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Coccidia (Apicomplexa: Eimeriidae) of amphibians of the world

DONALD W. DUSZYNSKI[1], MATTHEW G. BOLEK[2] & STEVE J. UPTON[3]

[1]*Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131. E-mail: eimeria@unm.edu*
[2]*Department of Biology, University of Nebraska at Kearney, Kearney, NE 68849. E-mail: bolekmg@unk.edu*
[3]*Division of Biological Sciences, Kansas State University, Manhattan, Kansas 66506. E-mail: coccidia@ksu.edu*

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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, or on vertebrate animals. They also are among the least studied and understood, with the exception of those species that cause pathology in domesticated hosts. Here we review and evaluate all published descriptions of coccidians within the largest family of the phylum, Eimeriidae Minchin 1903, because there has never been a detailed taxonomic summation for those species that infect amphibians. About 35 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*, *incertae sedis*, or *nomen nuda*. The class Amphibia has three orders, 56 families, 464 genera and 6009 species (Frost *et al*. 2006). There are no coccidia known from 41 of the 56 (73%) families, 436 of the 464 (94%) genera and 5964 of the 6009 (>99%) species. In the Anura (frogs), only 14 of the 44 (32%) families (Bombinatoridae, Bufonidae, Dicroglossidae, Hylidae, Hyperoliidae, Leptodactyllidae, Limnodynastidae, Megophyridae, Microhylidae, Pipidae, Ptychadenidae, Pyxicephalidae, Ranidae, Rhacophoridae), 30 of the 388 (8.8%) genera, and 67 of the 5283 (1.2%) species have been examined for coccidia and 30 coccidia are known (18 *Eimeria*, 9 *Isospora*, 2 *Goussia*, and 1 *Hyaloklossia* species). In the Urodela (salamanders), 7 of the 9 (78%) families (Ambystomatidae, Amphiumidae, Cryptobranchidae, Plethodontidae, Proteidae, Salamandridae, Sirenidae), 18 of the 64 (28%) genera and 45 of the 553 (8%) species have been examined and 21 coccidia are known (19 *Eimeria* and 2 *Isospora* species). In the Gymnophiona (caecilians), only 1 of 3 (33%) families, 1 of 12 (8%) genera, and only 1 of the 173 (0.6%) species, *Dermophis mexicanus* (family Caeciliidae), have been examined and 1 *Eimeria* species is known. Also in the Amphibia, there are 10 *species inquirendae* (a species of doubtful identity), 22 *incertae sedis* (uncertain taxonomic position), and 5 names are considered *nomen nuda*. In general, herpetologists are encouraged to be more receptive to working with parasitologists to use comparative parasite data that might provide insights into amphibian evolution and habitat use. The eimeriid coccidia are ideal parasites for such cooperative efforts because they can be collected easily by noninvasive fecal collections.

Key words: Eimeriidae, *Eimeria*, *Isospora*, *Goussia*, *Hyaloklossia*, review article

Introduction

The Amphibia, with 3 orders, 56 families, 464 genera, and circa 6009 species (Frost *et al*. 2006), is one of the most understudied vertebrate classes when it comes to their parasite fauna (Lannoo 2005). With habitat loss, acid rain, pollution of waterways by insecticides and herbicides from farmland runoff, and other perturbations due to continued human encroachment that seem to be increasing mortality among amphibian populations worldwide, it is critical that we learn more about their biology by investing heavily in multi-disciplinary approaches (Lannoo 2005). When amphibians (and other vertebrates, for that matter) are collected, we need to take more than carcass and, perhaps, frozen tissues; there is a tremendous harvest of parasite fauna and information that, most often, goes unused and is discarded. Such data may be able to contribute significantly to better understanding amphibian evolutionary relationships because some of their parasites, especially their coccidia, are often host-specific (at least in some other vertebrate groups), 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 are not there, but because we have not made a concerted effort to look for them (e.g. Duszynski *et al*. 1999; Duszynski & Upton 2000; Bolek *et al*. 2003; Jirků & Modrý 2005).

An overview of some of the species of coccidia known from amphibians was published over 13 years ago (Upton & McAllister 1988; McAllister 1989; Upton *et al*. 1993); however, they and Wilber *et al*. (1998), noted that most earlier authors who published descriptions of new species from amphibians and other vertebrate species 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 Amphibia worldwide up to 2006, make qualitative decisions about the validity of those species, standardize their descriptions, present illustrations (photomicrographs, when available, and line drawings) at the same scale for all of them, and provide in one place all of the known photosyntypes.

Methods

Methods followed are from Wilber *et al*. (1998) regarding the number of oocyst-sporocyst characters needed to validate a coccidium species and in the definition and deposition of specimens [United States National Parasite Collection (USNPC), Beltsville MD; Harold W. Manter Laboratory (HWML), University of Nebraska, Lincoln NE; Arkansas State University Museum of Zoology (ASUMZ), State University AR]. The type host, other hosts, type locality, 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 (1 example), and molecular analyses/systematics are reviewed. Most line drawings and all photomicrographs (Figs. 13–16; 21; 32; 35–37; 40; 53–66) are original. However, when original line drawings were considered useful/adequate, they were scanned from original sources (see Table 1). 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); micropyle cap (MC); oocyst residuum (OR); polar granule (PG); *sporocyst characters*: length (L), width (W), their ranges and ratio (L/W); Stieda body (SB); sub-Stieda body (SSB); para-Stieda body (PSB); sporocyst residuum (SR); sporozoites (SZ); refractile bodies (RB) and nucleus (N) in SZ. All measurements given are in µm and are from sporulated oocysts only. Amphibian taxonomic names are according to Frost *et al*. (2006).

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 our decision, we either accepted or rejected it as a valid species. If it was considered to be a valid species, we provided a standardized (boiler plate) description including all of the pub-

lished information to date; if certain structural features are unreported, they could not be included in the standardized description.

TABLE 1. List of the figures that were scanned from the original description with the permission of the authors and/or publishers.

Eimeria/*Goussia*/*Hyaloklossia*/*Isospora* spp. (Fig. No. in text)	Source of line drawing/Scanned From
E. algonquini (Fig. 22)	Chen & Desser (1989, Fig. 2)
E. ambystomae (Fig. 32)	Duszynski *et al.* (1972, Fig. 19)
E. belawini (Fig. 10)	Yakimoff (1930b, Fig. 4)
E. bufomarini (Fig. 3)	Paperna & Lainson (1995, Fig. 1)
E. canaliculata (Fig. 51)	Lavier (1936, Fig. 3d)
E. cyanophylyctis (Fig. 8)	Chakravarty & Kar (1952, Fig. 18)
E. dermophis (Fig. 53)	Asmundsson *et al.* (2000, Fig. 4)
E. distorta (Fig. 33)	Saxe (1955, Fig. A)
E. fitchi (Fig. 23)	McAllister *et al.* (1995, Fig. 1)
E. flexuosa (Fig. 12)	Upton & McAllister (1988, Fig. 9)
E. fragilis (Fig. 31)	Jirků & Modrý (2005, Fig. 10)
E. grobbeni (Fig. 48)	Rudovsky (1925, Fig. 25)
E. himalayana (Fig. 4)	Ray & Misra (1943, Fig. 14)
E. kermiti (Fig. 24)	Chen & Desser (1988, Fig. 3)
E. kingi (Fig. 34)	Saxe (1955, Fig. B)
E. laminata (Fig. 5)	Ray (1935, Fig. 11)
E. leptodactyli (Fig. 20)	Carini (1931c, Fig. 4)
E. longaspora (Fig. 46)	Barrow & Hoy (1960, Fig. 4)
E. mazzai (Fig. 1)	Yakimoff & Gousseff (1934, Fig. 2)
E. megaresidua (Fig. 47)	Barrow & Hoy (1960, Fig. 2)
E. microcapi (Fig. 35)	Duszynski *et al.* (1972, Fig. 20)
E. nipponensis (Fig. 41)	Matubayasi (1937, Fig. 11)
E. opacum (Fig. 36)	Upton *et al.* (1993, Fig. 1)
E. prevoti (Fig. 25)	Boulard (1975, Fig. A)
E. propria (Fig. 52)	Lavier (1936, Fig. 1a)
E. pyrrhogaster (Fig. 42)	Matubayasi (1937, Fig. 12)
E. ranae (Fig. 29)	Dobell (1909, Fig. 91)
E. ranarum (Fig. 26)	Laveran & Mesnil (1902a, Fig. 9)
E. saitamaensis (Fig. 43)	Matubayasi (1937, Fig. 10)
E. salamandrae (Fig. 49)	Dobell (1909, Fig. 566e)
E. spherica (Fig. 44)	Schneider (1887, Fig. 18)
E. streckeri (Fig. 13)	Upton & McAllister (1988, Fig. 10)
E. streckeri (Fig. 14)	Bolek *et al.* (2003, Fig. 5)
E. tarichae (Fig. 50)	Doran (1953, Fig. 2)
E. terraepokotorum (Fig. 9)	Jirků & Modrý, (2006a Fig. 11)

to be continued

TABLE 1. (continued)

Eimeria/*Goussia*/*Hyaloklossia*/*Isospora* spp. (Fig. No. in text)	Source of line drawing/Scanned From
E. tertia (Fig. 45)	Lavier (1936, Fig. 1c)
E. urodela (Fig. 37)	Duszynski *et al.* (1972, Fig. 21)
E. waltoni (Fig. 38)	Saxe (1955, Fig. C)
E. wambaensis (Fig. 18)	Jirků & Modrý (2005, Fig. 11)
G. hyperolisi (Fig. 19)	Paperna *et al.* (1997, Fig. 26)
G. neglecta (Fig. 27)	Molnár (1995, Fig. 1a)
H. lieberküehni (Fig. 28)	Laveran & Mesnil (1902b, Fig. 8)
I. brumpti (Fig. 7)	Lavier (1941, Fig. 1d)
I. cogginsi (Fig. 15)	Bolek *et al*. (2003, Fig. 10)
I. cruzi (Fig. 17)	Carini (1936, Fig. 1c)
I. delicatus (Fig. 16)	Upton & McAllister (1988, Fig. 11)
I. fragosum (Fig. 21)	Upton & McAllister (1988, Fig. 12)
I. hightoni (Fig. 40)	Upton *et al.* (1993, Fig. 2)
I. jeffersonianum (Fig. 39)	Doran (1953, Fig. 1)
I. neos (Fig. 30)	Kazubski & Grabda-Kazubska (1973, Fig. 2b)
I. stomatici (Fig. 2)	Chakravarty & Kar (1952, Fig. 2)
I. wenyoni (Fig. 6)	Chakravarty & Kar (1952, Fig. 18)
I. wladimirovi (Fig. 11)	Yakimoff (1930b, Fig. 2)

Results

In the Amphibia, there are 38 valid *Eimeria*, 11 *Isospora*, 2 *Goussia* and 1 *Hyaloklossia* species. Ten organisms or names (1 "Coccidium," 1 "Oocysts," 1 "Unsporulated Coccidian," 1 "*Goussia* sp." 1 "*Goussia*-like coccidian," 1 *Eimeria*, and 5 *Isospora* spp.) are considered *species inquirendae*; 5 organisms/names (2 "Coccidium," 2 *Eimeria*, 1 *Isospora*) are considered *nomen nuda*; and 22 organisms/names (10 *Eimeria*, 5 *Isospora*, 6 unsporulated oocysts, 1 *Isospora*-like) are considered *incertae sedis* (Table 2). There are no reports of coccidia in the following families because no species or few individuals in these families have ever been examined for coccidia, or the studies remain unreported: Anura (frogs): Alytidae, Amphignathodontidae, Aromobatidae, Arthroleptidae, Batrachophrynidae, Brachycephalidae, Brevicipitidae, Centrolenidae, Ceratobatrachidae, Ceratophryidae, Cryptobatrachidae, Cycloramphidae, Dendrobatidae, Heleophrynidae, Hemiphractidae, Hemisotidae, Hylodidae, Leiopelmatidae, Leiuperidae, Mantellidae, Micrixalidae, Myobatrachidae, Nyctibatrachidae, Pelobatidae, Pelodytidae, Petropedetidae, Pipidae, Phrynobatrachidae, Pyxicephalidae, Rhinophrynidae, Scaphiopodidae, Sooglossidae; Urodela (salamanders): Amphiumidae, Cryptobranchidae, Hynobiidae, Proteidae, Rhyacotritonidae, Sirenidae; Gymnophiona (caecilians): Ichthyophiidae, Rhinatrematidae (Upton & McAllister 1988; Upton *et al*. 1993; Asmundsson *et al*. 2000; Bolek *et al*. 2003; Jirků & Modrý 2006a, b). Amphibian species from which coccidia are known are listed by order, suborder, family and genus and life stage from which the coccidium was described, in the taxonomic sequence presented by Frost *et al*. (2006). Coccidia species are listed alphabetically under each host genus.

TABLE 2. Summary of all amphibian species and individuals that have been examined for coccidia and the known Eimeriidae described from Amphibians, through 2006.

Order/family Genus/species	No. infected/ No. examined	*Eimeria/Goussia/* *Hyaloklossia/Isospora*	Reference(s)
ANURA			
Bombinatoridae			
Bombina variegata	Unknown	*I. lieberkuehni*[c]	Golemansky & Bitseva (1975)
Bufonidae			
Amietophrynus garmani	0/6	0	Jirků & Modrý (2006a)
A. gutturalis	0/2	0	Jirků & Modrý (2006a)
Anaxyrus debilis	0/3	0	Upton & McAllister (1988)
A. valliceps	0/21	0	Upton & McAllister (1988)
A. woodhousii	0/22	0	Upton & McAllister (1988); Bolek *et al.* (2003)
Bufo bufo	Unknown	*E. mazzai*	Yakimoff & Gousseff (1934)
		Isospora sp.[b]	Wenyon (1926)
B. stomaticus	Unknown	*I. stomatici*	Chakravarty & Kar (1944)
Bufo sp. 1	0/2	0	Jirků & Modrý (2006a)
Bufo sp. 2	0/4	0	Jirků & Modrý (2006a)
Bufo sp. 3	Unknown	*Isospora* sp.[b]	Grassi (1882); Grassi & Feletti (1892); Labbe (1899); Walton (1941)
Chaunus marinus	6/30	*E. bufomarini*	Paperna & Lainson (1995)
	1/3	Unsporulated oocyst 1[b]	Rzepczyk (1976)
	1/3	Unsporulated oocyst 2[b]	Rzepczyk (1976)
	1/3	Unsporulated oocyst 3[b]	Rzepczyk (1976)
	1/3	Unsporulated oocyst 4[b]	Rzepczyk (1976)
	1/3	*Isospora*-like oocyst 5[b]	Rzepczyk (1976)
	0/389	0	Delvinquier & Freeland (1988)
Duttaphrynus himalayanus	1/1	*E. himalayana*	Ray & Misra (1943)
D. melanostictus	2/200	*E. laminata*	Ray (1935)
	2/several hundred	*I. wenyoni*	Ray & Das Gupta (1935)
Ollotis canalifera	1/7	*Eimeria* sp.[d]	Asmundsson (2003)
Pseudepidalea viridis	Unknown	*I. brumpti*	Lavier (1941)
Dicroglossidae			
Euphlyctis cyanophlyctis	Unknown	*E. cyanophlyctis*	Chakravarty & Kar (1944)
Fejervarya limnocharis	Unknown	*Isospora* sp.[b]	Chakravarty & Kar (1944)
F. vittigera	Unknown	*Eimeria* sp.[b]	Hegner & Chu (1930)
Hoplobatrachus occipitalis	2/5	*E. terraepokotorum*	Jirků & Modrý (2006a)
H. tigerinus	Unknown	*Isospora* sp.[b]	Chakravarty & Kar (1944)
Hylidae			
Acris crepitans	0/49	0	Upton & McAllister (1988); Bolek *et al*. (2003)

to be continued

TABLE 2. (continued)

Order/family Genus/species	No. infected/ No. examined	*Eimeria/Goussia/* *Hyaloklossia/Isospora*	Reference(s)
Hyla arborea	Unknown	*E. belawini*	Yakimoff 1930a, b; Walton (1940)
	Unknown	*I. wladimirovi*	Yakimoff (1930a, b)
	Unknown	*I. hylae*[c]	Mesnil (1907)
H. chrysoscelis	0/31	0	Bolek *et al*. (2003)
Litoria caerulea	Unknown	Unsporulated oocyst 6[b]	Rzepczyk (1976)
		Unsporulated oocyst 7[b]	Rzepczyk (1976)
		Isospora sp. 8[b]	Rzepczyk (1976)
Pseudacris clarkia	0/40	0	Upton & McAllister (1988)
P. streckeri	10/26	*E. flexuosa*	Upton & McAllister (1988)
	16/34	*E. streckeri*	Upton & McAllister (1988)
	5/34	*I. delicatus*	Upton & McAllister (1988)
P. illinoensis	1/8	*I. delicatus*	Upton & McAllister (1988)
P. triseriata	2/30	*E. streckeri*	Bolek *et al*. (2003)
	23/30	*I. cogginsi*	Bolek *et al*. (2003)
Scinax crospedospilus	Unknown	*I. cruzi*	Pinto & Vallim (1926)
S. fuscovarius	Unknown	*I. cruzi*	Pinto & Vallim (1926)
S. nasicus	Unknown	*I. cruzi*	Pinto & Vallim (1926)
S. ruber	Unknown	*I. cruzi*	Pinto & Vallim (1926)
Hyperoliidae			
Hyperolius viridiflavus	1/46	*E. wambaensis*	Jirků & Modrý (2005, 2006a)
	8/13	*G. hyperolisi*	Paperna *et al*. (1997)
H. kivuensis	0/20	0	Jirků & Modrý (2006a)
Kassina senegalensis	0/20	0	Jirků & Modrý (2006a)
Leptodactylidae			
Leptodactylus ocellatus	Unknown	*E. leptodactyli*	Carini (1931a, b, c)
L. fuscus	Unkonwn	Coccidian[c]	Paperna & Lainson (1995)
Limnodynastidae			
Limnodynastes tasmaniensis	1/1	*Goussia*-like coccidian[c]	Paperna *et al*. (1997)
Megophyridae			
Megophrys nasuta	9/9	"Oocysts"[c]	Griner (1982)
Microhylidae			
Gastrophryne carolinensis	0/2	0	Upton & McAllister (1988)
G. olivacea	14/95	*I. fragosum*	Upton & McAllister (1988)
Pipidae			
Xenopus sp.	0/65	0	Jirků & Modrý (2006a)
Ptychadenidae			
Ptychadena sp. 1	1/2	Coccidian[c]	Jirků & Modrý (2006a)
Ptychadena sp. 2	0/6	0	Jirků & Modrý (2006a)
Ptychadena sp. 3	0/3	0	Jirků & Modrý (2006a)

to be continued

TABLE 2. (continued)

Order/family Genus/species	No. infected/ No. examined	*Eimeria/Goussia/* *Hyaloklossia/Isospora*	Reference(s)
Pyxicephalidae	Unknown		
Amietia sp. 1	0/4	0	Jirků & Modrý (2006a)
Amietia sp. 2	0/4	0	Jirků & Modrý (2006a)
Tomopterna sp.	0/25	0	Jirků & Modrý (2006a)
Ranidae			
Lithobates berlandieri	0/2	0	Upton & McAllister (1988)
L. blairi	0/54	0	Upton & McAllister (1988); Bolek *et al*. (2003)
L. catesbeianus	26/214	*E. algonquini*	Chen & Desser (1989); Upton & McAllister (1988); Bolek *et al*. (2003)
	3/214	*E. kermiti*	Chen & Desser (1989); Upton & McAllister (1988); Bolek *et al*. (2003)
L. clamitans	3/25	*E. algonquini*	Chen & Desser (1989); Upton & McAllister (1988); Bolek *et al*. (2003)
	1/25	*E. kermiti*	Chen & Desser (1989); Upton & McAllister (1988); Bolek *et al.* (2003)
	2/4	*Eimeria sp.*[b]	Fantham & Porter (1947)
L. maculate	1/9	*Eimeria* sp.[d]	Asmundsson (2003)
L. pipiens	1/137	*I. lieberküehni*[c]	Labbé, (1894); Levine & Nye (1977)
L. septentrionalis	7/68	*E. algonquini*	Chen & Desser (1989)
	1/68	*E. kermiti*	Chen & Desser (1989)
L. sphenocephala	0/15	0	Upton & McAllister (1988)
L. sylvaticus	3/9	*E. algonquini*	Chen & Desser (1989)
	11/13	*E. fitchi*	McAllister *et al*. (1995)
	1/9	*E. kermiti*	Chen & Desser (1989)
Pelophylax lessonae	Unknown	*E. prevoti*	Laveran & Mesnil (1902a); Doflein (1909); Nöller (1913)
P. esculenta	Unknown	*I. ranae*[a]	Dobell (1909)
	Unknown	*E. ranarum*	Labbé (1894a); Doflein (1909)
	7/10	*G. neglecta*	Nöller (1920); Molnár (1995)
	>6/2,016	*H. lieberküehni*	Nöller (1913, 1923); Labbé, (1894a); Laveran & Mesnil (1902a); Kazubski & Grabda-Kazubski (1973, 1974); Voitková (1976); Modrý *et al*. (2001)
	Unknown	*Eimeria* sp. 1[b]	Eimer (1890); Upton & McAllister (1988)
	Unknown	*Eimeria* sp. 2[b]	Pachinger (1886); Upton & McAllister (1988)
P. ridibundus	19/38	G. neglecta	Molnár (1995)
Pelophylax sp.	Unknow	*I. lieberküehni*[c]	Labbé (1894a)
Rana arvalis	>1/38	*I. neos*	Yakimoff & Gousseff (1936); Kazubski & Grabda-Kazubska (1973, 1974)
		Isospora sp.[b]	Kazubski & Grabda-Kazubska (1973, 1974)

to be continued

TABLE 2. (continued)

Order/family Genus/species	No. infected/ No. examined	*Eimeria/Goussia/* *Hyaloklossia/Isospora*	Reference(s)
R. dalmatina	23/45	*Goussia* sp.	Jirků & Modrý (2006b)
R. temporaria	Unknown	*E. ranae*	Dobell (1908, 1909)
	Unknown	*E. ranarum*	Labbé (1894a)
	Unknown	*H. lieberküehni*	Laveran & Mesnil (1902b)
Rana sp.	Unknown	*E. pylori*[a]	Gebhardt, (1897); Levine & Becker (1933)
Rhacophoridae			
Chiromantis petersii kelleri	1/1	*E. fragilis*	Jirků & Modrý (2005)
URODELA			
Ambystomatidae			
Ambystoma laterale	0/14	0	Bolek (2000)
A. annulatum	0/4	0	Upton *et al*. (1993)
A. jeffersonianum	2/7	*I. jeffersonianum*	Doran (1953)
A. maculatum	0/22	0	Upton *et al*. (1993)
A. mavortium	17/17; Unknown	*E. ambystomae*	Duszynski *et al*. (1972); Bolek *et al*. (2003)
	1/17	*E. microcapi*	Duszynski *et al*. (1972)
	6/17	*E. urodela*	Duszynski *et al*. (1972)
A. opacum	1/5	*E. opacum*	Upton *et al*. (1993)
	1/1	*Eimeria* sp.6[b]	Rankin (1937)
	1/1	*Eimeria* sp.[b]	Walton (1942)
A. talpoideum	0/12	0	Upton *et al*. (1993)
A. texanum	12/61	*E. ambystomae*	Upton *et al*. (1993)
A. tigrinum	31/65	*E. ambystomae*	Doran (1953); Saxe (1955); Upton *et al*. (1993); Bolek (2000)
	Unknown	*E. distorta*	Saxe (1955)
	Unknown	*E. kingi*	Saxe (1955)
	1/1	*E. urodela*	Bolek (2000)
	Unknown	*E. waltoni*	Saxe (1955)
	Unknown	*Eimeria* sp. 1[b]	(Walton 1961a, b, c)
	Unknown	*Eimeria* sp. 2[b]	(Walton 1961a, b, c)
Amphiumidae			
Amphiuma tridactylum	0/2	0	Upton *et al*. (1993)
Cryptobranchidae			
Cryptobranchus bishopi	0/3	0	Upton *et al*. (1993)
Plethodontidae			
Aneides lugubris	0/7	0	Doran (1953)
atrachoseps attenuatus	0/65	0	Doran (1953)
B. major	0/4	0	Doran (1953)
Desmognathus auriculatus	0/1	0	Upton *et al*. (1993)

to be continued

TABLE 2. (continued)

Order/family Genus/species	No. infected/ No. examined	*Eimeria/Goussia/* *Hyaloklossia/Isospora*	Reference(s)
D. brimleyorum	0/6	0	Upton *et al*. (1993)
D. monticola	1/2	Coccidium[a]	Saxe (1955)
D. quadramaculatus	1/8	Coccidium[a]	Saxe (1955)
Eurycea cirrigera	0/1	0	Bolek (2000)
E. longicauda	0/1	0	Upton *et al*. (1993)
E. lucifuga	0/1	0	Upton *et al*. (1993)
E. multiplicata	0/1	0	Upton *et al*. (1993)
E. neotenes	0/8	0	Upton *et al*. (1993)
E. tridentifera	0/2	0	Upton *et al*. (1993)
E. tynerensis	0/36	0	Upton *et al*. (1993)
Hemidactylium scutatum	0/2	0	Upton *et al*. (1993)
Plethodon albagula	8/46	*I. hightoni*	Upton *et al*. (1993)
P. caddoensis	0/51	0	Upton *et al*. (1993); McAllister *et al*. (2002)
P. cinereus	0/4	0	Bolek (2000)
P. fourchensis	0/3	0	Upton *et al*. (1993)
P. kiamichi	1/16	*Eimeria* sp.[b]	McAllister *et al*. (2002)
P. neomexicanus	0/10	0	Upton *et al*. (1993)
P. ouachitae	0/9	1	Upton *et al*. (1993); McAllister *et al*. (2002)
P. serrautus	0/45	0	Upton *et al*. (1993); McAllister *et al*. (2002)
Proteidae			
Necturus maculosus	0/1	0	Upton *et al*. (1993)
Salamandridae			
Cynops pyrrhogaster	2/90	*E. nipponensis*	Matubayasi (1937); Upton *et al*. (1993)
	1/90	*E. pyrrhogaster*	Matubayasi (1937); Upton *et al*. (1993)
	2/90	*E. saitamaensis*	Matubayasi (1937); Upton *et al*. (1993)
Lissotrition helvetricus	Unknown	*E. canaliculata*	Lavier (1936)
	Unknown	*E. spherica*	Schneider (1887); Levine & Becker (1933)
L. vulgaris	Unknown	*E. canaliculata*	Lavier (1936)
	Unknown	*E. propria*	Schneider (1881); Doflein (1909)
	Unknown	*E. spherica*	Schneider (1887); Levine and Becker (1933)
Mesotriton alpestris	Unknown	*E. canaliculata*	Lavier (1936)
	Unknown	*E. propria*	Schneider (1881); Doflein (1909)
	Unknown	*E. spherica*	Schneider (1887); Levine & Becker (1933)
	Unknown	*E. tertia*	Lavier (1936)
Notophthalmus viridescens	13/157	*E. longaspora*	Barrow & Hoy (1960); Upton *et al*. (1993)
	22/144	*E. megaresidua*	Barrow & Hoy (1960)
Salamandra atra	Unknown	*E. grobbeni*	Rudovsky (1925)
	Unknown	*E. salamandraeatrae*	Phisalix (1927); Levine & Becker (1933)
	Unknown	*Eimeria* sp.[b]	Rudovsky (1925)

to be continued

TABLE 2. (continued)

Order/family Genus/species	No. infected/ No. examined	*Eimeria/Goussia/ Hyaloklossia/Isospora*	Reference(s)
S. salamandra	Unknown	*E. salamandrae*	Drüner (1894); Labbé (1894b); Simond (1897); Heidenhain (1888); Steinhaus (1889); Dobell (1909); Doflein & Reichenow (1953)
Taricha torosa	3/28	*E. tarichae*	Doran (1953); Levine (1980)
Triturus cristatus	Unknown	*E. canaliculata*	Lavier (1936)
	Unknown	*E. propria*	Schneider (1881); Doflein (1909)
	Unknown	*E. labbei*[a]	Labbé (1894); Hardcastle (1943)
Sirenidae			
Siren intermedia	0/16	0	Upton *et al*. (1993)
Gymnophiona			
Caeciliidae			
Dermophis mexicanus	2/5	*E. dermophis*	Asmundsson *et al*. (2000)
22 families, 50 genera, 113 species	342/5725 (5.9%)	39 *Eimeria*, 11 *Isospora*, 2 *Goussia*, 1 H*yaloklossia* spp.	

[a] *nomen nudum*, [b] *incertae sedis*, [c] *species inquirenda*, [d] Asmundsson (2003) examined 7 *Ollotis canalifera* and 9 *Lithobates maculata* from Guatemala, Sololá, San Lucas Tolimán, Finca Santo Tomás, Central America and reported finding a single toad and frog infected with 2 distinct *Eimeria* species respectively, however, both of these species superficially resembled rodent coccidia and we believe they were spurious parasites.

