SYSTEMATICS OF COCCIDIAN PARASITES (APICOMPLEXA) FROM AMPHIBIANS AND REPTILES IN NORTHCENTRAL TEXAS

DISSERTATION

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By

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Between February 1986 and October 1988, 863 amphibians and reptiles were collected in northcentral Texas and examined for coccidial parasites. Thirteen percent of amphibians (26% salamanders, 11% frogs and toads) and 28% of reptiles (54% turtles, 25% snakes) harbored 20 previously described and 16 new species of coccidia; overall prevalence of infection was 176/863 (20%).

Sixteen Ambystoma texanum were infected with Eimeria ambystomae which represents new host and geographic locality records for the coccidium. Forty anurans were found to be passing coccidia, including Pseudacris streckeri, Bufo valliceps and Gastrophryne olivacea. Four new species of coccidia were described from anurans and include Eimeria flexuosa, E. streckeri, Isospora delicatus and I. fragosum. However, oocysts found in B. v. valliceps were determined experimentally to represent pseudoparasites. Sixty-eight turtles were infected with coccidia, including Chelydra serpentina,

Kinosternon flavescens, Pseudemys texana, Terrapene ornata and Trachemys scripta elegans. Fourteen eimerians (5 of which are described as new species) were found in turtles. The new species from turtles include Eimeria cooteri, E. ornata, E. stylosa. E. texana and E. trachemydis. Interestingly, all 96 lizards examined were negative for coccidia. Fifty-three snakes including 11 colubrids and 1 viperid harbored coccidia of the genera Caryospora, Cryptosporidium, Eimeria and Sarcocystis; prevalence of infection was highest in 3 species of North American water snakes (Nerodia spp.). Seven new species of Eimeria were described from snakes, including E. conanti, E. infirmus, E. papillosum, E. rhombifera, E. serpenticola, E. striatula and E. tenuis.

There was no preference for coccidia between the sexes of any hosts. Based on limited data from a single anuran host, prevalence was higher during wetter months of spring than in summer. In addition, prevalence was higher in aquatic and semiaquatic snakes than in truly terrestrial species. Preliminary data suggested that using host specificity data of coccidia may be a method of studying host phylogeny and coevolutionary relationships in thamnophiine snakes.

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CHAPTER I

INTRODUCTION

The phylum Apicomplexa Levine, 1970, is composed of 5 major taxa of Protozoa (ca. 4,600 named species) that include gregarines, haemogregarines, coccidia, malarial parasites, and piroplasms. The taxonomy of the coccidia (suborder Eimeriorina), an economically and medically important group, was recently summarized by Levine (1988) and currently includes over 2,000 named species, of which approximately 46% occur in mammals, 14% in birds, 10% in reptiles, 3% in amphibians, 6% in fishes, and less than 1% in invertebrates.

Most available information on coccidia has derived from research on mammalian and avian hosts. This is due chiefly to the destructive effects that some coccidians have on economically important mammals and birds where entire stocks of domestic livestock and poultry can be lost in a matter of days. Reptiles and amphibians, which are not considered as economically important, have coccidia that are relatively unknown and/or inadequately described. Therefore, the extent of pathology caused by coccidia in poikilotherms is also largely unknown. Pellérdy (1974) provided descriptions of most amphibian

and reptilian coccidia reported through 1970 (ca. 175 species). Since 1970, only several new species have been added to the literature.

Although over 200 species of amphibian and reptilian coccidia have been reported, many of the original descriptions are in non-English journals, and are both hard to obtain and in need of translation. Additionally, most surveys for coccidia only have examined a single host species from an undefined geographic area. Most investigators conducting these surveys searched only the literature on coccidia known from the particular host species they were studying and, when none were listed, often described a new species based solely on the unconfirmed contention that as a group coccidia are host species specific. The consequence of that approach has often produced taxonomic inconsistencies with many synonyms. For instance, Pellérdy (1974) listed a number of oocysts, described from different birds and mammals, that are sufficiently similar morphologically to be the same species. Although hosts may (or may not) share a common phylogeny, they may have sufficient niche overlap for exposure to the same oocysts in their habitat. Therefore, it is essential to make careful morphometric comparisons of oocysts recovered from a particular host with those recovered from other syntopic hosts to avoid

incorrectly naming new species.

