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Coccidia (Apicomplexa: Eimeriidae) of the Mammalian Order Chiroptera

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Coccidia (Apicomplexa: Eimeriidae) of the Mammalian Order Chiroptera

DONALD W. DUSZYNSKI

Abstract

The coccidia are protists (phylum Apicomplexa) that, likely, are both the most abundant (numbers of individual zoites) and most speciose of all the kinds of parasites found in/on mammals. They also are among the least studied and understood, with the exception of those species that cause pathology in domesticated Artiodactyla. In this review, I focus only on the largest family of the phylum, Eimeriidae Minchin, 1903, because its members often are among the most prevalent apicomplexans of mammals, and because there has never been a taxonomic summation for those species that infect Chirpotera. In all published descriptions of bat coccidia, members of only one genus, *Eimeria*, have been discovered and named from oocysts found in fecal material; here, all published descriptions of *Eimeria* species that infect bats are reviewed and evaluated. Some of the named species are invalid, either because rules concerning the naming of new species (International Code of Zoological Nomenclature) were not followed and/or the original description was so incomplete as to be of little use; such names have been relegated to *species inquirendae.* Recently, oocysts of an *Isospora*-like species were found in the kidney and urine of *Eptesicus fuscus* (Vespertilionidae), but until a detailed description and a photosyntype or line drawing are available, this organism also must be considered a *species inquirendae.* The Chiroptera has 17 families, 177 genera and 925 species. There are no coccidia known from 11 families: Pteropodidae, Rhinopomatidae, Craseonycteridae, Nycteridae, Megadermatidae, Noctilionidae, Mormoopidae, Natalidae, Furipteridae, Myzopodidae, Mystacinidae, and for seven (64%) of these, no individuals in the family have been examined for coccidia. In the Emballonuridae, three genera—*Peropteryx, Rhynchonecteris* and *Taphozous*—have been examined and each has a unique *Eimeria* species; in the Rhinolophidae, only *Rhinolophus* has been examined with two *Eimeria* species known; in the Phyllostomidae, 15 genera have been examined, but only one *Eimeria* species has been found in a *Uroderma* species; in the Vespertilionidae, 13 genera have been examined and 20 *Eimeria* have been found in seven genera: *Antrozous* (1), *Myotis* (8); *Nyctalus* (2), *Nycticeius* (1), *Pipistrellus* (5), *Tomopea* (1) and *Vespertilio* (2); and in the Molossidae, five genera have been examined and five *Eimeria* species have been discovered in four of them: *Chaerephon* (2), *Eumops* (1), *Molossus* (1) and *Nyctinomops* (1). In all, 31 *Eimeria* species are now known from chiropteran hosts and eight *species inquirendae* are noted. In general, phyllostomids, exclusively New World bats, most of which are frugivorous, do not have coccidia, whereas other groups of bats that have been examined do. This may suggest that we are dealing with a phylogenetic explanation for this host-parasite association rather than an environmental, dietary or behavioral one. Mammalogists are encouraged to be more receptive to working with parasitologists to use comparative parasite data that might provide insights into bat evolution, habitat use and sociality. The eimeriid coccidia are ideal parasites for such cooperative efforts because they can be collected easily by noninvasive fecal (and urine?) collections.

Coccidia (Apicomplex: Eimeriidea) of the Mammalian Order Chiroptera, by D.W. Duszynski.

INTRODUCTION

The Chiroptera, with 925 species (Koopman 1993), is second only to rodents in the number of mammal species and, in terms of all the activities needed to carry on their daily lives (e.g., locomotion, feeding, behavior, morphology, body size, etc.), they show a greater degree of specialization than does any other order of mammals (Feldhamer et al. 1999). Because of their ability to fly, they are nearly cosmopolitan in their distribution and seem to be absent only from polar and arctic regions and, perhaps, some isolated oceanic islands (Vaughan 1978). Flight also has allowed them to fill a wide variety of feeding niches; although most species are insectivorous, others may be carnivorous, piscivorous, nectivorous, frugivorous or sanguinivorous. Because of this profusion of adaptation and dispersal, bats, their biology, and the communities they form have received a great deal of attention in recent decades (e.g., Findley 1993). Unfortunately, the parasites of bats, which certainly outnumber their hosts in both number and diversity, have been studied very little (e.g., Ubelaker et al. 1977).

With habitat loss, due to continued human encroachment, and increased mortality among bat populations worldwide, it is critical that we learn more about their biology by investing heavily in multi-disciplinary approaches. When bats are collected, we need to take more than skin, skull, skeleton, frozen tissue and chromosomes; there is a tremendous harvest of parasite tissue and information that, most often, goes unused and is discarded. Such data may be able to contribute significantly to better understanding bat evolutionary relationships because some of their parasites, especially their coccidia, are believed to be exceptionally host-specific, having shared a long evolutionary history with their host. Unfortunately, there is an enormous lack of information regarding the occurrence of coccidia in most host groups, not because they aren't there, but because we haven't made a concerted effort to look for them (e.g., Duszynski et al. 1999c; Duszynski and Upton 2000).

Coccidia are ubiquitous in vertebrates and represent some of the most prevalent parasites known. However, despite their widespread distribution, knowledge of their occurrence in most host groups is scarce because of the difficulties in dealing with such small (10–40 μm) protists. The coccidia have direct life cycles that include first asexual and then sexual reproduction, and both patterns (= endogenous development) occur within the epithelial or endothelial cells of the vertebrate gut or related structures (e.g., bile duct, renal tubular epithelium, oviduct epithelium, others). After fertilization, the resulting zygote often develops a thick outer wall (in terrestrial mammals), ruptures from the confines of its epithelial cell, and is the only stage to leave the host, usually in the feces; this transmission propagule is called the oocyst. Outside the host, in the presence of molecular oxygen, sufficient moisture, and usually a body temperature less than that of the host, the oocyst forms spores (= sporocysts), each of which contains a certain number of sporozoites, the actual infective unit of the parasite. Members of the genus *Eimeria* have oocysts that contain four sporocysts, each with two sporozoites, while those placed in the *Isospora* have two sporocysts, each with four sporozoites. The sporulated oocyst is highly resistant to abiotic environmental factors and is immediately infective to the next host that may ingest it.

The size and structure of sporulated oocysts of different coccidia species often (but not always) are structurally distinct enough to be able to distinguish between species, although sometimes these differences are subtle. Cross-transmission studies have demonstrated that coccidia from one host species do not infect hosts in other orders or classes. Only on rare occasions are they known to cross family boundaries, but generic borders seem to pose less of a hurdle, especially if the genera are closely related (Hnida and Duszynski 1999; Upton et al. 1992). Infections between congenerics are common. The details of the endogenous development are not known for almost all wild animal coccidia because of the difficulty finding and isolating the various tissue stages. Consequently, it is the description of the structures of the sporulated oocyst upon which the identity of most eimeriid coccidia is based. Unfortunately, traditional methods of fixation do not preserve oocysts in perpetuity (Duszynski and Gardner 1991), so the coccidia present a serious handicap when it comes to col-

lecting type specimens. Their endogenous stages are intracellular, transient (each lasting only a few hours or days), difficult to collect, and impossible to identify under field conditions, and there is no known method to preserve oocysts long term. Thus, those who describe coccidia base their "new species" decisions on: 1) mensural and qualitative observations of the sporulated oocyst; 2) the species of the host; 3) the geographic locality of the host; and 4) a composite line drawing of the sporulated oocyst. Only recently have parasite protistologists accepted the concept of using photomicrographs (= photosyntypes, see Duszynski 1999) to help document new coccidia species along with traditional methods.

The general taxonomy, life cycles, and species of the coccidia known from wild mammals was reviewed recently by Duszynski and Upton (2001); however they, and Wilber et al. (1998), noted that most earlier authors who published descriptions of new species from mammals did not apply, or even loosely follow, the International Code of Zoological Nomenclature (Ride et al. 1985, 2000). Here we review all published papers on the coccidia (Eimeriidae) reported from all Chiroptera worldwide, make qualitative decisions about the validity of those species, standardize their descriptions, present illustrations (line drawings) at the same scale for all of them, and provide—in one place—all of the known photosyntypes.

METHODS

Methods followed were those of Wilber et al. (1998) regarding the number of oocyst–sporocyst characters needed to validate a coccidia species and in the definition and deposition of specimens (USNPC = United States National Parasite Collection, Beltsville MD; MSB = Museum of Southwestern Biology, The University of New Mexico, Albuquerque, NM). The type host, type locality, other hosts, geographic distribution, prevalence (no. infected/no. examined), sporulation, prepatent and patent periods, site of infection, description of endogenous stages, pathology, deposition of specimens, cross-transmission studies (when available), and molecular analyses/systematics (one example) are reviewed. Most line drawings (Figs. 1–31) are original; however, when original line drawing were considered useful/adequate, they were scanned from original sources (see Table 2). Abbreviations used in species descriptions are standardized (Wilber et al. 1998): *oocyst characters*: length (L), width (W), their ranges and ratio (L/W); micropyle (M); residuum (OR), polar granule (PG); *sporocyst characters*: length (L), width (W), their ranges and ratio (L/W); Stieda body (SB); substieda body (SSB); parastieda body (PSB); residuum (SR); sporozoites (SP); refractile bodies (RB) and nucleus (N) in SP. All measurements given are in μm and are for sporulated oocysts only. Family, genera and binomial species names of hosts are those of Koopman (1993) and most common names are those used by Nowak (1991).

Each species description was examined in its chronological order of appearance in the literature and evaluated based on all previous descriptions from that host group, if any; then, following the guidelines of the International Code, the minimal criteria needed to support a valid description (per Wilber et al. 1998), and any new information that supported my decision, I either accepted or rejected it as a valid species. If it was considered to be a valid species, I provided a standardized (boiler plate) description including all of the published information to date; if certain structural features are unreported, they could not be included in the standardized description.

RESULTS

In the Chiroptera, there are 31 valid *Eimeria* species. Eight organisms (one "Coccidium," six *Eimeria* and one *Isospora* species) are considered *species inquirendae*. Hosts are listed by order, suborder and family in the taxonomic sequence presented by Koopman (1993); *Eimeria* species are listed alphabetically under each host genus.

CHIROPTERA

(17 families, 177 genera, 925 species)

Family Pteropodidae Gray, 1821

(2 subfamilies, 42 genera, 166 species)

Subfamily Pteropodinae Gray, 1821
(36 genera, 154 species)

Only 20 specimens of *Cynopterus sphinx* have been examined, but no coccidia are described from this subfamily to date.

Subfamily Macroglossinae Gray, 1866
(6 genera, 12 species)

No species in this subfamily have been examined for coccidia to date.

Family Rhinopomatidae Bonaparte, 1838
(1 genus, 3 species)

No species in this family have been examined for coccidia to date.

Family Craseonycteridae, Hill, 1974
(1 genus, monotypic)

The only species in this family has not been examined for coccidia.

Family Emballonuridae Gervais, 1856
(13 genera, 47 species)

Host Genus *Peropteryx* Peters, 1867
(3 species)

***Eimeria bragancaensis* Lainson and Naiff, 2000 (Fig. 1)**

Type host: *Peropteryx macrotis* (Wagner, 1843), Lesser dog-like bat.

Type locality: SOUTH AMERICA: Brazil, Pará State, primary forest near Bragança (1°03′ S, 46°46′W).

Geographic distribution: SOUTH AMERICA: Brazil: Pará.

Description of sporulated oocyst: Oocyst shape: spheroidal (50%) to subspheroidal; wall consists of 2 layers: outer, prominently striated (pitted), yellow-brown, ~0.75 thick, easily separates from inner layer, which is smooth, thin (~0.25), colorless; L x W (N = 25): 15.9 x 14.6 (14–18 x 14–18); L/W ratio: 1.0 (1.0–1.2); M: absent; OR: absent; PG: 1 or 2 always present, irregular in shape, ~1–2 x 1. Distinctive features of oocyst: striated outer wall that easily (and frequently) separates from smooth inner layer.

Description of sporocysts and sporozoites: Sporocyst shape: pear-shaped; L x W (N = 35): 8.4 x 5.3 (6–9 x 4–6); L/W ratio: 1.6 (1.2–1.9); SB: small, button-like, inconspicuous; SSB: small, inconspicuous; PSB: absent; SR: present; SR characteristics: small number of globules and finer granules in center of sporocyst; SP: lengthwise in sporocyst, recurved at their ends (line drawings); RB: 2, anterior (smaller) and posterior (larger) in SP. Distinctive features of sporocyst: inconspicuous SB and SSB.

Prevalence: 1/3 (33%).

Sporulation: Presumably exogenous. Feces were taken from the rectum of one bat and placed in 2% aqueous potassium dichromate ($K_2Cr_2O_7$) solution left at 23–24°C; however, the material was not examined until several weeks later by which time most oocysts were sporulated.

Prepatent and patent periods: Unknown.

Site of infection: In the cytoplasm, above the nucleus, of the epithelial cells of the small intestine.

Endogenous stages: Segmented meronts were 10 x 8, with 10–20 merozoites that were ~5 x 15. Young macrogamonts were 4 x 4, with a "voluminous nucleus containing a prominent karyosome." Mature macrogamonts were 11 x 10, with type I (small) and type II (large) wall-forming bodies and as they grow, their cytoplasm becomes packed with small, ovoidal, colorless bodies (amylopectin granules ?). Early microgamonts have intensely staining and frequently angular nuclei, located around their periphery. Mature microgamonts with a conspicuous residuum of variable size were ~10, and produce many microgametes that are ~3 x 0.5.

Pathology: There was considerable sloughing of epithelium in the regions of the intestine where the majority of developmental stages were seen. The infected bat, however, appeared to be in good health.

Material deposited: None.

Remarks: The sporulated oocysts of this species differ in several ways from those of the two other eimerians recorded from bats in this family. They differ from those of *E. rhynchonycteridis* by being much smaller, having an oocyst wall with two layers (vs. 1), the outer of which is striated, and by having 1–2 PG, which *E. rhynchonycteridis* lacks; their sporocysts also are quite different. They differ from those of *E.*

andamanensis by being larger, having a pitted outer wall (vs. smooth) and by lacking the large OR that helps characterize *E. andamanensis*. There also are significant geographic and host differences.

Lainson and Naiff (2000) also found tissue cysts of what they called "an unidentified protozoan" in the *lamina propria* of the small intestine and in the parenchyma cells of the liver of the same bat infected with *E. bragancaensis*. The cysts were 16.7 x 13.7 (12.5–22.5 x 9–16) and contained either an undivided parasite with one nucleus or stages in the division to form two to four zoites. Individual zoites were 12.5 x 2.5. They were of the opinion that the tissue cysts were not extra-intestinal stages of *E. bragancaensis*, since they bore a striking resemblance to the latent cysts of *Hepatozoan* sp., which usually are found in various organs of snakes and lizards. After discussing the *Hepatozoan* life cycle in reptiles, they suggested that, "if the parasite can tolerate the change from a cold-blooded to a warm-blooded host there could be a snake–bat–snake life-cycle for the parasite."

Reference: Lainson and Naiff (2000).

Host Genus *Rhynchonycteris* Peters, 1867
(monotypic)

Eimeria rhynchonycteridis Lainson, 1968 (Fig. 2)

Type host: *Rhynchonycteris naso* (Wied–Neuwied, 1820), Brazilian long-nosed bat.

Type locality: CENTRAL AMERICA: Belize, Cayo District, Baking Pot, along the banks of the Belize River.

Geographic distribution: CENTRAL AMERICA: Belize: Cayo.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall consists of 1 layer, which is smooth, very delicate, colorless; L x W (N = 25): 25.5; L/W ratio: 1.0; M: absent; OR: absent; PG: absent. Distinctive features of oocyst: delicate, 1-layered, smooth wall and lacking M, OR and PG.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: 15.2 x 8.1; L/W ratio: 1.9; SB: small, nipple-like and in which lies a small, highly refractile granule; SSB and PSB: absent; SR: present; SR characteristics: scattered, delicate globules of various size; SP: lie at ends of sporocyst and are markedly recurved at their ends; RB: apparently absent (line drawing). Distinctive features of sporocyst: delicate wall, SB with highly refractile granule in or below (?) it.

Prevalence: 4/9 (44%).

Sporulation: Exogenous. Oocysts sporulated in 24 hr in 2% aqueous $K_2Cr_2O_7$ solution left at 26–28 °C.

Prepatent and patent periods: Unknown.

Site of infection: Uncertain, but probably the small intestine.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: The sporulated oocysts of this species differ from those of all other eimerians from bats by the delicate walls of both oocysts and sporocysts and by the presence of the highly refractile granule in/under the SB (this granule may be a SSB).

Reference: Lainson (1968).

Host Genus *Taphozous* E. Geoffroy, 1818
(13 species)

Eimeria andamanensis Mandal and Nair, 1973 (Fig. 3)

Type host: *Taphozous melanopogon* Temminck, 1841, Tomb bat.