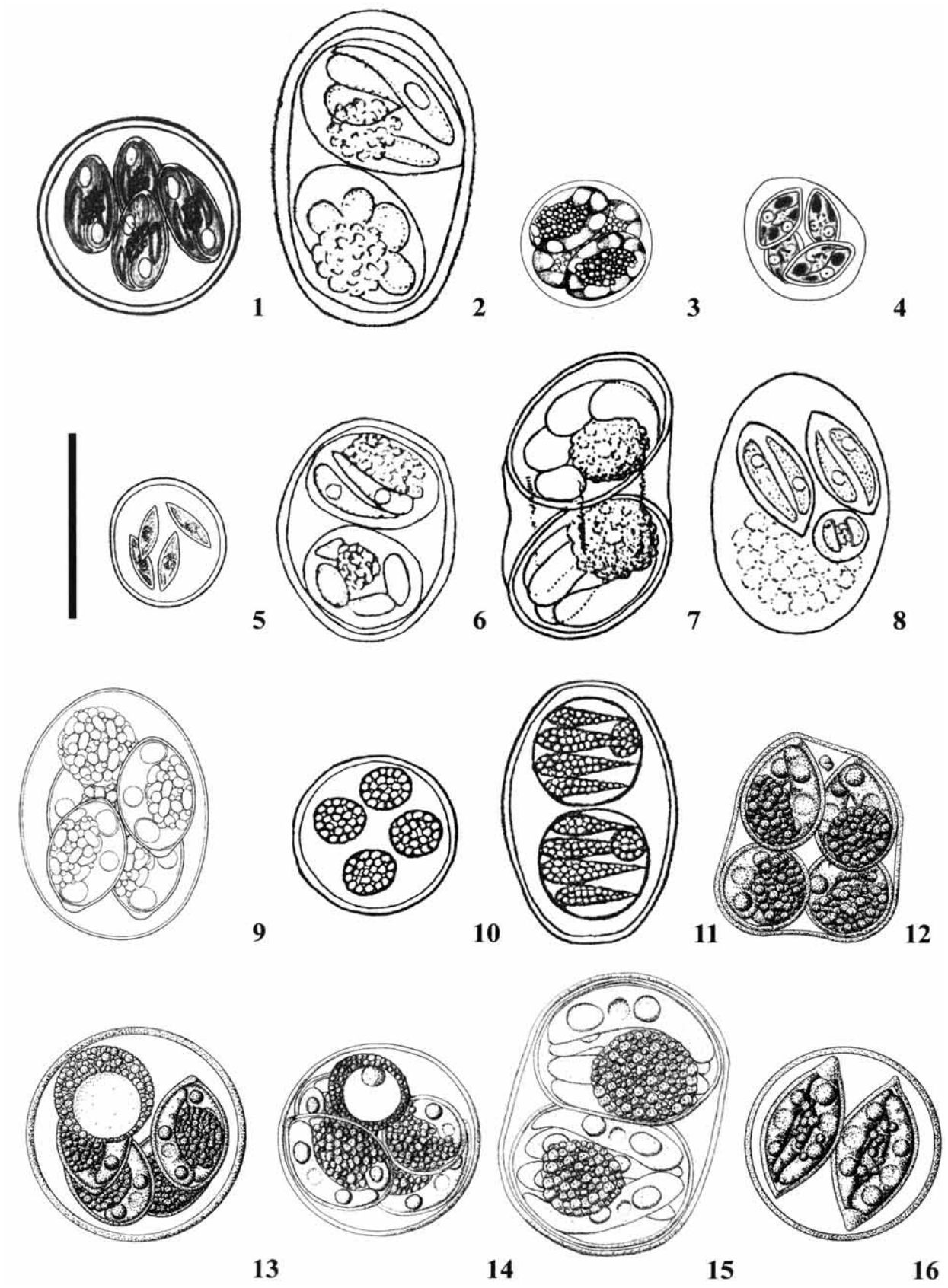
AMPHIBIA
(3 orders, 56 families, 464 genera, 6009 species)

ANURA Fischer von Waldheim 1813-Frogs
(44 families, 388 genera, 5283 species)

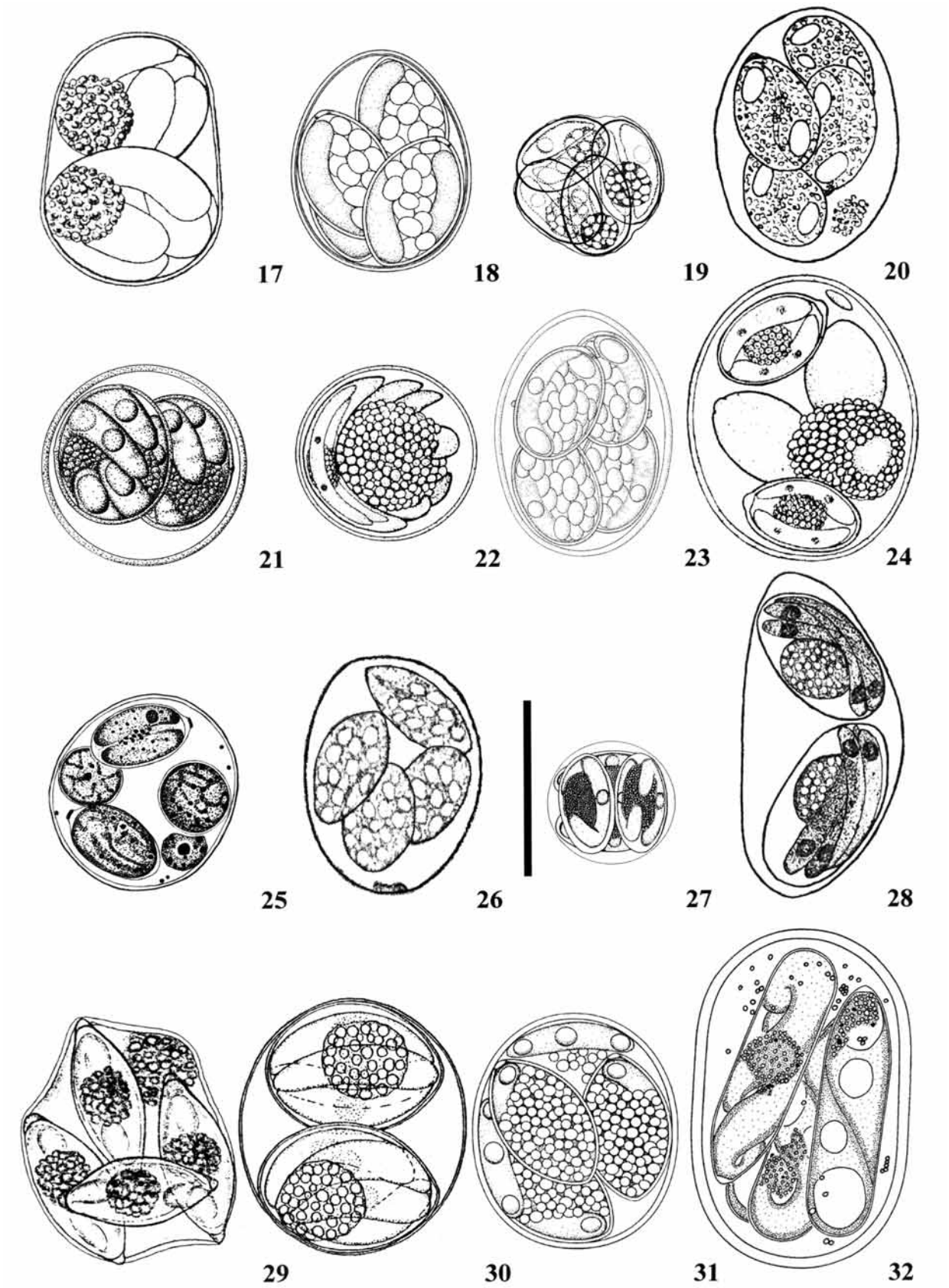
Family Bombinatoridae Gray 1825
(2 genera, 10 spp.)

Host genus *Bombina* Oken 1816
(8 spp.)

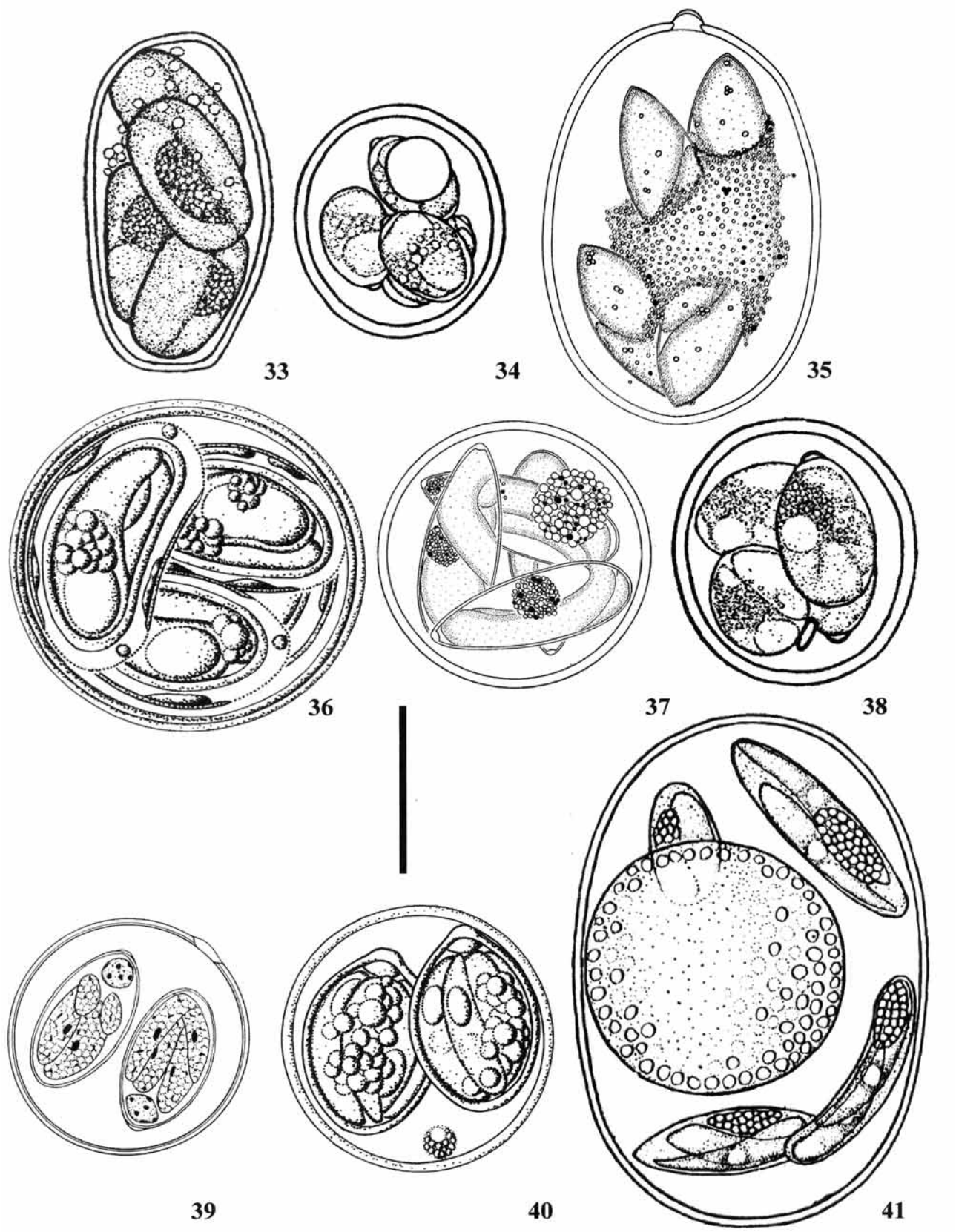
Remarks: The only time a coccidium was reported (to date) from a member of this genus was when Golemansky and Bitseva (1975) said they found *Isospora lieberkühni* in *B. variegata* (L.) in Bulgaria. However, *Isospora lieberkühni* has been an enigmatic organism that has perplexed coccidiologists since it was first reported by Lieberkühn (1854) as a renal coccidium of European water frogs. It was not until Modrý *et al*. (2001) sequenced the small-subunit (SSU) rRNA that its' true taxonomic position was established. What had been called *I. lieberkühni* is now placed in the newly re-erected genus *Hyaloklossia* Labbé 1896 (see *Remarks* under *Hyaloklossia liegerküehni*).



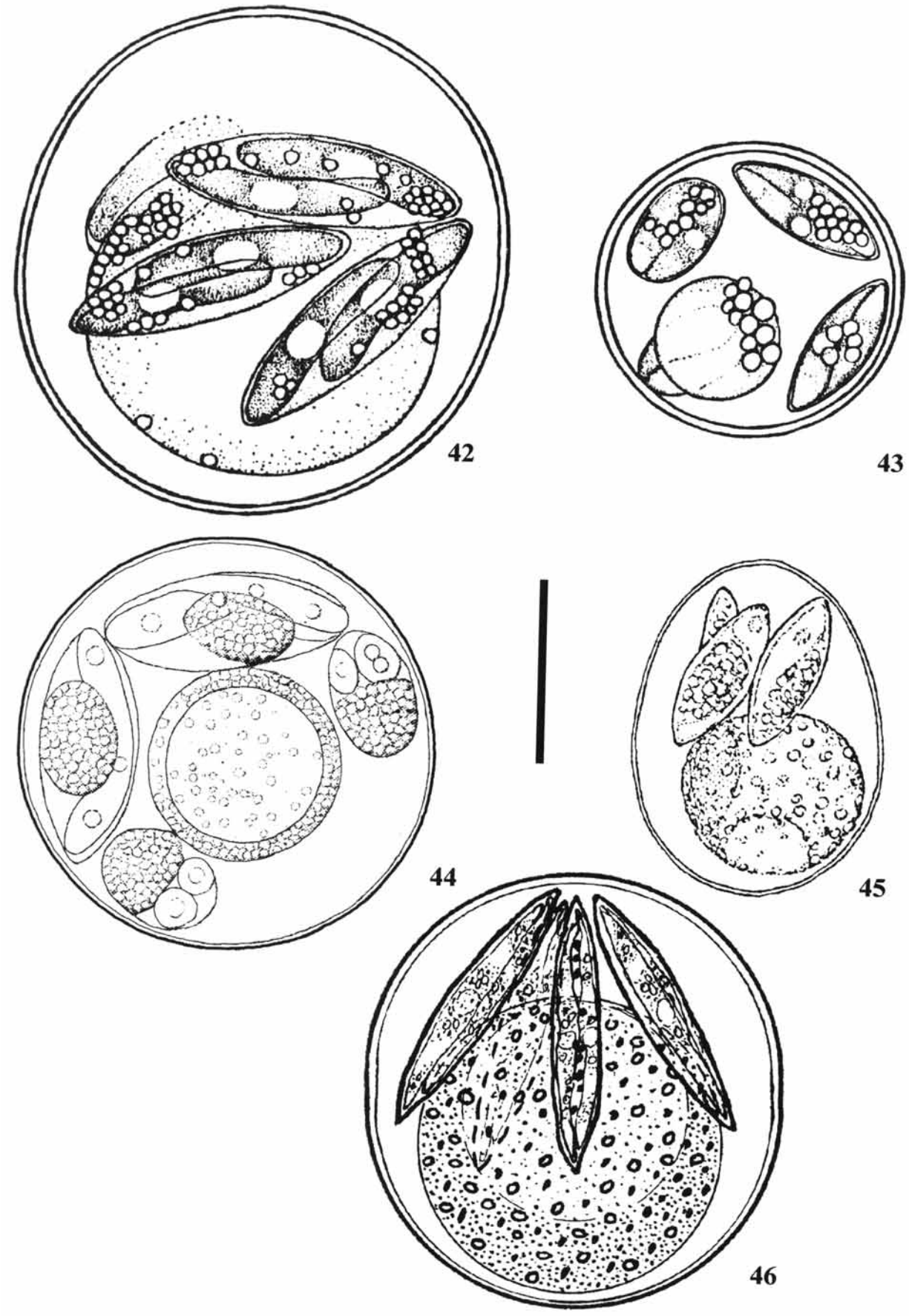
FIGURES 1–16. 1. *Eimeria mazzai.* **2.** *Isospora stomatici* **3.** *Eimeria bufomarini* **4.** *Eimeria himalayana* **5.** *Eimeria laminata* **6.** *Isospora wenyoni* **7.** *Isospora brumpti* **8.** *Eimeria cyanophlyctis* **9.** *Eimeria terraepokotorum* **10.** *Eimeria belawini* **11.** *Isospora wladimirovi* **12.** *Eimeria flexuosa* **13.** *Eimeria streckeri* from *Pseudacris streckeri* **14.** *Eimeria streckeri* from *Pseudacris triseriata.* **15.** *Isospora cogginsi* **16.** *Isospora delicatus.* Bar=15 µm.



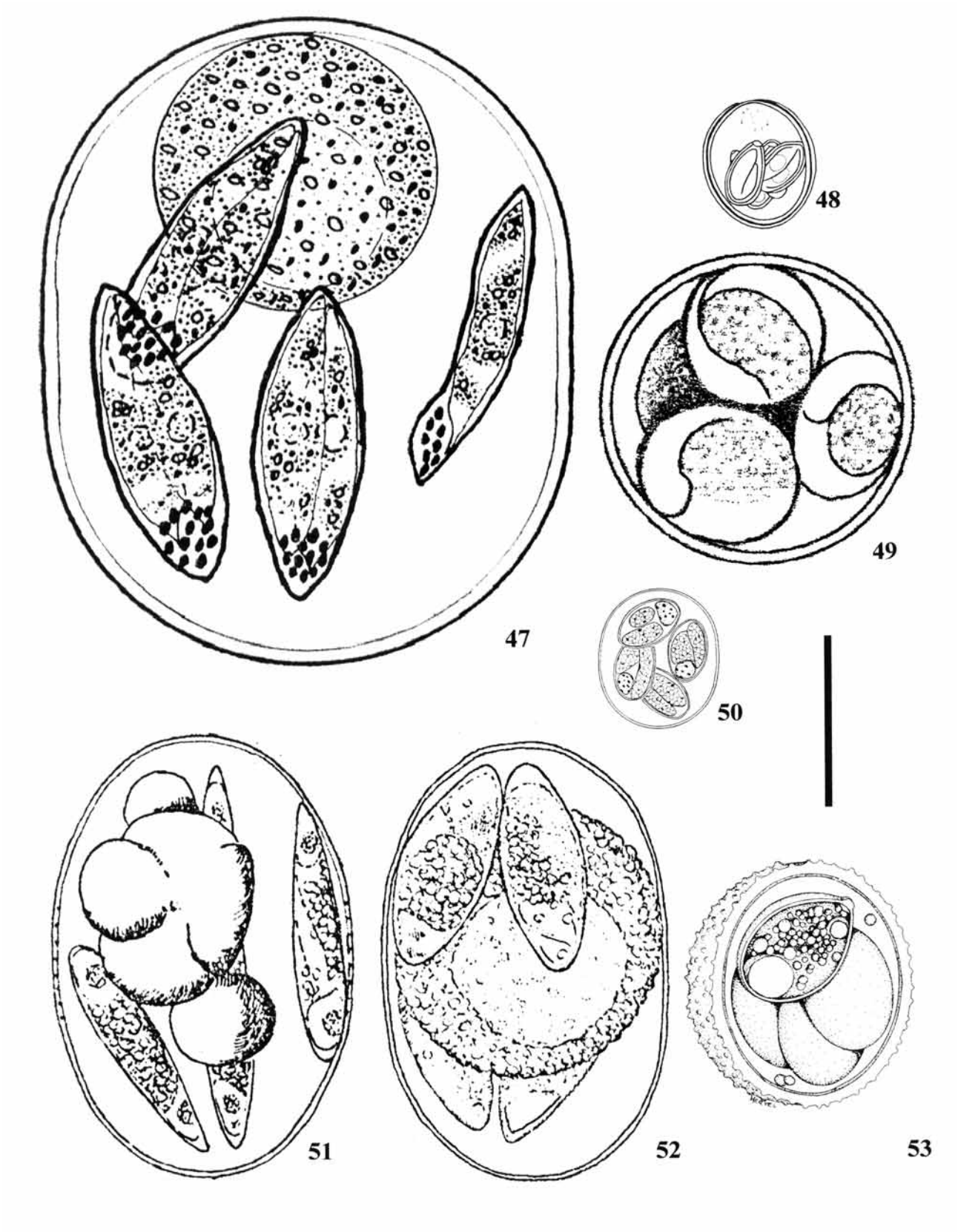
FIGURES 17–32. 17. *Isospora cruzi* **18.** *Eimeria wambaensis* **19.** *Goussia hyperolisi* **20.** *Eimeria leptodactyli* **21.** *Isospora fragosum* **22.** *Eimeria algonquini* **23.** *Eimeria fitchi* **24.** *Eimeria kermiti* **25.** *Eimeria prevoti* **26.** *Eimeria ranarum* **27.** *Goussia neglecta* **28.** *Hyaloklossia lieberküehni* **29.** *Eimeria ranae* **30.** *Isospora neos* **31.** *Eimeria fragilis* **32.** *Eimeria ambystomae.* Bar=15 µm.



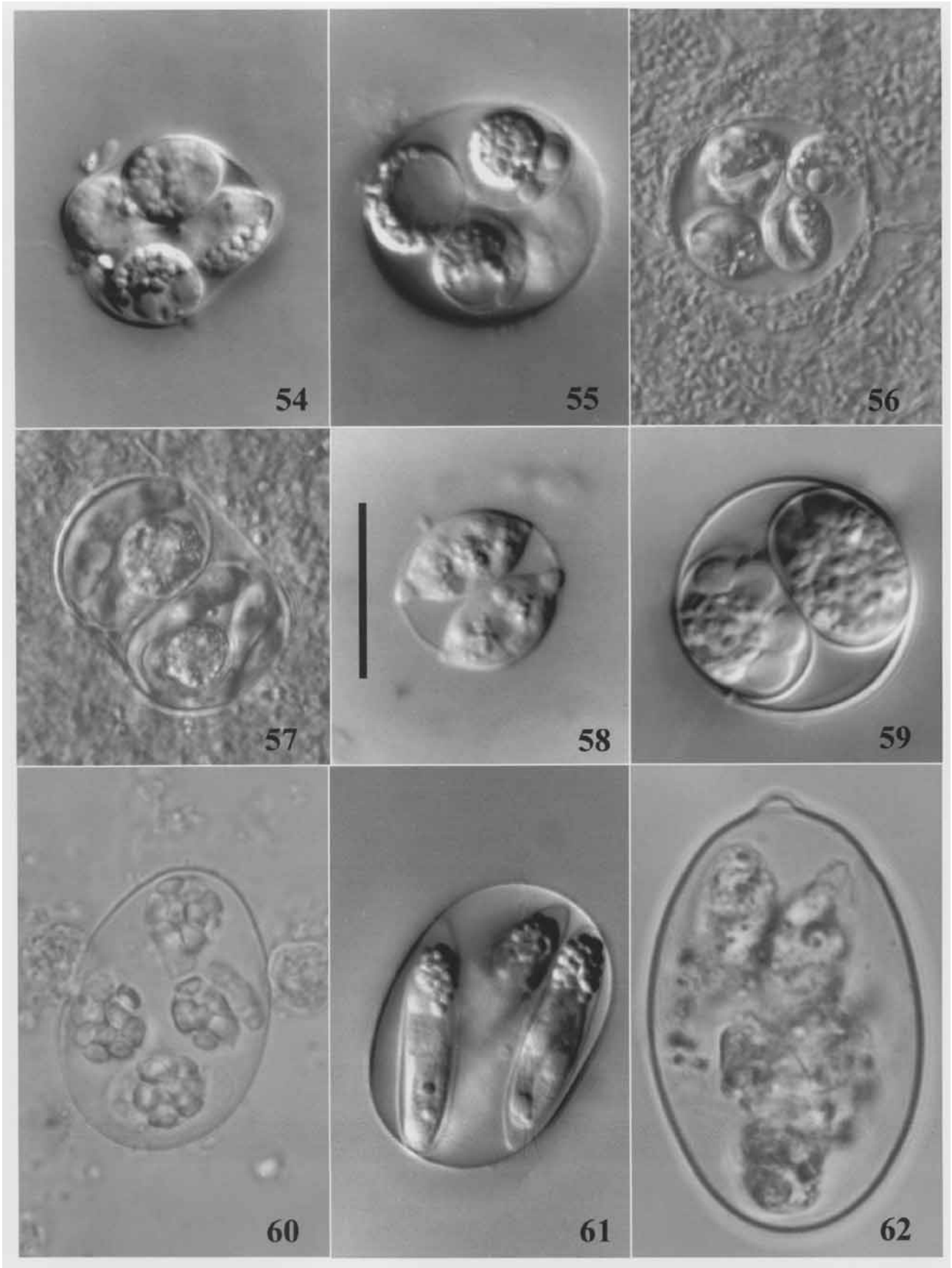
FIGURES 33–41. 33. *Eimeria distorta* **34.** *Eimeria kingi* **35.** *Eimeria microcapi* **36.** *Eimeria opacum* **37.** *Eimeria urodela* **38.** *Eimeria waltoni* **39.** *Isospora jeffersonianum* **40.** *Isospora hightoni* **41.** *Eimeria nipponensis*. Bar=15 μm.



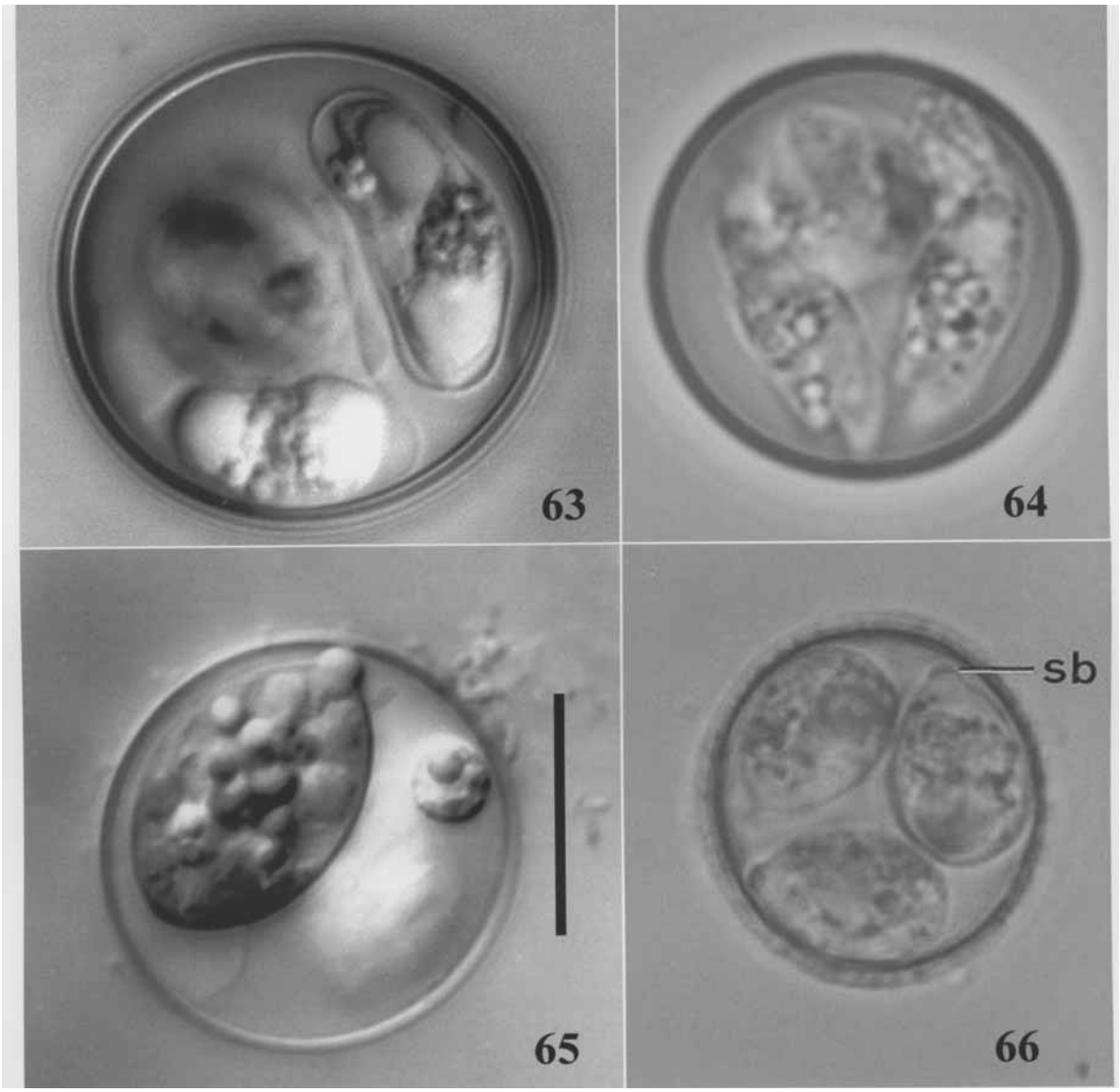
FIGURES 42–46. 42. *Eimeria pyrrhogaster* **43.** *Eimeria saitamaensis* **44.** *Eimeria spherica* **45.** *Eimeria tertia* **46.** *Eimeria longaspora*. Bar=15 µm.



FIGURES 47–53. 47. *Eimeria megaresidua* **48.** *Eimeria grobbeni* **49.** *Eimeria salamandrae* **50.** *Eimeria tarichae* **51.** *Eimeria canaliculata* **52.** *Eimeria propria* **53.** *Eimeria dermophis*. Bar=15 µm.



FIGURES 54–62. 54. *Eimeria flexuosa* **55.** *Eimeria streckeri* from *Pseudacris stechieri* **56.** *Eimeria streckeri* from *Pseudacris triseriata* **57.** *Isospora cogginsi* **58.** *Isospora delicatus* **59.** *Isospora fragosum* **60.** *Eimeria fitchi* **61.** *Eimeria ambystomae* **62.** *Eimeria microcapi*. Bar=15 µm.



FIGURES 63–66. 63. *Eimeria opacum* **64.** *Eimeria urodela* **65.** *Isospora hightoni* **66.** *Eimeria dermophis.* Bar=15 µm.

Family Bufonidae Gray 1825
(47 genera, 485 spp.)