Although there appears to be a renewed interest in the study of coccidia from amphibians and reptiles (e.g., Atkinson and Ayala, 1987; Chen and Desser, 1989; Matuschka, 1989), I am unaware of any publications concerning systematic relationships of the coccidian genera Eimeria, Isospora and Cryptosporidium known to infect common amphibian and reptilian taxa. Little is known about the affects these coccidia have on their hosts. Also, few comprehensive surveys of coccidia from amphibians and reptiles from defined geographical areas are available. Studies of this nature are important groundwork that allow for a synthesis of ecology and evolution of both the hosts and their coccidial parasite communities.

Because of the taxonomic confusion and paucity of systematic information, relatively little can be said about the phylogeny, ecology, evolution and pathology of coccidia in amphibians and reptiles. Without comprehensive studies of syntopic hosts within a defined geographic area, a theoretic foundation for experimental cross-transmission and life cycle studies is impossible. Thus, I began the 3-yr study presented herein with the following objectives:

(1) To recover both new and previously known species of coccidia from reptilian and amphibian hosts.

Since the majority of hosts are being surveyed for the first time and because no species of amphibian or reptilian coccidian have been reported previously within the geographic region studied herein, new species should be recovered.

(2) To determine if significant differences in prevalence occur in coccidia between host sexes.

(3) To examine prevalence of coccidial infections and establish whether they are significantly higher during the wetter months of spring and fall than in summer when oocysts should be more susceptable to dessication.

(4) To compare the overall prevalence of coccidia in aquatic and semiaquatic hosts versus terrestrial hosts. Coccidia found in the latter may need to circumvent dessication to survive and, thus, the morphologic structure of the oocyst wall may be thicker and more resistant than coccidia found in aquatic hosts.

(5) To see if it is possible to correlate oocyst structure with previously published data on host phylogeny (i.e., closely related host species may share more species of coccidia than poorly related species).

During this research, 16 new species of coccidia were found which are listed in the Appendix. Because the International Code of Zoological Nomenclature expressly forbids new species descriptions appearing in an

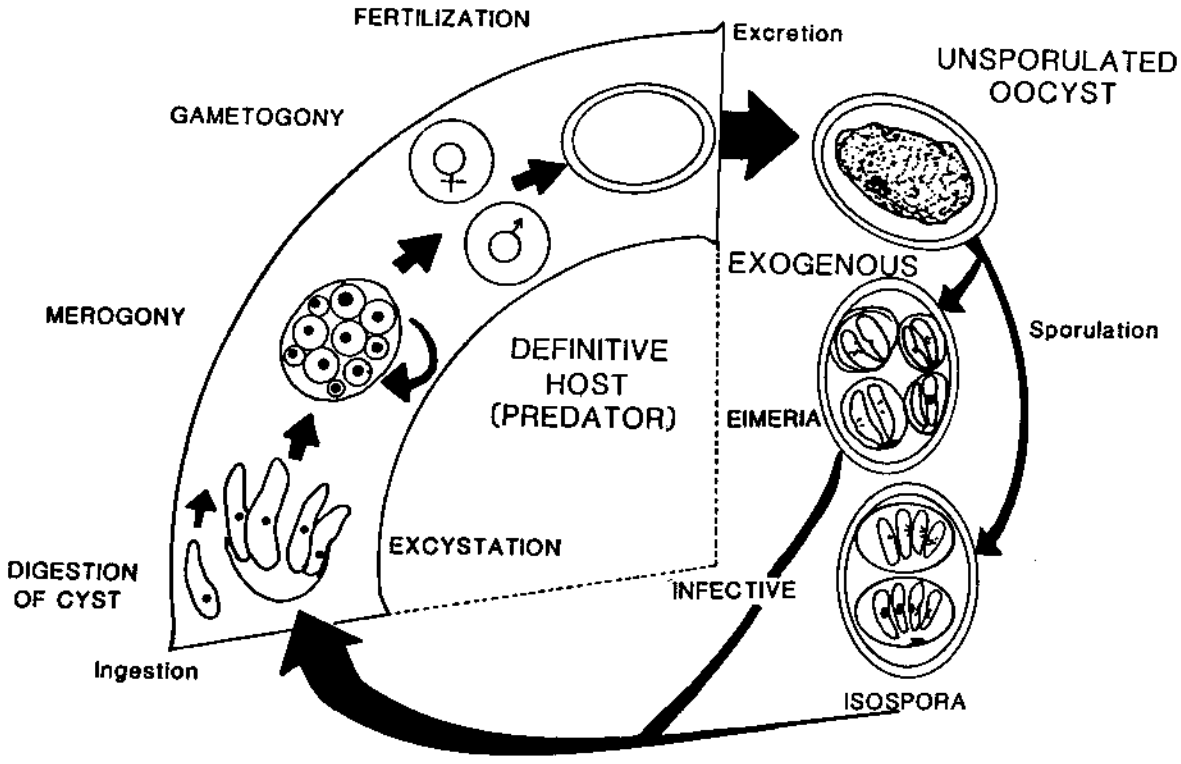
unpublished thesis for the first time (Ride et al., 1985), descriptions were originally published formally in the scientific literature and are cited herein.