Type locality: ASIA: India, Andaman Island, Haddo, Port Blair.

Geographic distribution: ASIA: India: Andaman Island.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall consists of 2 layers, ~0.4–0.5 thick: outer, is smooth, thin; inner, slightly thicker, pinkish; L x W: 13.5 (12.5–16.5); L/W ratio: 1.0; M: absent (?); OR: present; OR characteristics: a spheroidal mass of large globules, ~4.5–5.5, located to 1 side of oocyst; PG: present, 1. Distinctive features of oocyst: very small with thin, smooth wall (≤0.5) and massive OR of large globules.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal to broadly pyriform; L x W: 5.3 x 3.8 (4.5–6.5 x 3–4.5); L/W ratio: 1.5; SB: thick, prominent, at pointed end; SSB and PSB: absent; SR: present; SR characteristics: scattered granules of various size that fill sporocyst and sometimes obscure SP; SP: elon-

gate bodies that lie head to tail (line drawing) and have a large RB ("hyaline mass") at posterior end. Distinctive features of sporocyst: very small size.

Prevalence: 2/30 (7%).

Sporulation: Exogenous. Oocysts sporulated in 24–36 hr in 2.5% $K_2Cr_2O_7$ solution, presumably left at room temperature.

Prepatent and patent periods: Unknown.

Site of infection: Uncertain, but probably the small intestine.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: "Holotype (?)" deposited in the National Collection of Zoological Survey of India, Calcutta, Reg. No. Pt 1581. Unfortunately, the authors do not indicate what stage of the parasite life cycle comprises the holotype.

Remarks: Mandal and Nair (1973, p. 244) state that a M is present, but their line drawing does not show this structure. This is the smallest *Eimeria* species yet described from any bat.

Reference: Mandal and Nair (1973).

Family Nycteridae Van der Hoeven, 1855
(1 genus, 12 species)

No species in this family have been examined for coccidia to date.

Family Megadermatidae H. Allen, 1864
(4 genera, 5 species)

No species in this family have been examined for coccidia to date.

Family Rhinolophidae Gray, 1825
(2 subfamilies, 10 genera, 130 species)

Subfamily Rhinolophinae Gray, 1825
(1 genus, 64 species)

Host Genus *Rhinolophus* Lacépède, 1799
(64 species)

***Eimeria hessei* Lavier, 1924 (Fig. 4)**

Type host: *Rhinolophus hipposideros* (Bechstein, 1800), Lesser horseshoe bat.

Type locality: EUROPE: France.

Geographic distribution: EUROPE: France.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall consists of 1 layer, which is smooth, colorless; L x W: 16–22 (spheroidal forms) and 16–18 x 13–15 (sub-spheroidal forms); L/W ratio: 1.0; M: absent; OR: absent; PG: absent. Distinctive features of oocyst: small size and lacking M, OR and PG.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: not given; L/W ratio: not given; SB, SSB and PSB: all absent. SR: present; SR characteristics: coarse granules that occupy the middle ⅔ of sporocyst and obscure SP (line drawing); SP: oriented head to tail, presumably with a RB present at rounded end of SP (line drawing). Distinctive features of sporocyst: large SR filling most of sporocyst.

Prevalence: 3/15 (20%).

Sporulation: Exogenous. Oocysts sporulated in 13 days in 0.5% chromic acid solution at 15 and 25°C.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the upper ⅓ of the small intestine.

Endogenous stages: Meronts were spheroidal, 5–7 wide, with a highly chromophilic, large nucleus and produced 8–10 banana-shaped merozoites, 5–6 x 1.5. Microgametocytes were spheroidal, 10–12 wide, and produced many arcuate microgametes, 2–2.5 long. Mature macrogametocytes also are rounded, 10–12 wide, with a vesicular nucleus 3–4 wide. Lavier (1924b) said that fertilization occurred before the oocyst wall is laid down.

Pathology: Unknown.

Material deposited: None.

Remarks: Lavier (1924a) first named and later (1924b) described the oocyst and several of the endogenous stages. His description of the sporulated oocyst, however, is lacking in many details (e.g., there are no mensural data for the sporocysts), but he did provide line drawings of both the oocyst and the endogenous stages.

References: Lavier (1924a,b); Levine and Ivens (1981).

***Eimeria mehelyi* Musaev and Gauzer, 1971 (Fig. 5)**

Type host: *Rhinolophus mehelyi* Matschie, 1901, Mehely's horseshoe bat.

Type locality: SOUTHWESTERN ASIA: Azerbaidzhan.

Geographic distribution: SOUTHWESTERN ASIA: Azerbaidzhan.

Description of sporulated oocyst: Oocyst shape: ellipsoidal or ovoidal; wall consists of 1 layer, which is smooth, colorless, 1.5–2.0; L x W: 41.1 x 35.3 (36–46 x 28–40); L/W ratio: 1.2; M: absent; OR: absent; PG: 1–3 present (line drawing). Distinctive features of oocyst: thick, smooth, 1-layered wall; this is the largest *Eimeria* species yet described from any bat.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: 18.8 x 13.1 (12–20 x 8–16); L/W ratio: 1.4; SB: present, SSB: apparently present (line drawing), about same width as SB; PSB: absent. SR: present; SR characteristics: coarse granules dispersed between SP (line drawing); SP: banana-shaped, oriented head to tail, with N visible, but without RB (line drawing). Distinctive features of sporocyst: size, elongate-ovoidal shape with SB and SSB.

Prevalence: Unknown, 1/25 (4%) (?).

Sporulation: Exogenous. Oocysts sporulated in 14 days in 2.5% $K_2Cr_2O_7$ solution at 15–25°C.

Prepatent and patent periods: Unknown.

Site of infection: Unknown.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: Musaev and Gauzer (1971) compared these oocysts to *E. hessei* and felt they were sufficiently different to name it a different species; neither one has been found since their original descriptions. In their survey, Musaev and Gauzer (1971) also examined 87 other bats representing 10 different species, none of which they named. Of these 87 bats, 15 were of one species (unnamed) and in 1/15 (7%) they said they found 12 oocysts, which they did not describe.

References: Levine and Ivens (1981); Musaev and Gauzer (1971).

Subfamily Hipposiderinae Lydekker, 1891
(9 genera, 66 species)

No species in this subfamily have been examined for coccidia to date.

Family Noctilionidae Gray, 1821
(1 genus, 2 species)

Only two specimens of *Noctilio albiventris* have been examined for coccidia (Table 1), but no species of coccidia have been described from any member in this family to date.

Family Mormoopidae Koch, 1862-3
(2 genera, 8 species)

Only one individual of *Mormoops megalophyla* has been examined for coccidia (Table 1), but no species of coccidia have been described from any member of this family to date.

Family Phyllostomidae Gray, 1825
(8 subfamilies, 49 genera, 143 species)

Subfamily Phyllostominae Gray, 1825
(11 genera, 33 species)

Five species in five genera from this subfamily have been examined for coccidia (Table 1), but no species of coccidia have been described from any member of this family to date.

Subfamily Lonchophyllinae Griffiths, 1982
(3 genera, 9 species)

No species in this subfamily have been examined for coccidia to date.

Subfamily Brachyphyllinae Gray, 1866
(1 genus, 2 species)

No species in this subfamily have been examined for coccidia to date.

Subfamily Phyllonycterinae Miller, 1907
(2 genera, 3 species)

No species in this subfamily have been examined for coccidia to date.

Subfamily Glossophaginae Bonaparte, 1845 (10 genera, 22 species)

Only three species in three genera from this subfamily have been examined for coccidia (Table 1), but no species of coccidia have been

described from any member of this subfamily to date.

Subfamily Carolliinae Miller, 1924
(2 genera, 7 species)

Only two species of *Carollia* have been examined for coccidia (Table 1), but no species of coccidia have been described from any member of this subfamily to date.

Subfamily Stenodermatinae Gervais, 1856
(17 genera, 62 species)

Host Genus *Uroderma* Peters, 1866
(2 species)

***Eimeria magnirostrumi* Duszynski, Scott and Zhao, 1999 (Figs. 6, 32)**

Type host: *Uroderma magnirostrum* (Davis, 1969), Tent-building bat.

Type locality: SOUTH AMERICA: Bolivia, Santa Cruz, 10 km north of San Ramon, 16°36′ S, 62°42′ W.

Geographic distribution: SOUTH AMERICA: Bolivia: Santa Cruz.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall ~1.5 thick, consisting of 2 layers: outer, yellowish-brown, uniformly mammillated, ~⅔ of total thickness, gives a striated appearance in optical cross-section; inner, smooth; L x W (N = 56): 23.8 x 20.8 (20–26 x 19–24); L:W ratio 1.1 (1.0–1.4); MP absent; OR absent; 1–3 PG present, ~2.3 wide. Distinctive features of oocyst: thick, mammillated oocyst wall.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 56): 11.6 x 8.6 (10–12 x 7–10); L:W ratio 1.4 (1.1–1.8); SB present, ~1.3 wide; SSB ~2.6 wide, prominent, but PSB absent; SR dispersed in center of sporocyst, composed of spheroid globules; SP with a large, posterior RB. Distinctive features of sporocyst: SSB twice as wide as SB.

Prevalence: 1/2 (50%).

Sporulation: Presumably exogenous. Oocysts sporulated in 2% aqueous (w/v) $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC, no. 88104. Symbiotype host, *U. magnirostrum*, MSB 55908 (NK 12988, 8 August 1985).

Remarks: *Eimeria magnirostrumi* is most similar to *Eimeria macyi* Wheat, 1975 from *Pipistrellus sublavus* from Alabama, USA (Wheat 1975b) in that they both have a rough outer wall, have SB and SSB, and lack an OR. They differ because *E. magnirostrumi:* has a thicker wall than *E. macyi* (1.5 vs. 1); has two wall layers (vs. 1); is somewhat larger than *E. macyi* (24 x 21 vs. 19 x 18); and has a SSB that is twice as wide as its SB, whereas both structures in *E. macyi* are of equal width (Fig. 1 in Wheat 1975b).

References: Duszynski et al. (1999b); Scott and Duszynski (1997); Wheat (1975a, b).

Subfamily Desmodontinae Bonaparte, 1845 (3 genera, 3 species)

Only three specimens of *Desmodus rotundus* have been examined for coccidia (Table 1), but no species of coccidia have been described from any member of this subfamily to date.

Family Natalidae Gray, 1866
(1 genus, 5 species)

Only one specimen of *Natalus stramineus* from Mexico has been examined for coccidia (Table 1), but no species of coccidia have been described from any member of this subfamily to date.

Family Furipteridae Gray, 1866
(2 genera, 2 species)

No species in this family have been examined for coccidia to date.

Family Thyropteridae Miller, 1907
(1 genus, 2 species)

Only one specimen of *Thryoptera* sp. has been examined for coccidia (Table 1), but no species of coccidia have been described from any member of this family to date.

Family Myzopodidae Thomas, 1904
(1 genus, monotypic)

No species in this family have been examined for coccidia to date.

Family Vespertilionidae Gray, 1821
(5 subfamilies, 35 genera, 318 species)

Subfamily Kerivoulinae Miller, 1907
(1 genus, 22 species)

No species in this subfamily have been examined for coccidia to date.

Subfamily Vespertilioninae Gray, 1821
(30 genera, 269 species)

Host Genus *Antrozous* H. Allen, 1862
(2 species)

***Eimeria antrozoi* Duszynski, Scott, Aragon, Leach and Perry, 1999 (Figs. 7, 33)**

Type host: *Antrozous pallidus* Le Conte, 1854, Pallid bat.

Type locality: NORTH AMERICA: USA, New Mexico, San Juan Co., Upper Pump Canyon, near Twin Tanks, 36°51′80″ N, 107°47′40″ W.

Other localities: See Scott and Duszynski 1997 (= *E. arizonensis*-like).

Geographic distribution: NORTH AMERICA: USA: New Mexico; Mexico: Baja California Sur.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall 1.2–1.5 thick with 2 layers; outer, strongly sculptured, ~¾ of total thickness; inner, smooth; L x W (N = 78): 24.8 x 21.6 (22–27 x 19–24); L:W ratio 1.15 (1.0–1.3); MP absent; OR present; OR characteristics: usually a large lipid-like sphere, ~8, but sometimes 2–3 smaller spheres; 1 highly refractile PG present, ~3. Distinctive features of oocyst: sculptured nature of oocyst wall plus lipid-like OR.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: 11.5 x 7.8 (9–13 x 7–10); L:W ratio 1.5 (1.2–1.7); prominent SB, ~3 wide, but SSB and PSB absent; SR of many large granules sometimes obscuring SP; SP with a spheroid RB at rounded end. Distinctive features of sporocyts: prominent SB, prominent SR that obscures SP.

Prevalence 2/17 (12%).

Sporulation: Presumably exogenous. Oocysts sporulated in 2% (w/v) aqueous $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC no. 88094. Type host: *Antrozous pallidus*, NK 41192, 10 July 1996 (animal released).

Remarks: These sporulated oocysts first were reported in 12/85 (14%) pallid bats from two of five collection localities in New Mexico and Mexico (Scott and Duszynski 1997); it wasn't named then because of the similarity of these oocysts to those of *E. arizonensis*, a known parasite of rodents. The authors suggested naming this form be delayed until cross-infection and/or molecular studies could be completed to demonstrate the bat and rodent species as distinct. However, the regularity and the high prevalence in some bat populations strongly suggest this is not a spurious infection; it now has been found in 14/36 (39%) pallid bats from two counties in New Mexico (6/11, 55%, Eddy Co.; 2/17, 12%, San Juan Co.) and in Baja California Sur, Mexico (6/8, 75%), but not in 66 palid bats from Bernalillo, Sandoval, or Lincoln counties in New Mexico (Duszynski et al. 1999a; Scott and Duszynski 1997). Recently, Zhao et al. (2001) demonstrated conclusively that partial plastid 23S and nuclear 19S rDNA genes that were amplified from both *E. antrozoi* and *E. arizonensis* clearly separated them, confirming that *E. antrozoi* is a valid species. Interestingly, additional phylogenies based on a combined data set of both plastid and nuclear partial gene sequences grouped two bat (*E. antrozoi*, *E. rioarribaensis*) and three morphologically similar rodent *Eimeria* species (*E. arizonensis*, *E. albigulae*, *E. onychomysis*) into two separate clades with high bootstrap support (100% and 85%, respectively). This may suggest that some *Eimeria* species from bats may be derived from rodent *Eimeria* species and may have arisen as a result of lateral

host transfer between rodent and bat hosts. This is an exciting area that needs much further study.

Structurally, *Eimeria antrozoi* is most similar to *E. tomopea* and to *E. redukeri*. It differs from the former by having smaller oocysts (25 x 22 vs. 31 x 25) and sporocysts (11.5 x 8 vs. 14 x 9) and in having a large, prominent SB vs. one that is not easily seen unless the sporocysts are freed from the oocyst. It differs from *E. redukeri* by having a thicker oocyst wall (1.5 vs. 1), larger oocysts (25 x 22 vs. 20 x 18) and a wide, conspicuous SB, and by having a prominent SR of many large granules vs. one with only 1–3 spheroids.

References: Duszynski et al. (1988; 1999a); Scott and Duszynski (1997); Zhao et al. (2001).

Host Genus *Myotis* Kaup, 1829
(84 species)

***Eimeria californicensis* Duszynski, Scott, Aragon, Leach and Perry, 1999 (Figs. 8, 34)**

Type host: *Myotis californicus* (Audubon and Bachman, 1842), California myotis.

Type locality: NORTH AMERICA: USA, California, El Dorado Co., 9.7 km east of Somerset.

Other localities: USA, New Mexico, San Juan Co., 36°52′09″ N, 107°41′22″ W.

Geographic distribution: NORTH AMERICA: USA: California, New Mexico.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall 1.3–1.5 thick, consisting of 2 layers: outer, rough ~⅔ of total thickness; inner, dark, smooth; L x W (N = 41): 20.7 x 18.2 (19–23 x 16–20); L:W ratio 1.1 (1.0–1.3); MP absent; OR absent; 1–7 tiny PG present. Distinctive features of oocyst: numerous tiny PGs.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 41): 11.2 x 7.3 (10–12 x 7–8); L:W ratio 1.6 (1.4–1.7); SB present, pointed, but SSB and PSB absent; SR of 4–8 medium-sized granules between the SP or along 1 wall of sporocyst; SP with 1 posterior RB. Distinctive features of sporocyst: none.

Prevalence: 3/5 (60%) El Dorado Co., California; 3/33 (9%) San Juan Co., New Mexico.

Sporulation: Presumably exogenous. Oocysts sporulated in 2% aqueous (w/v) $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 88096. Symbiotype host: *Myotis californicus*, MSB 40654 (NK 576, 10 June 1979).

