light of data presented here and the cases discussed above. As Long and Millard (1976) suggest, use of corticosteroids or other immunosuppressant therapy may allow for detection of occult eimerian stages in host tissue.

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