Host genus *Bufo* Laurenti 1768
(13 spp.)

Eimeria mazzai Yakimoff and Gousseff 1934 (Fig. 1)

Synonym: *Eimeria transcaucasica* Yakimoff and Gousseff 1936a.

Type host: *Bufo bufo* L. 1758 (Syn. *B. vulgaris*), European common toad.

Other hosts: None reported to date.

Type locality: ASIA: Azerbaijan.

Geographic distribution: ASIA: Azerbaijan.

Description of sporulated oocyst: Oocyst shape: spheroidal; number of walls: 2; wall thickness: unknown; L x W: 16–18 x 16–18; L/W ratio: ~1.0; M, OR, PG: absent. Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: elongate ellipsoidal; L x W: 6–8 x 4; SB: not described, but probably present (line drawing); SSB and PSB: absent; SR: present; SR characteristics:

small, irregular granular mass between SZ (line drawing); SZ: comma-shaped with 1 RB at rounded end (line drawing). Distinctive features of sporocyst: none.

Prevalence: Unknown.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: The description of this species is only marginally useful; it is retained as a valid species only because modest mensural data for the oocyst and sporocysts and an original line drawing were given. Yakimoff and Gousseff (1936a) described *E. transcaucasica* from *Bufo bufo*; their description is almost identical to their earlier description of *Eimeria mazzai*. Thus, *E. transcaucasica* is considered the same species.

Isospora stomatici Chakravarty and Kar 1944 emend. Levine 1985 (Fig. 2)

Synonym: *Isospora stomaticae* Chakravarty and Kar 1944.

Type host: *Bufo stomaticus* Lütken 1864, Marbled toad.

Other hosts: None reported to date.

Type locality: ASIA: India, Calcutta suburbs.

Geographic distribution: ASIA: India, Calcutta.

Description of sporulated oocyst: Oocyst shape: broadly ellipsoidal to slightly ovoidal; number of walls: 2; wall thickness: very thin; L x W: 25.5 x 17.5 (24–26 x 15–20); L/W ratio: 1.5; M, OR, and PG: absent (line drawing). Distinctive features of oocyst: unsporulated oocysts are initially ovoidal or spheroidal, but become broadly ellipsoidal to ovoidal after sporulation; also, the very thin and fragile, 2-layered wall.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 15.4–17.6 x 11.0; L/W ratio: unknown; SB: absent (Chakravarty & Kar 1952) or present (Mandal 1976), SSB and PSB: absent; SR: present; SR characteristics: generally a conspicuous mass of large granules (line drawing), but it is eventually absorbed with development of the SZ: elongate bodies with one end slightly pointed, 13.2 x 3.3 (12.5–15 x 2.5–4.5); L/W ratio: 1.5; an obvious N is centrally located. Distinctive features of sporocyst: SR prominent in freshly sporulated forms, but disappears with time.

Prevalence: Unknown.

Sporulation: Exogenous, 48–60 h (Mandal 1976).

Prepatent and patent periods: Unknown.

Site of infection: Intestine.

Endogenous development: Mature meronts are spheroidal and contain 8–12 merozoites, ~6.6 x 3.2, each with a central N and an obvious karyosome. Microgamonts are ovoidal, 17.1–19.3 x 8.6–12.8, with comma-shaped microgametes, ~3.2–4.3 long. Macrogomonts vary from spheroidal to ovoidal with a diameter of ~15; their cytoplasm is granular with a deeply-staining N.

Pathology: None reported.

Materials deposited: None.

Remarks: This species was named and briefly described in an abstract by Chakravarty and Kar (1944), but without a line drawing; thus, initially, it was a *species inquirenda*. Later, the same authors (Chakravarty & Kar 1952) provided a more detailed account including information on the endogenous stages and provided a line drawing to document their observations. Mandal (1976) added further descriptive information which was nearly identical to that of the original description in mensural data of the oocyst and sporocysts; the only significant difference was that in his description of the sporocysts there was a knob-like structure at the anterior

end (SB). Levine (1985) emended the spelling of the specific epitaph when he pointed out that the genitive of *-us* is *-i*, not *-ae*.

Host genus *Chaunus* Wagler 1828
(44 spp.)

Eimeria bufomarini Paperna and Lainson 1995 (Fig. 3)

Type host: *Chaunus marinus* (L. 1758), Cane toad.

Other hosts: None reported to date.

Type locality: SOUTH AMERICA: Brazil, Pará State, Island of Marajo, Salvaterra.

Geographic distribution: SOUTH AMERICA: Brazil: Pará State, Island of Marajo.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; number of walls: 1; wall thickness: unknown; wall characteristics: colorless and very delicate; L x W: 9.2 x 9.0 (9–10 x 9–10); L/W ratio: 1.0 (1.0–1.1); M, OR, PG: all absent. Distinctive features of oocyst: colorless, fragile wall.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal; L x W: 6.3 x 3.7 (6–7 x 4); L/W ratio: 1.7 (1.6–1.7); SB: almost imperceptible, knob-like; SSB and PSB: absent; SR: present; SR characteristics: irregular mass of small and large globules that fills much of the sporocyst; SZ: mostly obscured by SR, but 2 RB detected by TEM. Distinctive features of sporocyst: massive SR that obscures the SZs.

Prevalence: 5 of 17 (29%) in Salvaterra, 1 of 13 (8%) in Belém, Pará.

Sporulation: Endogenous, oocysts sporulate within epithelial cells and usually mature sporocysts, but rarely intact oocysts, are discharged into the gut lumen.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the intestine.

Endogenous stages: Both merogony and gamogony occur in the tips of epithelial cells just below the brush border. Developing meronts, microgamonts and undivided parasites were difficult to distinguish from one another. Two different dividing stages were seen: 1) with pale blue cytoplasm (Giemsa-stained), had up to 11 N when 4.2 in diameter, 26 N when 8.4 in diameter, and 36 N when about 10.5 x 10 wide; and 2) with a more darkly staining cytoplasm with 6–8 N and measuring 8–15 x 7. Two types of mature meronts were seen: 1) produced 15 long, thin merozoites, 5.6–8.4 x 1.0–1.4, and 2) produced only up to 8 merozoites, which were stouter, 7.0 x 2.1. Early developing macrogamonts had a large, pale N with a distinct nucleolus and were 4–5 x 3 in smears. Developing microgamonts were not found in smears, but in tissue sections mature forms were 7 x 8, with up to 10 microgametes. Zygotes in tissue sections were subspheroidal, 7.5 x 5.0. Unsporulated oocysts in smears were subspheroidal, 10.5 x 8.0, but rounded up to 10 x 10 when sporulated.

Ultrastructural study of meronts showed that, at first, merozoites shared their common parasitophorous vacuole (PV), but that as they matured each became separated into an individual, adjoining vacuole. Some merozoites divided prior to the formation of the next generation of meronts, presumably by endodyogeny. Thus, merozoites with their own pellicle and subcellular organelles (micronemes, rhoptries, etc.) were found together in the same PV with stages that had differentiated into the next generation of juvenile meronts within their own limiting membrane. Both juvenile and dividing meronts, and gamonts, contained food vacuoles (?) and electron-dense globules that sometimes occupied the width of the parasite. Differentiation of merozoites was by exogenesis.

Ultrastructurally, developing microgamonts have peripherally arranged N, adjoined to centrioles and a mitochondrion. Their cytoplasm contains a Golgi complex and an ER network, and mature stages are filled with amylopectin granules. Macrogamonts gradually accumulate amylopectin granules as they mature and their cytoplasm also contains large food vacuoles, scattered and aggregated ribosomes, a network of rough ER, mitochondria, Golgi-like aggregates and Type I wall-forming bodies. Young oocysts (zygotes) are filled

with large amylopectin granules, some lipid vacuoles and the remains of electron-dense bodies first seen in macrogamonts. No sign of a rigid oocyst wall is found either in young oocysts or in mature oocysts containing sporocysts with developed SZ. After sporulation, a second, delicate membrane appeared below the limiting membrane (wall?) of the oocyst, which lies in close contact with the PV wall. SZ each have 2 RB and the bulky SR contains many amylopectin granules.

Pathology: No evidence of pathology was found in any of the infected hosts.

Materials deposited: Tissue sections of intestine are deposited in the Museum National dHistoire Naturelle, Paris (303LN). Other sections and intestinal smears are in the Department of Parasitology, Instituto Evandro Chagas, Belém, Pará, Brazil and in the Department of Animal Sciences, Faculty of Agriculture, Rehovot, Israel.

Remarks: The oocysts of *E. bufomarini* are similar in size to those of *E. laminata* (Fig. 5) and *E. himalayani* (Fig. 4, below), both of which are described from 2 bufonids in the genus *Duttaphrynus* in India, but Paperna and Lainson (1995) considered conspecificity unlikely due to geographic and host species differences, a concept with which we agree.

Host genus *Duttaphrynus* Frost *et al.* 2006
(6 spp.)

Eimeria himalayana Ray and Misra 1943 (Fig. 4)

Synonym: *Eimeria himalyanum* Ray and Misra 1941, *lapsus calami* and *species inquirenda*.

Type host: *Duttaphrynus himalayanus* (Günther 1864), Himalayan toad.

Other hosts: None reported to date.

Type locality: ASIA: India, U.P. Mukteswar-Kumaun (2500 m).

Geographic distribution: ASIA: India, Mukteswar.

Description of sporulated oocyst: Oocyst shape: spheroidal; number of walls: 2; wall thickness: very thin; L x W: 9.2 (7.5–10.5) along broadest diameter; L/W ratio: 1.0; M, OR, PG: all absent (line drawing). Distinctive features of oocyst: sporulation occurs intracellularly and the wall is very thin.

Description of sporocyst and sporozoites: Sporocyst shape: naviculoidal (spindle-shaped); L x W: 5.2 x 2.8 (4.5–6.5 x 2.5–3.5); L/W ratio: 1.9; SB, SSB, PSB: all absent; SR: present; SR characteristics: globular mass of small granules between SZ; SZ: club-shaped, 4.0 x 1.4, with 1 RB and a centrally-located N with a karyosome. Distinctive features of sporocyst: sporulation occurs intracellularly and sometimes SZs excyst and lie free within the oocyst in the host cell cytoplasm.

Prevalence: 1 of 1 (100%).

Sporulation: Endogenous, strictly intracellular.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the intestine.

Endogenous stages: The entire life-cycle, including formation of sporulated oocysts, takes place in epithelial cells of the small intestine. Two kinds of meronts were found. Micromeronts measured 1.8 x 2.2 and had a ragged appearance with a faintly developed N membrane, while macromeronts were 5.2 wide with a homogeneous cytoplasm and a prominent N membrane. The smaller meronts were found either distal to the N of the epithelial cell or they passed beyond it toward the basement membrane of the cell to complete merogony. These formed 16–32 merozoites which were 4–6 x 0.4. Mature micromerozoites had a ragged cytoplasm and a deeply staining area at 1 pole. Ray and Misra (1943) believed that these micromerozoites (from their micromeronts) produced the microgamont, which is about 6–8 wide when mature with about 8 microgametes that aggregate around the periphery of the cytoplasm. Microgametes were 2.6 x 0.9, but flagella were not seen.

In contrast, the larger meronts have a cytoplasm that stains homogeneously and a central N with a prominent karyosome. Fully developed macromeronts, found below or above the N, were 10–12 wide and contained up to 32 elongate merozoites; these measured 4.3 x 0.7, with a homogeneously staining cytoplasm and a central N with a central karyosome. Ray and Misra (1943) stated that these merozoites produced macrogamonts that were 7–12 x 6–10, and had a spheroidal N, about 3–5, with a karyosome. At this later stage, the nuclear membrane becomes irregular in outline and formed a fertilisation spindle parallel to the long axis of the gamont.

Pathology: Unknown.

Material deposited: None.

Remarks: Ray and Misra (1941) first named this species in an abstract for a paper read at the 28th session of the Indian Science Congress, held in Benares in 1941. Technically, of course, this violated the International Code of Zoological Nomenclature and made the name a *nomen nudum* since no species description existed in the published literature and no specimen was deposited in an accredited museum. Two years later they named it as new, again, when they published the name as *E. himalayanum*. In their published species description, Ray and Misra (1943) describe merogony and sporogony occuring at the same time in this 1 individual. Mandal (1976) gives a sporulation time of 48–72 h, conflicting with the original description of endogenous sporulation (Ray & Misra 1943).

Eimeria laminata Ray 1935a (Fig. 5)

Type host: *Duttaphrynus melanostictus* (Schneider 1799), Black-spined toad.

Other hosts: None reported to date.

Type locality: ASIA: India, Calcutta.

Geographic distribution: ASIA: India, Calcutta.

Description of sporulated oocyst: Oocyst shape: spheroidal; number of walls: 1 (line drawing of Ray 1935a) or double layered with outer one thicker (Mandal 1976); wall thickness: unknown; wall characteristics: colorless and very delicate; L x W: 9.8 (8–11 x 8–11); L/W ratio: 1.0; M, OR, PG: all absent. Distinctive features of oocyst: colorless, thin, fragile wall.

Description of sporocyst and sporozoites: Sporocyst shape: fusiform or spindle-shaped (pointed at both ends); L x W: 4.5–6.5 x 3; L/W ratio: ~2.0 (Mandal 1976); SB, SSB, PSB: all absent; SR: present; SR characteristics: irregular mass of small granules in center of sporocyst (line drawing); SZ: sausage-like (line drawing of Ray 1935a) with 1 end more pointed than the other and a centrally-located N. Distinctive features of sporocyst: small, spindle-shaped body pointed at both ends and 4 of them do not fill the interior of the oocyst (line drawing).

Prevalence: 2 of 200 (1%).

Sporulation: Endogenous, strictly within host intestinal epithelial cell.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the small intestine.

Endogenous stages: There are two kinds of meronts: macromeronts, 12 x 6, which release 20–30 merozoites, which develop into macrogamonts, and micromeronts, producing 6–8 merozoites, 3 x 1.3, which give rise to microgamonts with numerous uniflagellate microgametes. Early micromeronts were readily distinguished from macromeronts by the absence of darkly staining granules in their cytoplasm; early forms were 6 x 2 and mature forms were 12 x 5.5 with 6–8 merozoites, arranged parallel to the long axis of the meront. Ray (1935a) said that it was these merozoites that produced the male forms of the parasite. The mature microgamonts measured ~13 x 9 and showed numerous N at the periphery. Fully formed microgametes were 2.8–3 x ~1, with a single flagellum at 1 end about the same length as its body. Early macromeronts have “from a very early stage dark-staining granules scattered through the cytoplasm” (Ray 1935a). Fully mature macromeronts within the host cell were spheroidal, 9–10 wide when filled with up to 30 merozoites, each with darkly-stain-

ing granules in their cytoplasm. Fully developed macrogamonts were 11 x 5.6 with a spherical N, ~3. Both micro- and macromeronts were seen to have a structure at one end that Ray (1935a) called a hyaline laminae. Fertilization, oocyst formation, and sporulation all occurred intracellularly.

Pathology: Unknown.

Materials deposited: None.

Remarks: Ray (1935a) looked at fresh smears of frog rectal and intestinal contents in saline and saw what he said were, "active gregarinulae...in large numbers," which he later said were liberated merozoites of two sizes. Very little information about the sporulated oocyst is included in the original description, although description of other life stages is given. Mandal (1976) gives a sporulation time of 60–72 h, conflicting with the original description of endogenous sporulation (Ray 1935a, b).

Isospora wenyoni Ray and Das Gupta, 1935 (Fig. 6)

Type host: *Duttaphrynus melanostictus* (Schneider 1799), Black-spined toad.

Other hosts: *Fejervarya limnocharis* (Gravenhorst 1829), Indian cricket frog and *Hoplobatrachus tigerinus* (Daudin 1802), Turkey frog.

Type locality: ASIA: India, Bengal, Calcutta.

Geographic distribution: ASIA: India, Bengal, Calcutta.

Description of sporulated oocyst: Oocyst shape: subcylindroidal; number of walls: double contoured with the inner more prominent than the outer; wall thickness: unknown; L x W: 16–20 x 11–14; L/W ratio: unknown; M, OR, PG: all absent (line drawing). Distinctive features of oocyst: unsporulated oocysts are ovoidal or spheroidal, but become broadly ellipsoidal or ovoidal after sporulation; also, the very thin, fragile, 2-layered wall.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal; L x W: 8 x 4; L/W ratio: ~2; SB, SSB, PSB: all absent (photomicrograph); SR: present; SR characteristics: scattered granules (photomicrograph); SZ: unknown. Distinctive features of sporocyst: their long axis is at a right angle to the long axis of the oocyst.

Prevalence: Two of several hundred (~1%) *Duttaphrynus melanostictus*.

Sporulation: Exogenous, oocysts sporulated in ~3 days when kept in 1% chromic acid.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the small intestine.

Endogenous stages: Young undivided meronts (trophozoites) were 10 x 3; when mature they measured 20–25 wide and had 8–12 spindle-shaped merozoites which were 12 x 5. Each merozoite was reported to possess a pair of hyaline blades or lamina at their anterior end, similar to those reported in the merozoites of *E. laminata* by Ray (1935a). Young microgamonts were difficult to distinguish from developing meronts, but as they aged, a large number of N were seen around the periphery of the gamont. Individual microgametes were reported to measure 2.4 x 1.5. Early macrogamonts were easily distinguished by darkly staining cytoplasmic granules and a spheroidal N with a karyosome. Mature macrogamonts were 16–20 x 11–14, have the posterior end usually turned upon itself giving the impression of a short tail, and have an elongate N in which the karyosome fragments into many small granules scattered irregularly.

Pathology: Unknown.

Materials deposited: None.

Remarks: In an abstract, Chakravarty and Kar (1944) (erroneously?) mentioned finding oocysts of this species in two dicroglassid species, *F. limnocharis* and *H. tigerinus*. Later, in 1952, they redescribed the oocysts and sporocysts from these same hosts saying the oocysts were 19.8–15.4 x 15.4–13.3 and sporocysts 13.2–9.9 x 9.8–7.7, much larger than in the original description by Ray and Das Gupta (1935). Mandal (1976) said the oocysts were 17.5 x 14.5 (15–20.5 x 13.5–15.5) with a shape index of 1.2 and that an OR was present, but he did not show it in his line drawing; he also said the sporocysts were 11.8 x 8.5 (10–13.5 x 7.5–9.5), with

L/W ratio 1.3, measurements that are significantly larger than in the original description. Finally, Mandal (1976) noted that the sporulation time he observed was 60–70 h, similar to the 2–3 days cited by Ray and Das Gupta (1935) in their original description. It is our opinion that both Chakravarty and Kar (1944) and Mandal (1976) were dealing with oocysts of a species that was not *I. wenyoni*.

Host genus *Pseudepidalea* Frost *et al.* 2006
(11 spp.)

Isospora brumpti Lavier 1941 (Fig. 7)

Synonym: *Diplospora brumpti* (Lavier 1941) Grasse, 1953.

Type host: *Pseudepidalea viridis* (Laurenti 1768), Green toad.

Other hosts: None to date.

Type locality: ASIA: Syria.

Geographic distribution: ASIA: Syria, Turkmenistan.

Description of sporulated oocyst: Oocyst shape: ovoidal to ellipsoidal (line drawing); number of walls: 1 (line drawing); wall thickness: 0.3–0.5; wall characteristics: colorless; L x W: 24 x 16 (20–25 x 11–17); L/W ratio: 1.5; M, OR, PG: all absent. Distinctive features of oocyst: colorless, thin, fragile wall that collapses around the sporocysts and ruptures and vanishes soon after sporulation.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal; L x W: 15–19 x 10–14; L/W ratio: unknown; SB, SSB, PSB: all absent; SR: present; SR characteristics: granular body situated between SZ; SZ: banana-shaped, 13 x 3, lying head to tail, partly obscured by SR. Distinctive features of sporocyst: large granular SR.

Prevalence: Unknown.

Sporulation: Usually 24–48 h or less; some oocysts in fresh feces already have 2 sporoblasts.

Prepatent and patent periods: Unknown.

Site of infection: Within the first segments of the small intestine, but can also extend down the full length of the intestine.

Endogenous stages: Intracellular forms occupy a position between the center and the top of the epithelial cells. When a merozoite first enters a cell it is ~14 x 3; after rounding up and nuclear fragmentation it gives rise to 12–14 arched merozoites with pointy ends, which measure 12–14 x 3 and are tightly packed together. Frequently, one finds in a single vacuole up to 50 older merozoites, which appear to be segregating into several groups. Early microgamonts are indistinguishable from immature meronts, but as they mature they are easily distinguished by the N divisions that are happening at their surface. Lavier (1941) suggested that he saw 6–8 elongated chromosomes at this stage. By the time microgametogenesis is completed, the microgamont is ovoidal, and measures ~20 x 12. Lavier (1941) said that the macrogamont stays elongated for a long time (gregariniforme) while increasing in size, sometimes exceeding that of the oocyst. Mature macrogamonts are spheroidal and highly granular.

Pathology: Unknown.

Materials deposited: None.

Remarks: According to Pellérdy (1974), Lavier (1941) was unable to infect *B. bufo* (=*B. vulgaris*) with (sporulated ?) oocysts. Ovezmukhammedov and Annakuliyeva (1973) said they found this species in 4 of 46 (8.7%) *P. viridis* from the Ashkhabad and Tedzlien regions of Turkmenistan, but not in 121 *Pelophylax ridibunda* (Pallas 1771). The oocysts they measured were 20.9 x 16.5 (19–22 x 13.5–19), the sporocysts were 11.5 x 9.5 (11–13.5 x 8–11), and the sporozoites were 8.8 (8–11) x 2.7. These oocysts were thus shorter and wider than those in the original description (and, therefore, had a smaller L/W ratio, a feature that often is quite constant in the oocysts representing a single species) with shorter sporozoites. Thus, it is not clear

whether Ovezmukhammedov and Annakuliyeva (1973) were looking at a different species of *Isospora* or if these size differences in the sporulated oocysts was just a geographic variant.

Family Dicroglossidae Anderson 1871
(13 genera, 151 spp.)

Host genus *Euphlyctis* Fitzinger 1843
(4 spp.)

Eimeria cyanophlyctis Chakravarty and Kar 1952 (Fig. 8)

Type host: *Euphlyctis cyanophlyctis* (Schneider 1799), Skipping frog.

Other hosts: None reported to date.

Type locality: ASIA: India, Calcutta suburbs.

Geographic distribution: ASIA: India, Calcutta.

Description of sporulated oocyst: Oocyst shape: ovoidal to ellipsoidal; number of walls: 1; wall thickness: very thin; wall characteristics: transparent; L x W: 19.8–15.4 x 17.6–15.4; L/W ratio: unknown; M and PG: absent; OR: present; OR characteristics: an irregular mass of granules containing a large globule. Distinctive features of oocyst: thin, transparent outer wall and the prominent OR with a large globule embedded in it.

Description of sporocyst and sporozoites: Sporocyst shape: spindle-shaped, with one end tapering more than the other; L x W: 11 x 4.4–6.6; L/W ratio: unknown; SB, SSB, PSB: all absent; SR: absent; SZ: elongate with the anterior end pointed and a N (RB?) present at the broader end. Distinctive features of sporocyst: small size and spindle shape with one end more pointed (SB?) than the other.

Prevalence: Unknown.

Sporulation: Exogenous, 60–75 h (Mandal 1976).

Prepatent and patent periods: Unknown.

Site of infection: Intestine (Mandal 1976).

Endogenous stages: Early, uninucleate meronts are spheroidal, ~2.2 wide. These develop into meronts with 8 N. Microgamonts were 4.4 wide with a large number of chromatin granules that transformed into comma-shaped microgametes. Mature macrogamonts were 11 wide with a central N in a matrix of highly granular cytoplasm.

Pathology: None observed to date.

Materials deposited: None.

Remarks: This species was named and briefly described in an abstract by Chakravarty and Kar (1944), but there was no line drawing; thus, initially, it was a *species inquirenda*. In 1952, the same authors provided a more detailed account of the oocyst, modest information on the endogenous stages, and a line drawing to document their observations. Mandal (1976) added further descriptive information, but the oocysts he measured were 17.9 x 16.7 (15.5–20 x 13.3–15.5) with a L/W ratio of 1.1; these differ in width, and thus, in L/W ratio. The sporocysts Mandal (1976) measured were 11.5 x 5.5 (10.5–12.5 x 4.5–6.5) with a L/W ratio of 2.1, very similar to those in the original description. Mandal (1976) described the oocysts as ovoidal to subspheroidal in shape, yet his drawing shows them to be ovoidal.

Host genus *Hoplobatrachus* Peters 1863
(4 spp.)

Eimeria terraepokotorum Jirků and Modrý 2006a (Fig. 9)

Type host: *Hoplobatrachus occipitalis* (Günther 1858), African tigrine frog.

Other hosts: None reported to date.

Type locality: AFRICA: Kenya, Nginyang, Rift Valley Province (01° 09’ 33” N, 37° 15’ 47” E).

Geographic distribution: AFRICA: Kenya, Nginyang.

Description of sporulated oocyst: Oocyst shape: variable both in size and shape, ovoidal to broadly ellipsoidal; number of walls: 1; wall thickness: ~0.6; wall characteristics smooth and colorless; L x W: 20.2 x 16.0 (18–24.5 x 13.5–18.5); L/W ratio: 1.3 (1.1–1.4); M and PG: Absent; OR present; OR characteristics: spherical to subspherical (7–11) composed of spherical to subspherical mass of granules resembling those forming SR. Distinctive features of oocyst: colorless, thin, smooth wall, granules of the OR are of 2 types, elongate ones and distinctly finer spherical granules.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 9.8 x 7.2 (8.5–11.5 x 6–8); L/W ratio: not stated; sporocyst pole, opposite to SB is usually slightly pointed; SB: present at 1 end (1.5–2 x 0.5–0.7); SSB and PSB: absent; SR: present; SR characteristics: composed of numerous granules completely filling space between SZ or forming a subspheroidal mass; granules of the SR are of 2 types: elongate ones (2–2.5 x 1–1.5) and finer spheroidal granules (0.5–1); SZ: size not stated; finely granulated without visible striations, containing probably 2 RBs; RB usually spheroidal, (2–3 x 1.5–2); distinct N (2 x 2) located between the RBs. Distinctive features of sporocyst: granules of SR are of 2 types: elongate ones and finer spherical granules.

Prevalence: 2 of 5 (40%).

Sporulation: Exogenous.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the entire small intestine, extranuclear.

Endogenous stages: Mature meronts were spheroidal to broadly ellipsoidal 8–12 x 5–8 and contained ~20, somewhat spirally arranged merozoites. Mature macrogamonts were spheroidal or ellipsoidal, 16–19 x 13–17, and contained a few distinct wall-forming bodies (1.5–2). Microgamonts were ellipsoidal, 10–12 x 6–9, containing numerous relatively thick-bodied microgametes.

Pathology: Unknown.

Materials deposited: Photosyntypes of oocysts in various stages of sporulation and hematoxylin and eosin (H &E) stained paraffin sections with endogenous stages, along with type-host liver in 95% ethanol, were deposited in the collection of the Department of Parasitology, University for Veterinary and Pharmaceutical Sciences Brno, Czeck Republic (R 113/05). A voucher specimen of *H. occipitalis* was deposited in the herpetological collection of the National Museum of Kenya, Nairobi (NMK A/4246).

Remarks: Only 3 other eimerians from anurans are similar enough to this species to be compared. *Eimeria cyanophlyctis* (Fig. 8) from India differs in having distinctly narrower (11 x 4–7 *vs*. 9.8 x 7.2 [8.5–11.5 x 6–8] in *E. terraepokotorum*), spindle-shaped sporocysts lacking SR (Chakravarty & Kar 1952). *Eimeria* leptodactyli (Fig. 20) from South America, most closely resembling *E. terraepokotorum* in oocyst and sporocyst size, however, they differ in the appearance of the OR. *Eimeria streckeri* (Figs. 13, 14, 55, 56) from North America differs in its oocyst shape (spheroidal), the presence of a distinct vacuole within the OR, and presence of an indistinct SB.

Family Hylidae Rafinesque 1815
(46 genera, 814 spp.)

Host genus *Hyla* Laurenti 1768
(32 spp.)

Eimeria belawini Yakimoff 1930 (Fig. 10)

Type host: *Hyla arborea* (L. 1758), European treefrog.

Other hosts: None reported to date.

Type locality: CAUCASIA.

Geographic distribution: CAUCASIA.

Description of sporulated oocyst: Oocyst shape: spheroidal; number of walls: 1 (from line drawing); wall thickness and characteristics: unknown; L: 12; L/W ratio: 1.0; M, OR, PG: all absent (line drawing). Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: spheroidal; L x W: 4 x 4; L/W ratio: 1.0; SB, SSB, PSB and SR: all absent (line drawing); SZ: unknown. Distinctive features of sporocyst: none.

Prevalence: Unknown.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Unknown.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: This is the only *Eimeria* species described from a treefrog of the genus *Hyla*. Because most amphibian eimerians do not cross generic boundaries we feel that Yakimoff's (1930a, b) species is valid, but poorly described.

Isospora wladimirovi Yakimoff 1930a (Fig. 11)

Type host: *Hyla arborea* (L. 1758), European treefrog.

Other hosts: None reported to date.

Type locality: CAUCASIA.

Geographic distribution: CAUCASIA.

Description of sporulated oocyst: Oocyst shape: ovoidal to ellipsoidal; number of walls: 1 (line drawing); wall thickness and characteristics: unknown; L x W: 21.4 x 17.6 (18–25 x 15–21); L/W ratio: 1.2; M, OR, PG: all absent (line drawing). Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: subspheroidal; L x W: 13 x 9; L/W ratio: 1.4; SB, SSB, PSB: all absent (line drawing); SR; present; distinct (line drawing); SZ: elongate 8.9 x 4.4. Distinctive features of sporocyst: none.