Remarks: Sporulated oocysts of *E. californicensis* have some features similar to those of *E. eumopos* in that they both have SB, but lack a MP, SSB, and OR. They differ from *E. eumopos* by being smaller (21 x 18 vs. 35 x 28), having a thinner oocyst wall (1.5 vs. 1.9) without radial striations, and by having smaller and more numerous PGs. *Eimeria californicensis* differs from three other, similar, *Eimeria* species described from *Myotis* as follows: *E. catronensis* is ellipsoidal and has a MP; *E. pilarensis* is small and spheroidal (15.0 x 14.1) with a smooth outer oocyst wall; and *E. kunmingensis* is smaller (17.5 x 16) and has a smooth outer wall.

Reference: Duszynski et al. (1999a).

***Eimeria catronensis* Scott and Duszynski, 1997 (Figs. 9, 36)**

Type host: *Myotis lucifugus* Le Conte, 1831, Little brown bat.

Other hosts: *Myotis yumanensis* H. Allen, 1864, Yuma myotis.

Type locality: NORTH AMERICA: USA, New Mexico, Catron County, Gila National Forest, Bill Lewis Cienega, 33°27.6′ N, 108°37.9′ W.

Geographic distribution: NORTH AMERICA: USA: New Mexico.

Description of sporulated oocyst: Oocyst shape: ovoidal; wall ≤1thick, with 2 layers of equal thickness: outer, rough; inner, dark, smooth; L x W (N = 30): 22.2 x 14.8 (18–25 x 14–17); L:W ratio 1.5 (1.3–1.7); M present, ~2 wide, usually asymmetrically located near more pointed end of oocyst, but not seen in unsporulated oocysts; OR absent; 1–4 PG present. Distinctive features of oocyst: presence of asymmetrically located M.

Description of sporocysts and sporozoites: Sporocyst shape: football-shaped L x W (N = 30): 8.1 x 6.6 (8–11 x 5–7); L:W ratio 1.2 (1.1–1.8); SB present, but SSB and PSB absent; SR a

spheroidal granular mass sometimes obscuring SP. Distinctive features of sporocyst: football-shape with distinct SB at one end and spheroid, granular SR.

Prevalence: 3/27 (11%) type host; 8/29 (28%) *M. yumanensis*.

Sporulation: Presumably exogenous. Oocysts sporulated in 2% aqueous (w/v) $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Remarks: This species differs from other bat eimerians except *E. andamanensis* (?) and *E. levinei* (?) by having a M; *E. catronensis* differs from *E. andamanensis* by being ellipsoidal rather than spheroidal and has 1–4 PG; it differs from *E. levinei* by lacking an OR. Also, it is questionable, as noted elsewhere, if *E. andamanensis* and *E. levinei* actually have a M.

Reference: Scott and Duszynski (1997).

***Eimeria evoti* Duszynski, Scott, Aragon, Leach and Perry, 1999 (Figs. 10, 35)**

Type host: *Myotis evotis* (H. Allen, 1864), Gleaning myotis.

Type locality: NORTH AMERICA: USA, New Mexico, Socorro Co., San Mateo Mountains, Bear Trap Canyon.

Geographic distribution: NORTH AMERICA: USA: New Mexico.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall ~1.2 thick, with 2 layers; outer, yellowish, lightly pitted ~⅔ of total thickness; inner, smooth; L x W (N = 46): 21.3 x 18.6 (20–24 x 15–20); L:W ratio 1.2 (1.1–1.3); MP absent; OR absent, but 1 highly refractile PG present, ~3. Distinctive features of oocyst: pitted outer wall and large, refractile PG in combination with absence of OR.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 46): 12.2 x 8.0 (11–13 x 7.5–9); L:W ratio 1.5 (1.4–1.7); small, nipple-like SB present, as is a thin, difficult-to- see SSB 2 to 3 times wider than SB, but a PSB is absent; SR absent; SP clearly seen, with an elongate RB that composes ½ their length. Distinctive features of sporocyst: large SSB, large RB.

Prevalence: 1/13 (8%).

Sporulation: Presumably exogenous. Oocysts sporulated in 2% aqueous (w/v) $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 88099. Symbiotype host: *Myotis evotis*, MSB 53788 (NK 4803, 13 September 1980).

Remarks: The outer oocyst wall is pitted rather than mammillated, so it does not resemble any of the oocysts in the key provided by Scott and Duszynski (1997). In addition, the unique combination of structural features (pitted outer wall), tiny SB, or their absence (neither OR nor SR), distinguish the sporulated oocysts of this species from all those described previously from bats.

References: Duszynski et al. (1999a); Scott and Duszynski (1997).

***Eimeria humboldtensis* Duszynski, Scott, Aragon, Leach and Perry, 1999 (Figs. 11, 37)**

Type host: *Myotis californicus* (Audubon and Bachman, 1842), California myotis.

Type locality: NORTH AMERICA: USA, California, Humboldt Co., 12.8 km north, 2.4 km east of Arcada.

Geographic distribution: NORTH AMERICA: USA: California.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall 1.5 thick, with 2 layers: outer, rough ~⅔ of total thickness; inner, dark; L x W (N = 50): 23.1 x 20.7 (20–26 x 19–23); L:W ratio 1.1 (1.0–1.3); MP absent; OR present; OR characteristics: a large globule ≤9, but sometimes 2–3 smaller globules ~3 each; 1 PG present. Distinctive features of oocyst: rough outer wall combined with presence of OR and PG.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: 12.5 x 7.2 (11–14 x 7–8); L:W ratio 1.7 (1.5–2.0); SB present, but SSB and PSB absent; SR present; SR characteristics: composed of small granules or globules, often as a compact mass, but sometimes dispersed along edge of sporocyst; SP with 1

posterior RB. Distinctive features of sporocyst: none.

Prevalence: 1/5 (20%).

Sporulation: Presumably exogenous. Oocysts sporulated in 2% (w/v) aqueous $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 88100. Symbiotype host: *Myotis californicus*, MSB 40676 (NK 623, 13 June 1979).

Remarks: Sporulated oocysts of *E. humboldtensis* are most similar to those of *E. redukeri* from a pipistrelle from Japan, in size and in that they both have a rough outer wall, OR, PG, and SB. They differ, however, in host and geographic distribution and because the oocyst wall in *E. redukeri* is heavily mammillated, causing a striated appearance, whereas the wall of *E. humboldtensis*, although rough, is not striated in appearance. Also, the OR of *E. redukeri* is one globule, ~2–4, whereas in *E. humboldtensis* it is larger, ~9, or as 2–3 globules ~3 each. This species differs from some other *Eimeria* species described from *Myotis* as follows: *E. catronensis* is ellipsoidal and smaller and has a MP; *E. pilarensis* (15 x 14) and *E. kunmingensis* (17.5 x 16) are smaller and both have smooth outer oocyst walls; and *E. californicensis* lacks an OR.

Reference: Duszynski et al. (1999a).

***Eimeria kunmingensis* Yang-Xian and Fu-Qiang, 1983 (Fig. 12)**

Type host: *Myotis ricketti* (Thomas, 1894), Little brown bat.

Type locality: ASIA: China, Yunnan, Kunming, Huahong Cave.

Geographic distribution: ASIA: China: Yunnan.

Description of sporulated oocyst: Oocyst shape: subspheroidal to broadly ellipsoidal; wall ~1.3 thick, with 2 layers; outer, light yellow, smooth, ~¾ of total thickness; inner, smooth; L x W (N = 100): 17.5 x 16.4 (15–20 x 14–18); L:W ratio 1.1 (1.0–1.2); MP absent; OR absent; 1–3 ellipsoidal PG present. Distinctive features of oocyst: thick, smooth outer wall.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 100): 11.8 x 7.8 (10–13 x 7–10); L:W ratio 1.5 (1.3–1.8); SB: present, prominent, nipple-like; SSB and PSB absent; SR: present; SR characteristics: dispersed, small granules in center of sporocyst; SP elongate, head to tail in sporocyst, with 2 RB, larger 1 at rounded end, smaller 1 at pointed end. Distinctive features of sporocyst: nipple-like SB and SP with 2 RBs.

Prevalence: 105/151 (69.5%).

Sporulation: Exogenous. Oocysts sporulated in 60 hr at 26°C.

Prepatent and patent periods: Unknown.

Site of infection: Small intestine.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: This species differs from *E. levinei* and *E. andamanensis* by lacking a M and OR, from *E. eumopos, E. macyi* and *E. zakirica* by having an outer oocyst wall that is smooth, from *E. hessei* and *E. rhynchonycteridis* by having a two-layered wall, and from *E. vespertilii* and *E. mehelyi* by having smaller oocsyts.

Reference: Yang-xian and Fu-qiang (1983).

***Eimeria nigricani* Duszynski, Scott and Zhao, 1999 (Figs. 13, 38)**

Type host: *Myotis nigricans* (Schinz, 1821), Little brown bat.

Type locality: SOUTH AMERICA: Bolivia, Santa Cruz, 4.0 km south of Buena Vista, 17° 28′ S, 63°42′ W.

Geographic distribution: SOUTH AMERICA: Bolivia: Santa Cruz.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall ~1.3 (1.0–1.4) thick, with 2 layers; outer, brownish, rough, ~⅔ of total thickness, but does not appear striated in optical cross-section; inner, smooth; L x W (N = 91): 18.9 x 16.9 (17–23 x 14–20); L:W ratio 1.1 (1.0–1.3); MP absent; OR present; OR characteristics: 6–8 spheroidal globules dispersed throughout oocyst; 1 refractile PG present. Distinctive features of oocyst: subtle (see *Remarks*).

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 91): 10.1 x 7.4 (7–14 x 5–10); L:W ratio 1.4 (1.0–2.1); SB ~1.5 with a faint SSB, ~3 wide, flat on the bottom, but PSB absent; SR a mass of 3–4 round

globules (~1.0 in diameter); SP with 1 or 2 prominent RBs. Distinctive features of sporocyst: faint, wide SSB.

Prevalence: 2 of 4 (50%).

Sporulation: Presumably exogenous. Oocysts sporulated in 2% (w/v) aqueous $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes in the USNPC, no. 88105. Symbiotype, *M. nigricans*, MSB 58759 (NK 15201, 2 August 1987).

Remarks: The presence of a rough outer wall and SB and SSB make sporulated oocysts of *E. nigricani* similar to those of *E. magnirostrumi* and *E. macyi*. However, those of *E. nigricani* differ from *E. magnirostrumi* by having smaller oocysts (19 x 17 vs. 24 x 21) with a rough, but not distinctly mammillated outer wall, by having an OR of dispersed globules, by having SP with two RBs (vs. 1) and a SSB that is somewhat larger (3.0 vs. 2.6) and flat, rather than rounded, at the bottom. They differ from those of *E. macyi* in more subtle ways: by the presence of a two-layered outer wall (vs. 1), the presence of an OR, and by having a SSB that is twice as wide as the SB vs. one that is not wider than the SB and rounded on the bottom.

Reference: Duszynski et al. (1999b).

***Eimeria pilarensis* Scott and Duszynski, 1997 (Figs. 14, 39)**

Type host: *Myotis ciliolabrum* (Audubon and Bachman, 1942), Western small-footed myotis.

Other hosts: *Myotis yumanensis* H. Allen, 1864, Yuma myotis.

Type locality: NORTH AMERICA: USA, New Mexico, Taos County, Pilar, Orilla Verde.

Other localities: NORTH AMERICA: USA, California (*M. yumanensis*).

Geographic distribution: NORTH AMERICA: USA: California, New Mexico.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall ≤1.0 thick, with 2 layers of approximately equal thickness: outer, yellowish, smooth; inner, dark, smooth; L x W (N = 30): 15.0 x 14.1 (14–16 x 14–16); L:W ratio 1.1 (1.0–1.2); MP absent; OR absent; 1 PG present. Distinctive features of oocyst: small size, smooth, thin wall.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 30): 7.1 x 5.9 (6–9 x 5–7); L:W ratio 1.2 (1.1–1.5); SB present, small; SSB and PSB absent; SR present; SR characteristics: a singular, refractile mass, ~2.0, or as disbursed granules obscuring SP; SP with a spheroidal RB, at posterior end. Distinctive features of sporocyst: small size, indistinct SB.

Prevalence: 1/12 (8%) in type host; 4/70 (6%) in *M. yumanensis*.

Sporulation: Presumably exogenous. Oocysts sporulated in 2% (w/v) aqueous $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes in the USNPC, no. 86938. Symbiotype, *M. ciliolabrum*, in MSB (NK 32306, 22 June 1995).

Remarks: *Eimeria pilarensis* is most similar to *E. vejsovi* and *E. kunmingensis* except that it is smaller than the former (15 x 14 vs. 21 x 18) and the latter has an inner wall that is wrinkled. Also, *E. pilarensis*, like *E. rhynconyteridis*, differs from all other New World bat eimerians by having a smooth wall, but *E. rhynconycteridis* is larger (25.5 diameter) and has a thin wall with one obvious layer, whereas *E. pilarensis* is much smaller and has an oocyst wall with two layers.

Reference: Scott and Duszynski (1997).

***Eimeria rioarribaensis* Duszynski, Scott, Aragon, Leach and Perry, 1999 (Figs. 15, 40)**

Type host: *Myotis ciliolabrum* (Audubon and Bachman, 1942), Western small-footed myotis.

Type locality: NORTH AMERICA: USA, New Mexico, Rio Arriba Co., Quintana Tank, 36°36′ N, 107°23′ W, elev. 2040.

Other localities: Mexico, Baja California Norte, 3.2 km northeast of Rosarito.

Geographic distribution: NORTH AMERICA: USA: New Mexico; Mexico: Baja California Norte.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall ~1.5 thick, with 2 layers; outer, yellowish, rough ~⅔ of total thickness; inner, dark, smooth; L x W (N = 50): 24.9 x 20.1 (18–27 x 17–23); L:W ratio 1.2 (1.1–1.3); MP absent; OR absent, but 1–2 PG present, ~2 each. Distinctive features of oocyst: thick, rough outer wall.

Description of sporocysts and sporozoites: Sporocyst shape: ellipsoidal; L x W: 12.5 x 9.0 (8–14 x 7–10); L:W ratio 1.4 (1.2–1.5); SB ~1.5 wide, SSB ~2–3 wide, but PSB is absent; SR present; SR characteristics: 8–10 globules, often dispersed along edge of sporocyst; SP with an elongate RB in posterior half. Distinctive features of sporocyst: SSB twice as wide as SB.

Prevalence: 4/22 (18%) in New Mexico; 1/21 (5%) in Mexico.

Sporulation: Presumably exogenous. Oocysts sporulated in 2% (w/v) aqueous $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 88107. Type host: *Myotis ciliolabrum*, NK 27915, 13 June 1995 (animal released).

Remarks: Structurally, sporulated oocysts of *E. rioarribaensis* are most similar to those of *E. macyi* in that they both have a rough outer wall, SB and SSB and PG, and both lack an OR. They differ, however, in that *E. rioarribaensis* is larger (25 x 20 vs. 19 x 18) with a two-layered wall (vs. 1) and it is thicker (1.5 vs. 1). This species differs from some other similar *Eimeria* spp. from *Myotis* in that: *E. catronensis* is ellipsoidal and smaller and has a MP; *E. pilarensis* (15 x 14) and *E. kunmingensis* (17.5 x 16) are smaller and both have smooth outer oocyst walls; and *E. californicensis* and *E. humboldtensis* lack a SSB.

References: Duszynski et al. (1999a); Scott and Duszynski (1997).

Host Genus *Nyctalus* Bowdich, 1825
(6 species)

***Eimeria nyctali* Gottschalk, 1974 (Fig. 16)**

Type host: *Nyctalus noctula* (Schreber, 1774), Noctule bat.

Type locality: EUROPE: Germany.

Geographic distribution: EUROPE: Germany.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall ~1.9 thick with 2 layers: outer, thick, smooth, may be lightly speckled; inner, thin, dark; L x W: 20.0 x 18.0 (17–23 x 16–20); L:W ratio 1.1; MP: absent; OR: absent; PG: absent. Distinctive features of oocyst: thick, smooth outer wall, dark thin inner wall and absence of MP, OR, and PG.

Description of sporocysts and sporozoites: Sporocyst shape: ellipsoidal, not always symmetrical; L x W: 11 x 8 (10–13 x 6–9); L:W ratio 1.4; SB, SSB, PSB: all absent; SR: absent; SP lie head to tail and fill sporocyst; RB absent (line drawing). Distinctive features of sporocyst: absence of SB, SSB, SR and RB.

Prevalence: 1/1 (100%).

Sporulation: Exogenous. Oocysts sporulated in 1 day in 2% $K_2Cr_2O_7$ solution.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: This species has not been seen since its original description.

Reference: Gottschalk (1974).

***Eimeria vejsovi* Černá, 1976 (Fig. 17)**

Type host: *Nyctalus noctula* (Schreber, 1774), Noctule bat.

Type locality: EUROPE: Czechoslovakia, at Srbsko near Prague.