CHAPTER II

LIFE CYCLE AND HOST SPECIFICITY

To better understand how coccidial parasites infect various vertebrates, the life cycle of a typical coccidian is shown in Fig. 1. For the most part, species in the genera Eimeria and Isospora complete development within the intestine of a single host and are usually thought to be specific for that host species. Initially, unsporulated oocysts from an infected animal are passed in the feces and sporulate exogenously in a matter of days. Sporulated oocysts are ingested by another host and the vermicular infective sporozoites excyst and enter host intestinal epithelial cells. There they develop asexually by multiple fission (merogony = schizogony) forming a variable number of merozoites. These merozoites enter new host cells and again multiply by merogony. Eventually, the last generation merozoites enter new host cells and undergo gametogony (sexual reproduction). Most gamonts develop without further multiplication into macrogametes while others (microgametocytes) divide asexually by multiple fission to form a large number of flagellated sperm-like microgametes. After fertilization, an exterior wall

FIGURE 1. Life cycle of Eimeria and Isospora. (Redrawn from Fayer, 1982).


FERTILIZATION
Excretion
UNSPORULATED
OOCYST
GAMETOGONY
EXOGENOUS
MEROGONY
Sporulation
DEFINITIVE
HOST
(PREDATOR)
EIMERIA
EXCYSTATION
DIGESTION
OF CYST
INFECTIVE
Ingestion
ISOSPORA

1

forms around the zygote cytoplasm and forms the oocyst wall. The oocyst ruptures out of the host cell and is shed into the environment with host feces (terrestrial hosts in soil, aquatic hosts in water). Under the proper conditions of oxygen, humidity and temperature, the oocyst completes sporulation and becomes infective for the next appropriate host.

Although the majority of coccidia develop as described above, some coccidia have oocysts that are passed in the feces fully sporulated (e.g., species that sporulate in the gall bladder of some reptiles and some infecting hosts inhabiting aquatic environments). In addition, oocysts of coccidia from aquatic animals are less resistant to dessication than terrestrial species because the oocyst walls tend to be thinner.

There appears to be a high degree of host specificity in coccidian parasites, especially within the genus Eimeria. Marquardt (1981) noted that closely related species may serve as adequate hosts, but cross-transmission between genera seldom occurs and cross-transmission between families is extremely rare. However, it appears that the initial process of infection itself is non-specific. When oocysts are administered to nearly any species of potential host they will excyst and the infective sporozoites enter host cells. After rounding up, however, parasites

developing in an abnormal host disappear completely within 48 hr. Although these observations imply host cell physiology may be an important cue that affects further development of the coccidian, no studies have been published addressing this hypothesis. Marquardt (1981) further pointed out that certain strains or populations of hosts can be susceptable to a coccidian species, whereas other members of the same host species may be completely refractory. These observations suggest that both host genetics and, perhaps, ecological relationships (i.e., food habits, behavior) may be important factors determining whether a species of coccidian will successfully infect a particular host. Mayberry et al. (1982) reported that Eimeria separata from the Norway rat (Rattus norvegicus) could be transmitted to some, but not all, genetic strains of house mice (Mus musculus).