Prevalence: Unknown.

Sporulation: Unknown, but Yakimoff (1930a) reported finding oocysts in a sporulated state in the intestinal content.

Prepatent and patent periods: Unknown.

Site of infection: Unknown.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: This is the only *Isospora* species described from a treefrog of the genus *Hyla*. Because most amphibian isosporans probably do not cross generic boundaries, we feel that Yakimoff's (1930a, b) species is valid, but poorly described.

Host genus *Pseudacris* Fitzinger 1843
(16 spp.)

Eimeria flexuosa Upton and McAllister 1988 (Figs. 12, 54)

Type host: *Pseudacris streckeri* Wright and Wright 1933, Strecker's chorus frog.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: U.S.A. Texas, Dallas County.

Geographic distribution: NORTH AMERICA: U.S.A. Texas.

Description of sporulated oocyst: Oocyst shape: irregular; number of walls: 1; wall thickness: ~0.5; wall characteristics: flexible and encloses sporocysts tightly; L: 17.0 (15–19); M and OR: absent; PG: present; 1 (rarely more), 1.6–2.5 wide. Distinctive features of oocyst: Single-layered, flexible wall that tightly encloses the sporocysts.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 10.3 x 7.3 (10–12 x 6–8); L/W ratio: 1.4 (1.3–1.6); SB: present as slight thickening at pointed end; SSB and PSB: absent; SR: present; SR characteristics: 6.6 x 5.1 (5–8 x 4–6) composed of numerous coarse granules, each up to 2.5 wide, but sometimes diffuse with scattered granules; SZ: 9.4 x 2.4 (8–10 x 2–3) *in situ*, each with 2 RB; anterio-central RB usually spheroidal, 2.0 (1–3), while posterior RB is spheroidal, 1.7 (1–2); indistinct N located between the RBs. Distinctive features of sporocyst: large SR made up of large, coarse granules.

Prevalence: 10 of 34 (29%).

Sporulation: Presumably endogenous.

Prepatent and patent periods: Unknown.

Site of infection: Unknown (see *Remarks*).

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: Only 2 other eimerians from anurans are described with oocyst walls thin enough to adhere to the sporocysts and that produce irregularly-shaped oocysts: *G. neglecta* and *E. ranae*. This species is distinguished from the former (Fig. 27) by its larger oocysts (17 *vs*. 9–10) and sporocysts (10 x 7 *vs*. 3.5–4). Although the oocysts and sporocysts of *E. ranae* are similar in size to those of *E. flexuosa*, the latter (Fig. 12) lacks an OR which is present in *E. ranae*. Upton and McAllister (1988) reported the site of infection for *E. flexuosa* as the intestine, but their oocysts were recovered from the feces and no attempt was made to check what organs were infected with developmental stages of this species; therefore, the site of infection is unknown.

Eimeria streckeri Upton and McAllister 1988 (Figs. 13, 14, 55, 56)

Type host: *Pseudacris streckeri* Wright and Wright 1933, Strecker's chorus frog.

Other hosts: *Pseudacris triseriata* (Wied-Nuweid 1838), Western chorus frog.

Type locality: NORTH AMERICA: USA, Texas, Dallas County.

Other localities: NORTH AMERICA: USA, Nebraska, Lancaster County, Pawnee Lake (40° 51’ 10.8” N, 96° 53’ 6.6” W).

Geographic distribution: NORTH AMERICA: USA, Texas, Nebraska.

Description of sporulated oocyst: Oocyst shape: spheroidal, rarely subspheroidal; number of walls: 1; wall thickness: ~0.7; wall characteristics: smooth; L x W: 18.8 x 18.7 (17–21.5 x 17–21); L/W ratio: 1.0 (1.0–1.1); M: absent; OR: spheroidal, 8.0 (6–11), composed of numerous coarse granules surrounding a large vacuolated or globular area; PG: absent (usually), although 1 may be found rarely. Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 11.1 x 7.7 (10–13 x 7–9); L/W ratio: 1.5 (1.2–1.7); SB: present as slight thickening at pointed end, indistinct; SSB and PSB: absent; SR: present; SR characteristics: an aggregate of granules bound by a limiting membrane, 6.6 x 5.7 (5–8 x 4–7), but additional granules are often found free among the SZ; SZ: 11.0 x 2.6 (10–13 x 2–3) *in situ*, each with 2 RB; anterior-central RB spheroidal to slightly ovoidal, 2.2 x 2.0 (1–3 x 1–2); posterior RB spheroidal, 1.6 (1–2); N located between the 2 RBs. Distinctive freatures of sporocyst: none.

Prevalence: 16 of 34 (47%) in *P. streckeri* in Texas (Upton & McAllister 1988); 2 of 30 (7%) in *P. t. triseriata* in Nebraska (Bolek *et al*. 2003)

Sporulation: Presumably endogenous.

Prepatent and patent periods: Unknown.

Site of infection: Unknown (see *Remarks*).

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: Photosyntypes of sporulated oocysts in the HWML, Lincoln, NE (HWML 16977).

Remarks: About half of the known eimerians from anura have spheroidal to subspheroidal sporulated oocysts. Of these, only 5 are reported to possess an OR: *E. algonquini*, *E. cyanophlyctis*, *E. leptodactyli*, *E. prevoti* and *E. streckeri*. Sporulated oocysts of this species differ from *E. algonquini* (Fig. 22) by having larger oocysts and much smaller sporocysts that have a SB, which those of *E. algonquini* lack. This species' oocysts and sporocysts are distinguished from those of *E. cyanophlyctis* (Fig. 8) by being more spheroidal and the presence of a SR, which *E. cyanophlyctis* lacks. They differ from *E. leptodactyli* (Fig. 20) by having smaller and more spheroidal oocysts and larger sporocysts, and from *E. prevoti* (Fig. 25) by its more spheroidal shape and much larger OR. The oocysts seen by Bolek *et al*. (2003) in *P. t. triseriata* from Nebraska were remarkably similar to those in the original description (Upton & McAllister 1988) in size and shape. The major difference was that those from Nebraska had a distinctive globular body in the OR, which remained constant in form during a period of 6 mo while being refrigerated in 2.5% $K_2Cr_2O_7$ solution. Upton and McAllister (1988) reported the site of infection for this species as the intestine, but their oocysts were recovered from the feces and no attempt was made to check what organs were infected with the developmental stages of *E. streckeri*; therefore, the site of infection of this species is unknown.

Isospora cogginsi Bolek, Janovy and Irizarry-Rovira 2003 (Figs. 15, 57)

Type host: *Pseudacris triseriata* (Wied-Nuweid 1838), Western chorus frog.

Other hosts: None to date.

Type locality: NORTH AMERICA: USA, Nebraska, Lancaster County, Pawnee Lake (40° 51' 10.8" N, 96° 53' 6.6" W).

Geographic distribution: NORTH AMERICA: USA, Nebraska.

Description of sporulated oocyst: Oocyst shape: ovoidal, rarely subspheroidal; number of walls: 1; wall thickness: ~0.5; wall characteristics: smooth, colorless; L x W: 19.3 x 15.1 (18–23 x 11–20); L/W ratio: 1.3 (1.1–1.6); M, OR, PG: all absent. Distinctive features of oocyst: wall frequently ruptures after sporulation, releasing free sporocysts.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal with a thin, colorless wall, ~0.4; L x W: 13.3 x 9.9 (11–15 x 9–13); L/W ratio: 1.3 (1.0–1.6); SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal, 5.5 x 5.3 (4–7 x 4–7) with numerous coarse granules bound by a membrane; SZ: elongate, 12.8 x 3.2 (10–15 x 2.5–4), arranged so that 2 SZ lie in one direction and the other 2 lie in the opposite direction; each with 2 RBs; anterior-central RB spheroidal to ovoidal, 2.3 x 2.4 (2–3 x 2–3); posterior RB spheroidal to ovoidal, 2.6 x 2.4 (2–3 x 2–3); N, indistinct, located between RBs. Distinctive features of sporocyst: SR bound by a distinct membrane.

Prevalence: 23 of 30 (70%) of adult frogs; 4 of 16 (25%) of tadpoles.

Sporulation: Exogenous; oocysts passed unsporulated or semi-sporulated in the sporoblast stage and become fully sporulated in 12–24 h at room temperature.

Prepatent and patent periods: Unknown.

Site of infection: Supra-nuclear in luminal epithelial cells of the posterior small intestine, although in heavily infected frogs, endogenous stages are found throughout the small intestine.

Endogenous stages: Mature meronts were 14.8 x 8.8 (12–19 x 7–10) and contained 8–9 banana-shaped

merozoites, 6.1 x 1.4 (5–7 x 1–2). Developing microgamonts with peripherally located N were 11.6 x 9.3 (10–16 x 7–12), mature microgamonts with numerous microgametes were 18.2 x 14.8 (16–22 x 13–17), and mature macrogamonts with numerous granules and vacuoles were 11.9 x 10.3 (10–14 x 8–13). Freshly released oocysts with basophilic sporoplasm and numerous granules were 14.1 x 11.7 (12–15 x 10–13); these began sporulating in the gut lumen.

Pathology: Unknown.

Materials deposited: Sporulated oocysts preserved in 70% ethanol in the HWML (HWML 16978) as are photosyntypes of sporulated oocysts (HWML 16979), histological sections of adult frog small intestine (HWML 16980) and histological section of tadpole small intestine (HWML 16981); the symbiotype host is in the University of Nebraska State Museum (ZM-23844).

Remarks: Of the 22 isosporans reported from anuran hosts, this species most closely resembles *I. cruzi* Pinto and Vallim, 1926, from *Scinax* spp. (Hylidae) from South America (Pinto & Vallim 1926; Carini 1936; Walton 1947). Sporulated oocysts of this species differ from those of *I. cruzi* (Fig. 17) in being a little smaller (19.3 x 15.1 *vs.* 20.7 x 17.2) and more ovoidal in shape (1.3 *vs.* 1.2). Additionally, the SR is bound by a distinct membrane not mentioned in *I. cruzi*. Based on these subtle differences as well as differences in hosts and geographic location, Bolek *et al*. (2003) were justified in naming this species from *Pseudacris* as distinct.

Isospora delicatus Upton and McAllister 1988 (Figs. 16, 58)

Type host: *Pseudacris strecker* Wright and Wright 1933, Strecker's chorus frog.

Other hosts: *Pseudacris illinoensis* Smith 1951, Illinois chorus frog.

Type locality: NORTH AMERICA: USA, Texas, Dallas County.

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

Description of sporulated oocyst: Oocyst shape: spheroidal, rarely subspheroidal; number of walls: 1; wall thickness: ~0.6; wall characteristics: smooth; L x W: 15.8 x 15.7 (13–17 x 13–17); L/W ratio: 1.0 (1.0–1.1); M, OR, PG: all absent. Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: spindle-shaped and pointed at both ends; L x W: 13.5 x 8.0 (11–15 x 7–10); L/W ratio: 1.7 (1.5–1.8); SB: present as a large thickening at 1 pointed end; SSB: absent; PSB: not described, although the end opposite of the SB tapers markedly; SR: present; SR characteristics: numerous coarse granules scattered among the SZ; SZ: elongate, 11.9 x 2.4 (10–14 x 2–3) *in situ*, each with 2 RBs; anterior RB spheroidal, 1.8 (1–2); posterior RB slightly larger, also spheroidal, 2.0 (1–3); N, indistinct, located between the 2 RBs. Distinctive features of sporocyst: distinct spindle-shape, pointed at both ends, resembling the oocysts of *Monocystis* species from earthworms.

Prevalence: 5 of 34 (15%) in type host; 1 of 8 (12.5%) in adult *P. illinoensis*.

Sporulation: Presumably endogenous.

Prepatent and patent periods: Unknown.

Site of infection: Unknown (see *Remarks*).

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: Only *I. wenyoni* (Fig. 6) has oocysts that are similar in size to those of this species. They differ, however, in that those of *I. delicatus* are more spheroidal and have larger sporocysts. Also, no other species of *Isospora* from an anuran has such spindle-shaped sporocysts. Although Upton and McAllister (1988) reported the site of infection for this species as the intestine, the oocysts were recovered from the feces and no attempt was made to check what organs were infected with *I. delicatus*; therefore, the site of infection of this species is unknown.

Host genus *Scinax* Wagler 1830
(91 spp.)

Isospora cruzi Pinto and Vallim 1926 (Fig. 17)

Type host: *Scinax crospedospilus* (Lutz 1925) (syn. *Ololygon crospedospila* [Lutz 1825] Fouquette and Delahoussaye 1977), Campo Belo snouted treefrog.

Other hosts: *Scinax fuscovarius* (Lutz 1925), Snouted treefrog, *Scinax nasicus* (Cope 1862), Lesser snouted treefrog, *Scinax ruber* (Laurenti 1768), Red snouted treefrog.

Type locality: SOUTH AMERICA: probably Brazil.

Geographic distribution: SOUTH AMERICA.

Description of sporulated oocyst: Oocyst shape: elongate-ellipsoidal, asymmetrical, being more pointed at one end than the other (line drawing, Carini 1936); oocyst wall: 1 thin layer (line drawing), smooth; L x W: 20.7 x 17.2 (20–22 x 17–18); L/W ratio ~1.2; M, OR, PG: all absent. Distinctive features of oocyst: asymmetrically ellipsoidal, more pointed at one end than at the other.

Description of sporocyst and sporozoites: Sporocyst shape: subspheroidal; L x W: 14 x 13.8 (Pinto & Vallim 1926) or 14 x 10 (Carini 1936); SB, SSB, PSB: all absent; SR: present; SR characteristics: compact spheroidal mass of large and small granules, ~6–7, usually confined to one end of sporocyst (line drawing); SZ: sausage-shaped without visible RB or N (line drawing). Distinctive features of sporocyst: subspheroidal shape.

Prevalence: Not given.

Sporulation: Presumably exogenous.

Prepatent and patent periods: Unknown.

Site of infection: Near the tips of the villi in the small intestine (line drawing).

Endogenous development: Mature meronts, spheroidal, 16–20, with 8–12 merozoites, each irregularly triangular, that assume the shape of a small rosette; each merozoite is 6–8 x 4–5. Microgametocytes are spheroidal, 15–18 wide, with each microgamete ~1.5 wide. Macrogamonts are spheroidal to ovoidal, 18–20 x 16–18, with heavily granulated protoplasm.

Pathology: Unknown.

Materials deposited: None.

Remarks: Pinto and Vallim (1926) found oocysts in the feces of several species of South American tree frogs, presumably from Brazil. Their oocysts were subspheroidal to ellipsoidal (line drawing), 20.7 x 17.2, with subspheroidal sporocysts, 13.8 x 14. Pinto and Vallim (1926) provided a line drawing of an unsporulated oocyst and a second drawing of an oocyst with 2 sporocysts filled with large globules, but there was no mention whether these were undeveloped sporocysts or if they were packed with a large SR. It was not until 1936 when Carini again found this species in *S. ruber* and documented that the two sporocysts actually had 4 SZ each. Carini (1936) also fixed some frog intestinal tissue for histological sections and described several of the endogenous stages.

Family Hyperoliidae Laurent 1943
(17 genera, 198 spp.)

Host genus *Hyperolius* Rapp 1842
(125 spp.)

Eimeria wambaensis Jirků and Modrý 2005 (Fig. 18)

Type host: *Hyperolius viridiflavus* (Duméril & Bibron 1841), Common reed frog.

Other hosts: None reported to date.

Type locality: AFRICA: Kenya, Wamba (Rift Valley province, 00° 56' 58.4" N, 37° 20' 56.9" E).

Geographic distribution: AFRICA, Kenya.

Description of sporulated oocyst: Oocyst shape: ellipsoidal to ovoidal; number of walls: 2; outer, 0.5–0.7, smooth; inner, 0.1–0.2; L x W: 17–13 (15–18.5 x 11–14); L/W ratio: 1.4 (1.2–1.6); M, OR, PG: all absent. Distinctive features of oocyst: wall tightly encloses the sporocysts such that they sometimes appear deformed.

Description of sporocyst and sporozoites: Sporocyst shape: navicular (slightly pointed at both ends); L x W: 8.7 x 6.0 (8–10.5 x 5.5–7); L/W ratio: 1.4 (1.2–1.6); SB: present, but barely visible as slight thickening at one end of sporocyst; SSB and PSB: absent; SR: present; SR characteristics: composed of coarse granules of irregular shape, each 1.5–2 wide, and these completely fill the sporocyst leaving only small parts of SZ visible; SZ: arranged head to tail, each with 1 spheroidal N visible, 1.5 wide, in center of SZ. Distinctive features of sporocyst: thin, single-layered wall and navicular shape.

Prevalence: 1 of 2 (50%) frogs from Wamba; 0 of 40 frogs from the Kakamega forest.

Sporulation: Exogenous.

Prepatent and patent periods: Unknown.

Site of infection: Intranuclear in epithelial cells of both small and large intestines.

Endogenous stages: All endogenous stages are surrounded by a PV and develop in the N of epithelial cells of the small and large intestine. Early trophozoites were 3.5 x 2–3, located within a vacuole insde the host cell N. Mature microgamonts were spheroidal to ellipsoidal, ~10–15 x 8–10. Microgamonts in various stages of development were 11–16 x 7–12 and contained a large N and numerous eosinophilic granules resembling wall-forming bodies. No meronts were observed.

Pathology: None described.

Materials deposited: Photosyntypes of sporulated oocysts and histological sections with (undescribed) endogenous stages deposited in the Department of Parasitology, University of Veterinary and Pharmaceutical Sciences Brno, Czech Republic (R 65/04). Symbiotype host (*sensu* Frey *et al*. 1992) in the herpetology collection of the National Museum of Kenya, Nairobi (A/4130).

Remarks: This is the first emerian described from this host genus. Its oocysts differ in both quantitative and qualitative features from all other known anuran eimeriids. Further, the geographic origin and host phylogeny make the conspecificity with other *Eimeria* spp. unlikely.

Goussia hyperolisi Paperna, Ogara and Schein 1997 (Fig. 19)

Type host: Tadpole of *Hyperolius viridiflavus* (Duméril & Bibron 1841), Common reed frog.

Other hosts: None reported to date.

Type locality: AFRICA: Kenya, Sagana fish ponds.

Geographic distribution: AFRICA, Kenya.

Description of sporulated oocyst: Oocyst shape: subspheroidal; number of walls: initially a typical plasma membrane (see *Remarks*, below), but as the oocyst matures this envelope seems to merge with the wall of the PV that surrounds it; wall characteristics: membranous; L x W: 7.7 (7–10) or 7–9 x 6–8; L/W ratio: 1.1–1.3; M, OR, PG: all absent. Distinctive features of oocyst: the plasma membrane of the oocyst merges with the membrane of the PV and then becomes surrounded and enclosed by a yellow body, which may be an accumulation of degenerate intraepithelial lymphocytes resulting as part of a host defense process.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal (line drawing); L x W: 7.2 x 4.9 (6–8 x 4–6); L/W ratio: 1.5; SB, SSB, PSB: all absent; SR: present; SR characteristics: a ball of large granules/globules that gradually disintegrates and disappears once SZ differentiation is completed; SZ: 7 x 1.4–2, with a RB ~4.2–5.6 x 2.8. Distinctive features of sporocyst: a double-layered wall, 7.7–8.5 (?) thick, with distinct longitudinal sutures, characteristic of the genus, and a SR that disappears once the SZ differentiate.

Prevalence: 8 of 13 (61.5%) tadpoles, 0 of 4 (0%) post-metamorphosis, and 0 of 11 (0%) adult frogs.

Sporulation: Endogenous.

Prepatent and patent periods: Unknown.

Site of infection: Variable. Early developmental stages are found located in cells of the gut epithelium between the N and the brush border (Paperna *et al*. 1997, p. 82), while the host cells of oocyst stages in the tadpoles resemble intraepithelial leuckocytes rather than ordinary mucosal epithelial cells (Paperna *et al*. 1997, p. 87).

Endogenous stages: Early meronts were 4.5–5 x 2–4 and these later formed merozoites that the authors first said were 9.5 x 4 (Paperna *et al*. 1997, p. 80), but later (Paperna *et al*. 1997, p. 82) said were "very elongated," 7–8 long. Young macrogamonts were 7–9 x 4–5 and contained within a PV. Microgamonts were not seen.

Pathology: Progressive cytoplasmic degradation of infected host cells that causes them to round up and separate from the surrounding host tissue.

Materials deposited: None.

Remarks: In addition to the discrepancy noted above, regarding length of the merozoites, there are a few other discrepancies by Paperna *et al*. (1997) that make our interpretation of some of their data tenuous. First, Paperna *et al*. (p. 85), stated that "early oocysts...were 7.7 (7.0–9.8) and sporoblasts 9.45 (8.4–10.6) in diameter." Our view is that early oocysts and sporoblasts are one and the same. Second, early in their results they stated (p. 82), "Neither refractile nor crystalloid bodies could be identified in the newly formed sporozoites," but later (p. 85) they said that SZs contained a RB, 4.2–5.6 x 2.8.

A number of *Eimeria* species described from anurans have very thin walled oocysts that undergo endogenous sporulation and some of these have sporocysts with longitudinal sutures rather than a SB. This led Molnár (1995) to place *E. neglecta*, which he redescribed, into the genus *Goussia*, of mostly piscine coccidian (see Steingagen 1991 and Steingagen & Körting 1990), but the members of which all share this unique sporocyst feature.

This is only the second eimeriid coccidium described from tadpoles; both are *Goussia* species and both seem to share some unique developmental features. Nöller (1920), who first described *E. neglecta* (= *G. neglecta*), noticed the disappearance of infection from the tadpoles as they neared metamorphosis into frogs. Likewise, Paperna *et al*. (1997) found that the infections in *H. viridiflavus* also were found naturally only in tadpoles (8 of 13), but never in young post metamorphosis frogs (0 of 4) or in adult frogs (0 of 11). They also noted that infections terminated in tadpoles which failed to develop to the metamorphosis stage, suggesting to them that infection is time-restricted and expires independently of the metamorphosis process.

The sporulated oocysts of this species are similar in size to those of *G. neglecta* described from *P. rhidibundus* and *P. esculenta* tadpoles in Hungary. However, the sporocysts of this species are smaller (6.6 x 4.8) and have a smaller L/W ratio, 1.4, than those of *G. neglecta*, which are larger (8.8 x 4.8) with a larger L/W ratio, 1.8. This was the first coccidium described from anurans on the African continent.

Family Leptodactylidae Werner 1896
(4 genera, 91 spp.)

Host genus *Leptodactylus* Fitzinger 1826
(82 spp.)

Eimeria leptodactyli Carini 1931a, b, c (Fig. 20)

Type host: *Leptodactylus ocellatus* (L. 1758), Criolla frog.

Other hosts: None reported to date.

Type locality: SOUTH AMERICA: Brazil: outskirts of São Paulo.

Geographic distribution: SOUTH AMERICA: Brazil: outskirts of São Paulo.

Description of sporulated oocyst: Oocyst shape: ovoidal; number of walls: 1; wall thickness: "thin;" wall characteristics: colorless; L x W: 23 x 17; M and PG: absent (line drawing); OR: present, often arranged in a rosette-like pattern. Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal; L x W: 9 x 6.5; SB: present; SSB, PSB: both absent; SR: present; SR characteristics: scanty. Distinctive features of sporocyst: none.

Prevalence: Not given.

Sporulation: Exogenous.

Prepatent and patent periods: Unknown.

Site of infection: Unknown.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: About half of the known eimerians from anura have ovoidal sporulated oocysts. Of these, five other species are reported to possess an OR: *E. cyanophlyctis* from Asia (Fig. 8), *E. kermiti* from North America (Fig. 24), *E. prevoti* (Fig. 25) and *E. ranae* (Fig. 29) from Europe, and *E. terraepokotorum* from Africa (Fig. 9). However, sporulated oocysts of *E. leptodactyli* are larger than oocysts of *E. cyanophlyctis*, *E. terraepokorum*, *E. prevoti* and *E. ranae*, and smaller than oocysts of *E. kermiti*. Additionally this is the only *Eimeria* species known from a *Leptodactylus* species (additionally see Carini 1931a, b, c; Walton 1945). Based on these differences as well as differences in hosts and geographic location, we consider this species from *Leptodactylus ocellatus* as distinct.

Family Microhylidae Günther 1858
(43 genera, 413 spp.)

Host genus *Gastrophryne* Fitzinger 1843
(5 spp.)

Isospora fragosum Upton and McAllister 1988 (Figs. 21, 59)

Synonym: *Isospora* sp. of McAllister and Upton 1987b.

Type host: *Gastrophryne olivacea* (Hallowell 1856), Great Plains narrowmouth toad.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Texas, Somervell County.

Geographic distribution: NORTH AMERICA: USA, Texas.

Description of sporulated oocyst: Oocyst shape: spheroidal; number of walls: 1; wall thickness: ~0.8; wall characteristics: smooth, thin, ruptures 1–3 days after sporulation, releasing sporocysts; L x W: 18.5 (17–21); M, OR, PG: all absent. Distinctive features of oocyst: thin wall that ruptures after sporulation, freeing sporocysts.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 12.7 x 10.9 (11–14 x 10–12); L/W ratio: 1.2 (1.1–1.3); SB, SSB, PSB: all absent; SR: present; SR characteristics: coarsely granular, spheroidal or ovoidal, 7.9 x 6.9 (5–11 x 5–10); SZ: elongate, 12.6 x 3.4 (12–14 x 3–4) *in situ*, with 2 SZ in one direction and 2 in the opposite direction, each with 2 RBs; anterior RB spheroidal, 2.3 (1.2–2.4) and posterior RB spheroidal to ovoidal, 3.0 x 2.3 (2–4 x 2–3); N located between the 2 RBs. Distinctive features of sporocyst: sometimes, slight thickenings may be seen at opposite ends and at sides of sporocysts suggesting the presence of sutures.

Prevalence: 14 of 95 (15%). The prevalence in adult frogs, given by month, appears to fluctuate seasonally: February, 0 of 16 (0%); March 4 of 9 (44%); April 4 of 16 (25%); May 3 of 19 (16%); June 1 of 21 (5%); July 0 of 2 (0%); September 2 of 7 (29%); and October 0 of 5 (0%).

Sporulation: Exogenous, oocysts recovered from feces were unsporulated, partially sporulated or, rarely, fully sporulated.

Prepatent and patent periods: Unknown.

Site of infection: Unknown (see *Remarks*).

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: This species most closely resembles *I. neos* (Fig. 30) reported from *R. arvalis* in the former USSR. (Yakimoff & Gousseff 1936b); however, its oocysts are smaller than those of *I. neos* and its sporocysts have a large, highly distinctive SR, which those of *I. neos* lack. Kazubski and Grabda-Kazubska (1973) reported an isosporan from *R. arvalis* in Poland that is slightly larger than *I. fragosum* and has a SR. Even though Yakimoff and Gousseff (1936b) stated specifically that *I. neos* lacked a SR, Kazubski and Grabda-Kazubska (1973) identified the form they found as *I. neos* because, according to Kheysin (1967, as cited in Kazubski and Grabda-Kazubska, 1973), the SR is used to provide nutrition to the SZ and, thus, may disappear with time. Upton and McAllister (1988) considered this hypothesis unlikely and suggested that the isosporan reported by Kazubski and Grabda-Kazubska (1973) may be a separate, yet undescribed, species. However, recently we were able to observe changes in the SR and OR of *I. cogginsi* (Fig. 15) stored at room temperature in 2.5% $K_2Cr_2O_7$ solution for a period of 14 mo and determined that both the SR and OR disappeared in this species, suggesting that researchers working on new descriptions should report the time period elapsed between collection and species description of coccidians. Upton and McAllister (1988) reported the site of infection for this species as the intestine. However, the oocysts were recovered from the feces and no attempt was made to check what organs were infected with developmental stages of *I. fragosum*; therefore, the site of infection of this species is unknown.

Family: Ranidae Rafinesque 1814
(18 genera, 316 spp.)

Host genus *Lithobates* Fitzinger 1843
(49 spp.)

Eimeria algonquini Chen and Desser 1989 (Fig. 22)

Type host: *Lithobates catesbeianus* (Shaw 1802), American bullfrog.

Other hosts: *Lithobates clamitans* (Latreille *In* Sonnini de Manoncourt and Latreille 1801), Green frog; *Lithobates septentrionalis* (Baird 1854), Mink frog; *Lithobates sylvaticus* (LeConte 1825), Wood frog.

Type locality: NORTH AMERICA: Canada, Ontario, Algonquin Park, Lake Sasajewun.

Geographic distribution: NORTH AMERICA: Canada, Ontario.

Description of sporulated oocyst: Oocyst shape: spheroidal; number of walls: 1; wall thickness: thin; wall characteristics: smooth; L x W: 15.8 (14.5–16); L/W ratio: 1.0; M and PG: absent; OR: present; OR characteristics: spheroidal, 10 (9–11), composed of coarse granules. Distinctive features of oocyst: colorless, thin, smooth wall and the massive size of the OR which mostly obscures the sporocysts (line drawing).

Description of sporocyst and sporozoites: Sporocyst shape: banana-shaped; L x W: 19.5 x 4.2 (19–20 x 4–5); L/W ratio: 4.6; SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of small, coarse granules (line drawing); SZ: elongate, 13.8 x 1.6 (13.5–14 x 1–2), 2 spheroid RBs present, located one on

each side of an indistinct N. Distinctive features of sporocyst: very thin wall that is almost invisible (line drawing) and a L/W ratio that is the largest of any amphibian coccidium.

Prevalence: 26 of 162 (16%) *Lithobates catesbeianus*; 3 of 25 (12%) *Lithobates clamitans*; 7 of 68 (10%) *Lithobates septentrionalis*; 3 of 9 (33%) *Lithobates sylvaticus*.