Geographic distribution: EUROPE: Czechoslovakia.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall a faint brown, ~1.0–1.5 thick, as a "doubly outlined membrane," smooth; L x W (N = 30): spheroidal forms, 18.0 (16–20) and subspheroidal forms, 21.0 x 18.0 (19–22 x 17–20); L:W ratio 1.0–1.2; MP absent; OR absent; 1 PG present. Dis-

tinctive features of oocyst: smooth wall and lacking OR.

Description of sporocysts and sporozoites: Sporocyst shape: elongate–ovoidal; L x W: 8–10 x 4–5; L:W ratio not given; SB: present, small; SSB and PSB: absent; SR present; SR characteristics: granular, spheroidal, 3.5 wide, may be membrane-bound; SP banana-shaped with 1 RB at rounded end. Distinctive features of sporocyst: small SB, membrane-bound SR.

Prevalence: 1/1 (100%).

Sporulation: Presumably exogenous. "Oocysts from the intestine of the bat were left to sporulate in 1.5% $K_2Cr_2O_7$," but the time and temperature were not stated.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells throughout the length of the (small?) intestine.

Endogenous stages: Meronts were 11 x 10 and had 3 (?) sickle-shaped merozoites that were 8–9 x 2. Microgametocytes were ovoidal, 11–13 x 8–10 and contained 30–40 microgametes each. Macrogametocytes were spheroidal, ~10, or ovoidal, 11–13 x 8–11, with a large (4 x 3.5) nucleus containing a large nucleolus, ~2 wide.

Pathology: Unknown.

Material deposited: None.

Remarks: Meronts reproduce asexually by multiple events of binary fission, which ought to result (generally) in even numbers of merozoites. Thus, it seems unusual to have a meront with only three merozoites. This species has not been seen since its original description.

Reference: Černá (1976).

Host Genus *Nycticeius* Rafinesque, 1819
(6 species)

Eimeria jacksonensis Duszynski, Scott, Aragon, Leach and Perry, 1999 (Figs. 18, 41)

Type host: *Nycticeius humeralis* Rafinesque, 1818, Evening bat.

Type locality: NORTH AMERICA: USA, South Carolina, Richland Co., Fort Jackson, South Carolina Army National Guard Leesburg Training, Red Diamond Road Bridge over Colonel's Creek.

Geographic distribution: NORTH AMERICA: USA: South Carolina.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall 1.3–1.5 thick, with 2 layers of equal thickness; outer, yellowish, mammillated; inner, dark, smooth; L x W (N = 50): 22.4 x 18.0 (21–24 x 17–20); L:W ratio 1.3 (1.1–1.5); MP absent; OR absent, but 1–3 PG present. Distinctive features of oocyst: uniformly mammillated outer layer of wall which can give a striated appearance in optical cross-section (line drawing).

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: 10.9 x 7.7 (9–12 x 6–8); L:W ratio 1.4 (1.2–1.6); SB present, but SSB and PSB absent; SR present; SR characteristics: composed of a granular mass sometimes obscuring SP; at least 1 RB located either at the end or in the middle of the SP. Distinctive features of sporocyst: none.

Prevalence: 2/2 (100%).

Sporulation: Presumably exogenous. Oocysts sporulated in 2% (w/v) aqueous $K_2Cr_2O_7$ solution in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 88101. Host released after it was measured and identified and its feces was collected.

Remarks: The sporulated oocysts of this species are most similar to those of *E. macyi*, *E. rioarribaensis*, *E. eumopos* and *E. californicensis* in that they all have rough-walled oocysts and all lack an OR. However, *E. macyi* and *E. rioarribaensis* have a SSB that *E. jacksonensis* lacks, and *E. eumopos* is much larger than *E. jacksonensis* (35 x 28 vs. 22 x 18) and has a thicker oocyst wall (1.9 vs. 1.4). The differences between oocysts of this species and those of *E. californicensis* are very subtle. In addition to host genus and geographic separation, the number and size of the PG differs between the two species as do the L/W ratios of their oocysts and granulation, size and distribution of their SR.

Reference: Duszynski et al. (1999a).

Host Genus *Pipistrellus* Kaup, 1829
(48 species)

***Eimeria chiropteri* Alyousif, 1999 (Fig. 19)**

Type host: *Pipistrellus kuhlii* (Kuhl, 1817), Asian pipistrelle.

Type locality: SOUTHWEST ASIA: Saudi Arabia, Central region, Riyadh City.

Geographic distribution: SOUTHWEST ASIA: Saudi Arabia.

Description of sporulated oocyst: Oocyst shape: subspheroidal to broadly ellipsoidal; wall 1.2 (1.1–1.3) thick, with 2 layers; outer, light yellow, mammillated, ~⅔ of total; inner, yellow-brown, smooth; L x W (N = 50): 23.5 x 20.6 (19–26 x 16.5–25); L:W ratio 1.1 (1.1–1.3); M: absent; OR: present; OR characteristics: a coarse, granular sphere 4.7 (4.3–5.6) that appears membrane-bound (line drawing); 1 spherical PG present. Distinctive features of oocyst: mammillated outer wall and membrane bound OR.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 50): 10.8 x 7.5 (10–12 x 7–8); L:W ratio 1.4; SB: present; SSB and PSB: absent; SR: present; SR characteristics: composed of numerous dispersed, small, homogenous granules; SP: elongate, with 1 RB at rounded end. Distinctive features of sporocyst: nipple-like SB.

Prevalence: 4/20 (20%).

Sporulation: Exogenous. Oocysts sporulated in 2.5% (w/v) aqueous $K_2Cr_2O_7$ solution in 6 days at 26 ± 2°C.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Oocysts in 10% formalin and photosyntypes of sporulated oocysts in the Parasitological Collection, Zoology Department, College of Science, King Saud University, Riyadh, Saudi Arabia, KSUC No. 107. Hosts were released after they was measured and identified and their feces were collected.

Remarks: Sporulated oocysts of this species differ from those of *E. macyi* in having a bilayered wall and an OR; they differ from those of *E. redukeri* in having a larger OR as a spherical mass consisting of several globules, a spheroidal PG, and in the number of SR granules; finally, they differ from those of *E. pipistrellus* in being smaller in size, broadly ellipsoidal in shape, and in having a mammillated outer oocyst wall, while that of *E. pipistrelllus* is smooth.

Reference: Alyousif (1999a).

***Eimeria kuhliensis* Alyousif, 1999 (Fig. 20)**

Type host: *Pipistrellus kuhlii* (Kuhl, 1817), Asian pipistrelle.

Type locality: SOUTHWEST ASIA: Saudi Arabia, Central region, Riyadh City.

Geographic distribution: SOUTHWEST ASIA: Saudi Arabia.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall 0.8 (0.6–1.0) thick, with only 1 obvious layer that is slightly stirated and light greenish-yellow, mammillated; L x W (N = 30): 27.6 x 25.9 (25–32 x 23–30); L:W ratio 1.1 (1.0–1.2); M: absent; OR: present; OR characteristics: irregular in size and shape, consisting of several globules, 0.8–5.0; 1 spheroidal PG present. Distinctive features of oocyst: 1-layered, striated wall.

Description of sporocysts and sporozoites: Sporocyst shape: elongate–ovoidal; L x W (N = 30): 12.6 x 8.5 (12–14 x 8–9); L:W ratio 1.5 (1.4–1.6); SB: present at slightly tapered end of sporocyst as a flat, dark structure; SSB reported to be present (?), but this was not evident either in the photomicrographs or in the original line drawing; PSB: absent; SR: present; SR characteristics: composed of many dispersed, small granules that sometimes obscure SP; SP: elongate, each with 1 RB located at broad end and 1 smaller RB at pointed end. Distinctive features of sporocyst: flat, opaque SB.

Prevalence: 4/15 (27%).

Sporulation: Exogenous. Oocysts sporulated in 2.5% (w/v) aqueous $K_2Cr_2O_7$ solution in 7 days at 26 ± 2°C.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from intestinal contents.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Oocysts in 10% formalin and photosyntypes of sporulated oocysts in the Parasitological Collection, Zoology Department, College of Science, King Saud University, Riyadh, Saudi Arabia, KSUC No. 106.

Remarks: The sporulated oocysts of this species differ from those of *E. macyi* in having larger oocysts and sporocysts, in the presence of

an OR and by having a spheroidal PG. They differ from those of *E. redukeri* in having larger oocysts and sporocysts, a single, striated oocyst wall, an OR of several globules, a spheroidal PG, and an SR of many small granules. Finally, they differ from those of *E. pipistrellus* and *E. chiropteri* in having larger oocysts and sporocysts, a single, striated oocyst wall, and in having an OR of several globules.

Reference: Alyousif (1999b)

***Eimeria macyi* Wheat, 1975a (Fig. 21)**

Type host: *Pipistrellus subflavus* (F. Cuvier, 1832), Eastern pipistrelle.

Type locality: NORTH AMERICA: USA, Alabama, Clarke County, Lion's Den Cave.

Geographic distribution: NORTH AMERICA: USA: Alabama, Arkansas.

Description of sporulated oocyst: Oocyst shape: subspheroidal to broadly ellipsoidal; wall 1.0 thick, with 1 (?) layer that is rough, light brown, pitted and appears striated in optical cross-section; there is an inner, dark membrane that probably is a second layer; L x W (N = 100): 19.0 x 17.6 (16–21 x 15–19); L:W ratio 1.1 (1.0–1.2); MP absent; OR absent, but 1–2 ellipsoidal PGs present. Distinctive features of oocyst: striated appearance of outer wall.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 100): 11.0 x 7.0 (10–12 x 6–8); L:W ratio 1.6; SB: present, prominent, knob-like; SSB: present, about same width as SB; PSB: absent; SR: present; SR characteristics: composed of several dispersed granules; SP: elongate, lying lengthwise or toward end of sporocyst, partly curled around each other, each with a small, anterior and larger posterior RB. Distinctive features of sporocyst: presence of SB and SSB and 2 RB in SP.

Prevalence: 2/3 (67%) in Alabama; 2/5 (40%) in Arkansas.

Sporulation: Unknown, but presumably exogenous. Oocysts sporulated during 1 week at 22–25 °C in 2.5% $K_2Cr_2O_7$ solution.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from cecal contents.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: Twenty-five years after Wheat's (1975a,b) original description, McAllister et al. (2001) found and redescribed the sporulated oocysts of *E. macyi* that they collected from *P. subflavus* in Arkansas. The oocysts and sporocysts from Arkansas bats were slightly larger than those described by Wheat: 22.2 x 20.5 vs. 20.3 x 18,1 and 12.4 x 8.3 vs. 10.6 x 6.6, respectively. McAllister et al. (2001) measured sporozoites *in situ* (16.4 x 3.4), which Wheat (1975a,b) did not do, and they also provided the first photomicrograph of a sporulated oocyst (which I did not have access to when this manuscript went to press). They did not, however, deposit photosyntypes into an accredited museum.

References: McAllister et al. (2001); Wheat (1975a,b).

***Eimeria pipistrellus* Alyousif, Al-Dakhil and Al-Shawa, 1999 (Fig. 22)**

Type host: *Pipistrellus kuhlii* (Kuhl, 1817), Asian pipistrelle.

Type locality: SOUTHWEST ASIA: Saudia Arabia, Shagrah.

Geographic distribution: SOUTHWEST ASIA: Saudia Arabia.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall 1.3 thick, consisting of 2 layers of equal thickness: outer, smooth, light brownish-yellow; inner, dark, smooth; L x W (N = 50): 24.8 x 23.2 (22–27 x 20–25); L:W ratio 1.1 (1.0–1.2); MP: absent; OR: present; OR characteristics: 1–3 large globules, 5.2 (4.5–6.0); PG: present, ~1.6. Distinctive features of oocyst: large size, smooth outer wall, dark inner wall plus both OR and PG are present.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 50): 11.6 x 8.3 (10.5–13 x 7.5–9); L:W ratio 1.45 (1.4–1.5); SB: present at slightly pointed end of sporocyst; SSB and PSB: absent; SR: present; SR characteristics: numerous minute, dispersed granules; SP: elongate, lying head to tail each with 1 posterior RB. Distinctive features of sporocyst: thin wall (line drawing) and flat, opaque SB.

Prevalence: 3/12 (25%).

Sporulation: Presumably exogenous. Oocysts sporulated after 1 week at 26 ± 2 °C in 2.5% aqueous $K_2Cr_2O_7$ solution.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from intestinal contents.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Oocysts in 10% formalin and a photosyntype are deposited in the Parasitology Collection, Department of Zoology, College of Science, King Saud University, Riyadh, Saudia Arabia, KSUC 105.

Remarks: In addition to significant geographic and host differences, this species differs considerably from *E. macyi* and *E. redukeri*, the two most similar species, by having larger oocysts with a smooth (vs. rough) outer wall. In addition, it differs from the former because it has an OR and lacks a SSB and from the latter in having a larger OR composed of 1–3 globules, larger sporocysts with a smaller L:W ratio, and a SR of small, dispersed granules, rather than 1–3 large globules.

Reference: Alyousif et al. (1999).

***Eimeria redukeri* Duszynski, 1997 (Figs. 23, 42)**

Type host: *Pipistrellus javanicus* (Gray, 1838), Asian pipistrelle.

Type locality: ASIA: Japan, Honshu, Niigata, Shiunji, Shium Golf Country Club.

Geographic distribution: ASIA: Japan: Honshu.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall ~1.0 thick, consisting of 2 layers: outer, mammillated, ⅔ of total thickness; inner, smooth; L x W (N = 150): 20.3 x 18.1 (16–25 x 14–21); L:W ratio 1.1 (1.0–1.3); MP: absent; OR: present; OR characteristics: a singular globule, 2.0 x 3.8; PG: 1, small. Distinctive features of oocyst: rough outer wall and both OR and PG are present.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 150): 10.6 x 6.6 (8–12 x 5–8); L:W ratio 1.6 (1.2–1.9); SB: present as small, dark structure at slightly pointed end of sporocyst; SSB and PSB: absent; SR: present; SR characteristics: 1–3 refractile spheroids; SP: lie head to tail, each with 1 RB. Distinctive features of sporocyst: SR of large, refractile spheroids.

Prevalence: 1/4 (25%).

Sporulation: Presumably exogenous. Unfortunately, the feces from these bats were collected and stored in 2% (v/v) H_2SO_4; this was a mistake because, unlike 2.5% aqueous (w/v) $K_2Cr_2O_7$ solution, it is especially detrimental to the structural integrity, and ability to sporulate, of many of the oocysts stored in it.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from intestinal contents.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 86899. Symbiotype host: *Pipistrellus javanicus*, MSB 45547 (NK 6280, 26 June 1982).

Remarks: The sporulated oocysts of this species differs from those of other eimerians described from *Pipistrellus* spp. as noted in the four *Remarks* sections (above).

Reference: Duszynski (1997).

Host Genus *Vespertilio* Linnaeus, 1758
(2 species)

***Eimeria vespertilii* Musaev and Veisov, 1961 (Fig. 24)**

Type host: *Vespertilio murinus* Linnaeus, 1758, Frosted bat.

Type locality: EUROPE: Russia, Nakhichevanskoi.

Geographic distribution: EUROPE: Russia, Nakhichevanskoi.

Description of sporulated oocyst: Oocyst shape: described as ovoidal, but illustrated as subspheroidal; wall of uniform thickness, ~3.0, consisting of 2 (description) or 3 (line drawing) layers: outer, smooth, colorless, ~1.5; inner, smooth, yellowish, ~1.5; their line drawing shows a third, innermost layer that is thin, dark; L x W: 25.0 x 21.0 (20–27 x 18–24); L:W ratio 1.2; M: absent; OR: present; OR characteristics: a spheroid, homogeneous, lipid-like globule; PG: present, small. Distinctive features of oocyst: thick, 2–3 layered wall and OR a lipid-like globule.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal, highly pointed at 1 end; L x W: 9.0 x 5.0 (6–10 x 4–6); L:W ratio 1.8; SB: prominent, pointed; SSB and PSB: absent; SR: present; SR characteristics: a few scattered granules; SP: small, bean-shaped, without RB. Distinctive features of sporocyst: highly

pointed shape; small, bean-shaped SP (degenerate?).

Prevalence: 1/1 (100%).

Sporulation: Exogenous. Oocysts sporulated in 3 days in 2.5% $K_2Cr_2O_7$ at 25–30°C.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from intestinal contents.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: This species has not been recorded since its original description.

Reference: Musaev and Veisov (1961).

***Eimeria zakirica* Musaev, 1967 (Fig. 25)**

Type host: *Vespertilio murinus* Linnaeus, 1758, Frosted bat.

Type locality: EUROPE: Russia, Nakhichevanskoi.

Geographic distribution: EUROPE: Russia, Nakhichevanskoi.