CHAPTER III

THE STUDY AREA

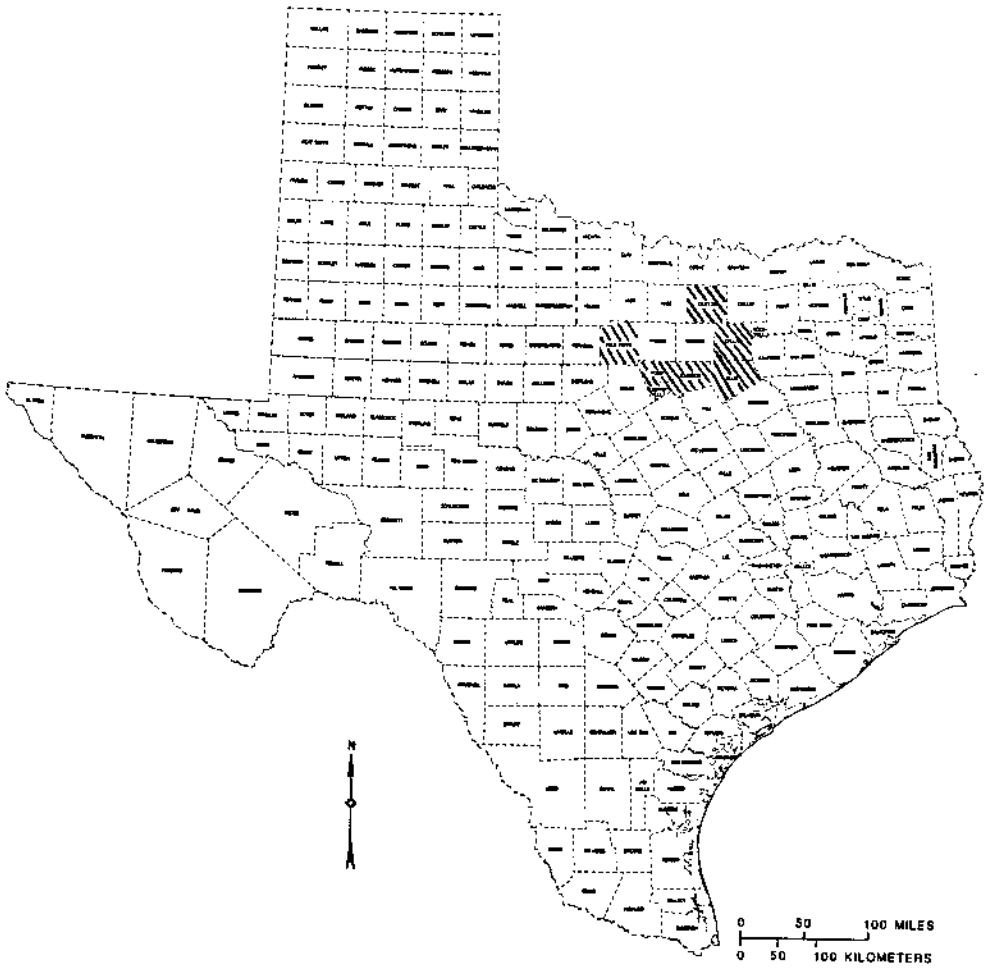
The state of Texas and its 254 counties are geographically situated at the junction of 4 major physiographic divisions of North America, including the Rocky Mountains, Great Plains, eastern forests and southwestern deserts. The state is ecologically diverse with unusually rich environments made up of numerous different habitats supporting a herpetofauna of 204 species and 283 taxa of amphibians and reptiles (Dixon, 1987). Northcentral Texas is at a crossroads where herpetofauna from tropical Mexico and subtropical Texas mix with those of the Great western High Plains, and species of the western high mountains and deserts intermingle with others from the humid lowlands of the eastern forest and south Gulf coastal regions. Therefore, areas within the boundaries of northcentral Texas provide a unique opportunity for studying the coccidia of such a diverse mix of amphibians and reptiles.

The overall study area includes portions of Dallas, Hood, Johnson, and Somervell counties in the Cross Timbers (oak-hickory forest community) of northcentral

Texas (Fig. 2). Principal study sites are located on ranch lands in western Johnson (Georges Creek Ranch), southeastern Hood (Diamond-L Ranch, Hinton-Parker Ranch, Russell Ranch, and Fort Spunky) and northeastern Somervell (Fry Ranch and Nemo) counties. The major study site (Georges Creek Ranch) includes more than 4,452 ha. A small secondary study site is located west of DeSoto, in rural Dallas County, and includes abandoned pastureland and an intermittant stream that flows into a small cattle tank. In addition, minor collecting sites are located in central Denton and northwestern Ellis counties and along the Brazos River in northcentral Palo Pinto County.

The major area of study is characterized by open prairie grasslands and juniper-covered limestone hills on uplands and sandy areas along the Brazos River. The region is also interspersed with numerous small streams, lakes, stock ponds and cattle tanks in the Trinity-Brazos watershed. Habitat consists primarily of cedar glade, pastureland where domestic cattle are allowed to graze, and disturbed tall-grass prairie. Dominant grasses include: big bluestem (Andropogon gerardi), little bluestem (Schizachyrium scoparium), indiangrass (Sorghastrum spp.), switchgrass (Panicum virgatum), sideoats grama (Bouteloua curtipendula), hairy grama (B. hirsuta), Texas grama (B. rigidiseta),

FIGURE 2. Map of Texas showing counties (hatched lines) included in the region of study.