Sporulation: Presumably endogenous.

Prepatent and patent periods: Unknown.

Site of infection: Unknown (see *Remarks*).

Endogenous stages: Unknown.

Pathology: None observed, to date.

Materials deposited: None.

Remarks: There are four other species of amphibian *Eimeria* that have spheroidal oocysts similar to those of *E. algonquini*. Sporulated oocysts of *E. belawini* (Fig. 10), *E. laminata* (Fig. 5), and *E. mazzai* (Fig. 1) are smaller, while those of *E. streckeri* (Figs. 13, 14, 55, 56) are larger than those of *E. algonguini*. In addition, sporocyst sizes, hosts and geographical locations are different between these five species.

The authors suggested that due to the method of obtaining fecal samples (gently squeezing the abdomen or giving the frog an enema with 85% saline), only moderate to heavy infections were detected, while lighter infections may have been missed. Thus, actual prevalence in examined frogs may have been higher than what they found. Young bullfrogs, based on size, were most frequently infected. This might be due to sporulated oocysts released into the water being ingested by larger invertebrates and, or, tadpoles, the prey of young bullfrogs (Korschgen & Baskett 1963; Fulk & Whitaker 1969). Chen and Desser (1989) reported the site of infection for *E. algonquini* as the intestine, but oocysts were recovered from the feces and no attempt was made to examine the intestine for developing stages of *E. algonquini*; therefore, the site of infection for this species is unknown.

Eimeria fitchi McAllister, Upton, Trauth and Bursey 1995 (Figs. 23, 60)

Type host: *Lithobates sylvaticus* (LeConte 1825), Wood frog.

Other hosts: None reported to date.

Type locality: NORTH AMERICA, USA, Arkansas, Izard County, 6.0 km SW of Melbourn, off State Highway 9.

Geographic distribution: NORTH AMERICA, USA, Arkansas.

Description of sporulated oocyst: Oocyst shape: ovoidal; number of walls: 1; wall thickness: 0.5; wall characteristics: smooth; L x W: 21.9 x 14.3 (20–24 x 13–15); L/W ratio: 1.5 (1.3–1.7); M and OR: absent; PG: usually absent, but sometimes 1–3 fragments are attached to the outer wall of the sporocysts. Distinctive features of oocyst: very thin wall and fragments of debris (former PG?) attached to outer wall of sporocysts.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 10.9 x 7.4 (10–11 x 7–8); L/W ratio: 1.5 (1.3–1.6); SB: present (?) as a slight thickening at one end of sporocyst; SSB and PSB: absent; SR: present; SR characteristics: 3.6 x 1.6, consisting of ~25 large, coarse, scattered granules; SZ: elongate, 11.1 x 1.7 (10–12 x ~2) *in situ*, with 2 RBs, 1 an anterio-central, spheroidal, ~1.1 wide, and a posterior RB, subspheroidal to ovoidal, 2.9 x 1.6 (2–3 x 1.4–1.6); an indistinct N lies between the 2 RBs, 1 anterio-central, spheroidal, ~1.1 wide, and a posterior RB, subspheroidal to ovoidal, 2.9 x 1.6 (2–3 x 1.4–1.6); an indistinct N Lies between the 2 RBs. Distinctive features of sporocyst: none.

Prevalence: 11 of 13 (85%).

Sporulation: Exogenous, complete within 5 days at 23° C.

Prepatent and patent periods: Unknown.

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

Endogenous stages: Unknown.

Pathology: None observed to date.

Material deposited: Photosyntype of sporulated oocysts in USNPC (No. 84163). Symbiotype host deposited at ASUMZ (Cat. No. 19434).

Remarks: The host frogs and their oocysts were collected in February, 1994; this was the first ranid frog in the United States documented to harbor coccidia. This species can be easily distinguished from *E. kermiti* and *E. algonquini* described from *L. sylvaticus* in Ontario, Canada. Sporulated oocysts of *E. kermiti* (Fig. 24) are larger and have an OR and PG, and sporocysts with a distinct SB while those of *E. algonquini* (Fig. 22) are spheroidal, with very thin-walled sporocysts.

Eimeria kermiti Chen and Desser 1988 (Fig. 24)

Type host: *Lithobates catesbeianus* (Shaw 1802), American bullfrog.

Other hosts: *Lithobates clamitans* (Latreille *In* Sonnini de Manoncourt and Latreille 1801), Green frog; *Lithobates septentrionalis* (Baird 1854), Mink frog; *Lithobates sylvaticus* (LeConte 1825), Wood frog.

Type locality: NORTH AMERICA: Canada, Ontario, Algonquin Park, Pee Wee Lake.

Geographic distribution: NORTH AMERICA: Canada, Ontario.

Description of sporulated oocyst: Oocyst shape: ovoidal; number of walls: 1; wall thickness: "thin;" wall characteristics: smooth; L x W: 25.1 x 19.5 (25–27 x 18–20); L/W ratio: 1.3; M: absent; OR: present; OR characteristics: spheroidal to subspheroidal, 8.3 x 7.3 (8–9 x 7–7.5), composed of a large vacuole surrounded by coarse granules; PG: present. Distinctive features of oocyst: very thin, single-layered wall.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 9.9 x 6.6 (9–10 x 6–7); L/W ratio: 1.5; SB: present as a small, nipple-like structure at one end of sporocyst; SSB and PSB: absent; SR: present; SR characteristics: spheroidal to subspheroidal body, 3.3 x 2.4 (4–5 x 2–3), composed of coarse granules between SZ; SZ: elongate, 8.6 x 2.3 (8–9 x 2–3), indistinct N lies between 2 small RBs. Distinctive features of sporocyst: none.

Prevalence: 3 of 162 (2%) *Lithobates catesbeianus*; 1 of 25 (4%) *Lithobates clamitans*; 1 of 68 (2%) *Lithobates septentrionalis*; 1 of 9 (11%) *Lithobates sylvaticus*.

Sporulation: Presumably endogenous.

Prepatent and patent periods: Unknown.

Site of infection: Unknown (see *Remarks*).

Endogenous stages: Unknown.

Pathology: None observed.

Materials deposited: None.

Remarks: This species is distinguished from *E. ranarum* (Fig. 26) by its larger oocysts (25 x 19.5 *vs*. 18–20 x 12–16) as well as from those of *E. leptodactyli* (23 x 17, Fig. 20). The authors suggest that due to the method of obtaining fecal samples (gently squeezing the abdomen or giving the frog an enema with 85% saline) only moderate to heavy infections were detected, while lighter infections may have been missed. Thus, the prevalences in the frogs they examined may be higher than what they reported. Young bullfrogs, based on host size, were most frequently infected. This might be due to sporulated oocysts that are released into the water being ingested by larger invertebrates and tadpoles, the prey of young bullfrogs (Korschgen & Baskett 1963; Fulk & Whitaker 1969). Chen and Desser (1989) reported the site of infection for *E. kermiti* as the intestine, but oocysts were recovered from the feces and no attempt was made to examine the intestine for developing stages of *E. kermiti*; thus, the site of infection for this species is unknown.

Host genus *Pelophylax* Fitzinger 1843
(24 spp.)

Eimeria prevoti (Laveran and Mesnil 1902a, b) Doflein 1909 (Fig. 25)

Synonyms: *Paracoccidium prevoti* Laveran and Mesnil 1902a; *Eimeria prevunti* (Laveran and Mesnil

1902a), Yakimoff and Matikaschwili 1933, *lapsus*.

Type host: *Pelophylax lessonae* (Camerano 1882) Pool frog.

Other hosts: None reported to date.

Type locality: EUROPE: France, west of Paris.

Geographic distribution: EUROPE: France.

Description of sporulated oocyst: Oocyst shape: mostly globoidal to ovoidal; number of walls: 1; wall thickness: "thin;" wall characteristics: smooth; L x W: variable; globoidal forms are 16–18, while ovoidal forms are 20–22 x 12–15; L/W ratio: variable; M and PG: absent; OR: present; OR characteristics: spheroidal, ~5–6 wide, composed of a large vacuole surrounded by coarse granules. Distinctive features of oocyst: thin, single-layered wall and an OR with a vacuole surrounded by granules.

Description of sporocyst and sporozoites: Sporocyst shape: initially fusiform, but the sporocyst wall eventually disappears leaving 8 SZ free in oocyst; L x W: unknown; L/W ratio: unknown; SB: present as a small, nipple-like structure at one end of sporocyst; SSB and PSB: absent; SR: present; SR characteristics: small mass composed of coarse granules between SZ; SZ: elongate, ~10–12 long, with 1 obvious RB. Distinctive features of sporocyst: sporocyst wall disappears soon after sporulation is completed, leaving the 8 SZ and the remaining OR and SR free within the oocyst.

Prevalence: Unknown.

Sporulation: Unknown. The initial sporoblast, ~7 µm wide, elongates to form the sporocysts and OR. Upon sporocyst formation, the SZ are arranged head to tail therein.

Prepatent and patent periods: Unknown.

Site of infection: Mid-gut epithelial cells.

Endogenous stages: Both merogony and gamogony occur above the N of the intestinal epithelial cell. Young meronts were round, ~4, and limited by a fine membrane. Ripe meronts were ovoidal, ~21.5 x 16.8, and produced up to 40 merozoites (38–44), each ~6.2 x 1.5. Mature microgamonts were 21.4 x 19.8 and give rise to comma-shaped microgametes, 5–6 x 0.7, with 2 flagella which are unequal in length (11 and 8 long). A vacuole is visible within the granular cytoplasm of the mature macrogamonts, which are round, ~10, and have a distinct N with a conspicuous karyosome. Doflein (1909) said that the macrogamont formed the covering only after fertilization and that the sporoblast of the zygote did not go through a pyramid stage, as seen in many coccidia.

Pathology: Unknown.

Materials deposited: None.

Remarks: Laveran and Mesnil (1902a) created the subgenus *Paracoccidium* in their belief that disintegration of the sporocyst wall soon after sporulation was completed might represent an intermediate phylogenetic type of development; however, work with other amphibian coccidia (e.g. *E. canaliculata*; *E. fragilis*) shows that this is not an uncommon phenomenon. Doflein's (1909) line drawing of *E. prevoti* (Fig. 25) shows that the oocysts he saw were ellipsoidal. Boulard (1975) redescribed the species and its endogenous development, also from pool frogs, which he caught in Normandy and most of the measurements above are from his paper. Boulard (1975) provided a detailed line drawing of a sporulated oocyst that showed a distinct SB on the sporocysts before they disintegrated, a detail omitted by Laveran and Mesnil (1902a) in their original work. Boulard's (1975) young oocysts taken from feces measured 16.5 x 12.8 (15–17 x 12–14), with a L/W ratio of 1.3; after sporulation, the oocysts were 17.4 x 12.6 with a L/W ratio of 1.4. The OR was a spherical mass of granules, ~4.5 x 3.

Eimeria ranarum (Labbé 1894b) Doflein 1909 (Fig. 26)

Synonyms: *Acystis parasitica* (Labbé 1894b), pro parte; *Caryophagus ranarum* Labbé 1899; *Coccidium ranarum* (Labbé 1894b) Laveran and Mesnil 1902a; *Karyophagus ranarum* Labbé 1894b.

Type host: *Pelophylax esculenta*, (L. 1758), Pool frog.

Other hosts: *Rana temporaria*, L. 1758, Grass frog.

Type locality: EUROPE: France.

Geographic distribution: EUROPE: France.

Description of sporulated oocyst: Oocyst shape: ellipsoidal to ovoidal; number of walls: 1; wall thickness: "thin;" wall characteristics: smooth; L x W: 18–20 x 12–16; L/W ratio: unknown; M: present (line drawing in Laveran & Mesnil 1902a); OR and PG: both absent. Distinctive features of oocyst: presence of a small M.

Description of sporocyst and sporozoites: Sporocyst shape: spindle-shaped with both ends tapering to a point; L x W: 7 x 4; L/W ratio: 1.8; SB, SSB, PSB: all absent; SR: present; SR characteristics: scattered ovoid globules; SZ: about the same length as the sporocysts (line drawing). Distinctive features of sporocyst: very small and spindle shaped.

Prevalence: Unknown.

Sporulation: Exogenous; but oocysts passed in the feces in an advanced state of sporulation.

Prepatent and patent periods: Unknown.

Site of infection: Development is exclusively within the N of small intestinal epithelial cells.

Endogenous stages: Meronts contain 25–30 small merozoites, ~5–6 long, arranged in irregular rows. Microgametes are also small, ~3 long. Ellipsoidal macrogametes are filled with large granules and are ~17 x 12 when discharged into the lumen of the small intestine; at that time they have a distinct M, through which Laveran and Mesnil (1902a) believed the microgametes entered.

Pathology: Atrophy of the infected host cell N.

Materials deposited: None.

Remarks: The history of the discovery and naming of this coccidium is convoluted and confusing and is best summarized by Dobell (1909) who wrote that Labbé (1894b) mentioned that he found a parasite, like that occurring in newts, in the N of the intestinal epithelium of *Rana temporaria*. Without giving any further description he bestowed the name *Karyophagus ranarum* n. sp. upon it. But on the very next page (p. 212) he said that he believed that this parasite is identical with *Karyophagus salamandrae* Steinhaus, and *Cytophagus salamandrae* Steinhaus, and he proposed to call them all *Acystis parasitica*! Later, Labbé (1899) retained the name *Caryophagus ranarum* Labbé for the intestinal coccidium of the frog, but gave the host as *Rana esculenta* (=*Pelophylax esculenta*), and gave no further description of it. It is obviously useless to attach much importance to these names, and impossible to identify the animal(s). Walton (1941, 1961) erroneously reported 2 *Ambystoma* spp. as hosts for this coccidium.

Goussia neglecta (Nöller 1920) Molnár 1995 (Fig. 27)

Synonym: *Eimeria neglecta* Nöller 1920.

Type host: Tadpoles of *Pelophylax esculenta* (L. 1758), Pool frog.

Other hosts: Tadpoles of *Pelophylax ridibundus* (Pallas 1771), Marsh frog; possibly tadpoles of *Pelophylax lessonae* (Camerano 1882), Little water frog; possibly tadpoles of *Rana temporaria* L. 1758, Grass frog.

Type locality: EUROPE: Germany, near Hamburg.

Geographic distribution: EUROPE: Germany, Hungary.

Description of sporulated oocyst: Oocyst shape: round occasionally in groups of 2 or 3 enclosed in yellow bodies; number of walls: 1; wall thickness: thin, fragile; wall characteristics: smooth (see *Remarks*); L x W: 10.6 (8.5–12.5); L/W ratio: 1.0; M, OR, PG: all absent. Distinctive features of oocyst: very thin, single-layered wall that is often carried with the intestinal epithelial cell when these are shed into the lumen.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal (Nöller 1920) to ellipsoidal (Molnár 1995), with 1 side slightly flattened, with distinct longitudinal sutures (see *Remarks*); L x W: 8.8 x 4.8 (6.5–10 x 4–6); L/W ratio: 1.8; SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal to subspheroidal body composed of large granules/globules (line drawings), 5–7.5 x 3–4 in young oocysts and spheroidal, ~2,

in older oocysts; SZ: vermiform with one end reflexed, 8.2 x 1.8 (6–10 x 1.5–2) with indistinct, centrally located N. Distinctive features of sporocyst: very thin walls with one side slightly flattened and with distinct longitudinal sutures, characteristic of the genus, recurved SZs.

Prevalence: Unknown for type host in Germany; 19 of 38 (50%) *P. ridibundus* and 7 of 10 (70%) *P. esculenta* in Hungary (Molnár 1995).

Sporulation: Endogenous.

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the intestine.

Endogenous stages: Nöller (1920) found merogony to occur in the epithelial cells of the tadpole, but not in those of the adult. Molnár (1995) indicated that meronts contained 8–16 merozoites arranged in parallel. Meronts, gamonts, and immature oocysts were observed both in apical and basal cytoplasm of the epithelial cells.

Pathology: Unknown.

Materials deposited: None.

Remarks: This was the first coccidium described from tadpoles (Nöller 1920) and to date is only the second named species of *Goussia* known from amphibians. The description given above is a composite from Nöller's (1920) original description (which was grossly inadequate, but did include a crude line drawing) and Molnár's (1995) re-description. Finally, Walton (1949b), in an abstract, mentioned *G.* (*E.*) *neglecta* as a parasite of *R. temporaria* from Europe, but provided no other information. Molnár (1995) indicated that the oocysts of this species consisted of 2 halves joined by a suture and because of this observation transferred *Eimeria neglecta* to the genus *Goussia*. However, his line drawing of the oocyst does not show the 2 halves, and we suspect that he meant that the sporocysts contained 2 halves joined by a suture which is the characteristic feature of the genus *Goussia* and this was misstranslated from Hungarian to English. Both Nöller (1920) and Molnár (1995) reported *G. neglecta* in tadpoles of *Pelophylax* spp. and possibly tadpoles of *Pelophylax lessonae*, but not adult frogs. Molnár (1995) noted that the highest prevalence of infection was observed during July in tadpoles that had hindlimbs, but that the prevalence was lower in tadpoles with hindlimbs and emerged forelimbs and lowest in those with no limbs. Sporulated oocysts were found in mucus and feces and in groups of 2 or 3 enclosed in yellow bodies. Molnár (1995) speculated how the oocysts of *G. neglecta* might survive after leaving the tadpole, given the very fragile nature of their oocyst and sporocyst walls; he suggested the species might overwinter as sporozoites in tubificid oligiochaetes as was shown for *G. carpelli* in the common carp (Steinhagen & Körting 1990). Molnár (1995) also mentioned seeing developmental stages of another coccidium in the N of the epithelial cells in the frogs he examined, but that these seem to represent another species. Recently Jirků and Modrý (2006b) reported a *Goussia* sp. similar in morphology to *G. neglecta* from a forest pond at Zajetchee potok, Brno, Czeck Republic in 23 of 45 (51%) tadpoles of the agile frog, *Rana dalmatina*, Fitzinger *In* Bonaparte, 1839. Because measurements of the sporocysts of their isolate differed slightly, but overlapped in range with *G. neglecta* from the original description by Nöller (1920) and as reported by Molnár (1995), they took the conservative approach and refer to their isolate as a species of *Goussia*. Importantly, their examinations of tadpoles indicated that they found developmental stages of *Goussia* sp. in the intestine, and fully sporulated oocysts in the intestine and the sinuses of the liver. They allowed tadpoles of *R. dalmatina* to metamorphose to assess the fate of *Goussia* infections in these hosts. All juvenile and subadult frogs which metamorphosed in the laboratory and were examined 2 wk to 15 mo after metamorphosis contained oocysts of *Goussia* sp. in the liver, but not in the intestine. Only individual or clusters of oocysts were observed in the liver, and these were not enclosed by yellow bodies or macrophages. This study was the first to demonstrate *Goussia* sp. infections in an extraintestinal location in an amphibian host. The authors suggested that the extraintestinal oocysts of amphibian *Goussia* sp. in metamorphosed frogs may serve as a reservoir for colonization of tadpoles at new breeding sites or when ponds dry up. They suggested that oocysts of *Goussia* sp. in the liver of adult frogs are not likely to leave the host by the feces, and tadpoles may become infected by consuming dead frogs with oocysts in their liver.

Hyaloklossia lieberküehni (Labbé 1894b) Laveran and Mesnil 1902b (Fig. 28)

Synonyms: *Diplospora lieberkühni* (Labbé 1894b) Grasse 1953; *Hyaloklossia lieberkühni* (Labbe 1894b) Labbé 1896; *Klossia lieberkühni* Labbé 1894b; *Isospora lieberküehnk* (Labbe 1894b) Laveran and Mesnil 1902b.

Type host: *Pelophylax esculenta* (L. 1758), Pool frog.

Other hosts: *Lithobates pipiens* (Schreber 1782), Northern leopard frog; *Pelophylax ridibunda* (Pallas, 1771), Marsh frog; *Rana temporaria* L. 1758, Grass frog; *Bombina variegata* (L. 1758), Yellowbelly toad.

Type locality: EUROPE: France.

Geographic distribution: EUROPE: Bulgaria, Czeck Republic, France, Poland; NORTH AMERICA: Wisconsin.

Description of sporulated oocyst: Oocyst shape *in situ*: asymmetrically ellipsoidal; number of walls: 1; wall thickness: "very thin;" wall characteristics: transparent, elastic, and fragile; L x W: 35–45 x 20–25; L/W ratio: unknown; M, OR, PG: all absent. Distinctive feature of oocyst: intracellular development and sporulation.

Description of sporocyst and sporozoites: Sporocyst shape: broadly spindle-shaped to ellipsoidal; L x W 25–30 x 14–16; L/W ratio: unknown; SB, SSB, PSB: all absent; SR: present; SR characteristics: spheroidal to subspheroidal cluster of irregular granules; 9.5–17 x 7–12; SZ: elongate, banana-shaped, 17–21 x 3–4 with a small, round RB at their rounded end (line drawing). Distinctive feature of sporocyst: very thin wall.

Prevalence: Usually not stated, but 1 of 137 (<1%) *L. pipiens* in Wisconsin (Levine & Nye 1977); in 2 of >2000 (<0.1%) *P. esculenta* in Poland (Kazubski & Grabda-Kazubski 1973); 4 of 16 (25%) frogs during April and May and 0 of 18 (0%) frogs in July in the Czeck Republick (Modrý *et al*. 2001) and Vojtková (1976) not stated; and Laveran and Mesnil (1902b) in France and Nöeller (1923) in Germany both reported a high degree of infection in young *P. esculenta*.

Sporulation: Endogenously, within the tubular epithelial cells of the kidney.

Prepatent and patent periods: Unknown, but oocysts may rupture intracellularly releasing sporocysts into the renal tubules.

Site of infection: Epithelium of the renal tubules.

Endogenous stages: According to Laveran and Mesnil (1902b), within only 48 h after ingesting oocysts, the parasite produces an intense infection in various organs of the body with both meronts and gamonts. Nöller (1923) found sporozoites in the spleen of 16 day old tadpoles after he had infected them with sporocysts. Merogony occurred in the spring in the glomerular epithelium of the kidneys of young frogs, but did not develop to gamonts until the summer. Merozoites were short and crescent-shaped with a central N. Gamonts also developed in glomerular epithelial cells. Macrogamonts were elongate ovoidal to ellipsoidal bodies with a large N and a granular cytoplasm. Mature microgamonts had peripherally arranged N and each microgamete had 2 flagella. Levine and Nye (1977) found from 1–12 merozoites per host cell in the cytoplasm of kidney tubule epithelial cells where they completely destroyed the cytoplasm, but left the N intact although sometimes shrunken. The merozoites they saw were elongated and slightly curved, ~6–7 long, with a central or subcentral spherical or squarish N, ~1, and similar to those described by Nöller (1923).

Pathology: Produces marked pathological changes in the kidneys where they form large, whitish cyst-like structures filled with granular contents consisting of mostly immature oocysts (Kazubski & Grabda-Kazubski 1973).

Material deposited: SSU rRNA sequences in GenBank (AF298623).

Remarks: Lieberkühn (1854) was the first to find this renal coccidium in *P. esculenta* in France. Later, Labbé (1894b) described it under the name *Klossia lieberkühni* and two years later, in 1896, after re-evaluating its status, he erected the genus *Hyaloklossia* to accommodate this species. Later authors (Laveran & Mesnil 1902b; Minchin 1903) placed *H. leiberküehni* into the genus *Diplospora* Labbé 1893; still others (Nöller 1923; Doflein & Reichenow 1953) placed it into the genus *Isospora* (Schneider 1881). Recognizing that the

genus *Isospora* is now known to be polyphyletic, Modrý *et al.* (2001) collected "*I.*" *lieberküehni* from *P. esculenta* in the Czech Republic, extracted DNA, and amplified and sequenced the SSU rRNA gene. Using various phylogenetic analyses to examine the phylogenetic position of this enigmatic organism to species in both the Eimeriidae (*Isospora, Eimeria, Cyclospora*) and the Sarcocystidae (*Sarcocystis, Toxoplasma, Hammondia, Neospora,* and others) they concluded that, the unique combination of morphological, biological and phylogenetic features was sufficient to re-erect and emend the oldest available synonym, *Hyaloklossia* with *H. liberküehni* as the type species.

Nöller (1923) believed that the endogenous stages reported in organs other than the kidneys by Laveran and Mesnil (1902b) were actually *Lankesterella minima*, and that the endogenous stages of *H.* (=*I.*) *lieberküehni* are limited to the kidney. Nöller (1923) also gave the details of the life history noting that oocysts deposited in the water were swallowed by tadpoles in which the SZ make their way to the glomeruli of the kidneys, where merogony takes place in the epithelial cells. Resulting merozoites then invade the tubule epithelium, which was found heavily infected with other meronts in young frogs during late April and early May. Several weeks later, macro- and microgamonts were found in tubule cells where the oocysts formed (Wenyon 1926). Nöller (1923) said microgametes were biflagellate. Levine and Nye (1977) reported the infection in 1 *L. pipiens* from Wisconsin, USA, as a new host and geographic record based solely on merozoites seen in the kidney tubule epithelial cells. We feel that Levine and Nye (1977) had no justification in identifying *H. lieberküehni* based on merozoites seen in the kidney tubules and their report may represent an undescribed species of apicomplexan from the northern leopard frog. Pellérdy (1974, p. 725) indicated that this species, along with *I. mesnili, E. ranarum* and *E. salamandrae*, are all intranuclear parasites.

Host genus *Rana* Linnaeus 1758
(43 spp.)

Eimeria ranae (Dobell 1908) Dobell 1909 (Fig. 29)

Synonym: *Cytospermium ranae* Rivolta 1878; *Coccidium ranae* Dobell 1908.

Type host: *Rana temporaria* L. 1758, Grass frog.

Other hosts: *Pelophylax esculenta* (L. 1758), Pool frog.

Type locality: EUROPE: England, Cambridge.

Geographic distribution: EUROPE: England, Germany.

Description of sporulated oocyst: Oocyst shape: spheroidal to ovoidal; number of walls: 1; wall thickness: "thin;" wall characteristics: smooth; L x W: 18–22 x 18–22; L/W ratio: 1.0; M and PG: absent; OR: present; OR characteristics: spheroidal mass composed of large granules (line drawing). Distinctive features of oocyst: very thin, single-layered wall that collapses around sporocysts or disintegrates releasing the sporocysts.

Description of sporocyst and sporozoites: Sporocyst shape: spindle-shaped with both ends tapering to a point; L x W: 14 x 7; L/W ratio: 2.0; SB: present as a small, nipple-like structure at 1 end of sporocyst; SSB: absent; PSB: present as a small, nipple-like structure at opposite end of sporocyst (see *Remarks*); SR: present; SR characteristics: spheroidal body composed of coarse granules between SZ; SZ: longer than sporocyst with their ends curled over one another; an indistinct N lies in the middle of each SZ. Distinctive features of sporocyst: presence of both SB and PSB, giving the sporocyst a strong resemblance to those of *Monocystis* spp.

Prevalence: ~15% of all *R. temporaria* (Dobell 1909).

Sporulation: Unknown; however, Dobell (1909) stated that it usually occured in the gut lumen of the lower small intestine and the large intestine (see *Remarks*).

Prepatent and patent periods: Unknown.

Site of infection: Unknown; however, Dobell (1909) speculated, "It appears most probable that schizog-

ony (= merogony) takes place in the small intestine in the upper part and is completed before any of the parasites proceed to spore formation."

Endogenous stages: Unknown. Dobell (1909) said that he repeatedly examined the intestinal epithelium, the liver, and the kidneys of frogs that were passing "spores" (oocysts and/or sporocysts) and those that were uninfected and never could find any endogenous stages.

Pathology: Unknown.

Materials deposited: None.

Remarks: Dobell (1908, 1909) found this species in *R. temporaria* near Cambridge and Munich and once in *P. esculenta* near Munich. He originally named it in 1908, but provided no mensural data and no line drawing, thus creating a *species inquirenda*. In 1909 he gave a more detailed description, providing both measurements and a line drawing. The most interesting and/or disturbing aspect about his species description is the structure of the sporocysts, which strongly resemble the spores of *Monocystis* spp. However, Dobell (1909) said that he carefully followed the sporulation process and watched the sporocysts change from what he called "oval" (his Fig. 95) to spindle-shaped (his Figs. 96, 97), with a nipple-like structure on each end. He was clearly aware of the existence of *Monocystis* spores because he said, "Their resemblance to the spores of *Monocystis* is often very striking in early stages of development. As I have already noted (p. 206), these spores are not uncommon in frogs. Of course, when fully formed the octozoic *Monocystis* spores cannot possibly be mistaken for the dizoic spores of the *Eimeria*." If his description is accurate, this is 1 of only 2 amphibian coccidia to possess a PSB (the other being *E. spherica* from *Mesotriton alpestris*, from France). The other interesting aspect of Dobell's (1909) work is that he stated he always encountered sporogony to occur in the lower end of the frog's gut about the posterior half of the small intestine, together with the large intestine. However, the timeline he gives for sporulation to occur is as follows: unsporulated oocyst to 4 sporoblast stage, 12–20 h; sporoblasts into spores, 20 h; development of the "sporal residuum," 6–7 h; from the sporal residuum to sporozoite formation, development proceeds more slowly, but no time is given. Thus, sporulation, which he says takes place in the lower small intestine and the large intestine takes, minimally, 38+ h. Our observations on ranid and other anurans maintained in the laboratory indicate that, unless they are fed, they may not defecate for up to a week. Taken together these data suggest that the observation of fully sporulated oocysts in the feces of anurans may not indicate that their development is endogenous and the only way to document endogenous development may be by documenting fully sporulated oocysts in infected host cells. Walton (1949a, b) lists *E. ranae* as a parasite of *P. esculenta* (1949a) and *R. temporaria* (1949b), both from Europe, but provides no other information.