Description of sporulated oocyst: Oocyst shape: ellipsoidal (original line drawing), but measurements indicate subspheroidal; wall of uniform thickness, ~1.0, with 1 smooth, colorless layer; L x W: 25.0 x 22.5 (20–30 x 16–26); L:W ratio 1.1; M: absent; OR: absent; PG: 1, small. Distinctive features of oocyst: thin, smooth wall, without OR.

Description of sporocysts and sporozoites: Sporocyst shape: ellipsoidal; L x W: 11.0 x 8.0 (8–14 x 6–10); L:W ratio 1.4; SB, SSB and PSB: all absent; SR: present; SR characteristics: a few scattered granules between SP (line drawing); SP: small, pear- or bean-shaped, usually at ends of sporocyst and lacking RB (line drawing). Distinctive features of sporocyst: ellipsoidal shape without SB and with small, bean-shaped SP.

Prevalence: 1/1(100%).

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from intestinal contents.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: This species has not been recorded since its original description.

Reference: Musaev (1967).

Subfamily Murininae Miller, 1907
(2 genera, 16 species)

No species in this subfamily have been examined for coccidia to date.

Subfamily Miniopterinae Dobson, 1875
(1 genus, 10 species)

No species in this subfamily have been examined for coccidia to date.

Subfamily Tomopeatinae Miller, 1907
(1 genus, monotypic)

Host Genus *Tomopeas* Miller, 1900

***Eimeria tomopea* Duszynski and Barkley, 1985 (Figs. 26, 43)**

Type host: *Tomopeas ravus* Miller, 1900, Peruvian crevice bat.

Type locality: SOUTH AMERICA: Peru, Departmento Lambayeque, Cerro la Vieja, 7 km S Motupe; ~150 m.

Geographic distribution: SOUTH AMERICA: Peru: Lambayeque.

Description of sporulated oocyst: Oocyst shape: ellipsoidal to subspheroidal; wall of uniform thickness, ~1.0, consisting of 2 layers: outer, yellowish, mammillated, ⅔ of total thickness; inner, smooth, colorless; L x W (N = 100): 30.6 x 24.6 (26–34 x 20–28); L:W ratio 1.2 (1.2–1.35); MP: absent; OR: present; OR characteristics: variable from a spheroid, homogeneous, lipid-like globule, ~5.0, to multiple bodies, to a coarse, granular spheroid and sometimes there is a membrane-like structure associated with the sphere; PG: present, small. Distinctive features of oocyst: rough outer wall plus both OR, which is highly variable in structure from oocyst to oocyst, and PG.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W (N = 100): 13.9 x 9.0 (12–15 x 8–10); L:W ratio 1.5 (1.4–1.8); SB: present, small, somewhat flattened structure at slightly pointed end of sporocyst; SSB and PSB: absent; SR: present; SR characteristics: large scattered granules; SP: lie head to tail, each with 1 posterior RB. Distinctive features of sporocyst: thin wall with tiny, flattened SB.

Prevalence: 2/17 (12%).

Sporulation: Presumably exogenous. Oocysts sporulated in 2.5% aqueous (w/v) $K_2Cr_2O_7$ solution after 1 week at ~23°C after being returned to the lab from Peru.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from intestinal contents.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 86004. Symbiotype host: *Tomopeas ravus* in the Louisiana State University Museum of Zoology, LSUMZ 25067 (7 July 1981).

Remarks: The sporulated oocysts of this species most closely resemble those of *E. eumopos*. They differ, however, by being smaller (31 x 25 vs. 35 x 28), by having a distinct OR that *E. eumopos* lacks, by having larger sporocysts (14 x 9 vs. 12 x 5) with a large, granular SR, and by having a SB that is indistinct.

Reference: Duszynski and Barkley (1985).

Family Mystacinidae Dobson, 1875
(1 genus, 2 species)

No species in this family have been examined for coccidia to date.

Family Molossidae Gervais, 1856
(12 genera, 80 species)

Host Genus *Chaerephon* Dobson, 1874
(13 species)

Eimeria dukei Lavier, 1927 (Fig. 27)

Type host: *Chaerephon pumila* (Cretzschmar, 1830) (Syn. *Nyctinomus pumilus*; Syn. *Tadarida pumila*), Lesser mastiff bat.

Other hosts: *Tadarida lobata* (Thomas, 1891)? (see *Remarks*).

Type locality: AFRICA: Uganda, Entebbe.

Geographic distribution: AFRICA: Uganda.

Description of sporulated oocyst: Oocyst shape: subspheroidal to broadly ellipsoidal; wall "quite thick," although his line drawing shows it to be a thin, 1-layered structure; L x W: 23–25 x 18–22; L/W ratio: not given; M: absent; OR: present; OR characteristics: a large sphere of coarse granules taking up about ½ of the space within the oocyst (line drawing); PG: absent. Distinctive features of oocyst: large sphere of coarse granules that displace sporocysts to one end of oocyst.

Description of sporocysts and sporozoites: Sporocyst shape: slightly ovoidal; L x W: 7–9 x 6–7; L/W ratio: not given; SB, SSB and PSB: apparently all absent. SR: present; SR characteristics: a few small granules between SP (line drawing); SP: elongate, with 1 RB located at rounded end (line drawing). Distinctive features of sporocyst: SB, SSB, PSB all absent.

Prevalence: 3/11 (27%).

Sporulation: Exogenous. Oocysts sporulated in 4 days in 0.5% chromic acid solution at 18–20°C.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: Lavier (1927) described this species from 3/11 (27%) *C. pumila* (= *N. pumilus*) from Entebbe, Uganda. Pellérdy (1974) listed "*Tadarida limbata*" [sic] (probably *T. lobata*) as a host, but gave no mention why he did so. Černá and Ryšavý (1976) measured 27 sporulated oocysts from *Taphozous nudiventris* Cretzschmar, 1830 (Emballonuridae), which they suggested were *E. dukei*. Their oocysts were 21–25 x 18–23 with a thin, membranous wall without a M, but with "an enormously large residual body (10–13 in diameter);" the sporocysts were ovoidal, 7–9 x 4–5 with an indistinct SB and an SR of "individual residual granules only." Their oocysts sporulated in ~20 h at 30°C. They suggested that the oocysts they observed may be those of *E. dukei* and "that this coccidian from African bats may utilize a wide range of hosts." Unfortunately, we know so little about the coccidia from bats that we do not know if some *Eimeria* species of bats can transfer between host genera (which is possible) or between host families (which is unlikely). Levine and Ivens (1981) included *E. dukei* in their brief summary of coccidia from bats, but made no mention of the observations of Černá and Ryšavý (1976).

References: Černá and Ryšavý (1976); Lavier (1927); Levine and Ivens (1981); Pellérdy (1974).

***Eimeria levinei* Bray, 1958 (Fig. 28)**

Type host: *Chaerephon bemmeleni* (Jentink, 1879) (Syn. *Tadarida bemmeleni*), Lesser mastiff bat.

Type locality: AFRICA: Liberia.

Geographic distribution: AFRICA: Liberia.

Description of sporulated oocyst: Oocyst shape: ovoidal, somewhat flattened and thickened at 1 end (line drawing); wall a 1-layered structure (line drawing); L x W: 21.6 x 18.2 (19–24 x 17–19); L/W ratio: 1.2; M: present (?); M characteristics: small, around which there is a somewhat flattened ridge (line drawing); OR: present; OR characteristics: "abundant" number of coarse granules that take up about the top ½ of the space within the oocyst (line drawing); PG: absent. Distinctive features of oocyst: 1 of the 3 (?) eimeriid oocysts from bats with a M (but see Discussion); the flattening at one end also set it apart from other species.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: 8.5 x 7.4 (8–9 x 7–8); L/W ratio: 1.1; SB: present, distinct; SSB and PSB: absent. SR: absent; SP: spherodial, 3.4 x 3.4 (3–4 x 3–4) and "hyaline;" RB: apparently absent. Distinctive features of sporocyst: SB present as a dark, pointed structure at one end of sporocyst; rounded, "hyaline" (degenerate?) SP.

Prevalence: 2/3 (67%).

Sporulation: Exogenous. Oocysts sporulated in 2–4 days in 2.0% chromic acid solution.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the posterior third of the small intestine.

Endogenous stages: Meronts had crescentic-shaped merozoites arranged with all pointed in the same direction. Microgametocytes had numerous nuclei and pronounced septa formation in the cytoplasm. Macrogametocytes were thin walled with a large eccentric vesicular nucleus that had a large, eccentric karyosome.

Pathology: Unknown.

Material deposited: None.

Remarks: This species has not been reported since its original description.

References: Bray (1958, 1964); Levine and Ivens (1981).

Host Genus *Eumops* Miller, 1906

***Eimeria eumopos* Marinkelle, 1968 (Fig. 29)**

Type host: *Eumops perotis* (Schinz, 1821) (Syn. *E. trumbulli*), Mastiff bat.

Type locality: SOUTH AMERICA: Columbia, Departménto Meta, Puerto López.

Geographic distribution: SOUTH AMERICA: Columbia: Meta.

Description of sporulated oocyst: Oocyst shape: asymmetrically ovoidal; wall consists of 2 layers: outer, brownish, ~1.6–2.6, rough, covered with pronounced pits and appears radially striated in optical cross-section; inner, thin, smooth, colorless; L x W: 34.9 x 28.0 (34–36 x 27–28); L/W ratio: 1.25; M: absent; OR: absent; PG: 1 or 2, ~2–4 in size. Distinctive features of oocyst: large size, thick, brown, bumpy striated wall and sometimes asymmetrical (line drawing).

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: 11.0 x 7.9 (10.5–12 x 6.5–8); L/W ratio: 1.4; SB: present (?) as small, nipple-like structure, ~0.6 x 1.0; SSB and PSB: absent. SR: present; SR characteristics: scattered, coarse granules; SP: banana-shaped, 10.0 x 3.9 (9–11 x 3–4) oriented head to tail and fill most of sporocyst; 1 large RB present at rounded end of SP. Distinctive features of sporocyst: very thin wall with small nipple-like SB.

Prevalence: 2/12 (17%).

Sporulation: Exogenous. Oocysts sporulated in 8–15 days in 2.5% $K_2Cr_2O_7$ solution left at 25°C.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the anterior part of the small intestine.

Endogenous stages: Meronts were 98 x 62, thick-walled, and contained up to 350 crescentic merozoites; the cytoplasm of the host cell formed a covering layer 2–3 thick around the meront. Microgametocytes measured 17 x 11 with ~48 microgametes. Young macrogametocytes are rounded and their cytoplasm is packed with granular matter, which is later transformed into dark-staining peripheral granules; the nucleus is "large," with a slightly eccentric nucleolus. Nearly mature macrogametocytes were 18.9 x 16.1 (18–23 x 14–18) Endogenous young oocysts were 21.6 x 19.1 (19–26 x 18–25) with a wall 0.3 thick.

Pathology: Unknown.

Material deposited: None.

Remarks: Marinkelle (1968) measured both sporulated and unsporulated oocysts and noted that oocyst size increased during sporulation by almost 20%. Interestingly, he found this species in 2/12 (17%) *E. perotis*, but found no other coccidian oocysts in more than 388 other bats representing 22 species found in Colombia; unfortunately, he did not name the other species he examined. Although reported to be present, his line drawing did not show a SB.

References: Levine and Ivens (1981); Marinkelle (1968).

Host Genus *Molossus* E. Goeffroy, 1805

***Eimeria molossi* Lainson and Naiff, 1998 (Fig. 30)**

Type host: *Molossus ater* Goeffroy, 1805, Velvety free-tailed bat.

Type locality: SOUTH AMERICA: Brazil, Amazonas, suburbs of Manaus.

Geographic distribution: SOUTH AMERICA: Brazil: Amazonas.

Description of sporulated oocyst: Oocyst shape: sometimes subspheroidal, but mostly broadly ellipsoidal; wall consists of 3 layers: outer 2 are closely contiguous, yellowish-brown, prominently striated in optical cross-section; inner, thin, smooth, colorless; L x W (N = 100): 23.4 x 17.5 (18–30 x 15–22.5); L/W ratio: 1.3 (1.0–1.6); M: absent; OR: absent; PG: 1–2, conspicuous, ellipsoidal, ~1.9 long. Distinctive features of oocyst: 3-layered wall giving a striated appearance.

Description of sporocysts and sporozoites: Sporocyst shape: broadly ellipsoidal to ovoidal; L x W: (N = 50) 10.3 x 7.5 (10–12.5 x 7.5); L/W ratio: 1.4 (1.3–1.7); SB: present as small, nipple-like structure; SB and PSB: absent. SR: present; SR characteristics: 4–12 relatively large spherules between SP; SP: oriented head to tail, longer than and filling most of sporocyst so that they recurve on themselves; 1 RB at rounded end of SP. Distinctive features of sporocyst: very thin wall and SP that are longer than sporocyst.

Prevalence: 17/38 (45%).

Sporulation: Exogenous. Sporulation time is unknown, but it was noted that sometimes ≥70% of the oocysts in a given fecal sample failed to sporulate when stored in 2.5% $K_2Cr_2O_7$ solution left at 23–24 °C.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the ileum with all stages positioned between the brush-border and the host cell nucleus, which becomes distended and later destroyed by the growing stages.

Endogenous stages: Meronts (N = 6) were 12.3 x 9.3 (11–14 x 8–10) and produced 8–12 merozoites, ~6 x 1. Microgametocytes measured 15.8 x 11.8 (15.5–17 x 11–12), had a bulky RB, 10 x 8, and shed >50 microgametes, 3 x 0.5. Young macrogametocytes are first spheroidal and later become ellipsoidal, 18 x 14; glycoprotein granules then become conspicuous and some are 2 in diameter. The oocyst wall is fully developed before the oocysts are shed into the gut lumen.

Pathology: No outward signs of disease, but histological sections showed damage of the epithelium presumed to be caused by the parasite and endogenous stages were commonly seen together with sloughed epithelial cell debris in the gut lumen

Material deposited: None.

Remarks: This is the only species described from *Molossus*. Its sporulated oocysts most closely resemble those of *E. eumopos* (from *Eumops trumbuli*, another molossid) and those of *E. macyi* (from *Pipistrellus subflavus*, Vespertilionidae), both of which have a roughish, striated outer oocyst wall. The oocysts of *E. eumopos* are larger than those of *E. molossi* (35 x 28 vs. 23 x 17) and the former has an oocyst wall with only two layers. In addition, there are significant size and number differences in the endogenous developmental stages between the two species. The oocysts of *E. macyi* are smaller, and more spheroidal in shape than those of *E. molossi* (19 x 17.6 vs. 23 x 17) and have sporocysts with a distinct SSB, which those of *E. molossi* lack. Finally, there are no cross-transmission studies done with the coccidia of any bat species, so we know nothing about host specificity within the Chiroptera. In at least one other mammalian lineage (e.g., Sciuridae), some *Eimeria* species apparently are successfully shared between host species in different genera (Wilber et al. 1998); however, in other mammals (e.g., Muridae), *Eimeria* species usually can be transferred between species in the same genus, but generally

not between hosts in different genera (Hnida et al. 1999). Thus, it is not possible to say with certainty whether eimerians with similarly structured oocysts can exist in more than one host genus.

Reference: Lainson and Naiff (1998).

Host Genus *Nyctinomops* Miller, 1902
(4 species)

***Eimeria tadarida* Duszynski, Reduker and Paker, 1988 (Figs. 31, 44)**

Type host: *Nyctinomops femorosaccus* (Merriam, 1889) (Syn. *Tadarida femorosacca*), Pocketed free-tail bat.

Type locality: NORTH AMERICA: Mexico, Sonora, 19.3 km E. Alamos by road, Rio Cuchujaqui.

Geographic distribution: NORTH AMERICA: Mexico: Sonora.

Description of sporulated oocyst: Oocyst shape: subspheroidal to ellipsoidal; wall of uniform thickness, ~1.5, with 2 layers: outer, mammillated, ⅔ of total thickness; inner, smooth, colorless; L x W (N = 100): 25.2 x 19.0 (20–30 x 16–23); L/W ratio: 1.3 (1.2–1.6); M: absent; OR: absent (?); PG: 1–3 fragments that may be remnants of an OR. Distinctive features of oocyst: rough outer wall.

Description of sporocysts and sporozoites: Sporocyst shape: ovoidal; L x W: (N = 100) 12.1 x 7.6 (10–14 x 6–9); L/W ratio: 1.6 (1.4–1.7); SB present as darkened line at 1 end of sporocyst and difficult to see; SSB present (?) (there always is a clear space below pointed end of sporocyst), asymmetrical, 2–3x wider than SB; PSB: absent. SR: present; SR characteristics: several small to large globules and granules sometimes obscuring SP; SP with 1 large, posterior RB. Distinctive features of sporocyst: asymmetrical SSB, 2–3 times wider than SB.

Prevalence: 1/18 (5.5%).