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Texas wintergrass (Stipa leucotricha) and rattail smutgrass (Sporobolus indicus). Climax vegetation includes upland hardwoods such as cedar elm (Ulmus crassifola), Texas oak (Quercus texana), live oak (Q. virginiana), common hackberry (Celtis occidentalis), eastern black walnut (Jugulans nigra), and pecan (Carya illinoensis), eastern red cedar (Juniperus virginiana) and honey mesquite (Prosopis glandulosa) in cedar glade, and Gulf black willow (Salix nigra), eastern cottonwoods (Populus deltoides) and American elm (U. americana) along stream habitat (Vines, 1982). The most common succulents found on the primary study site are prickly pear cactus (Opuntia rafinesquei) and yucca (Yucca sp.). Various wildflowers are found throughout the study area (Ajilvsgi, 1984), the most common types being antelope-horns (Asclepias asperula), bull nettle (Cnidoscolus texanus), coreopsis (Coreopsis basalis), bitterweed (Helenium amarum), common broomweed (Xanthocephalum dracunuloides), buffalo gourd (Curcubita foetidissima) buffalo bur (Solanum rostratum), indian blanket (Gaillardia pulchella), Texas bluebonnet (Lupinus texensis), Texas paintbrush (Castilleja indivisa), purple dalea (Dalea lasiathera), henbit (Lamium amplexicaule) and western wallflower (Erysimum capitalum).

The soil of southwestern Johnson County is

predominantly a dark-colored and alkaline prairie loam interspersed with red clay. Soils within the Georges Creek study site consist of a Bolar-Brackett-Aledo complex, which is strongly sloping to steep and very shallow to moderately deep, with some alkaline loamy, stony and gravelly soils on upland prairie (Coburn, 1985). At study areas in southeastern Hood and northeastern Somervell counties, soils consist of a Bastrop-Yahola or Tarrant-Purves complex with very shallow to shallow sandy red clays that formed in limestone on uplands (Coburn, 1978).

Surface geology of this region is largely lower Cretaceous rock (Papaw formation) and predominantly limestone with some marl, sandstone and clay. Over much of the area elevation ranges from 165-300 m; however, along the Brazos River valley, elevations typically are not more than 185 m.

Climatological conditions of the area are typical for north Texas and are generally hot in the summer and cool in winter. Precipitation falls at various times throughout the year, with spring and fall being wetter months than summer. However, there can be year-to-year or even within year variability in precipitation as evidenced by data gathered during the 3-yr study period and summarized in Table I. For example, 1986 was a

TABLE I. Precipitation data recorded during the study period (1986-1988) at the Cleburne Station*.

Year	Total precipitation (cm)	Departure from normal (+ or -) (cm)
1986	122.1	+39.9
1987	90.4	+8.2
1988	57.9	-24.4

*National Oceanic and Atmospheric Administration (NOAA) (1986, 1987, 1988).

wetter than normal year, while 1988 was very dry. This coincided with an extensive summer drought that occurred over much of the United States during 1988 (Trenberth et al., 1986). On the other hand, precipitation during 1987 was about average for this region of the state.

Annual temperature data for 1987 recorded at the Cleburne station (elevation = 239 m) in Johnson County (located ca. 15 km NE of the study area at 32^{o} 20'N, 97^{o} 24'W) averaged 7.6-30.0 C (mean overall annual temperature = 18.7 C) with extremes on 5 August (40.6 C) and 16 December (-6.1 C) (NOAA, 1987). Annual soil

temperature recorded at a depth of 10 cm was 7.8-39.5 C (mean = 24.7 C) in Hasse loam with 0% slope at neighboring Stephenville, Erath County (NOAA, 1987). Most rainfall was recorded in the month of May (24.0 cm) and the least amount fell during the months of April (0.61 cm) and August (1.02 cm) (NOAA, 1987). The site is subject to fluctuations in solar radiation as evidenced by a low of 250 langleys in January to a high, in July 1987, of 600 langleys.