Isospora neos Yakimoff and Gousseff 1936 a, b (Fig. 30)

Type host: *Rana arvalis* Nilsson 1842, Moor frog.

Other hosts: None reported to date.

Type locality: EUROPE: Belarus, Vitsyebskaya Voblasts, district of Polock.

Geographic distribution: EUROPE: Belarus, Poland.

Description of sporulated oocyst: Oocyst shape: ovoidal or spheroidal to subspheroidal; number of walls: 1 (line drawing); wall characteristics: transparent, smooth, and delicate; L x W: spheroidal, 23.7 (22–27) or subspheroidal, 26 x 22.4 (23–29 x 20–24); L/W ratio: 1.0 or 1.1; M, OR, PG: absent. Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal, slightly pointed at 1 end; L x W: 12.6–13.6 x 7.2–10.8; L/W ratio: unknown; SB, SSB, PSB: all absent (line drawing); SR: absent (original description) or present (Kazubski & Grabda-Kazubska 1973); SR characteristics: a membrane-bound ball of large granules (line drawing), 9–11 x 6–7. Distinctive features of sporocyst: the membrane-bound SR that is always on 1 side of the sporocyst.

Prevalence: 1 of 38 (<3%) (Kazubski & Grabda-Kazubska 1973).

Sporulation: Exogenous, but sporulation begins in transit down the intestine and is completed in 24 h at room temperature.

Prepatent and patent periods: Unknown.

Site of infection: Posterior half of the small intestine (Kazubski & Grabda-Kazubska 1973).

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: This species seems most similar to *I. brumpti* (Fig. 7) reported from a *Pseudepidalea viridis* in Syria. However, the oocysts of *I. brumpti* are longer and, thus, have a larger L/W ratio. Kazubski and Grabda-Kazubska (1973) redescribed *I. neos* as oval, 21–22 x 19–20 with a delicate wall that bursts after several hours. Their sporocysts were oval or slightly spindle-shaped, 16.2 x 12.8 (15–18.5 x 12–14.5), with a large granular SR (9–11 x 6–7) that was always on one side of the sporocyst and the SZ they measured were banana-shaped, 14–15 x 3–3.5. The main difference between the original description (Yakimoff & Gousseff 1936b) and the redescription by Kazubski and Grabda-Kazubska (1973) was that the latter authors described a large, apparently membrane-bound (line drawing) SR, not reported by Yakimoff and Gousseff (1936b). However, given the same host species and the geographic proximity of the hosts in both descriptions, they suggested that Yakimoff and Gousseff (1936b) simply missed it by saying, "its absence in the sporocysts seems to be hardly probable." Kazubski and Grabda-Kazubska (1973) also noted that unsporulated oocysts, 17–19 wide, were smaller than sporulated oocysts.

Family Rhacophoridae Hoffman 1932
(10 genera, 272 spp.)

Host genus *Chiromantis* Peters 1854
(15 spp.)

Eimeria fragilis Jirků and Modrý 2005 (Fig. 31)

Type host: *Chiromantis petersii kelleri* Boettger 1893, Central foam-nest tree frog.

Other hosts: None known to date.

Type locality: AFRICA: Kenya, Kula Mawe (Eastern province, 00° 34' 11.1" N, 38° 11' 56.3" E).

Geographic distribution: AFRICA: Kenya.

Description of sporulated oocyst: Oocyst shape: ellipsoidal; wall thickness: ~0.5; wall characteristics: smooth; L x W: 18.5 x 15.2 (17–19.5 x 14.5–16); L/W ratio 1.2 (1.1–1.3); M, OR, PG: all absent. Distinctive features of oocyst: thin, smooth wall that easily breaks down in hypertonic Sheather's sugar solution.

Description of sporocyst and sporozoites: Sporocyst shape: navicular (slightly pointed at both ends); L x W: 10.6 x 6.8 (9.5–12 x 6–7); L/W ratio 1.6 (1.5–1.7); SB: present as slightly thickened end of sporocyst, barely visible; SSB and PSB: absent; SR: present; SR characteristics: mass of fine refractile granules, each ~1 wide, so numerous they almost completely fill sporocyst leaving only parts of SZ visible; SZ: elongate, 10 x 2, with finely granulated cytoplasm and each with 2 spheroidal RB, 1–1.5, located at opposite ends of each SZ; N, ~1.5, in center of SZ. Distinctive features of sporocyst: SR that completely packs sporocyst obscuring SZ and tendency of sporocysts to disintegrate during storage and release free SZ into oocyst.

Prevalence: 1 of 1 (100%).

Sporulation: Presumably exogenous; oocysts were stored in 2.5% $K_2Cr_2O_7$ at room temperature for 4 wk and then at 6–7° C for 3 mo before being examined, some of which were not sporulated.

Prepatent and patent periods: Unknown.

Site of infection: Intranuclear in epithelial cells of the small intestine.

Endogenous stages: Early trophozoites, 3 x 2, were within a PV, 5 x 3.5–4, inside a host cell N. Meronts, with ~5 merozoites, were 6–7 x 4–5 and each merozoite was 5 x 1. Mature microgamonts are irregular in shape, ~10–15 x 7.5–14. Macrogamonts in various stages of maturity are 14–17 x 11–17 and have a large N and many eosinophilic granules, 0.5–1 wide. Sometimes multiple stages are found in a single host cell N, each within its own PV.

Patholgy: Unknown.

Materials deposited: Photosyntypes of sporulated oocysts and histological sections are deposited in the collection of the Department of Parasitology, University of Veterinary and Pharmaceutical Sciences, Brno, Czech Republic (R 60/04). Symbiotype host (*sensu* Frey *et al*. 1992) is in the herpetological collection of the National Museums of Kenya, Nairobi (A/4138).

Remarks: This is the only species, to date, described from this family of frogs. The oocyst wall is thin and fragile and the sporocysts have the tendency to disintegrate and release free SZ into the oocyst content. Jirků and Modrý (2005) first examined oocysts after 4 mo of storage, at which time they found that 80% of sporulated oocysts contained free SZ. Intranuclear development has only been reported in three other amphibian coccidia, *E. ranarum* (Fig. 26) from *P. esculenta* and *R. temporaria*, *E. wambaensis* (Fig. 18) from *H. viridiflavus*, and *E. grobbeni* (Fig. 48) from *S. atra*, the Alpine salamander. In addition, the geographic origin and host phylogeny make the conspecificity with other anuran eimerians unlikely.

URODELA (CAUDATA) Fisher von Waldheim 1813-Salamanders
(9 Families, 63 genera, 553 species)

Family Ambystomatidae Gray 1850
(2 genera, 35 species)

Host genus *Ambystoma* Tschudi 1838
(31 species)

Eimeria ambystomae Saxe 1955 (Figs. 32, 61)

Type host: Larval *Ambystoma tigrinum* (Green 1825), Tiger salamander.

Other hosts: *Ambystoma mavortium* Baird 1850, Barred tiger salamander; *Ambystoma texanum* (Matthes 1855), Smallmouth salamander.

Type locality: NORTH AMERICA: USA, Iowa, Dickinson County.

Geographic distribution: NORTH AMERICA: USA, Colorado, Indiana, Iowa, Nebraska, New Mexico, Texas.

Description of sporulated oocyst: Oocyst shape: ellipsoidal; wall thickness: 1 layer of uniform thickness, ~1; wall characteristics: smooth, colorless to pale yellow; L x W: 31.2 x 17.7 (24.5–36 x 15–20); M and PG: absent; OR: present; OR characteristics: spheroidal to subspheroidal body consisting of a hyaline sphere surrounded by small refractile granules, 12.7 x 11.4. Distinctive features of oocyst: large size, ellipsoidal shape, and large OR composed of a hyaline sphere with small refractile granules.

Description of sporocyst and sporozoites: Sporocyst shape: lanceolate; L x W: 21.9 x 5.1 (17–24.5 x 4–6); SB: present; SSB and PSB: absent; SR: present; SR characteristics: scattered refractile granules, sometimes aggregated into 2 groups; SZ: elongate, almost as long and as wide as sporocyst and arranged in sporocyst in a variety of twisted and parallel positions; SZ with 2 large RB, one near posterior end and the other above it near the middle of SZ. Distinctive features of sporocyst: lanceolate shape with a SB at slightly pointed end.

Prevalence: At least 13 of 56 (23%) *A. tigrinum* from Iowa between 1951–1954 (Saxe 1955); 1 of 1

(100%) *A. tigrinum* from Indiana (Bolek 2000); 17 of 17 (100%) *A. mavortium* from Colorado (5) and New Mexico (12) (Duszynski *et al*. 1972); *A. mavortium* from Nebraska not given (Bolek *et al*. 2003); and 11 of 51 (22%) *A. texanum* from Texas (McAllister & Upton 1987a; Upton *et al*. 1993). Saxe (1955) indicated that oocysts were noted in 1 of 8 *Desmognathus quadramaculatus* and in 1 of 2 *D. monticola* obtained from commercial sources, but never identified these oocysts to species.

Sporulation: Exogenous, 25–48 h; in one population, 80% sporulated within 48 h while in a second population 96% sporulated in 25 h (Saxe 1955).

Prepatent and patent periods: Unknown.

Site of infection: In the cytoplasm of epithelial cells of the small intestine from 2–10 cm above the rectum (Saxe 1955).

Endogenous stages: Saxe (1955) said he saw merozoites, macro- and microgametocytes in the cytoplasm of epithelial cells in stained sections of the lower small intestine from 3 larval *A. tigrinum*.

Pathology: Unknown.

Materials deposited: Photosyntypes of sporulated oocysts are deposited in the USNPC (No. 87478).

Remarks: Oocysts from *A. mavortia* from Colorado and New Mexico (Duszynski *et al*. 1972) and from *A. tigrinum* from Indiana (Bolek 2000) closely resembled those described from Iowa by Saxe (1955): oocysts from Colorado and New Mexico, 29.8 x 17.3 (24–38 x 15–25); oocysts from Indiana, 27 x 16.5 (27–28 x 15–17) *vs*. oocysts from Iowa, 31.2 x 17.7 (24.5–36 x 15–20); sporocysts from Colorado and New Mexico, 22.6 x 5.4 (16–27 x 5–7); sporocysts from Indiana, 15.4 x 5.1 (15–16 x 5–7) *vs*. sporocysts from Iowa, 21.9 x 5.7 (17–24.5 x 4–6). There were only 2 discrepancies between the 3 accounts: a) the size and composition of the OR: numerous scattered granules *vs*. a large hyaline structure surrounded by scattered granules; and b) Saxe (1955) did not mention the presence of a SB, while Duszynski *et al*. (1972) documented photographically that a SB was present. Saxe (1955) also said that the oocysts he saw may increase in size with time.

Eimeria distorta Saxe 1955 (Fig. 33)

Type host: Larval *Ambystoma tigrinum* (Green 1825), Tiger salamander.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Iowa, Dickinson County.

Geographic distribution: NORTH AMERICA: USA, Iowa.

Description of sporulated oocyst: Oocyst shape: elongate-ellipsoidal initially, but quickly becomes distorted in 3% $K_2Cr_2O_7$ solution when placed under a coverglass; wall thickness: 1 very thin layer (line drawing); wall characteristics: smooth; L x W: 29.2 x 15.5 (27–31 x 14–16); L/W ratio 1.9; M and PG: absent; OR: present; OR characteristics: scattered refractile granules. Distinctive features of oocyst: very thin wall that distorts easily when prepared for viewing with a light microscope.

Description of sporocyst and sporozoites: Sporocyst shape: elongate ellipsoidal; L x W: 12.4 x 7.3; L/W ratio 1.7; SR: present; SR characteristics: compact mass of small granules; SB, SSB, PSB: all absent; SZ: appear sausage-shaped (line drawing), slightly longer than sporocyst and without visible RB or N. Distinctive features of sporocyst: ellipsoidal shape and absence of SB; also, sporocysts appear tightly packed within confines of oocyst wall (line drawing).

Prevalence: Unknown.

Sporulation: Exogenous, 1/3 of the oocysts sporulated after 76 h, 2/3 sporulated after 5 days; the temperature at which they were maintained was not given.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: The type host was a larval *A. tigrinum*. Unsporulated oocysts were about the same size as sporulated ones, 27.5 x 15.5. This species has not been seen since its original description.

Eimeria kingi Saxe 1955 (Fig. 34)

Type host: *Ambystoma tigrinum* (Green 1825), Tiger salamander.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Iowa, Dickinson County, near the Lakeside Laboratory.

Geographic distribution: NORTH AMERICA: USA, Iowa.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall thickness: 1 thin layer (line drawing); wall characteristics: smooth; L x W: 20.4 x 18.3 (16–23 x 14–21); L/W ratio 1.1; M and PG: absent; OR: present; OR characteristics: starts as a compact mass of granules, becomes a single refractile sphere 5.2 wide ~6 days after leaving the host. Distinctive features of oocyst: OR changes from compact mass of granules to a refractile sphere.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 8.8 x 6.5 (7–10 x 5–8); L/W ratio 1.3; SB: present, small knob at pointed end of sporocyst; SSB and PSB: both absent; SR: present; SR characteristics: scattered refractile granules; no mention is made of SZ, RB or N. Distinctive features of sporocyst: none.

Prevalence: Unknown.

Sporulation: Exogenous, 4–6 days.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: This species was found in an adult *A. tigrinum*, the same host animals from which *E. waltoni* was described. It has not been seen since its original description.

Eimeria microcapi Duszynski *et al.* 1972 (Fig. 35, 62)

Type host: *Ambystoma mavortium* Baird 1850, Barred tiger salamander.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA: Colorado, Weld County.

Geographic distribution: NORTH AMERICA: USA: Colorado.

Description of sporulated oocyst: Oocyst shape: ellipsoidal; wall thickness: 1 thin layer of uniform thickness; wall characteristics: smooth; L x W: 38.1–25.3 (35–41 x 23–26); L/W ratio: 1.5 (1.3–1.7); M: present, 3.0 (2–4) wide, covered by a distinct MC; OR: present; OR characteristics: a large mass with no distinct shape, consisting of many small granules; PG: absent. Distinctive features of oocyst: large size, thin wall, presence of M and MC, and large, amorphous OR.

Description of sporocyst and sporozoites: Sporocyst shape: navicular (slightly pointed at both ends); L x W: 18.1 x 7.4 (16–19 x 6–8); L/W ratio: 2.5 (2.1–2.8); SB: if present (?), very small and difficult to distinguish at 1 end of sporocyst; SSB, PSB: both absent; SR: present; SR characteristics: composed of 5–15 scattered granules; SZ: tightly packed in sporocyst, without discernable N or RB visible. Distinctive features of sporocyst: navicular shape.

Prevalence: 1 of 5 (20%) salamanders from Colorado; 0 of 12 salamanders from New Mexico, U.S.A.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Unknown, oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: Photosyntypes of sporulated oocysts are deposited in the USNPC (No. 87486).

Remarks: Among the oocysts described from salamanders, only those of *E. canaliculata* Lavier, 1936 (Fig. 51) and *E. propria* (Schneider 1881) (Fig. 52) approach the size of *E. microcapi*, however, neither has a M or MC and the sporocysts of both are much longer than those of *E. microcapi*.

Eimeria opacum Upton, McAllister and Trauth 1993 (Figs. 36, 63)

Type host: *Ambystoma opacum* (Gravenhorst 1807), Marbled salamander.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA: Arkansas, Grant County, 6.4 km SW Sheridan.

Geographic distribution: NORTH AMERICA: USA: Arkansas.

Description of sporulated oocyst: Oocyst shape: spheroidal to slightly subspheroidal; wall thickness: ~1.0; wall characteristics: 2 layers, outer, smooth, ~1/2 of total thickness; L x W: 29.4 x 23.8 (27–32 x 25–31); L/W ratio: 1.0 (1.0–1.1); M, OR, PG: all absent. Distinctive features of oocyst: large size with 2 walls of equal thickness.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal when viewed from one side, but kidney-bean shaped when viewed from another side; L x W: 17.4 x 9.1 (16–21 x 8–11); L/W ratio: 1.7 (1.6–2.3); SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of 1–2 small clusters of coarse granules; SZ: 20–24 x 4–5, with large posterior RB 7.7 x 4.2 (5.5–9.5 x 4–5) and centrally located N. Distinctive features of sporocyst: each sporocyst is loosely enclosed in a secondary sporocyst wall, with ends of the secondary wall connected by frail, membrane-like material; 1–3 homogeneous globules present between primary and secondary sporocyst walls with other homogeneous globular material flattened against inner portion of secondary wall.

Prevalence: 1 of 5 (20%).

Sporulation: Exogenous. All oocysts were passed unsporulated and became fully sporulated within 1 wk at ~23° C.

Prepatent and patent periods: Unknown.

Site of infection: Unknown. Oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: Photosyntypes of sporulated oocysts are deposited in the USNPC (No. 83259). The symbiotype host (*sensu* Frey *et al.* 1992) was an adult male, 50 mm snout-vent length, collected 20 March 1992, and is deposited in the ASUMZ (Cat. No. 18276).

Remarks: Oocysts of *E. opacum* are unique among the coccidia because of the double-walled structure of the sporocysts; even the kidney-bean shape itself is rare. Rankin (1937) found unsporulated oocysts in *A. opacum* that were 17 x 12, measurements identical to those reported for the macrogametes/unsporulated oocysts of *E. ranarum* (Laveran & Mesnil 1902a), a parasite of ranids in Europe. Likewise, Walton (1942) mentioned an eimerian from an unspecified *Ambystoma* species, which Saxe (1955) later reported through personal communication with Walton as also being from *A. opacum*, but did not identify it.

Eimeria urodela Duszynski *et al.* 1972 (Figs. 37, 64)

Type host: *Ambystoma mavortium* Barid 1850, Barred tiger salamander.

Other hosts: *Ambystoma tigrinum* (Green 1825), Tiger salamander.

Type locality: NORTH AMERICA: USA: Colorado, Weld County.

Geographic distribution: NORTH AMERICA: USA: Colorado; Indiana.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall thickness: 1.0; wall characteristics: 1 smooth layer, colorless, of uniform thickness; L x W: 22.3–22.1 (14–26 x 14–26); L/W ratio: 1.0 (1.0–1.1); M

and PG: absent; OR: present; OR characteristics: consisting of large granules usually in a compact mass, ~5–7, but sometimes scattered throughout oocyst. Distinctive features of oocyst: spheroidal shape with large OR.

Description of sporocyst and sporozoites: Sporocyst shape: lanceolate; L x W: 16.3 x 5.8 (12–19 x 4–7); L/W ratio: 2.8 (2.0–3.6); SB: present, small, at pointed end of sporocyst; SSB, PSB: absent; SR: present; SR characteristics: usually compact spheroidal mass in center of sporocyst, but sometimes granules more diffuse in anterior of sporocyst; SZ: longer than sporocyst, crescent-shaped when within sporocyst, and arranged either side-by-side or intertwined with each other; neither N nor RB are visible. Distinctive features of sporocyst: the second largest L/W ratio in any amphibian coccidium, next to *E. longaspora* (see below).

Prevalence: 5 of 5 (100%) *A. mavortium* from Colorado during each of 3 collection periods; 0 of 12 *A. mavortium* from New Mexico (Duszynski, *et al*. 1972), and 1 of 1 *A. tigrinum* (100%) salamanders from Indiana (Bolek 2000).

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Unknown, oocysts collected from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: Photosyntypes of sporulated oocysts are deposited in the USNPC (No. 87489).

Remarks: Of the oocysts described from salamanders, only those of *E. spherica* (Schneider) (Fig. 44) and *E. waltoni* Saxe (Fig. 38) resemble *E. urodela*. Oocysts of *E. spherica*, redescribed by Lavier (1936), are much larger than those of *E. urodela*, with a mode of 35, and its sporocysts are much shorter and different in structure than those of *E. urodela*. Oocysts of *E. waltoni*, as described by Saxe (1955) are always subspheroidal, whereas those of *E. urodela* are distinctly spheroidal. Other differences between the 2 species include the size and shape of the OR and of the sporocysts.

Eimeria waltoni Saxe 1955 (Fig. 38)

Type host: *Ambystoma tigrinum* (Green 1825), Tiger salamander.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Iowa, Dickinson County, near the Lakeside Laboratory.

Geographic distribution: NORTH AMERICA: USA, Iowa.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall thickness: not stated; wall characteristics: 1 smooth wall of uniform thickness (line drawing); L x W: 22.2 x 19.2 (20–24 x 17–21); L/W ratio: 1.2; M: absent; OR: probably absent; PG: relatively small disc-like refractile granule described as the OR by Saxe (1955). Distinctive features of oocyst: closely resembles *E. kingi* in the unsporulated state, otherwise, none.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 12.2 x 7.2 (11–14 x 6–8); L/W ratio 1.7; SB: present as small knob a pointed end of sporocyst; SSB and PSB: both absent; SR: present; SR characteristics: loose aggregation of refractile granules; SZ, RB and N were not mentioned by Saxe (1955). Distinctive features of sporocyst: none.

Prevalence: Unknown.

Sporulation: Exogenous, ~66 h.

Prepatent and patent periods: Unknown.

Site of infection: Unknown, oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: The type host is the same individual as the type host of *E. kingi*. This species has not been found since its original description.

Isospora jeffersonianum Doran 1953 (Fig. 39)

Type host: *Ambystoma jeffersonianum* (Green 1827), Jefferson salamander, but see *Remarks*, below.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Minnesota, near Bemidji, Beltrami County.

Geographic distribution: NORTH AMERICA: USA, Minnesota.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall thickness: ~1.5; wall characteristics: 2 layers, outer, smooth, ~2/3 of total thickness (line drawing); L x W: 18.5–22.5; L/W ratio: 1.0; M: present, about 1.5–2 wide appearing as a small knob on oocyst wall; OR and PG: absent. Distinctive features of oocyst: presence of M.

Description of sporocyst and sporozoites: Sporocyst shape: elongate ovoidal, slightly pointed at one end; L x W: 15.5–16 x 7–8; L/W ratio: not given; SB: a small knob at pointed end of sporocyst; SSB and PSB: both absent; SR: present; SR characteristics: spheroidal, highly granular body, 2–2.7, that appears membrane-bound (line drawing); SZ: crescent-shaped, 6–7 long, with N equidistant between ends; RB not mentioned or shown in line drawing (Doran 1953). Distinctive features of sporocyst: membrane-bound SR.

Prevalence: 2 of 7 (29%).

Sporulation: Exogenous, 64–72 h.

Prepatent and patent periods: Unknown.

Site of infection: Unknown, oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: Doran (1953) lists the blue-spotted salamander *A. jeffersonianum* as the host. However, *A. jeffersonianum*, the Jefferson salamander, is not known to occur in Minnesota (Conant & Collins 1991; McAllister *et al*. 1993). Because the taxonomy of *A. jeffersonianum* and the blue-spotted salamander *A. laterale* was in a state of confusion (Bishop 1943) until Uzzel's work (1964), we think that the actual host Doran (1953) was dealing with was *A. laterale* or a hybrid species (Lowcock *et al*. 1987; Upton *et al*. 1993) which occurs commonly in Minnesota (Oldfield & Moriarty 1994).

Family Plethodontidae Gray 1850
(24 genera, 375 spp.)

Host genus *Plethodon* Tschudi 1838
(55 spp.)

Isospora hightoni Upton, McAllister and Trauth 1993 (Figs. 40, 65)

Synonym: *Isospora* sp. of McAllister, Upton and Trauth 1993.

Type host: *Plethodon albagula* Grobman 1944, Western slimy salamander.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Arkansas, Grant County, 6.4 km SW Sheridan.

Geographic distribution: NORTH AMERICA: USA, Arkansas.

Description of sporulated oocyst: Oocyst shape: spheroidal, rarely subspheroidal; wall thickness: ~1; wall characteristics: 2 layers, outer, smooth, ~1/2 of total thickness; L x W: 22.9 x 22.8 (21–24 x 21–24); L/W ratio: 1.0 (1.0–1.0+); M, PG: absent; OR: present; OR characteristics: a mass of small granules surrounding a central globule, all enclosed in a thin membrane, ~2.5–5 wide, but present in only 33% of the oocysts. Distinctive features of oocyst: unique OR that is present in only about 1/3 of the oocysts.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal, slightly pointed at one end; L x W: 16.6 x 11.1 (14.5–17.5 x 10.5–14); L/W ratio 1.5 (1.4–1.6); SB: present as large knob at pointed end, 1.2–1.6 high x 2–2.5 wide; SSB: present, 1.5–2.5 high x 2.5–3 wide; PSB: absent; SR: present; SR characteristics: composed of numerous coarse globules scattered among SZ; SZ: elongate sausage-shaped, 13.6 x 2.7 (12–14.5 x 2.5–3) each with 2 RB; anterior RB subspheroidal to ellipsoidal, 2.7 x 2.5 (2.5–3 x 2–3) and posterior RB smaller, spheroidal to subspheroidal, 2.3 x 2.2 (2–3 x 2–2.5); N located between refractile bodies. Distinctive features of sporocyst: large, distinct SB and SSB.

Prevalence: 8 of 46 (17%).

Sporulation: Exogenous, all oocysts were passed unsporulated and became fully sporulated within 1 wk at ~23° C.

Prepatent and patent periods: Unknown.

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

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes deposited in the USNPC (No. 83260). Symbiotype host (*sensu* Frey et al. 1992) a juvenile male, 25 mm snout-vent length, collected 20 March, 1992, deposited in the ASUMZ (Cat. No. 18277).

Remarks: The only other isosporan described from caudate amphibians is *I. jeffersonianum* (Fig. 39) from the blue-spotted salamander *A. laterale* (*=A. jeffersonianum*) from Minnesota. The latter possesses a knob or thickening in the oocyst wall that *I. hightoni* lacks and the sporocysts of *I. jeffersonianum* are more elongate than those of *I. hightoni*.

Family Salamandridae Goldfuss 1820
(20 genera, 74 spp.)

Host genus *Cynops* Tschudi 1838
(7 spp.)

Eimeria nipponensis Upton, McAllister and Trauth 1993 (Fig. 41)

Synonym: *Eimeria propria* of Matubayasi 1937, *pro parte*.

Type host: *Cynops pyrrhogaster* (Boie 1826), Japanese fire-bellied newt.

Other hosts: None reported to date.

Type locality: ASIA: Japan, exact locality unknown.

Geographic distribution: ASIA: Japan.

Description of sporulated oocyst: Oocyst shape: ellipsoidal; wall thickness: not given; wall characteristics: 1 smooth, colorless layer; L x W: 50.2 x 34.5 (44.5–55 x 31–38); L/W ratio: 1.5; M, PG: absent; OR: present; OR characteristics: a large spheroidal body that appears membrane bound, 25.1 (21–31), with many coarse granules at its periphery. Distinctive features of oocyst: large size and large OR.

Description of sporocyst and sporozoites: Sporocyst shape: spindle-shaped, L x W: not given; L/W ratio: unknown; SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of many granules aggregated into a tight mass; SZ: elongate, ~2/3 the length of sporocyst. Distinctive features of sporocyst: spindle shape.

Prevalence: 2 of 90 (2%).

Sporulation: Unknown. Although Matubayasi (1937) specifically stated, “Formation of the sporozoites in the oocyst are completed in the intestine of the host.” it is unclear if these oocysts sporulate in the intestinal cells (endogenous sporulation) of the host or in the lumen of the intestine (exogenous sporulation).

Prepatent and patent periods: Unknown.

Site of infection: Epithelial cells of the small intestine, between the cuticular layer and the N.

Endogenous stages: Merogony was observed in 1 animal experimentally infected with one oocyst and killed at eight days post-inoculation. The mature meront was ellipsoidal and contained ~20 crescent-shaped merozoites. Merozoites were 9.2 x 1.5 and their posterior half is narrower than the anterior, where a round N with a large karyosome is situated.

Pathology: Unknown.

Material deposited: None.

Remarks: This is the "second type" of oocyst reported by Matubayasi (1937) in *Triturus pyrrhogaster* (=*Cynops pyrrhogaster*), which he identified as *E. propria* by stating, "it may not be unreasonable to consider my form as identical with *E. propria*," in spite of also saying "although in dimensions they do not coincide with each other." The oocysts of *E. propria* (Fig. 52) are considerably smaller (30–36 x 20–36) and it is clear that the coccidium he was seeing represented a separate species.

Eimeria pyrrhogaster Upton, McAllister and Trauth 1993 (Fig. 42)

Synonym: *Eimeria propria* of Matubayasi 1937, *pro parte*.

Type host: *Cynops pyrrhogaster* (Boie 1826), Japanese fire-bellied newt.

Other hosts: None reported to date.

Type locality: ASIA: Japan, exact locality unknown.

Geographic distribution: ASIA: Japan.

Description of sporulated oocyst: Oocyst shape: subspheroidal to ovoidal; wall thickness: not given; wall characteristics: 1 smooth layer; L x W: 42.8 x 39.9 (38–45 x 34.5–45); L/W ratio: 1.1; M, PG: absent; OR: present; OR characteristics: a large, spheroidal body, 28.3 (24–31), composed of many granules that become coarse at its periphery, all enclosed in a thin membrane. Distinctive features of oocyst: large size and large, membrane-bound OR.

Description of sporocyst and sporozoites: Sporocyst shape: spindle-shaped, L x W: 22.2 x 8.2; L/W ratio: 2.7; SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of clusters of loose granules dispersed through sporocyst; SZ: shorter than length of sporocyst with a spheroidal RB (or N?) centrally located. Distinctive features of sporocyst: spindle-shaped and all 4 are always found attached to the surface of the OR.

Prevalence: 1 of 90 (1%).