Sporulation: Exogenous (?). Oocysts sporulated when stored in 2.5% $K_2Cr_2O_7$ solution while transported in the field.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts in the USNPC No. 86002. Symbiotype host: *Nyctinomops femorosaccus*, MSB 53835 (27 October 1980).

Remarks: This species somewhat resembles *E. tomopea, E. macyi* and *E. eumopos*. The oocysts of this form differ from those of *E. tomopea* by being smaller and lacking a PG; they also have smaller sporocysts that have a SSB that *E. tomopea* lacks, although in both species the SB is difficult to visualize. They differ from those of *E. macyi* by having larger oocysts and a larger L:W ratio (1.3 vs. 1.1) and by having a SSB that is two to three times wider than the SB vs. one that is the same width. They differ from those of *E. eumopos* by being much smaller (25 x 19 vs. 35 x 28), by having a thinner outer wall that is mammillated, not pitted, and by having sporocysts with a SSB that *E. eumopos* lacks.

Reference: Duszynski, Reduker and Parker (1988).

Species Inquirendae

Coccidium sp. Gruber et al. 1996

Original hosts: *Myotis mystacinus* (Kuhl, 1817), *Myotis nattereri* (Kuhl, 1817), *Nyctalus noctula* (Schreber, 1774) and *Pipistrellus pipistrellus* (Schreber, 1774) (Vespertilionidae).

Remarks: Gruber et al. (1996) diagnosed severe renal coccidiosis with cystic tubular dilatation in these four insectivorous bats in Hannover, Germany. Cystic dilatations occurred in the tubules of the renal medulla and cortex; these tubules were almost completely filled with both asexual and sexual stages. Meronts were 13–19 in diameter and contained 16–22 banana-shaped merozoites; free zoites were 1.5–2.3 x 7–10, without refractile bodies. Macrogamonts were 12–18 in diameter and could be identified (ultrastructurally) by their peripherially located, osmiophilic, electron-dense, wall-forming bodies that surrounded lipid bodies and polysaccharide granules. Microgamonts were 12–15 in diameter with numerous microgametes, 2.0–3.5 x 0.2–0.4, each with two flagella. Both asexual and sexual endogenous stages were released into the cystic tubular lumina from superficial renal epithelial cells. Only a few structures were seen that were thought to be unsporulated oocysts; these measured 11–17 in diameter. No urine was collected from these bats so precise identification was not possible since sporulated oocysts were never

available. Gruber et al. (1996) concluded that the consistent morphology of the parasite and the cystic dilated renal tubules with both asexual and sexual stages differed distinctly enough from a *Klossiella* sp. (Klossiellidae) found previously in the kidneys of *Myotis sodalis* Miller and Allen, 1928 by Kusewitt et al. (1977), to suggest a new, undescribed renal coccidium. Unfortunately, this species must remain a *species inquirendae* until its sporulated oocysts can be identified.

***Eimeria* (?) *myotis* Gottschalk, 1969**

Original host: *Myotis myotis* (Borkhausen, 1797) (Vespertilionidae).

Remarks: Gottschalk (1969) found some spheroidal–subspheroidal structures, 15 x 14.5 (12–21 x 11–20), in the large intestine and others, 14.4 x 13.8, in the small intestine, which he named *E. myotis*. Frank (1978) also reported seeing stages of this form in the jejunum of a *M. myotis* collected in Austria. However, since sporulated oocysts were never seen or described, some (Wheat 1975; Duszynski and Barkley 1985; others) have considered this name a *nomina nuda*. However, *species inquirendae*, defined by Ride et al. (1985) as "a doubtfully identified species needing further investigation," seems a more appropriate term. Thus, this form must remain a *species inquirendae* until it can be studied and described more completely.

***Eimeria* (?) *plecoti* Gottschalk, 1969**

Original host: *Plecotus auritus* (Linnaeus, 1758), Long-eared bat (Vespertilionidae).

Remarks: Gottschalk (1969) found spheroidal to subspheroidal oocysts (?) in the large intestine that measured 16 x 14 (13–18 x 12–16), with a colorless, thin wall. Since neither sporocysts nor sporozoites were described, this form cannot be placed in the genus *Eimeria* and must be considered a *species inquirendae* until it can be described more completely. The only other oocysts ever found in bats of this genus were those of *Klossia variabilis* (Adeleidae) by Levine et al. (1955), but they thought *K. variabilis* probably was a pseudoparasite of the bat and a true parasite of some invertebrate that it had eaten.

***Eimeria dukei* of Černá and Ryšavý, 1976**

Original host: *Taphozous nudiventris* Cretzschmar, 1830 (Emballonuridae).

Remarks: Černá and Ryšavý (1976) described this form from 27 sporulated oocysts they found in 1971 in the feces of one *T. nudiventris* collected in the vicinity of the village of Abu Rawash, close to the pyramids of Ziza (Egypt), and they called it *E. dukei* (see *Remarks* under *E. dukei*). Unfortunately, they did not present a photomicrograph or a line drawing nor did they archive specimens. Given that eimerians are reasonably host specific, it is unlikely that they are able to infect host species in different families. Thus, the form they saw must be considered a *species inquirendae*.

***Eimeria* sp. Duszynski, 1997**

Original host: *Rhinolophus ferrumequinum* (Schreber, 1774), Horseshoe bat (Rhinolophidae).

Remarks: Duszynski (1997) observed eimerian oocysts in 1/3 (33%) *R. ferrumequinum* from Japan. They were subspheroidal, 23.4 x 19.2 (19.5–26 x 17–22.5) with a rough wall, a PG and an OR; sporocysts were lemon-shaped with a SB, but only 2/25 oocysts were sporulated. Thus, given the guidelines of Duszynski and Wilber (1997), it was not realistic to describe this form as a new species based only on the structure of two sporulated oocysts. There is only one other mention of oocysts having been recovered from *R. ferrumequinum*. Labbé (1893) reported three types of "oocysts" from this host in France and named it *Coddidium viride*, a name later emended to *E. viridis* by Reichenow (1921). Lavier (1924a) and Pellérdy (1974) opined that Labbé (1893) had dealt with more than one species and relegated *E. viridis* to a *nomen nudum*; however, *species inquirenda*, a doubtfully identified species needing further investigation (Ride et al. 1985: 264), is a more technically correct designation.

***Eimeria* sp. Duszynski, Reduker and Parker, 1988**

Original host: *Lasiurus cinereus* (Beauvois, 1796), Hoary bat (Vespertilionidae).

Remarks: Duszynski et al. (1988) found this form in 2/22 (9%) *L. cinereus* (0/3, El Dorado Co., California, U.S.A.; 1/8, Hidalgo Co., New Mexico, U.S.A.; 1/11, Baja California Norte, Mexico). Unfortunately, no completely sporulated oocysts were observed, although several

sporulated sufficiently for them to determine it was an *Eimeria* species. The oocysts were subshperoidal, with a wall of uniform thickness ~2.0, with two layers: outer, mammillated, ~¾ of total thickness; inner, smooth. This form is similar in either size or shape to *E. eumopos, E. macyi, E. tomopea* and *E. zakirica*. A photosyntype was published in their description and the symbiotype host (MSB No. 42509) is deposited in the Division of Mammals, Museum of Southwestern Biology, The University of New Mexico, Albuquerque, New Mexico, U.S.A.

***Eimeria viridis* (Labbé, 1893) Reichenow, 1921**

Synonym: *Coccidium viride* Labbé, 1893.

Original host: *Rhinolophus ferrumequinum* (Schreber, 1774), Greater horseshoe bat (Rhinolophidae).

Remarks: Labbé said he found this species in 2/22 (9%) bats in France; he measured a few oocysts and said there were three structural types: ovoidal/pyriform (20 x 13), spheroidal (15) and pyriform (6–7?), the latter with a truncated micropyle. It is likely, as pointed out by Lavier (1924), Pellérdy (1974) and Levine and Ivens (1981), that Labbé (1893) was dealing with oocysts representing two or three species. Because Labbé (1893) gave no illustrations and no further structural information, this form must be considered a *species inquirendae*, at best.

***Isospora* sp. Sunderman, Greenwell, D'Andrea, Mendonca and Lindsay, 2000**

Original host: *Eptiscus fuscus* (Beauvois, 1796), Big brown bat (Vespertilionidae).

Remarks: At the 75th Anniversary Meeting of the American Society of Parasitologists in Puerto Rico, 20–24 June, 2000, Sundermann et al. published an abstract (No. 187) and presented a poster that documented the presence of *Isospora*-like oocysts (2 sporocysts, 4 sporozoites each) in the kidney of a big brown bat from a captive colony in Auburn, Alabama. At necropsy, they noticed a multilobular, 3-mm "cystic lesion" in one kidney; fresh smears and H&E-stained histological sections of this cyst showed numerous coccidian developmental stages including meront-like stages, gamonts, unsporulated and sporulated oocysts. The cyst wall was ~4.5 thick, gamonts were located near its periphery and the interior region of the cyst was filled with oocysts. They surveyed the colony, via urine samples, from which the original bat was collected and found 3/93 (3%) were excreting oocysts and/or sporocysts that were *Isospora*-like. The oocysts were 21.5 x 17.0; sporocysts were 14.5 x 7 with a SR, ~6, and SP ~8 long (*in situ*). This coccidium is unlike *Sarcocystis* species because both asexual and sexual satges were present in the kidney. However, this organism is different from most *Isospora* species in that many of the oocysts sporulated in the kidney and the oocyst wall was very thin and often broke, releasing many sporocysts into the urine. They speculated that transmission is direct when urine contaminates members of the colony and ingestion takes place via grooming. They did not observe any morbitity or mortality associated with this parasite. Since no photosyntypes or drawings of the sporulated oocyst exist at this time, this species must, for the moment, be considered another *species inquirindae*.

DISCUSSION

I have summarized the world's literature on the coccidia (Eimeriidae) known to infect bats. There are several related genera of parasitic protists—*Klossiella* (Klossiellidae), *Klossia* (Adeleidae), *Sarcocystis* and *Toxoplasma* (Sarcocystidae)—that have, from time to time, been reported from bats (Cook et al. 1955; Levine et al. 1955; Orio et al. 1958; Pokorney et al. 1961; Bray 1964; Galuzo et al. 1964, 1970; Levit 1968; Boulard 1975; Kusewitt et al. 1977; Taylor et al. 1979), but the review of these other families is not the purview of this study. The Chiroptera, comprised of 17 families, 177 genera and 925 species (Koopman 1993), is the second most speciose lineage of mammals next to Rodentia. Yet, only 86 species (9.3%), in 43 genera (24.3%) and 10 families (58.8%) of bats have been examined for coccidia; even more incredible is that only 2,119 individual bats, in all collections reported in the literature, have been examined for coccidia. Within these 86 bat species are found 31 named species reported from only 27/86 (31.4%) examined host species; interestingly, all are *Eimeria* species (Table 1). Eleven additional bat species were found to be discharging oocysts, some of which could be identified to the genus *Eimeria* and some of

which could only be identified as oocysts. These reports are widespread temporally and geographically and most represent only one collection event from one locality. Of the 27 infected bat species with named *Eimeria*, 19 (70%) were found to have only a single coccidia species that may (or may not) be unique to that host (Table 1); however, 14/19 (73.7%) had 15 or fewer host specimens examined, so it is likely that at least some harbor additional coccidia species as yet unknown to science. The remaining eight bat species that have been examined for coccidia, most of which had reasonable sample sizes (>30), each had two *Eimeria* species, a few of which were shared between congeners. Thus, if we assume that each extant bat species may have at least two unique coccidia species, there should be at least 1,800 more species of coccidia yet to be discovered from the 925 known bat species. Or put another way, to date, only about 1.6% of the total species of coccidia from bats have been discovered and described.

Or, have we simply not been looking in the right places? The recent reports by Gruber et al. (1996) and Sundermann et al. (2000) offer the intriguing suggestion that we need to reexamine how and *where* we look for coccidian oocysts. Both groups of authors conclusively documented asexual and sexual endogenous stages in the kidneys of four genera of vespertilionid bats, suggesting that this may not be a novel or uncommon occurrence, at least in that family. Traditionally, those who have collected hosts in the field to look for coccidian oocysts have been conditioned by their history to collect only fecal material. Perhaps we have been looking in the wrong excrement! And if, in future studies, we begin to examine both feces and urine, how many additional coccidia remain to be discovered in the epithelium of the kidneys and urinary tubules, beyond the number projected (above) just from intestinal-dwelling species? To say that the coccidia of bats have been understudied by chiropterologists and their parasitology colleagues is an understatement!

From the small sample of bat species examined to date and summarized here, we can speculate that their coccidia species can be shared between congenerics, but not between confamilials; however, we cannot say this with certainty. What else don't we know about the 31 *Eimeria* species described to date? Not one of the known species has been passed in hosts experimentally, under laboratory conditions, so we know nothing about the prepatent and patent periods of the parasites. Nothing is known about the conditions (time, temperature) under which sporulation will occur in 15/31 (48%). Nothing is known about the site of infection (endogenous development) in 24/31 (77%). Only one merogonous stage is known (there usually are 2–4 in most known *Eimeria* life cycles) and the gamonts have been described from only 6/31 (19%), while endogenous developmental stages are completely unknown for the other 25/31 (81%) *Eimeria* species in bats; thus, not one complete life cycle is known. There are no papers that examine ultrastructure of any stage from bats. There are no cross-transmission studies with *Eimeria* between bat species. There are no "type" materials of any kind on deposit in accredited museums for 14/31 (45%) *Eimeria* species. And there is molecular data available, in the form of partial plastid 23S and nuclear 18S rDNA gene sequences, on only two species, *E. antrozoi* (from *Antrozous*) and *E. rioarribaensis* (from *Myotis*) (Zhao et al. 2001). Overall, our knowledge of these 31 *Eimeria* species found in bats is dismal.

Only in one survey to date (Yang-Xian and Fu-Qiang 1983), were ≥100 individual bats of a single species, from the same locality and time period, examined for coccidia and in that survey 105/151 (69.5%) *Myotis ricketti* were reported to harbor only one species, *E. kunmingensis*. In the majority of other surveys, usually ≤30 individuals, of one bat species from one locality and time, were examined for coccidia and the number of bats found to be infected was small (Table 1). Is the overall prevalence of coccidia in bats lower than in other mammal lineages (e.g., Rodentia, Insectivora, etc.) and if so, why? Or is the prevalence artefactually low because so few species and such small sample sizes have been examined?

Other questions beg answers. Many bat species are specialists in their feeding (insects, fish, nectar, fruit, blood, etc.), roosting (solitary vs. communal, tight vs. open spaces), grooming and sociality (gregarious vs. solitary). How do the combination of these (and other) factors, which make each bat species unique, contribute to its ability to come in contact with potentially infec-

tive sporulated oocysts? One picture that seems to emerge from the limited available data is that phyllostomoids, most of which are frugivorous, aren't infected with eimeriid coccidia, while vespertilionids and molossids, many of which are aerial insectivores, are infected. This seems counterintuitive. Frugivores often land on trees to harvest their meals and may defecate there as well; feces so deposited could contaminate other fruit with oocysts and facilitate infection of subsequent visitors. Yet these bats are remarkably infection-free, whereas the insectivores harbor most of the known species. How do bats that feed primarily on insects in flight become infected with oocysts that previously were deposited via the feces of another conspecific or congeneric? How are cycles of infection with these coccidia maintained in nature in solitary bat species that feed "on the wing?" Do certain invertebrates act as transport hosts to bridge the gap between oocysts (that invariably end up on vegetation, the ground, or in the roost) and bats that feed in the air? Is it possible, contrary to what is known about eimeriid biology in all other mammals, that *Eimeria* species of bats might utilize intermediate or transport hosts to bridge the food gap for aerial feeders? How do abiotic factors in the roost microclimate (e.g., humidity, temperature) influence the development and maintenance of oocysts deposited there in the feces and/or urine and how do bats come in contact with such oocysts once they become infective (i.e., sporulated)? Why haven't more bats been examined for coccidia? How can one conceptualize about the host–parasite relationship when we know so little about only 31 putative species, when there could be as many as 2,000 coccidia species in bats? Given the paucity of our current knowledge, these are questions that cannot be answered yet.

When the feces of a bat are examined for coccidia oocysts, the possibility always exists that, if oocysts are found, they may be from a prey/food item that had been eaten by the bat being examined. Often, such oocysts are distorted and found in small numbers, whereas when many undistorted oocysts are recovered from feces of one or more host individuals, more credibility is lent that such oocysts actually are being produced in, and discharged from, the bat being examined. Duszynski (1997), for example, found thousands of oocysts of *E. redukeri* in the feces of *P. javanicus* from Japan. Thus, although confidence is higher that *E. redukeri* actually infects *P. javanicus*, there is no explanation how a bat that eats only small insects in flight (Nowak 1994) can become infected via fecal oocysts.