CHAPTER IV

MATERIALS AND METHODS

Host collection techniques

Fieldwork began on 17 February 1986 and continued until 21 October 1988. Host specimens were collected by a variety of methods. Amphibians were taken with dipnets from aquatic sites or by hand and excavation in terrestrial localities. Generally, larval salamanders and anuran tadpoles were captured in ponds and streams and adult salamanders under debris in woodland habitat. Adult anurans were taken in a similar manner, except that toads were most often collected by spotlighting at night on roads following spring rains. Aquatic turtles were collected with 2.5-cm-mesh wire hoop nets baited with sardines anchored in ponds and cattle tanks and terrestrial box turtles were taken on roadways. Most large snakes were collected with pilstrom snake tongs while smaller ones were taken by hand under rotten log and rock retreats. Lizards were stunned with rubber bands or shot with .22 caliber rat shot.

Freshly killed animals on the road (DOR) were collected and included in this study. Previous experience (McAllister, unpubl. data) with fresh DOR

animals has revealed that many species of coccidia are viable, as long as conditions in the carcass remain aerobic.

For each host species, the currently accepted scientific and standard common names of North American amphibians and reptiles are provided following Collins et al. (1982). Voucher specimens of hosts are deposited in the Arkansas State University Museum of Zoology (ASUMZ). Syntypes of many coccidians (oocysts in 10% formalin) are deposited in the United States National Parasite Collection, USDA, Beltsville, Maryland (USNM).

Host necropsy techniques

Hosts were transported to the laboratory in individual refrigerated (4 C) containers and processed within 24 hr. However, some turtles were placed individually in 38-L glass aquaria and, soon after defecation (usually within 48 hr), either retained for voucher specimens or returned to the original collection site. Amphibians were either killed by pithing or exposure to 0.2% ethyl-m-aminobenzoate (tricaine methanesulfonate) and reptiles overdosed with sodium pentobarbital.

After exposing host viscera by mid-ventral incision, the entire intestinal tract, from the duodenum to the rectum, was removed and placed in 0.6% isotonic

NaCl. Feces taken from the colon, along with slit portions of the intestines and contents of the gall bladder were placed in vials containing 2.5% aqueous (w/v) potassium dichromate solution. However, because certain amphibian coccidia were found during this study to possess fragile oocyst walls, feces from these hosts were placed in individual vials containing tap water supplemented with 100 IU/ml penicillin-G and 100 µg/ml streptomycin.

Observations were made directly on wet mounts of intestinal or gall bladder contents and feces from amphibians. Samples from reptiles were concentrated by coverslip flotation in a modified Sheather's sugar solution (sp. gr. 1.30) (Todd and Ernst, 1977). This effectively separates coccidian oocysts from fecal debris by low-speed centrifugation (500g x 5 min.). Unsporulated oocysts were sporulated at room temperature (ca. 22-23 C) for up to 1 wk in Petri dishes containing a thin layer of tap water supplemented with antibiotic or 2.5% potassium dichromate. Examinations and measurements were made on $\geq$ 25 parasites of each species using an Olympus BH-S photomicroscope equipped with a x100 SPlan objective, x1.25 optivar, Nomarski interference-contrast optics and a calibrated ocular micrometer (Olympus Inc., Tokyo, Japan) and are reported in micrometers (µm) with the mean followed by