Sporulation: Unknown. Although Matubayasi (1937) specifically stated, "Formation of the sporozoites in the oocyst are completed in the intestine of the host," it is unclear if these oocysts sporulate in the intestinal cells (endogenous sporulation) of the host or in the lumen of the intestine (exogenous sporulation).

Prepatent and patent periods: Unknown.

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

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: This is the "third type" of oocyst reported by Matubayasi (1937) in *T. pyrrhogaster* (= *C. pyrrhogaster*), which he identified as a variety of his second type, *E. propria*, although he also said, "It is hardly possible to determine for the present whether this type belongs to either *E. spherica* or *E. propria*, or to a new species." The oocysts of this species are considerably shorter than those of *E. propria* (Fig. 52). Thus, we agree with Upton *et al*. (1993) that it deserves separate species status.

Eimeria saitamaensis Upton, McAllister and Trauth 1993 (Fig. 43)

Synonym: *Eimeria spherica* of Matubayasi 1937.

Type host: *Cynops pyrrhogaster* (Boie 1826), Japanese fire-bellied newt.

Other hosts: None reported to date.

Type locality: ASIA: Japan, exact locality unknown.

Geographic distribution: ASIA: Japan.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall thickness; not given; wall characteristics: 1 smooth layer, colorless; L x W: 23–26 x 23–26; L/W ratio: 1.0; M, PG: absent; OR: present; OR characteristics: spheroidal body, ~14, and composed of a large homogeneous body with several granules seemingly attached at one pole on its periphery (line drawing). Distinctive features of oocyst: large OR with smaller granules attached at one end.

Description of sporocyst and sporozoites: Sporocyst shape: spindle-shaped, L x W: 15.4 x 6.1; L/W ratio: 2.5; SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of several scattered granules; SZ: nearly as long as sporocyst; RB at one end and a N in the center. Distinctive features of sporocyst: spindle shape.

Prevalence: 2 of 90 (2%).

Sporulation: Unknown, although Matubayasi (1937) indicated that formation of the SZ in the oocyst were completed in the intestine of the host. However, it remains to be seen if the oocysts sporulate endogenously in the host or exogenously.

Prepatent and patent periods: Unknown.

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

Endogenous stages: Unknown. However, Matubayasi (1937) did find “a small number of gametocyte-like forms” 8 days after infecting a newt with 1 oocyst, but concluded, “these were too small in number to be examined in stained preparation. Thus the experimental infection resulted in a failure.”

Pathology: Unknown.

Material deposited: None.

Remarks: This is the “first type" of oocyst reported by Matubayasi (1937) in *T. pyrrhogaster* (= *C. pyrrhogaster*) that he erroneously believed to be *E. spherica*. However, oocysts of *E. spherica* (Fig. 44) are 36 (22–38) in diameter, whereas those of this species are somewhat smaller, and the sporocysts are longer than those of *E. spherica*.

Host genus *Mesotriton* Bolkay 1927
(1 spp.)

Eimeria spherica (Schneider, 1887) Levine and Becker 1933 (Fig. 44)

Synonyms: *Coccidium sphericum* Schneider 1887; *Cytophagus tritonis* Steinhaus 1891, *pro parte*; *Eimeria tritonis* (Steinhaus 1891) Levine and Becker 1933; *Karyophagus tritonis* (Steinhaus 1891) von Wasielewski 1896; non *Eimeria spherica* of Matubayashi 1937; non *Eimeria spherica* Dogiel 1948, non *Eimeria dogieli* from fish.

Type host: *Mesotriton alpestris* (Laurenti 1768), Alpine newt

Other hosts: *Triturus cristatus* (Laurenti 1768), Crested newt; *Lissotriton helveticus* (Razoumovsky, 1789), Palmate newt; *Lissotriton vulgaris* (L. 1758), Common newt.

Type locality: EUROPE: France.

Geographic distribution: EUROPE: France.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall thickness: ~0.8; wall characteristics: 2 wall layers, (1 in line drawing), outer, smooth; inner thinner than outer; L x W: 35 (22–38); L/W ratio: 1.0; M,

PG: absent; OR: present; OR characteristics: large spheroidal mass, >25, that consists of a homogeneous central body surrounded by granules of various sizes that occupies about 2/3 volume of oocyst. Distinctive features of oocyst: spheroidal shape and very large OR.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal, slightly pointed at both ends; L x W: 12–15 x 6–7; L/W ratio: ~2.1; SB: may be present (line drawing); SSB: absent; PSB: may be present (line drawing); SR: present; SR characteristics: amorphous to ellipsoidal mass of large granules, not exactly median, but closer to one side of the sporocyst (line drawing); SZ: elongate, slightly pointed at one end, slightly rounded at the other, and slightly longer than sporocyst (line drawing). Distinctive features of sporocyst: the sporocyst looks similar to an oocyst of *Monocystis* (line drawing).

Prevalence: Unknown.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Intestinal mucosa.

Endogenous stages: Not described (?). However, Phisalix (1933) described endogenous stages of an *Eimeria* sp. from *Triton alpester* (=*Mesotriton alpestris*) collected from the Jura and Alpes mountain range at 800 m and 2100 m elevation respectively, and around Paris. Those oocysts were 35 wide and sporocysts were 14 x 7, as were the sporozoites, suggesting that the species may be *E. spherica*. In the descriptions, meronts were 12–25 x 10.5–20 and contained 8–24 merozoites which were 8.4–21 x 3–3.1. Fully formed microgametocytes were ovoidal, measured 23 x 27, and contained at least 150 microgametes; microgametes were 6 x 3. Mature macrogametes were oval, 20 x 25, and took up the entire host cell.

Pathology: Unknown.

Materials deposited: None.

Remarks: This species was first described by Schneider (1887) in a 1 page note and later redescribed in detail by Lavier (1936). It has not been reported since then.

Eimeria tertia Lavier 1936 (Fig. 45)

Type host: *Mesotriton alpestris* (Laurenti 1768), Alpine newt.

Other hosts: None to date.

Type locality: EUROPE: France.

Geographic distribution: EUROPE: France.

Description of sporulated oocyst: Oocyst shape: ovoidal; wall thickness: ~0.6; wall characteristics: 2 wall layers (but 1 in line drawing) outer, smooth; L x W: 26 x 21 (22–33 x 18–25); L/W ratio: 1.2; M, PG: absent; OR: present; OR characteristics: large spheroidal mass of granules of various sizes and occupies about 1/2 volume of oocyst. Distinctive features of oocyst: ovoidal shape and large OR.

Description of sporocyst and sporozoites: Sporocyst shape: ellipsoidal, slightly pointed at both ends; L x W: 12–15 x 6–7; L/W ratio: ~2.1; SB: may be present (line drawing); SSB, PSB: both absent; SR: present; SR characteristics: compact, ellipsoidal mass of large granules in center of sporocyst (line drawing); SZ: elongate, slightly pointed at one end, slightly rounded at the other, and slightly longer than sporocyst (line drawing). Distinctive features of sporocyst: none.

Prevalence: Unknown.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Intestinal mucosa.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: At the time, this was the third new species described by Lavier (1936). It has not been seen since its initial description.

Host genus *Notophthalmus* Rafinesque 1820
(3 spp.)

Eimeria longaspora Barrow and Hoy 1960 (Fig. 46)

Type host: *Notophthalmus viridescens* (Rafinesque 1820), Eastern newt.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Michigan, Douglas Lake, University of Michigan Biological Station.

Geographic distribution: NORTH AMERICA: USA, Michigan.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall thickness: not given; wall characteristics: 1 smooth layer; L x W: 34.9 x 33.1 (30–40 x 26–38); L/W ratio: 1.1; M, PG: absent; OR: present; OR characteristics: a large, spheroidal granular structure that contains a large hyaline sphere with a mean diameter of 25. Distinctive features of oocyst: very large OR that seems to push the sporocysts to one end of oocyst (line drawing); also, as the oocyst continues to age (mature) for 2 wk or more under refrigeration it increases in size such that older oocysts were 45.9 x 43.8 (44.5–48 x 42–46).

Description of sporocyst and sporozoites: Sporocyst shape: lanceolate, pointed at both ends; L x W: 24.0 (23–26.5) x 3.8; L/W ratio 6.3; SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of a few scattered refractile granules between SZ; SZ: also lanceolate (line drawing), 22.5 x 2; one end of each SZ projects past the other SZ into the opposite ends of the sporocyst; RB and N not visible. Distinctive features of sporocyst: the largest L/W ratio of any species from amphibians.

Prevalence: 13 of 144 (9%) over a 2 yr period.

Sporulation: Exogenous, all oocysts were passed unsporulated and 96% became fully sporulated within 48 h.

Prepatent and patent periods: Unknown.

Site of infection: Unknown, oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: The oocysts of this species are quite similar to those of *E. pyrrhogaster* (Fig. 42) described from *C. pyrrhogaster* from Japan (Matubayasi 1937), especially when you compare Fig. 4 in Barrow and Hoy (1960) with Fig. 12 in Matubayasi (1937). The striking thing about both drawings is that both show a massive OR (>25) that occupies ~2/3–3/4 the volume of the oocyst, thus compressing the lanceolate-spindle shaped sporocysts towards one end, giving the appearance they are attached to the OR. The size of older (and thus larger) oocysts of *E. longaspora* are quite similar to those of *E. pyrrhogaster* (45.9 x 43.8 *vs.* 42.8 x 39.9, respectively) as is the size of their ORs (25 *vs.* 28). However, their sporocysts are quite different in width, 24 x 3.8 (L/W 6.3) *vs.* 22.2 x 8.2 (L/W 2.7).

Eimeria megaresidua Barrow and Hoy 1960 (Fig. 47)

Type host: *Notophthalmus viridescens* (Rafinesque 1820), Eastern newt.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, Michigan, Douglas Lake, Sedge Point Pool, University of Michigan Biological Station.

Geographic distribution: NORTH AMERICA: USA, Michigan.

Description of sporulated oocyst: Oocyst shape: ellipsoidal; wall thickness: not given; wall characteristics: 1 smooth layer; L x W: 56.2 x 47.9 (55–58 x 45–49); L/W ratio: 1.2; M, PG: absent; OR: present; OR characteristics: a compact body of scattered granules, 19–30 wide, with a centric or an acentric hyaline sphere, 12–13 wide. Distinctive features of oocyst: OR increases during the first 2 wk outside the host.

Description of sporocyst and sporozoites: Sporocyst shape: lanceolate, pointed at both ends; L x W: 27.6 x 9.5 (18–34 x 8–10); L/W ratio 2.9; SB, SSB, PSB: all absent; SR: present; SR characteristics: composed of large granules that localize at one end of sporocyst; SZ: also lanceolate (line drawing), 18.9 x 4.7, with a centrally located N. Distinctive features of sporocyst: lanceolate shape.

Prevalence: 22 of 144 (15%) over a 2 yr period.

Sporulation: Exogenous; 65–70% of all oocysts were in various stages of sporulation when fecal samples were collected from the hosts and 95% became fully sporulated within 24 h.

Prepatent and patent periods: Unknown; however, Barrow and Hoy (1960) noted that all infections were recovered 4 to 7 days after newts were collected.

Site of infection: Unknown, oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: The oocysts of this species are similar to those of *E. nipponensis* (Fig. 41) described from *C. pyrrhogaster* from Japan (Matubayasi 1937), when their respective line drawings are compared (Fig. 2, Barrow & Hoy 1960; Fig. 11, Matubayasi 1937). However, the oocysts of *E. nipponensis* are smaller than those of *E. megaresidua* (50 x 34.5, L/W=1.5, *vs*. 56 x 48, L/W=1.2).

Host genus *Salamandra* Laurenti 1768
(6 spp.)

Eimeria grobbeni Rudovsky 1925 (Fig. 48)

Synonyms: non *Eimeria grobbeni* of Doran 1953; non *Eimeria grobbeni* of Walton 1961a, b.

Type host: *Salamandra atra* Laurenti 1768, Alpine salamander.

Other hosts: None reported to date.

Type locality: EUROPE: Austria.

Geographic distribution: EUROPE: Austria.

Description of sporulated oocyst: Oocyst shape: subspheroidal; wall thickness: ~1; wall characteristics: 2 layers, outer, smooth, ~2/3 of total thickness (line drawing); L x W: 10–11 x 9–10; L/W ratio: unknown; M: present, about 1.5 wide; OR, PG: both absent. Distinctive features of oocyst: presence of M.

Description of sporocyst and sporozoites: Sporocyst shape: pyriform (line drawing) to elongate-ovoidal, pointed at one end; L x W: 5–6 x 4; L/W: ~1.4; SB: present as small knob at tapered end of sporocyst; SSB, PSB: both absent; SR: rarely present; SR characteristics: a few scattered granules; SZ: crescent-shaped (line drawing) with RB at one end and N at the other. Distinctive features of sporocyst: pyriform shape.

Prevalence: Unknown.

Sporulation: Exogenous, 3–4 days at room temperature, but a few sporulated oocysts were also encountered in the intestine of infected hosts, especially the rectum.

Prepatent and patent periods: Unknown.

Site of infection: N of intestinal epithelial cells.

Endogenous stages: There is no mention of a first generation meront or where it develops. However, (later?) merozoites penetrate the host N and destroy it from within, and a PV arises in the N to surround the merozoite. The merozoite then rounds up and develops into either a small meront (4–5 wide) or a large meront (17–18 wide) and each is capable of giving rise to 20–30 merozoites that measure 10–12 x 1–1.5. Microgamonts are 5 wide and their N undergo repeated divisions producing microgametes tapered at one end; in some, a 2–3 x 1 wide vacuole is seen. About 70–90 microgametes arise around a central residuum from each microgamont. Macrogamonts are 4–5 wide and have a large karyosome. Many chromatin-rich granules gradually

migrate toward the periphery. The growing macrogamete destroys the host cell N.

Pathology: In the intestine, desquamation of the epithelium and infiltration of inflammatory cellular elements in the mucosa and submucosa are seen. Heavily infected salamanders show conspicuous depigmentation of the skin, particularly on the head, cervical and abdominal regions (Pellérdy 1974).

Material deposited: None.

Remarks: Rudovsky (1925) reported 2 small eimerians from *S. atra*: one he named *E. grobbeni*; it had a M, but no OR; the second, unnamed species, was of identical size, had an OR and an outer wall that collapsed easily. It is likely that the latter was *E. grobbeni* that sporulated improperly. The coccidium from *Taricha torosa* (=*Triturus torosus*) in California was improperly termed *E. grobberi* (sic) by Doran (1953). It is now *E. tarichae* (Levine 1980) (Fig. 50).

Eimeria salamandrae (Steinhaus 1889) Dobell 1909 (Fig. 49)

Synonyms: *Acystis parasitica* Labbé 1894b, *pro parte*; *Caryophagus salamandrae* (Steinhaus 1889) Druner 1894; *Coccidium salamandrae* (Steinhaus 1889) Simond 1897; *Cytophagus tritonis* Steinhaus 1891, *pro parte*; *Eimeria tritonis* (Steinhaus 1891) Walton 1941; *Karyophagus salamandrae* Steinhaus 1889; *Karyophagus tritonis* (Steinhaus 1891) von Wasielewski 1896.

Type host: *Salamandra salamandra* (L. 1758) (syn. *Salamandra maculata*), Fire salamander.

Other hosts: None reported to date.

Type locality: EUROPE: Exact country/locality unknown.

Geographic distribution: EUROPE.

Description of sporulated oocyst: Oocyst shape: spheroidal; wall thickness: ~1; wall characteristics: 2 layers, outer, smooth; L x W: 18–30; L/W ratio: 1.6; M, OR, PG: all absent. Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: unknown; L x W: unknown; L/W ratio: unknown; SB, SSB, PSB: all unknown; SR: present; SR characteristics: unknown; SZ: comma-shaped; RB, N: unknown. Distinctive features of sporocyst: unknown.

Prevalence: Unknown.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Intestinal epithelial cells.

Endogenous stages: According to Pellérdy (1974), “It was claimed that certain asexual stages penetrate the nucleus of the host cell deforming it to such an extent that it assumes a crescent shape and flatters (sic) closely against the schizont. There is, however, no recent evidence that such penetration takes place.” Later, von Wasielewski (1896) and Steinhaus (1889) depicted early meronts that look like those of any other known coccidium. Apparently, when these meronts grow in a host cell the N enlarges, elongates and narrows, and comes to recline in a semilunar shape near the edge of the PV (Pellérdy 1974). Meronts localize close to the host cell’s brush border; each produces 10–16 merozoites that taper toward one end. Microgametes develop around a central residuum in the microgamont.

Pathology: Unknown.

Material deposited: None.

Remarks: Doflein and Reichenow (1953) claimed that the oocyst wall develops prior to fertilization and that the microgametes penetrate the macrogamete through the M. This unusual feature was the basis for the “ephemeral” creation of the subgenus *Orthospora* (Pellérdy 1974).

Host genus *Taricha* Gray 1850
(3 spp.)

Eimeria tarichae Levine 1980 (Fig. 50).

Synonym: *Eimeria grobbeni* of Doran 1953.

Type host: *Taricha torosa* (Rathke 1833), California newt.

Other hosts: None reported to date.

Type locality: NORTH AMERICA: USA, California, Los Angeles County, San Bernardino Mountains, Fish Canyon.

Geographic distribution: NORTH AMERICA: USA, California.

Description of sporulated oocyst: Oocyst shape: subspheroidal to slightly ellipsoidal; wall thickness: not given; wall characteristics: 1 smooth layer; L x W: 11–13 x 10–12; L/W ratio: unknown; M, OR, PG: all absent. Distinctive features of oocyst: none.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal, slightly pointed at one end; L x W: not given; L/W ratio unknown; SB, SSB, PSB: all absent; SR: present; SR characteristics: a compact mass of fine and coarse granules that appear membrane-bound, usually found in more rounded end of sporocyst; SZ: shorter than length of sporocyst, generally sausage-shaped, without obvious RB or N (line drawing). Distinctive features of sporocyst: none.

Prevalence: 3 of 28 (11%).

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Unknown, oocysts recovered from feces.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: None.

Remarks: Doran (1953) found this eimerian in the feces of 3 of 28 California newts, *T. torosa*. He called it *E. grobbeni*, described from the Alpine salamander, *S. atra* (Rudovsky 1925), but he admitted that the oocysts from California newts may belong to a new species. Levine (1980) pointed out that the form observed by Doran (1953) differed from that species (*E. grobbeni*) in lacking a micropyle and in host genus and considered it a separate species which he named *E. trichae*.

Host genus *Triturus* Rafinesque 1815
(6 spp.)

Eimeria canaliculata Lavier 1936 (Fig. 51)

Type host: *Triturus cristatus* (Laurenti 1768), Crested newt.

Other hosts: *Mesotriton alpestris* (Laurenti 1768), Alpine newt; *Lissotriton helveticus* (Razoumovsky 1789), Palmate newt; *Lissotriton vulgaris* (L. 1758), Common newt.

Type locality: EUROPE: France.

Geographic distribution: EUROPE: France.

Description of sporulated oocyst: Oocyst shape: cylindroidal, symmetrical; wall thickness: ~1; wall characteristics: 2 wall layers (although line drawing shows 1), outer, smooth and contains, in the equatorial zone, 8–9 fine, radiating "canaliculi" that seem to terminate themselves in/on the internal layer of the oocyst wall (Lavier 1936) and are arranged in an equatorial band ~12–13 wide; inner, thinner than outer one; L x W: 39.5 x 24 (36–42 x 20–27); L/W ratio: 1.6; M, PG: absent; OR: present, as a large mass of lipid-like globules that mostly obscure sporocysts (line drawing). Distinctive features of oocyst: massive OR of oil-like globules

and an equatorial band, 12–13 wide, of fine radiating "canaliculi" in the oocyst outer wall that seem to encircle the oocyst wall.

Description of sporocyst and sporozoites: Sporocyst shape: lanceolate; L x W: 25–30 x 6; L/W ratio: ~4.5; SB: may be present (line drawing); SSB, PSB: absent; SR: present; SR characteristics: ovoidal mass of small granules, nearer the rounded end of the sporocyst; SZ: elongate, slightly longer than sporocyst, and pointed at one end, each with a small RB at rounded end (line drawing). Distinctive features of sporocyst: sometimes the sporocyst walls disintegrate leaving eight sporozoites free within the oocyst.

Prevalence: Unknown.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Intestinal mucosa.

Endogenous stages: Unknow.

Pathology: Unknown.

Materials deposited: None.

Remarks: Laveran and Mesnil (1902a) described an intestinal coccidium (*E. prevoti*) from *P. esculenta* for which they created the genus *Paracoccidium* because the sporocyst walls disappeared after sporulation releasing eight SZ into the oocyst, a phenomenon now known to be reasonably common among eimerians of reptiles and, apparently, some amphibians. *Eimeria canaliculata* and *E. propria* are morphologically similar and are found in the same hosts (see Lavier 1936). However, sporocysts of *E. canaliculata* are longer, the outer wall of the oocysts has an equatorial band of tubules, and the OR is a large mass of lipid-like globules. This combination of structural features makes the sporulated oocysts of *E. canaliculata* unique among all caudate eimerians.

Eimeria propria (Schneider 1881) Doflein 1909 (Fig. 52)

Synonyms: *Coccidium proprium* (Schneider 1881) Schneider 1887; *Orthosporo propria* Schneider 1881; *Pfeifferia* (*Coccidium*) *propria* Labbé (1896); non *Eimeria propria* of Matubayashi 1937.

Type host: *Triturus cristatus* (Laurenti 1768), Crested newt.

Other hosts: *Mesotriton alpestris* (Laurenti 1768), Alpine newt; *Lissotriton vulgaris* (Linnaeus 1758), Common newt.

Type locality: EUROPE: France.

Geographic distribution: EUROPE: France.

Description of sporulated oocyst: Oocyst shape: symmetrically cylindrical; wall thickness: ~0.8; wall characteristics: 2 wall layers (although line drawing shows 1), outer, smooth; inner, thinner than outer; L x W: 38–41 x 22–24; L/W ratio: ~1.7; M: absent (but see *Remarks*, below); OR: present; OR characteristics: up to or >22 wide; PG: present (Lavier 1936). Distinctive features of oocyst: large cylindrical shape with a large OR and a PG often attached to the internal surface of the oocyst wall (Lavier 1936, but not shown in his line drawing).

Description of sporocyst and sporozoites: Sporocyst shape: cylindroid and pointed at both ends; L x W: 18–22 x 7–8; L/W ratio: unknown; SB, SSB, PSB: all absent; SR: present; SR characteristics: compact ellipsoidal mass of large granules, ~10 x 7, in center of sporocyst; SZ: 15–18 x 2.5, sausage-shaped (line drawing), each with 2 small RBs, one at each end (line drawing). Distinctive features of sporocyst: shaped like a "fat cigar."

Prevalence: Unknown.

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Intestinal mucosa.

Endogenous stages: Unknown.

Pathology: Unknown.

Materials deposited: None.

Remarks: Schneider (1881) was the first to recover cylindroidal oocysts from the digestive tract of 2 salamanders, *T.* (=*Triton*) *cristatus* and *L.* (=*Triton*) *vulgaris*, near Poitiers (France) and he named the oocysts *O. propria* in a one page note. Later Schneider (1887), abandoned the genus *Orthospora* that he had created from this cylindrical form, and placed it, and a new spheroidal form (*E. spherica*), into the genus *Coccidium*. Labbé (1894a, 1896) considered the two species of Schneider (1881, 1887) to be a single coccidium, the oocyst of which could exhibit a variety of shapes, and called it *C. proprium* (Lavier 1936). This view prevailed for nearly half a century until Lavier (1936) dispelled it. Steinhaus (1891) described merogony of a coccidium under the name *Cytophagus tritonis*. In 1896, Labbé placed these intracellular stages and those known from *C. proprium* into his new genus, *Pfeiffera*, for no justifiable reasons (Lavier 1936). Schneider (1881) made no mention of a M, but described a structure at one end of the oocyst that he called an operculum; he also described a transverse radial structure (suture?) extending like a belt along the central part of the oocyst; however, Lavier (1936), who redescribed and presented line drawings for *E. propria*, did not see these structures. The description above follows that of Pellérdy (1974), which differs from the measurements and line drawing given in Doflein (1909). Walton (1941, 1961c, 1964a, b) lists *S. salamandra* (syn. *S. maculosa*) as a host for this species and Pellérdy (1974) listed *S. atra*; these are probably misidentifications. Lavier (1936, 1937) gave oocyst measurements as 36-43 x 20-27 and sporocysts 18–22 x 7–8 (line drawing of sporocyst strongly resembles an oocyst of *Monocystis*). Although this may represent a different coccidium, all other structural characteristics appear to match those of Schneider (1881).

GYMNOPHIONA Müller 1832-Caecilians

(3 families, 27 genera, 173 spp.)

Family Caeciliidae Rafinesque 1814

(22 genera, 120 spp.)

Host genus *Dermophis* Peters 1880

(7 spp.)

Eimeria dermophis Asmundsson, Campbell and Duszynski 2000 (Figs. 53, 66)

Type host: *Dermophis mexicanus* (Duméril & Bibron 1841), Mexican caecilian.

Other hosts: None reported to date.

Type locality: CENTRAL AMERICA: Guatemala, Departamento de San Marcos, Pacific versant on the lower slopes of Volcán Tajumulco, Finca San Ignacio, 14° 54’ 0” N, 92° 0’ 0” W.

Geographic distribution: CENTRAL AMERICA: Guatemala.

Description of sporulated oocyst: Oocyst shape: spheroidal to subspheroidal; wall thickness: ~1: wall characteristics: appears to be composed of 1 layer, pale yellow, with widely spaced bumps; L x W: 19.5 x 17.7 (16–23 x 15–21); L/W ratio: 1.1 (1.0–1.4); M, OR: both absent; PG: 3 or more, highly refractile, each spheroidal, ~1. Distinctive features of oocyst: outer wall that appears striated in optical cross section with widely spaced bumps on outer surface.

Description of sporocyst and sporozoites: Sporocyst shape: ovoidal; L x W: 11.0 x 7.2 (10–12 x 6–9); L/W ratio: 1.5 (1.2–2.0); SB: small, at pointed end of sporocyst; SSB: small, indistinct; PSB: absent; SR: present; SR characteristics: composed of small to medium granules that completely fill sporocyst; SZ: mostly obscured by SR, but with 1 spheroidal RB, ~3–4, at 1 end and a smaller RB at opposite end. Distinctive features of sporocyst: None.

Prevalence: 2 of 5 (40%).

Sporulation: Unknown.

Prepatent and patent periods: Unknown.

Site of infection: Unknown, oocysts recovered from fecal material.

Endogenous stages: Unknown.

Pathology: Unknown.

Material deposited: Photosyntypes of sporulated oocysts deposited in the USNPC, document no. 313 (No. 88840); symbiotype host deposited in the Herpetological Collection, the University of Texas, Arlington, TX (UTA A-52165).

Remarks: This is the first and only coccidia species to be described from any member of the order Gymnophiona. One of 2 hosts was very heavily infected; given the known diet of caecilians, Asmundsson *et al*. (2000) believed it unlikely that the oocysts found were from an infected food item. Although a few of the sporulated oocysts known from both anurans and caudatans (above) are similar in size to those of *E. dermophis*, there are sufficient differences between other quantitative and qualitative features of the oocysts and their sporocysts to easily distinguish them. Based on oocyst and sporocyst size, there are only 3 species with sporulated oocysts that are similar to those of *E. dermophis. Eimeria kingi* Saxe 1955 (Fig. 34), has a large globular oocyst residuum not seen in *E. dermophis.* Oocysts of *Eimeria waltoni* Saxe 1955 (Fig. 38), are similar in size to those of *E. dermophis*, but the outer oocyst wall is smooth and it has an oocyst residuum that appears as a single refractile granule. *Eimeria urodela* Duszynski *et al*. 1972 (Fig. 37), differs from *E. dermophis* by having a smooth oocyst wall, lacking polar granules, and possessing an oocyst residuum. For these reasons, we agree with the decision of Asmundsson *et al*. (2000) in designating *E. dermophis* as a valid species. In addition, no *Eimeria* species are known to cross ordinal boundaries, so the host species and its locality also help distinguish this eimerian as a distinct species.

Species inquirendae, incertae sedis, nomina nuda and non-valid designations

In this section, we place all those "coccidia" (Eimeriidae) about which too little is known from the published literature to decide whether they are real or not. Using definitions from the 4th edition of the *International Code of Zoological Nomenclature* (Ride *et al*. 2000), *species inquirenda* (pl. *species inquirendae*) refers to "a species of doubtful identity needing further investigation." Implicit in our use of this term is that the taxonomic unit, or "species," has been taxonomically named in some published document, but without existence of a type specimen of any kind (e.g. line drawing, photosyntype, stages in tissue sections, oocysts in preservative, etc.) and without sufficient qualitative and quantitative data on the most widely available stage in the life-cycle (i.e. the sporulated oocyst) to distinguish it from other, perhaps closely related, species.

The term *incertae sedis* as defined by the *Code*, means "of uncertain taxonomic position." Thus, this term applies to forms that are mentioned (e.g. as *Eimeria* sp. or *Isospora* sp.), but for which no mensural or qualitative data (e.g. number of sporocysts and sporozoites in the oocyst) were provided.

Finally, sometimes authors, especially in the older literature, gave new names to organisms they saw, but failed to conform to Article 12 of the *Code* if published before 1931 or, if published after 1930, failed to conform to Article 13 (Ride et al. 2000). These names become *nomen nudum* (pl. *nomena nuda*), and, thus, become preoccupied and unavailable names. However, the same name may be made available later for the same or a different concept, but in such a case it would take authorship and date from that act of establishment, not from any earlier publication as a *nomen nudum*.

ANURA (frogs)

***Incertae sedis* (16)**

Eimeria sp. 1 (Eimer, 1870) Upton and McAllister 1988, *incertae sedis*

Host: *Pelophylax esculenta*, (L. 1758), Pool frog.