Among the factors that contribute to the prevalence of eimeriid infections in most mammals include host specificity, acquired (age) immunity, and abiotic factors (Scott and Duszynski 1997). Wilber et al. (1994) suggested that UV radiation and relative humidity (RH) may drive the patterns seen in the prevalence of coccidia in Townsend's ground squirrels (*Spermophilus townsendii*) in Idaho. Although no one has demonstrated it empirically, the abiotic factors most likely to contribute to infection of bats by eimeriid coccidia are the stability of roost microclimate (e.g., RH, temperature) and bat roosting behavior (e.g., colonial vs. solitary). For example, bats that prefer crowded roosts with stable microclimates (maternity colonies in attics and caves) may be more likely to contact and ingest sporulated oocysts than bats that prefer to roost alone where microclimates may be highly variable (trees, leaf litter). Compact roost types (attics, tight crevices) may bring bats into contact with feces or urine more often than large, open roosts (e.g., caves). Bats that choose these compact roosts may have a greater prevalence of coccidia than bats that choose the larger, open roost, due to presumed continued contact with feces. Likewise, increased grooming that occurs within maternity colonies may contribute to a greater chance of them ingesting infective oocysts. Unfortunately, answers for such correlative type questions remain elusive.

In the absence of type material such as photosyntypes, certain portions of many descriptions must be viewed cautiously. For instance, some bat coccidia have been reported to vary greatly in size and shape, even ranging from spheroidal to ovoidal to ellipsoidal. Thus, it is likely that some of the descriptions (*E. mehelyi, E. vespertilii, E. dukei* of Pellérdy [1974], *E. dukei* of Černá and Ryšavý [1976]) represent multiple species that were being confused as one. Some of the morphologic characteristics of the oocyst wall should be considered dubious, or at least with caution. Oocysts are frequently reported to be yellow or orange in color, but how

much of this represents true color, light refraction by different types of lenses (achromatic vs. apochromatic), or potassium dichromate impregnating the wall is unknown. Thus, wall color should be viewed cautiously for several species (*E. evoti, E. kunmingensis, E. pilarensis, E. rioarribaensis, E. jacksonensis, E. chiropteri, E. vespertilii, E. tomopea*). Likewise, the number of wall layers reported frequently is erroneous because observations may be influenced by lens quality and overall inexperience in interpretation. Thus, many of the reports of one-layered walls in non-aquatic hosts may be in error.

Length of SPs *in situ* must always be viewed cautiously; SPs rapidly shorten and degenerate once they become non-viable, and the large posterior RB in some species commonly is confused with the SP itself. Thus, SP sizes given for *E. dukei, E. levinei* and *E. vespertilii* may be questionable. Another common mistake is for the PG, which sometimes becomes attached to the inner oocyst wall, to be confused with and called a M; this may be the case for *E. levinei*. In other descriptions, the SSB may be overlooked, considered a portion of the SB itself, or even imagined to be present with no supporting evidence; such may be the case for *E. kuhliensis*.

The coccidia are obligate, intracellular parasites that are closely tied to the genome of their definitive host(s). Within the enterocytes of their host they undergo both asexual (merogony) and sexual (gamogony) reproduction, culminating in the production of resistant propagules, the oocysts, which are discharged from the host most commonly in its feces; in addition, there is recent evidence (Gruber et al. 1996; Sundermann et al. 2000) that urine also may commonly contain oocysts. Thus, oocysts can be collected easily in the field and represent the stage most used, to date, in the identification of coccidia. Vertebrate biologists working on bats, other mammals, or even other vertebrate groups can play a pivotal role in our understanding of the coccidia from their particular host group simply by properly collecting fecal and urine samples. Before oocysts can be studied critically, however, they must be maintained properly to keep them viable so that their structural integrity remains intact. The methods for collecting and preserving coccidian oocysts in the field have been outlined in detail (Duszynski and Wilber 1997); it must be emphasized that the only preservation fluid known to keep oocysts alive for extended periods of time is 1–3% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution. Previous studies on bat coccidia have shown that other types of solutions sometimes used for coccidia (e.g., dilute sulfuric acid solution) fail to maintain parasite viability and oocyst integrity (Duszynski and Wattam 1988). Attempts to fix and preserve internal details of the oocysts also have failed and traditional fixatives such as 5–10% neutral buffered formalin or polyvinyl alcohol (PVA), which routinely are used to fix helminth fecal stages, should be avoided (Duszynski and Gardner 1991).

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Table 1. Summary of all bat species and individuals that have been examined for coccidia and the known Eimeriidae described through 2000 from Chiroptera (17 families, 177 genera, 925 species) worldwide.

Family/Subfamily *Genus/species*	No. infected/ No. examined	*Eimeria/Isospora* spp. described	Reference(s)
Pteropodidae			
Pteropodinae			
Cynopterus sphynx	0/20	0	Mandal & Nair 1973
Emballonuridae			
Peropteryx macrotis	1/3	*bragancaensis*	Lainson & Naiff 2000
Rhynchonecteris naso	4/9	*rhynchonycteridis*	Lainson 1968
Taphozous melanopogon	2/30	*andamanensis*	Mandal & Nair 1973
T. nudiventris	1/1	*E.* sp.	Černá & Ryšavý 1976
Rhinolophidae			
Rhinolophinae			
Rhinolophus cornutus	0/5	0	Duszynski 1997
R. ferrumequinum	1/3	*E.* sp.	Duszynski 1997
R. hipposideros	3/15	*hessei*	Lavier 1924
R. mehelyi	1/25	*mehlyi*	Musaev & Gauzer 1971
Noctilionidae			
Noctilio albiventris	0/2	0	Duszynski et al. 1999b
Mormoopidae			
Mormoops megalophyla	0/1	0	Scott & Duszynski 1997
Phyllostomidae			
Phyllostominae			
Macrophyllum macrophyllum	0/1	0	Scott & Duszynski 1997
Macrotus californicus	0/1	0	Duszynski et al. 1988
Phyllostomus hastatus	0/3	0	Scott & Duszynski 1997; Duszynski et al. 1999b
Tonatia silvicola	0/1	0	Scott & Duszynski 1997
Vampyrum spectrum	0/2	0	Duszynski et al. 1999b

Table 1 continued

Glossophaginae			
Anoura goeffroyi	0/3	0	Scott & Duszynski 1997
Choeronycteris mexicana	0/1	0	Duszynski et al. 1988
Leptonycteris curasoae	0/2	0	Duszynski et al. 1988
Carolliinae			
Carollia brevicauda	0/1	0	Scott & Duszynski 1997
C. perspicillata	0/9	0	Scott & Duszynski 1997; Duszynski et al. 1999b
Stenodermatinae			
Artibeus anderseni	0/1	0	Scott & Duszynski 1997
A. cinereus	0/1	0	Duszynski et al. 1999b
A. lituratus	0/10	0	Scott & Duszynski 1997; Duszynski et al. 1999b
A. obscurus	0/3	0	Scott & Duszynski 1997
A. planirostris	0/5	0	Scott & Duszynski 1997
Chiroderma villosum	0/2	0	Duszynski et al. 1999b
Platyrrhinus infuscus	0/1	0	Scott & Duszynski 1997
P. lineatus	0/2	0	Duszynski et al. 1999b
Pygoderma bilabiatum	0/1	0	Scott & Duszynski 1997
Sturnira erythromos	0/2	0	Scott & Duszynski 1997
S. lilium	0/1	0	Scott & Duszynski 1997
S. oporaphilum	0/1	0	Scott & Duszynski 1997
Uroderma magnirostrum	1/3	*magnirostrumi*	Scott & Duszynski 1997; Duszynski et al. 1999b
Desmodontinae			
Desmodus rotundus	0/3	0	Duszynski et al. 1999b
Natalidae			
Natulus stramineus	0/1	0	Duszynski et al. 1988
Thyropteridae			
Thyroptera sp.	0/1	0	Scott & Duszynski 1997

Table 1 continued

Family/Subfamily *Genus/species*	No. infected/ No. examined	*Eimeria/Isospora* spp. described	Reference(s)
Vespertilionidae			
Vespertilioninae			
Antrozous pallidus	14/115	*antrozoi*	Scott & Duszynski 1997; Duszynski et al. 1988, 1999a
Eptesicus brasiliensis	0/1	0	Scott & Duszynski 1997
E. fuscus	5/255	*E.* sp., *I.* sp.	Scott & Duszynski 1997; Duszynski et al. 1988, 1999a; Sundermann et al. 2000
Euderma maculatum	0/4	0	Scott & Duszynski 1997; Duszynski et al. 1999a
Idionycteris phyllotis	0/2	0	Duszynski et al. 1999a
Lasionycteris noctivagans	0/61	0	Scott & Duszynski 1997; Duszynski et al. 1988
Lasiurus borealis	0/7	0	Scott & Duszynski 1997; Duszynski et al. 1988
L. cinereus	2/54	*E.* sp.	Scott & Duszynski 1997; Duszynski et al. 1988, 1999a
L. ega	0/1	0	Duszynski et al. 1988
L. intermedius	0/1	0	Duszynski et al. 1999b
L. seminolis	0/1	0	Duszynski et al. 1999a
Myotis albescens	0/3	0	Scott & Duszynski 1997
M. auriculus	2/27	*E.* sp.	Scott & Duszynski 1997; Duszynski et al. 1999a
M. californicus	7/71	*californicensis, humboldtensis*	Scott & Duszynski 1997; Duszynski et al. 1999a
M. ciliolabrum	6/79	*pilarensis, rioarribaensis*	Duszynski & Scott 1997; Duszynski et al. 1999a
M. evotis	1/26	*evoti,* spp.	Scott & Duszynski 1997; Duszynski et al. 1999a

Table 1 continued

M. lucifugus	4/31	*catronensis,* sp.	Scott & Duszynski 1997; Duszynski et al. 1999a
M. macrodactylus	0/4	0	Duszynski 1997
M. mystacinus	1/1	coccidium sp.	Gruber et al. 1996
M. nattereri	1/1	coccidium sp.	Gruber et al. 1996
M. nigricans	2/4	*nigricani*	Duszynski et al. 1999b
M. oxyotus	0/3	0	Scott & Duszynski 1997
M. thysanodes	1/36	*E.* sp.	Scott & Duszynski 1997; Duszynski et al. 1999a
M. nigricans	2/4	*nigricani*	Duszynski et al. 1999b
M. ricketti	105/151	*kunmingensis*	Yang-Xian & Fu-Qiang 1983
M. velifer	0/4	0	Scott & Duszynski 1997; Duszynski et al. 1999a
M. vivesi	1/25	*E.* sp.	Duszynski et al. 1999a
M. volans	1/80	*E.* sp.	Scott & Duszynski 1997; Duszynski et al. 1999a
M. yumanensis	15/97	*pilarensis, catronensis*	Scott & Duszynski 1997; Duszynski et al. 1999a
Nyctalus noctula	3/3	*vejsovi, nyctali,* coccidium sp.	Černá 1976; Gottschalk 1974; Gruber et al. 1996
Nycticeius humeralis	2/2	*jacksonensis*	Duszynski et al. 1999a
Pipistrellus hesperus	0/30	0	Scott & Duszynski 1997; Duszynski et al. 1988, 1999a
P. javanicus	1/4	*redukeri*	Duszynski 1997
P. kuhlii	11/47	*chiropteri, kuhliensis, pipistrellus*	Alyousif et al. 1999; Alyousif 1999a,b
P. pipistrellus	1/1	coccidium sp.	Gruber et al. 1996
P. subflavus	4/8	*macyi*	Wheat 1975a,b; McAllister et al. 2001
Plecotus auritus	0/1	0	Duszynski 1997
P. townsendii	0/4	0	Scott & Duszynski 1997; Duszynski et al. 1999a
Vespertilio murinus	2/2	*vespertilii, zakirica*	Musaev & Veisov 1961; Musaev 1967
V. superans	0/22	0	Duszynski 1997

Table 1 continued

Family/Subfamily *Genus/species*	No. infected/ No. examined	*Eimeria/Isospora* spp. described	Reference(s)
Tomopeatinae			
Tomopeas ravus	2/17	*tomopea*	Duszynski & Barkley 1985
Molossidae			
Chaerephon bemmeleni	2/3	*levinei*	Bray 1958
C. pumila	3/11	*dukei*	Lavier 1927
Eumops perotis	2/12	*eumopos*	Marinkelle 1968
Molossus ater	17/39	*molossi*	Lainson & Naiff 1998; Duszynski et al. 1999b
M. molossus	0/50	0	Scott & Duszynski 1997; Duszynski et al. 1999b
Nyctinomops macrotus	0/4	0	Scott & Duszynski 1997
N. femorosaccus	1/18	*tadarida*	Duszynski et al. 1988
Tadarida brasiliensis	0/41	0	Scott & Duszynski 1997; Duszynski et al. 1988, 1999a
Unknown genera/species	1/475+	coccidium sp.	Marinkelle 1968; Musaev & Gauzer 1971
10 families, 43 genera, 86 species	236/2119 (11%)	31 *Eimeria*, 1 *Isospora* spp.	

Table 2. List of figures that were scanned from the original description with the permission of the anthors and/or publishers.

Figure/*Eimeria* sp.	Source of line drawing
1. *bragancaensis*	Scanned from Lainson & Naiff (2000, Fig. 28)
12. *kunmingensis*	Scanned from Yang-Xian & FuQiang (1983, Fig. 1)
19. *chiropteri*	Scanned from Alyousif (1999a, Fig. 5)
20. *kuhliensis*	Scanned from Alyousif (1999b, Fig. 4)
21. *macyi*	Scanned from Wheat (1975a, Fig. 1)
22. *pipistrellus*	Scanned from Alyousif et al. (1999, Fig. 4)
29. *eumops*	Scanned from Marinkelle (1968, Fig. 1C)
30. *molossi*	Scanned from Lainson & Naiff (1998, Fig. 25)

LEGEND TO FIGURES

Figures 1–31. Line drawings of the 31 *Eimeria* species known from bats. Bar = 10 μm. Most line drawings are from our own work cited herein. Some (as noted below), which we felt were of inferior quality, were redrawn from the original publication, while a few, which were of good quality, were scanned from the original publications.

Figures 32–44. Photomicrographs of sporulated oocysts of *Eimeria* species from bats that are on deposit as photosyntypes in the U.S. National Parasite Collection, Beltsville, MD. Bar = 10 μm.

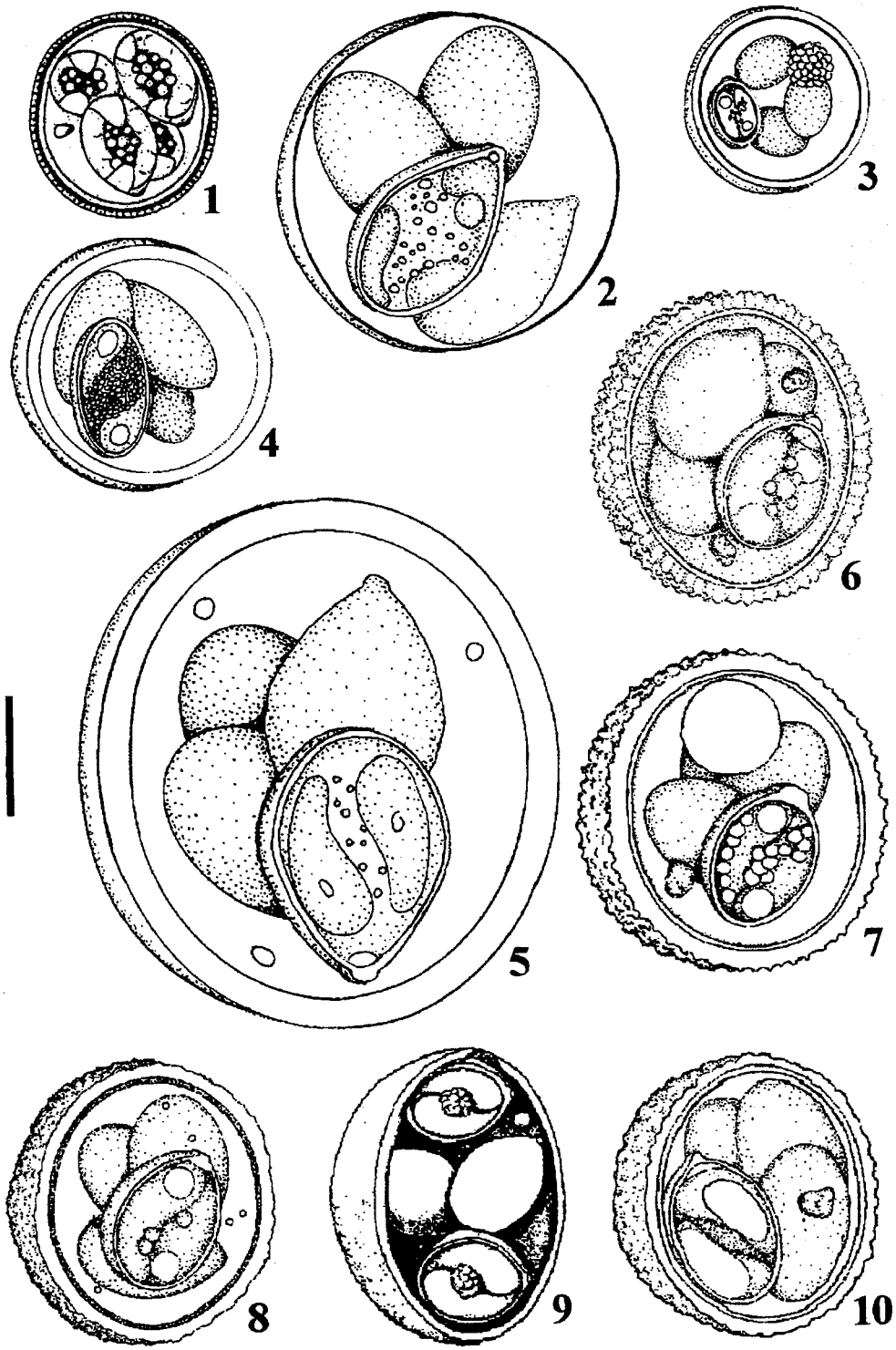

Plate I. Figures 1–10.