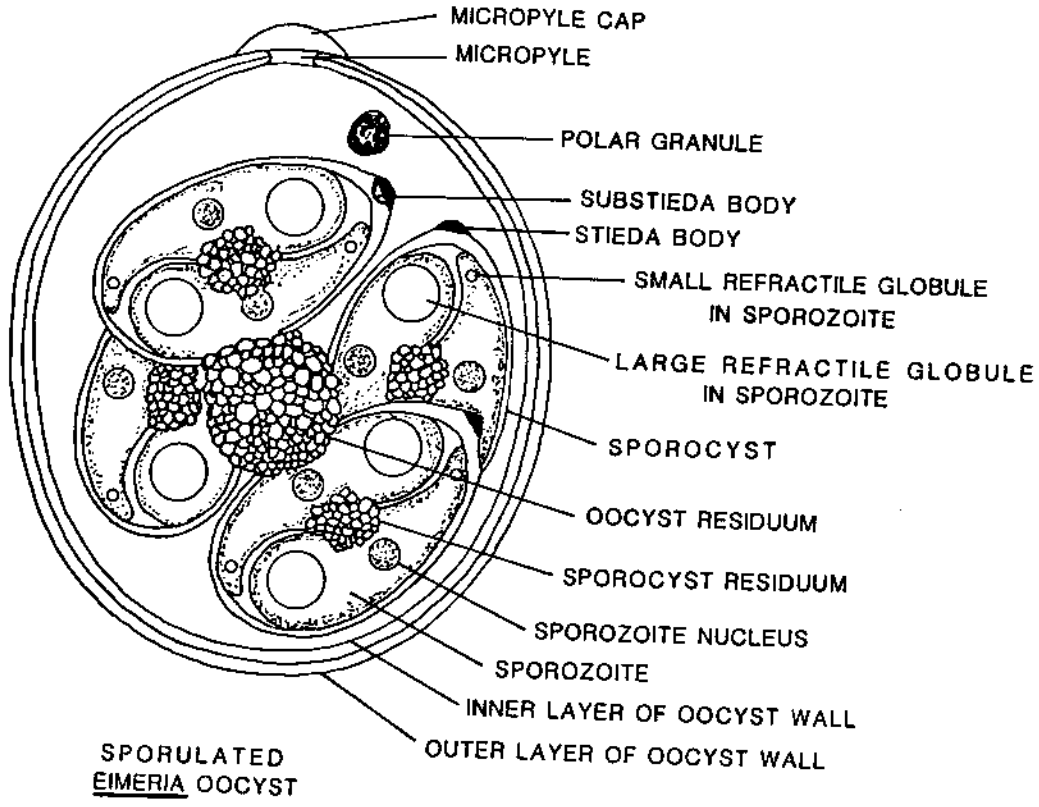
the ranges in parentheses. Species identification of coccidia were determined by examining the structure of the sporulated oocyst (Fig. 3) and line drawings were made of each new and 2 previously known species.

Experimental infections

An unknown species of adelid (Apicomplexa: Adeleidae) was recovered from Gulf Coast toads (Bufo valliceps). Because most members of this family infect invertebrates, experimental infections were attempted. Two B. valliceps were collected and housed individually in clean oocyst-free 38-L glass aquaria and fed homogenized dog chow with vitamin supplements ad lib. Over the next 3 wk, feces was examined from each of the toads to assure the absence of coccidia. At the end of this period, each was inoculated orally with 20,000 3-wk old sporocysts. Feces from experimentally infected toads were checked periodically over the next 2 wk for presence of coccidian oocysts. When oocysts were recovered, oocysts in each fecal sample were counted by hemacytometer to quantify the number of shed oocysts. Tissue samples of the small intestine, stomach, large intestine, gall bladder, and liver were fixed in 10% formalin to check for the developmental stages at 21 DPI.

An unknown species of Sarcocystis Lankester, 1882

FIGURE 3. Sporulated Eimeria sp. oocyst showing the structures used to distinguish species. (Redrawn from Levine, 1978).



SPORULATED
EIMERIA OOCYST

3

(Apicomplexa: Sarcocystidae), found in the feces of a western diamondback rattlesnake (Crotalus atrox), was also inoculated orally into experimental animals. Four ICR outbred Mus musculus (Harlan Sprague-Dawley) were housed in preautoclaved rodent cages and fed commercial rodent mash pellets and water ad lib. Sporocysts were removed from 2.5% potassium dichromate 20 days after the fecal sample was collected and placed in phosphate buffered saline (PBS) at a concentration of 1.5 million sporocysts/ml in a total of 10 mls and stored at 4 C. Two of the mice were inoculated per os with 3,000 and 8,000 sporocysts, respectively, whereas the other 2 were used as uninfected controls. Mice were killed 15 wks post-inoculation and squash preparations of the diaphragm and tongue examined both macroscopically and microscopically for sarcocysts.

Data analyses

Similar morphological types of oocysts from a given host group were divided into groups based on obvious qualitative and quantitative features (oocyst wall texture, oocyst length and width, oocyst length/width ratio, sporocyst length and width, sporocyst length/width ratio, appearance of a sporocyst residuum, number of polar granules, and number of refractile bodies). Measurements were made on the features and, if

necessary, differences between the groups tested for significance using the nonparametric Wilcoxon Mann-Whitney U-Test. For this test, as for many nonparametric procedures, actual measurements were not employed, rather, ranks of the measurements were utilized; data were ranked from the lowest to the highest values. The term prevalence (number of hosts infected per hosts examined) follows the definition of Margolis et al. (1982). Chi-square analysis of 2 x 2 contingency tables (Sokal and Rohlf, 1969) was used to analyze host-parasite interactions. The terms significant or significantly different refer to statistical significance at $P \leq 0.05$.