Remarks: No oocysts were measured or described (see Eimer 1870; Upton & McAllister 1988).

Eimeria sp. of Fantham and Porter 1947, *incertae sedis*

Host: *Lithobates clamitans* (Latreille *In* Sonnini de Manoncourt & Latreille 1801) Green frog.

Remarks: Fantham and Porter (1947) collected 1 *Necturus maculosus*, 1 *Anaxyrus americanus*, 5 *L. catesbeianus*, 3 *L. pipiens*, and 3 *L. clamitans* from Lad Des Sableets, north-west of Montreal, Canada and reported seeing a few *Eimeria* oocysts in a single female green frog without giving any description of the oocysts.

Eimeria sp. of Hegner and Chu 1930, *incertae sedis*

Host: *Fejervarya vittigera* (Wiegmann 1834), Luzon wart frog.

Remarks: The report of Hegner and Chu (1930) is of an unidentified coccidium in *F. vittigera* from the Philippines; it is not complete enough, and makes this species of *Eimeria* of uncertain taxonomic position.

Eimeria sp. 2 (Pachinger 1886) Upton and McAllister 1988, *incertae sedis*

Synonym: *Molybdis entzii* Pachinger 1886.

Host: *Pelophylax esculenta*, (L. 1758), Pool frog.

Remarks: Mention was made only of an ovoidal oocyst, 30 x 13.

Isospora sp. of Chakravarty and Kar 1944, *incertae sedis*

Synonym: *Eimeria wenyoni* Ray and Das Gupta 1935 of Chakravarty and Kar 1944.

Hosts: *Fejervarya limnocharis* (Gravenhorst 1829), Indian cricket frog; *Hoplobatrachus tigerinus* (Daudin 1802), Tiger frog.

Remaks: See *Remarks* in *Isospora wenyoni*.

Isospora sp. of Grassi, 1882, *incertae sedis*.

Host: *Bufo* spp. (?).

Remarks: Mention has been made of an isosporan in *Bufo* spp. (?) by a number of authors (Grassi 1882; Grassi & Feletti 1892; Labbé 1899; Walton 1941), but little else is known about it.

Isospora sp. of Kazubski and Grabda-Kazubska 1973, *incertae sedis*

Host: *Rana arvalis* Nilsson 1842, Moor frog.

Remarks: Oocysts are subspheroidal, 21–22 x 19–20 and sporocysts are 16.2 x 12.8 (15–18.5 x 12–14.5); this species was found in Poland.

Unsporulated oocyst 1 of Rzepczyk, 1976, *incertae sedis*

Host: *Chaunus (=Bufo) marinus* (L. 1758), Cane toad.

Remarks: Rzepczyk (1976) mentioned seeing 1 spheroidal, unsporulated oocyst in the intestinal contents of a cane toad, *C. marinus*.

Unsporulated oocyst 2 of Rzepczyk 1976, *incertae sedis*

Host: *Chaunus (=Bufo) marinus* (L. 1758), Cane toad.

Remarks: Rzepczyk (1976) found what she said was a subspheroidal unsporulated oocyst, 28 x 26.6, in the intestinal contents of a second cane toad *C. marinus*.

Unsporulated oocyst 3 of Rzepczyk 1976, *incertae sedis*

Host: *Chaunus (=Bufo) marinus* (L. 1758), Cane toad.

Remarks: Rzepcyzk (1976) found 2 unsporulated oocysts of a third coccidium in the intestinal contents of a third cane toad, *C. marnius*. These were 28 x 28 and 26.6 x 23.6 and were were similar to her unsporulated oocyst 2, but neither sporulated.

Unsporulated oocyst 4 of Rzepczyk 1976, *incertae sedis*

Host: *Chaunus (=Bufo) marinus* (L. 1758), Cane toad.

Remarks: Rzepcyzk (1976) found two other oocysts in the third cane toad. The first was another unsporulated oocyst, 26.6 x 26.6, with a thick brown wall and an "elaborate" M.

Isospora-like oocysts/sporocysts 5 of Rzepczyk 1976, *incertae sedis*

Host: *Chaunus (=Bufo) marinus* (L. 1758), Cane toad.

Remarks: In the third cane toad mentioned above, she also diagnosed *Isospora* sporocysts with four sporozoites. Sporocysts (N=12) were 19.2 x 10.0 (22–16 x 10–8), L/W of 1.9 (1.6–2.1) and with a "prominent" sporocyst wall and an ovoidal SR, 6.4 x 4.5.

Unsporulated oocyst 6 of Rzepczyk 1976, *incertae sedis*

Host: *Litoria caerulea* (White 1790), Whites treefrog.

Remarks: In 6 of 12 treefrogs she saw 3 distinct coccidian types, but no treefrogs had more than one type. The first morphotype she saw was an unsporulated oocyst that was heart-shaped, 39.2 x 33.6, with a thick, brown wall and an "elaborate" M. She only saw 2 oocysts in 1 frog.

Unsporulated oocyst 7 of Rzepczyk 1976, *incertae sedis*

Host: *Litoria caerulea* (White 1790), Whites treefrog.

Remarks: Her second morphotype was seen in each of 3 of the 12 treefrogs examined; in these she saw 1 unsporulated oocyst; each of which was broadly ovoidal, 28 x 25.

Isospora (?) sp. 8 of Rzepczyk 1976, incertae sedis

Host: *Litoria caerulea* (White 1790), Whites treefrog.

Remarks: The third morphotype she reported in the *L. caerulea* she examined were spheroidal to ovoidal, colorless oocysts that sporulated in 6 days in $K_2Cr_2O_7$. She identified these oocysts as being an *Isospora* sp. that measured 16.8–20.7 x 14.0–16.8. This form was found in only 2 frogs with "only 1–4 oocysts in the total rectal contents of each frog."

Isospora sp. of Wenyon 1926, *incertae sedis*

Host: *Bufo bufo* (L. 1758), Common European toad.

Remarks: Endogenous sporulation in epithelial cells of the intestine.

***Nomena nuda* (2)**

Eimeria pylori (Gebhardt 1897) Levine and Becker 1933, *nomen nudum*

Synonym: *Coccidium pylori* Gebhardt 1897.

Host: *Rana* sp. (?).

Remarks: No oocysts were measured or described (see Gebhardt 1897; Levine & Becker 1933; Walton 1941, 1949c).

Isospora ranae (Rivolta 1878) Dobell 1909 of Walton 1941, *nomen nudum*

Synonym: *Cytospermium ranae* Rivolta 1878

Host: *Pelophylax esculenta*, (L. 1758), Pool frog.

Remarks: No oocysts were measured or described (see Dobell 1909; Pellérdy 1974; Rivolta 1878; Walton 1941).

***Species inquirendae* (9)**

"Coccidian" of Paperna and Lainson 1995, *species inquirenda*

Host: *Leptodactylus fuscus* (Schneider 1799), Rufous frog.

Remarks: In their paper describing the life history and ultrastructure of *E. bufomarini*, Paperna and Lainson (1995) mentioned finding another, as yet undescribed coccidium, in the Brazilian frog, *Leptodactylus fuscus* and said that this undescribed species also demonstrated endogenous sporogony in the epithelial cells of the intestine. Unfortunately, they never published this work.

Goussia sp. of Jirků and Modrý 2006b, *species inquirenda*

Host: *Rana dalmatina* Fitzinger *In* Bonaparte 1839, Agile frog.

Remarks: Jirků and Modrý (2006b) reported on the extra-intestinal localization of *Goussia* sp. oocysts in *R. dalmatina* from the Czech Republic. Their sporocysts were remarkably similar to *G. neglecta* and overlapped in their dimensions. However, because *G. neglecta* is known to parasitize *P. esculenta* and *P. ridibunda* and recent findings that some *Goussia* spp. parasitizing fish have narrow host specificity (Molnár *et al*. 2005) these authors took a conservative approach and did not name their species of *Goussia* until experimental infections and molecular data can be obtained.

"Goussia-like coccidian" of Paperna *et al*. 1997, *species inquirenda*

Host: *Limnodynastes tasmaniensis* Günther (1858), Spotted marsh frog.

Remarks: Paperna *et al.* (1997) in their description paper on *G. hyperolisi* reported that L. Berger of the CSIRO Australian Animal Health Laboratory, Geelong, Victoria, Australia, presented them with a histological slide prepared from the intestine of a *Limnodynastes tasmaniensis* (=*Lymnodynastes tasmanicus*) tadpole heavily infected with sporulating *Goussia*-like oocysts. Unfortunately these authors never described the species, and nothing is known about it.

Isospora lieberküehni (Labbé 1894) of Levine and Nye 1977, *species inquirenda*

Synonym: *Isospora lieberküehnk* (Labbé 1894b) Laveran and Mesnil 1902b.

Host: *Lithobates pipiens* (Schreber 1782), Northern leopard frog.

Remarks: Levine and Nye (1977) reported the infection in 1 *L. pipiens* from Wisconsin, USA, as a new host and geographic record based solely on merozoites seen in the kidney tubule epithelial cells. It is difficult to tell what group of apicomplexans Levine and Nye (1977) were dealing with, however, because no oocysts were recovered and this species has been reported from European *Pelophylax* spp. It is doubtful that these authors were dealing with *I. lieberküehni.*

Isospora hylae Mesnil 1907, *species inquirenda*

Host: *Hyla arborea* (L. 1758), European treefrog.

Remarks: Mesnil (1907) found oocysts in the digestive tract of *H. arborea* specimens from the outskirts of Paris. They were described as ellipsoidal, flattened at one end, 30–35 x 20–25 without an OR and sporocysts were ovoidal 23 x 17 with a SR. Mesnil (1907) said that endogenous development occured in the epithelial cells of the small intestine, while oocysts remained in the rectum of the frog. Neither line drawing nor photomicrograph(s) accompanied Mesnil's description.

Isospora lieberkühni Labbé 1894 of Golemansky and Bitseva (1975), *species inquirenda*

Host: *Bombina variegata* (L. 1758), Yellow-bellied Toad.

Remarks: Golemansky and Bitseva (1975) said they found *I. lieberkühni* in this host in Bulgaria. Because of host and geographic differences, this seems highly unlikely (also see Modrý *et al.* 2001).

Isospora lieberkühni Labbé 1894, *species inquirinda*

Host: *Pelophylax* spp. European water frogs.

Remarks: This has been an enigmatic organism that has perplexed coccidiologists since it was first reported by Lieberkühn (1854) as "Psorospermus," a renal coccidium of water frogs (*Pelophyla* spp.). However, Modrý *et al*. (2001) sequenced its SSU rRNA and found that its' true taxonomic position belongs in their re-erected (2001) genus, *Hyaloklossia* Labbé 1896. Thus, what was probably best considered a *species inquirenda* prior to 2001 is now known to be a valid species of *Hyaloklossia* (see *Remarks* under *Hyaloklossia lieberküehni*).

"Oocysts" of Griner, 1982, *species inquirenda*

Host: *Megophrys nasuta* (Schlegel 1858) Malayan horned frog.

Remarks: Griner (1982) reported seeing oocysts in the glomeruli and tubules of 9 *Megophrys nasuta* necropsied from the San Diego Zoo and Wild Animal Park, California, as routine histological studies of postmortem animals. He also reported no evidence of any significant pathology compared to normal frog kidney tissue. He indicated that the oocysts in the horned frogs suggested that they may have been coccidia.

"Unsporulated Coccidian" of Jirků and Modrý 2006a, *species inquirenda*

Host: *Ptychadena* sp. 1.

Remarks: In a study describing the endogenous and exogenous stages of *E. terraepokotorum* from *Hoplobatrachus occipitalis* from Kenya, Jirků and Modrý (2006a) examined 16 taxa of anurans and reported seeing unsporulated coccidian oocysts in 1 of 2 *Ptychadena* sp. Unfortunately, the oocysts did not sporulate and it is not clear what coccidium this was.

URODELA (salamanders)

Incertae sedis (6)

Eimeria sp. of McAllister et al. 2002, *incertae sedis*

Host: *Plethodon kiamichi* Highton *in* Highton, Maha, and Maxson 1989, Kiamichi slimy salamander.

Remarks: McAllister *et al*. (2002) surveyed 4 endemic *Plethodon* species from Arkansas and Oklahoma and found 1 of 16 (6%) *P. kiamichi* passing oocysts they identified as an *Eimeria* species, but did not describe or name it.

Eimeria sp. of Rankin 1937, *incertae sedis*

Synonym: non *Eimeria ranarum* (Labbé 1894) Doflein 1909 of Rankin 1937.

Host: *Ambystoma opacum* (Gravenhorst 1807), Marbled salamander.

Remarks: Although Rankin (1937) and Walton (1942) list *A. opacum* as a host for *E. ranarum*, a review of the literature of the known species of coccidia infecting amphibia suggests they may be at least genus specific. Thus, it is unlikely that *E. ranarum*, a parasite of frogs, infects a salamander.

Eimeria sp. of Rudovsky 1925, *incertae sedis*

Host: *Salamandra atra* Laurenti 1768, Alpine salamander.

Remarks: Rudovsky (1925) reported two small eimerians from *S. atra*. One, *E. grobbeni*, was reported to possess a M, but no OR; the second was of identical size, had an OR and an outer wall that collapsed easily, but he did not name it. We suggest that the latter may be a separate species or he may have seen oocysts of *E. grobbeni* that did not sporulate properly.

Eimeria sp. of Walton 1942, *incertae sedis*

Synonyms: non *Eimeria ranarum* (Labbé 1894a) Doflein 1909 of Walton 1942; non *Eimeria ranarum* (Labbé 1894) Doflein 1909 of Rankin 1937.

Host: *Ambystoma opacum* (Gravenhorst 1807), Marbled salamander.

Remarks: Walton (1942) originally reported an unnamed eimerian in an *Ambystoma* sp. Later, Saxe (1955) stated that he'd communicated with Walton and learned that the original observation was by Dr. H. Kirby. Kirby thought he had seen *E. ranarum* in *A. opacum*. This was clearly a misidentification.

Eimeria sp. 1 of Walton 1961, *incertae sedis*

Synonym: non *Eimeria grobbeni* of Walton 1961a.

Host: *Ambystoma tigrinum* (Green 1825), Tiger salamander.

Remarks: Walton (1961a) reported *E. grobbeni*, a parasite of *Salamandra atra* in Europe, from *A. tigrinum* in North America. This is certainly a misidentification.

Eimeria sp. 2 of Walton 1961, *incertae sedis*

Synonym: non *Eimeria ranarum* (Labbe 1894) Doflein, 1909.

Host: *Ambystoma tigrinum* (Green 1825), Tiger salamander.

Remarks: Walton (1961a) reported *E. ranarum*, a coccidian of *Pelophylax esculenta* and *Rana temporaria* in Europe, from *A. tigrinum* in North America. This is certainly a misidentification.

***Nomena nuda* (3)**

Coccidium of Saxe, 1955, *nomen nudum*

Host: *Desmognathus monticola* Dunn 1916, Seal salamander.

Remarks: Saxe (1955) reported that coccidian oocysts (genus and species not given) were found.

Coccidium of Saxe, 1955, *nomen nudum*

Host: *Desmognathus quadramaculatus* (Holbrook 1840), Black-bellied salamander.

Remarks: Saxe (1955) reported that coccidian oocysts (genus and species not given) were found.

Eimeria labbei (?) (Labbe 1894) Hardcastle 1943, *nomen nudum*

Synonyms: *Eimeria tritonis* (Labbé 1896) Levine and Becker 1933; *Pfeifferella tritonis* (Labbé 1896) Labbé 1899; *Pfeifferia* sp. of Labbé 1894; *Pfeifferia tritonis* Labbé 1896; non *Eimeria tritonis* (Steinhaus 1891) Walton 1941, a synonym of *Eimeria salamandrae*.

Hosts: *Triturus cristatus* (Laurenti 1768), Crested newt; *Lissotriton vulgaris* (L. 1758), Common newt.

Remarks: There is nothing in Labbé's description that would permit Hardcastle (1943) to make a species characterization. Labbé (1899) considered that his material might represent stages in the life-cycle of *E. propria*. Siedlecki (1898) identified *P. tritonis* with *E. propira* (see Saxe 1955). Only endogenous stages were described. Thus, this is a *nomen nudum*. These were probably *E. canaliculata, E. propria, E. spherica,* or *E. tertia*.

***Species inquirendae* (1)**

Eimeria salamandraeatrae (Phisalix 1927) Levine and Becker 1933, *species inquirenda*

Synonym: *Coccidium salamandrae atra* Phisalix 1927

Host: *Salamandra atra* Laurenti 1768, Alpine salamander.

Remarks: This species was first found somewhere in the Alps at 800–1400 m by Phisalix (1927). Spheroidal oocysts were 27 x 23 with M, OR and PG all absent. Sporocysts spheroidal, 10.5 wide. Development was reported in intestinal epithelial cells with 3 types of meronts. Type 1 meronts are granular, spheroidal, 15 wide, and produce 6–10 short, piriform merozoites, 4.2 x 2.1. Type 2 meronts undergo maturation in the lumen of the intestine where they form 8–16 merozoites, each 12.6 x 6.3 with a central N. Type 3 meronts are 31.5 x 27.3 and produce 12–20 merozoites which are "flexed," 21 x 3–4, and taper toward both ends. Gametogony takes place in the epithelial cell layer. Young microgamonts are 15 x 10.5, but may reach 35 x 27, or larger, by maturity; they have large refractile granules and vacuoles that migrate toward the periphery of the gamont, become flattened, and form >100 flexed microgametes, each 6–7.5 x 1. Macrogamonts are ovoidal, granular bodies, 15 x 10.5, and may be found subepithelially; they pass into the intestinal lumen for fertilization where they develop into oocysts. Unfortunately, no drawings or photomicrographs exist.

GYMNOPHIONA (caecilians)

None.

Non-valid designations

Eimeria princeps (Labbe 1894) Levine and Becker 1933 of Walton 1941, 1948, *lapsus*, is not a valid anuran coccidium. See Upton and McAllister (1988).

Discussion

Lieberkühn (1854) was the first to describe "psorosperms" in amphibians from Germany. He found these in the kidneys of frogs, not in the intestine. The parasite described by him is now known as *Hyaloklossia lieberküehni* (Labbé 1894). Since that first description, most named species of amphibian coccidia originate from the Holarctic region and Asia (see Upton & McAllister 1988; Upton *et al*. 1993) with only 4 species descibed from the African continent (3 *Eimeria*, 1 *Goussia*), and 4 species described from Central and South America (3 *Eimeria*, 1 *Isospora*) (Pinto & Vallim 1926; Carini 1931; Paperna & Lainson 1995; Asmundson *et al.* 2000; Jirků & Modrý 2006a).

Although numerous host-parasite lists and indexes were published throughout the middle of the 20th century by Walton (1940, 1941, 1942, 1945, 1947, 1948, 1949a, b, c, 1961a, b, c, 1964a, b, 1966, 1967), numer-

ous errors and unsubstanitated data reside within these compilations. Here we attempt to define most of these errors and summarize the world's literature (through 2006) on the coccidian parasites known to infect amphibians. The class Amphibia has 3 orders, 56 families, 464 genera and 6009 species (Frost *et al*. 2006). There are no coccidia known from 42 of 56 (75%) of the families, 431 of 464 (93%) of the genera and 5964 of 6009 (>99%) of the species. In the Anura (frogs), 30 coccidia are known (18 *Eimeria*, 9 *Isospora*, 2 *Goussia* and 1 *Hyaloklossia* species), in the Urodela (salamanders), 21 coccidia are known (19 *Eimeria* and 2 *Isospora* species), and in the Gymnophiona (caecilians), only 1 *Eimeria* species is known. These reports are widespread temporally and geopgraphically and most represent only single collections with few individuals examined for coccidian parasites (Table 2). Within the 113 species of amphibians that have been examined for coccidia parasites (Table 2), no data is provided for 23 species, and 54 species had 15 or fewer individuals examined for coccidians. Sixteeen amphibian species are reported to have only a single coccidian species that appears to be unique to that host; 20 amphibian species have 2 to 6 coccidian species reported from them, and 17 of these coccidian species appear to be unique to a single species of amphibian. Finally, 14 coccidian species are shared among 2 or more amphibian species and appear to be genus and/or family specific (Table 2).

Host Specificity

Historically, few studies exist on host specificity of coccidian parasites of amphibians, and to our knowledge only one experimental cross-transmission study between species exists in the literature. Lavier (1941) was unable to infect *B. bufo* with *I. brumpti* recovered from *D. brumpti*. Saxe (1955) reviewed the literature and indicated that Matubayasi (1937), Lavier (1936), Rankin (1937) and Doran (1953) all supported that certain *Eimeria* species of Amphibia were widely distributed geographically and not rigidly host-specific. However, in their comprehensive reviews of anuran and salamander coccidia, Upton and McAllister (1988) and Upton *et al*. (1993) suggested reasonably strict host specificity for anuran coccidia and genus and/or family host specificity for salamander coccidia.

The only study we are aware of that has examined multiple species, genera, and families of amphibians for coccidian parasites from a single location and time period is that of Bolek *et al*. (2003). They examined six species of frogs and a toad in five genera and three families from Pawnee Lake Nebraska (USA) and found that only the western chorus frog, *P. t. triseriata,* was infected with coccidia. Of interest is that at their study site, all six species were collected from the same general location and all six species overlapped in habitat use, particularly during the breeding season. Both bullfrogs, *L. catesbeianus,* and plains leopard frogs, *L. blairi,* were noted to commonly feed on *P. t. triseriata* (Bolek & Janovy 2004) and, thus, had a high probability of ingesting sporulated oocysts of *E. streckeri,* but were never found infected with this eimerian. Additionally, Bolek *et al*. (2003) maintained tadpoles of *P. triseriata* and *L. blairi* in the same tank for a period of four weeks, a time frame adequate for oocysts to be infective, and only tadpoles of *P. triseriata* shed oocysts of *I. cogginsi*. In addition to the study by Bolek *et al*. (2003), studies by Chen and Desser (1989) and Upton and McAllister (1988) indicate that some anuran coccidia species can infect multiple species of frogs. However, all of these studies found that anuran species of coccidia are genus and family specific. From the data provided above, and when enough information is given in the older literature to know what species of coccidia and/or anurans the investigators were dealing with, it appears that some anuran coccidia are host specific whereas others can infect multiple species of frogs in the same genus, but none is known to cross generic boundaries.

Coccidia of salamanders, however, appear to show a lesser degree of host specificity, and a number of species are known to infect multiple species of salamanders and newts in different genera (Upton *et al*. 1993). However, none are known to cross family boundries. Virtually nothing is known about the host specificity of coccidians of cecielans since only a single species of cecielan has been examined for these parasites (Asmundsson *et al*. 2000). Clearly, more ecological work and laboratory host specificity studies using laboratory-reared amphibians need to be conducted on anuran, salamander and cecilian coccidian parasites, to

understand if any real differences exist in host specificity of amphibian coccidia within and among the three orders of amphibians.

Life-Cycle and Oocyst

When known, most amphibian coccidia species infect the epithelial cells of the small and/or large intestine with one exception, *H. lieberküehni,* which infects the epithelial cells of the kidneys. To our knowlage, only two experimental life-cycle studies exists on anuran and urodel coccidia, and it is assumed that amphibian coccidia have direct life-cycles as has been shown for other eimerians of vertebrates (Nöller 1923; Matubayasi 1937; Pellérdy 1974). Nöller's (1923) study on the life history of *H. lieberküehni* indicates that sporulated oocysts are deposited in the water by frogs and are swallowed by tadpoles in which the SZ invade the glomeruli of the kidneys, where merogony takes place in the epithelial cells. Resulting merozoites then invade the tubule epithelium. In his study, young field collected frogs were found infected in late April and early May suggesting that tadpoles may be important in the transmission of this species to adult frogs.

Among other genera of amphibian coccidia, field studies indicate that *Eimeria* spp. have only been reported from adult anurans, whereas some eimerian species can apparently infect both adult and larval salamanders (Bolek *et al*. 2003). Until recently, *Isospora* spp. only have been reported from adult amphibians. Bolek *et al*. (2003) were the first to report *I. cogginsi* from field collected adult frogs and tadpoles of the western chorus frog. They indicated that very few studies have actually examined tadpoles for coccidia and the lack of reports on coccidia from tadpoles is due to the fact that we have not made a concerted effort to look for them in those life stages of anurans. Finally, studies on *Goussia neglecta* and *G. hyperolisi* indicate that only the tadpole stage becomes infected with these species and metamorphosed and adult frogs are never infected (Nöller 1920; Molnár 1995; Paperna *et al*. 1997).

The importance of tadpoles in the transmission of anuran coccidia should not be overlooked when considering that many anuran coccidia have delicate oocyst walls that break easily in a manner similar to those of piscine coccidian (Paperna & Cross 1985; Lom *et al*. 1991; Paperna & Lainson 1995), suggesting that they may not survive outside of an aquatic habitat. Studes by Jirků and Modrý (2006b) on an unnamed *Goussia* sp. in *Rana dalmatina* indicate that merogony only occurred in the tadpole stage of this host. However, their study also indicated that fully sporulated oocysts of this species were found in the sinuses of the liver of metamorphosed froglets and juvenile frogs up to 15 months post-metamorphosis. This study was the first to provide a potential mechanism for the survival of the delicate anuran oocysts in the environment before another round of transmission occurs in the anuran host.

In contrast to anuran oocysts, morphological studies on oocysts of salamanders and caecilians which do not have tadpole stages indicate that unlike anuran oocysts, oocysts of caudatans and gymnophionids have thick walls (Upton *et al*. 1993; Asmundsson *et al*. 2000). Comparative studies will have to be conducted on the transmission and survival of thin-walled anuran oocysts and thick-walled caudatan and gymnophionid oocysts to see if there is any relationship between thickness of oocyst walls and survival of these oocysts in the external environment.

Finally, sporulation is believed to be endogenous in most anuran coccidia (Pellérdy 1974; Upton & McAllister 1988; Chen & Desser 1988); whereas it is exogenous in caudatan species and the single known gymnophionid coccidian (Upton *et al*. 1993; Asmundsson *et al*. 2000), again suggesting differences in transmission strategies between anuran, and salamanders and caecilian coccidia. Recovering unsporulated oocysts in the feces of an amphibian host clearly indicates that they must sporulate in the external environment. However, finding fully sporulated oocysts in an amphibian host's feces does not discriminate between those oocysts sporulating in infected host cells (endogenous development) or sporulating in the host's gut lumen (exogenous development). This is particularly important in anuran hosts which may not defacate in the laboratory for up to a week and few studies have examined anurans for endogenous stages of their coccidians. Examples of species that have true endogenous development include *E. himalayani* (Ray & Misra 1941), *E.*

laminata (Ray 1935), *G. neglecta* (Nöller 1920), and *E. prevoti* (Laveran & Mesnil 1902a; Boulard 1975). Recently one of us (MGB) documented exogenous developing eimerian and isosporan species in tadpoles that have been reported to have endogenous development in adult frogs (Upton & McAllister 1988; unpublished data). These observations indicate that those who investigate the coccidian of amphibians need to examine internal host organs for developmental stages of these parasites to better determine if the development is endogenous or exogenous.

Future Studies on Amphibian Coccidia

Clearly a variety of amphibian species from a variety of habitats need to be sampled and resampled, and examined for coccidian parasites in order to get a better understanding of the true diversity of these parasites in this fascinating group of hosts. Studies, when possible, should examine all host life stages, including tadpoles and larvae of amphibian hosts, and multiple species of amphibians from the same location. To our knowledge, no long-term studies on amphibian coccidia exist, and most reports are based on one time examinations from a few individuals of a particular species (see Table 2). Additionally, when tadpoles are infected with other genera of coccidia, can they maintain infection during metamorphosis? It is known that caudate amphibians commonly infect adult, immature and larval salamnders of the same species (Bolek *et al*. 2003). These observations suggest that comparative studies on the transmission of anuran and caudatan coccidia may be very rewarding, and may give us a better evolutionary understanding of the differences and similarities between the coccidia of these groups of animals.

Finally molecular phylogenetic studies need to be conducted on amphibian coccidia to understand the position of amphibian coccidia among other parasite groups. To our knowledge the only amphibian coccidium that has been sequenced is *H. lieberküehni* (Modry *et al*. 2001). The few existing studies on endogenous development of anuran *Goussia* and *Eimeria* species by Paperna *et al*. (1997) and Paperna and Lainson (1995) indicate the absence of wall-forming bodies in macrogamonts in the anurans that have been examined by TEM. These observations on the absence of wall-forming bodies indicate similarities to piscine coccidia (Paperna 1991), in contrast to the presence of wall-forming bodies that occur in reptilian, avian and mammalian coccidia. In this context, it is also worth noting the observed merging of the oocyst envelope with the PV wall, which recalls the process of oocyst wall formation in several piscine coccidia (Desser & Li 1984; Paperna 1991; Steingagen 1991). Additionally, certain fish coccidia (Paperna 1991) are known to have newly formed merozoites divide, usually by endodyogeny, a process noted in the marine toad coccidium *E. bufomarini*. These observations suggest association of some anuran coccidia with those of fish that may imply primitive characters parallel to those seen not only in the piscine coccidian, but also among the coccidia of invertebrate hosts and in some tissue-cyst forming coccidia (e.g. *Sarcocystis*, *Frenkelia*). In order to undersand if this is a general characteristic of anuran or amphibian coccidia we need to construct molecular phylogenies of coccidian species specific to salamanders, caecilians, and adult and tadpole anurans.

We hope that our comprehensive review encourages both parasitologists and herpetologists to be more receptive toward working together and to use comparative parasite data that might provide insights into amphibian evolution and habitat use to be able to give us a better understanding of the diversity and basic biology of amphibian coccidia.

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