1. *E. bragancaensis* (scanned from Lainson and Naiff 2000, Fig. 28). **2.** *E. rhynchonycteridis* (redrawn from Lainson 1968). **3.** *E. andamanensis* (redrawn from Mandal and Nair 1973). **4.** *E. hessei* (redrawn from Lavier 1924). **5.** *E. mehelyi* (redrawn from Musaev and Gauzer 1971). **6.** *E. magnirostrumi*. **7.** *E. antrozoi*. **8.** *E. californicensis*. **9.** *E. catronensis*. **10.** *E. evoti*.

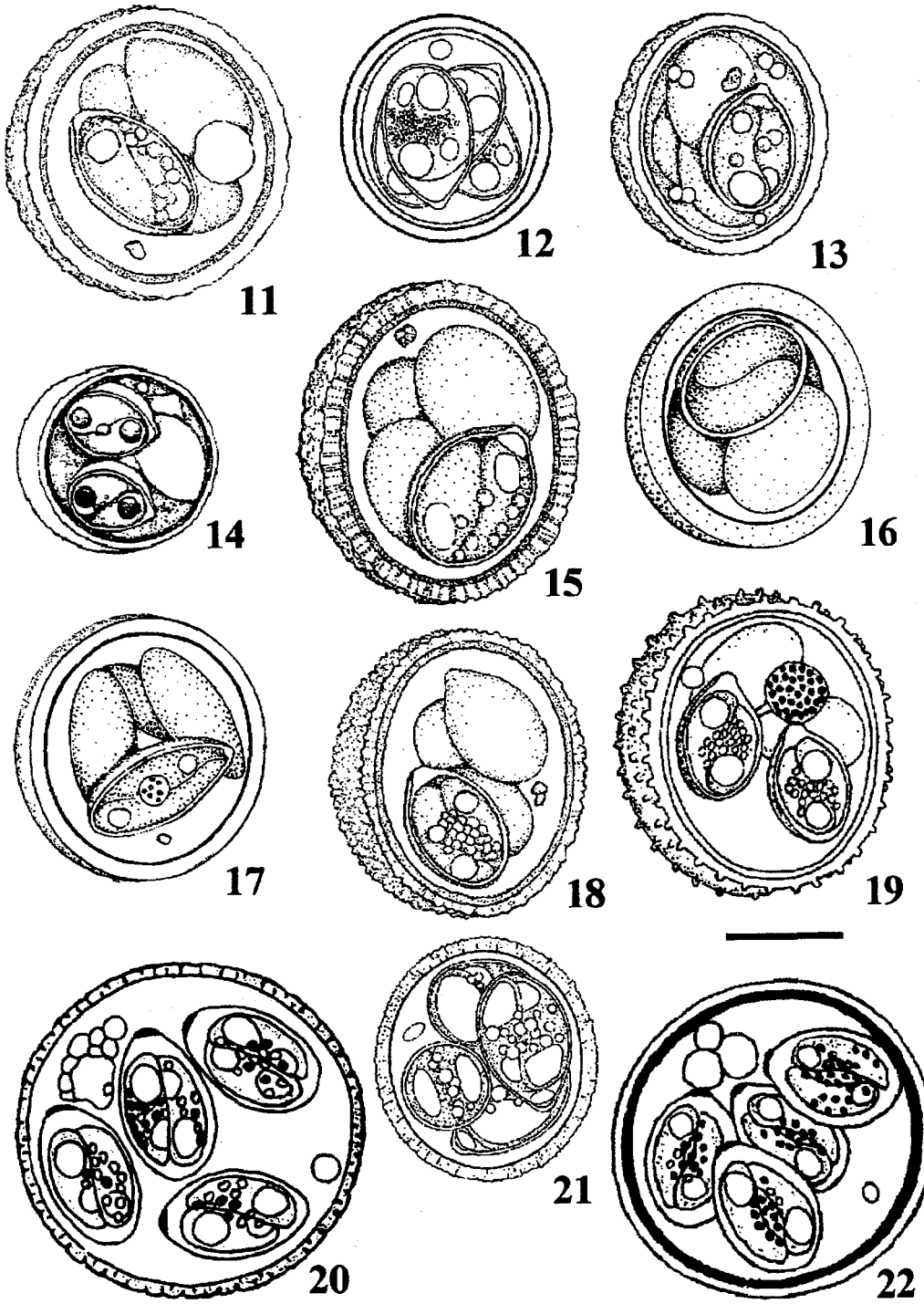

Plate II. Figures 11–22.

11. *E. humboldtensis*. **12.** *E. kummingensis* (scanned from Yang-Xian and Fu-Qiang 1983, Fig. 1). **13.** *E. nigricani*. **14.** *E. pilarensis*. **15.** *E. rioarribaensis*. 16. *E. nyctali* (redrawn from Gottschalk 1974). **17.** *E. vejsovi* (redrawn from Černá 1976). **18.** *E. jacksonensis*. **19.** *E. chiropteri* (scanned from: Alyousif 1999a, Fig. 5). **20.** *E. kuhliensis* (scanned from Alyousif 1999b, Fig. 4). **21.** *E. macyi* (scanned from Wheat 1975a, Fig. 1). **22.** *E. pipistrellus* (scanned from Alyousif, Al-Dakhil and Al-Shawa 1999, Fig. 4).

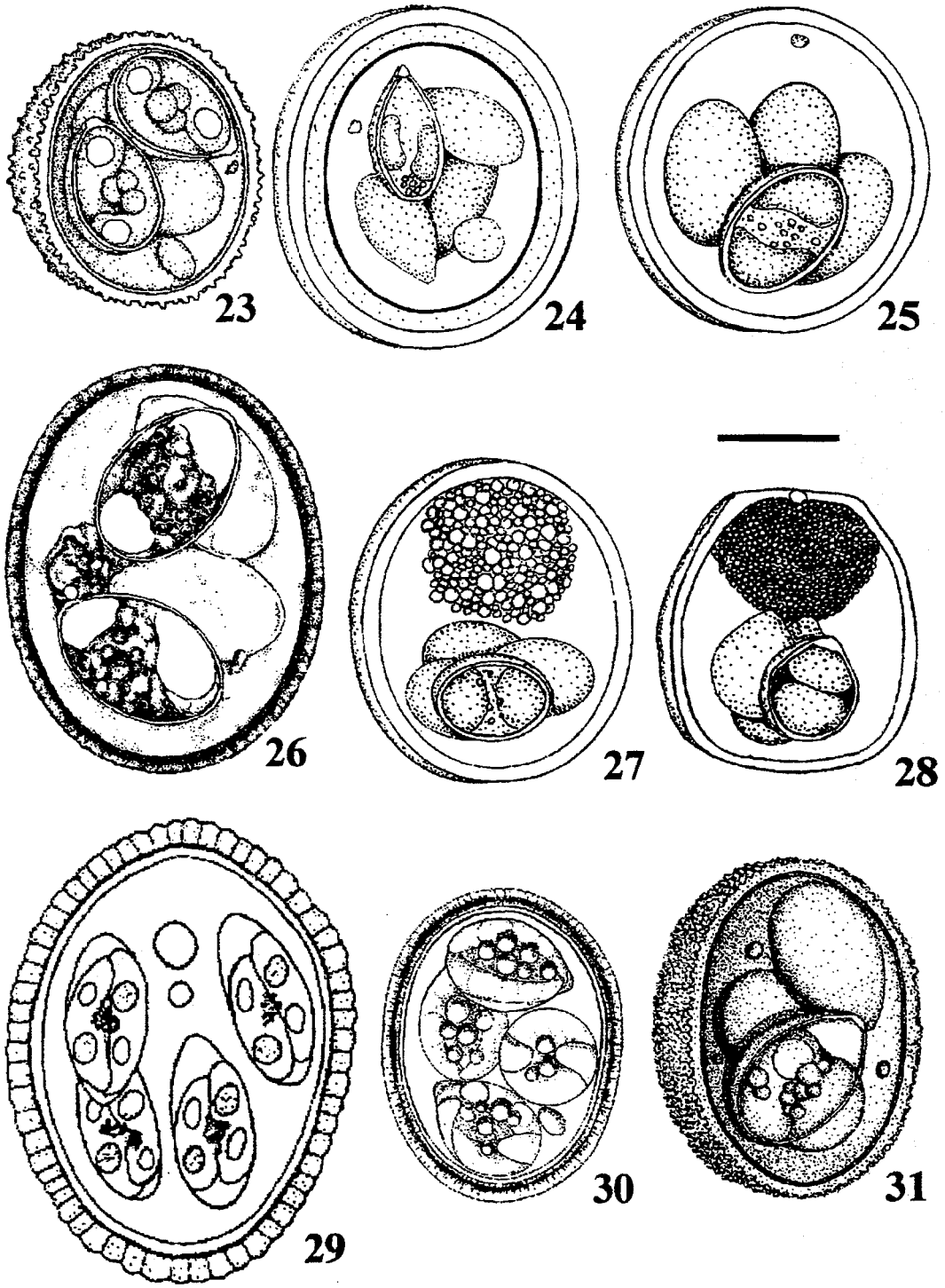

Plate III. Figures 23–31.

23. *E. redukeri*. **24.** *E. vespertilii* (redrawn from Musaev and Veisov 1961). **25.** *E. zakirica* (redrawn from Musaev 1967). **26.** *E. tomopea*. **27.** *E. dukei* (redrawn from Lavier 1927). **28.** *E. levinei* (redrawn from Bray 1958). **29.** *E. eumops* (scanned from Marinkelle 1968, Fig. 1C). **30.** *E. molossi* (scanned from Lainson and Naiff 1998, Fig. 25). **31.** *E. tadarida*.

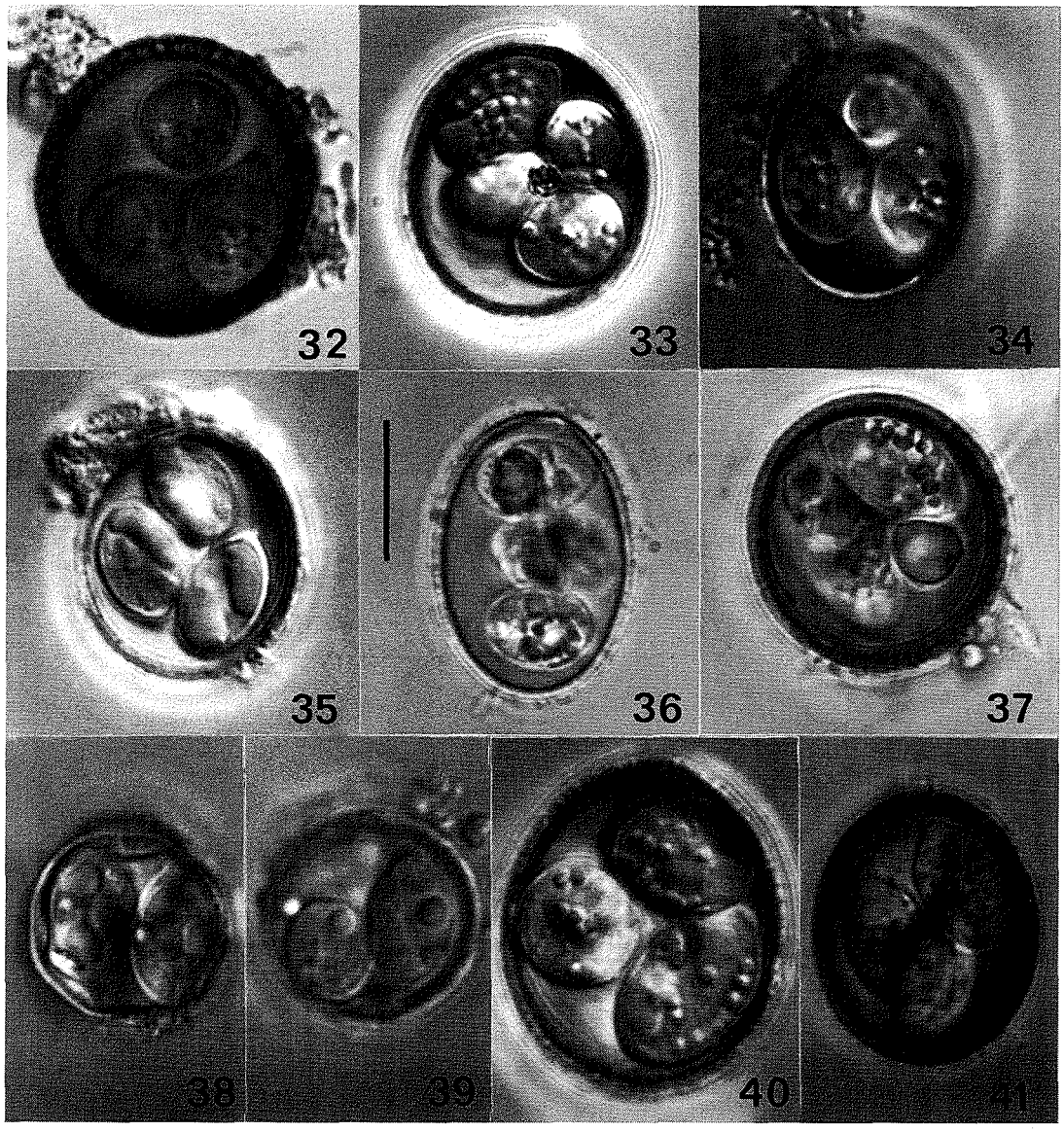

Plate IV. Figures 32–41.

32. *E. magnirostrumi.* **33.** *E. antrozois.* **34.** *E. californicensis.* **35.** *E. evoti.* **36.** *E. catronensis.* **37.** *E. humboldtensis.* **38.** *E. nigricani.* **39.** *E. pilarensis.* **40.** *E. rioarribaensis.* **41.** *E. jacksonensis.*

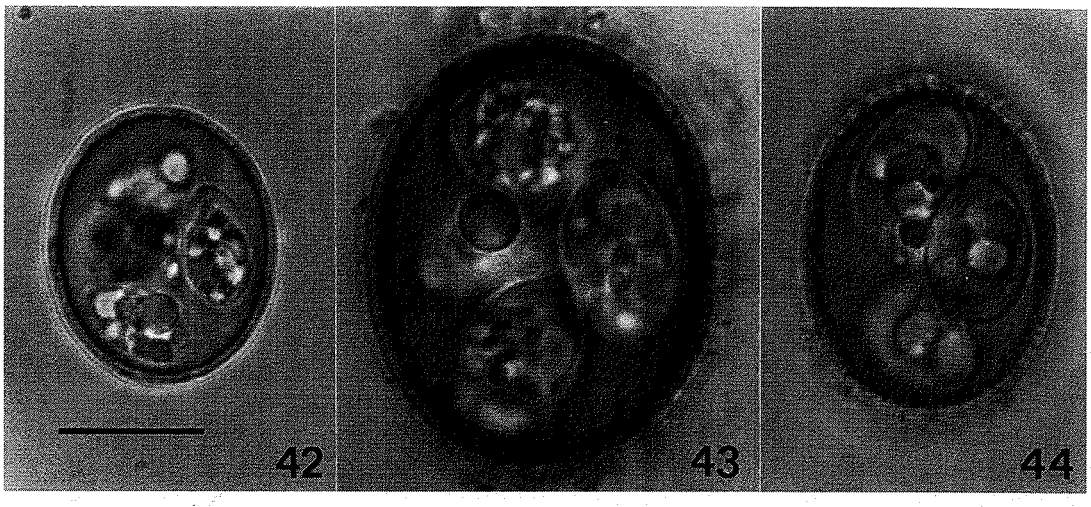

Plate V. Figures 42–44.
42. *E. redukeri.* **43.** *E. tomopea.* **44.** *E. tadarida.*

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