Because the walls of Cryptosporidium spp. in semiaquatic Nerodia spp. appeared to be thinner than isolates from terrestrial hosts, it was necessary to examine whether shrinkage during prolonged exposure to the flotation medium (Sheather's sucrose solution) was an important consideration of this study. Oocysts collected from Nerodia h. harteri were measured under 3 separate conditions: (1) exposure to 2.5% potassium dichromate only; (2) flotation in Sheather's sugar solution followed by measurements within 30 min; and (3) flotation followed by 1 hr period prior to measuring.

CHAPTER V

RESULTS

Systematics and prevalence data

A total of 863 specimens, representing 49 species within 15 families of amphibians (12 species, 5 families) and reptiles (37 species, 10 families), were collected and examined for coccidial parasites. These included 1 species (61 specimens) of salamander, 11 species (367 specimens) of frogs and toads, 7 species (125 specimens) of turtles, 7 species (96 specimens) of lizards, and 23 species (214 specimens) of snakes.

Overall prevalence of infection with at least 1 coccidian for all groups was 176/863 (20.4%), including 13.1% of the amphibians and 27.6% of the reptiles (Fig. 4). When individual host groups are compared, 26.2% of the salamanders, 10.9% frogs and toads, 0% lizards, 54.4% turtles, and 24.8% snakes harbored 1 or more species of coccidia (Fig. 5).

The remaining systematic and prevalence results are presented according to each amphibian or reptile host group and are further subdivided at the ordinal/subordinal level, beginning with the primitive salamanders and ending with the more advanced snakes.

FIGURE 4. Prevalence of infection of at least 1 coccidian among 863 amphibians and reptiles. Numbers above bars are number infected/number examined.

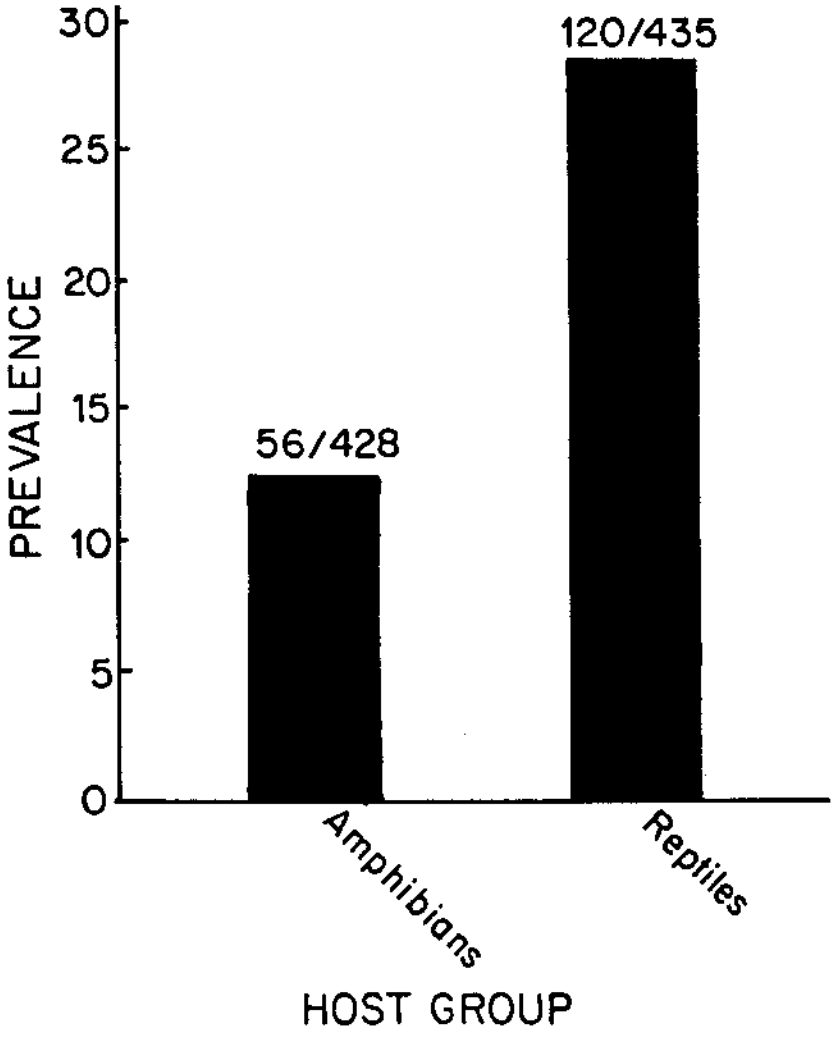
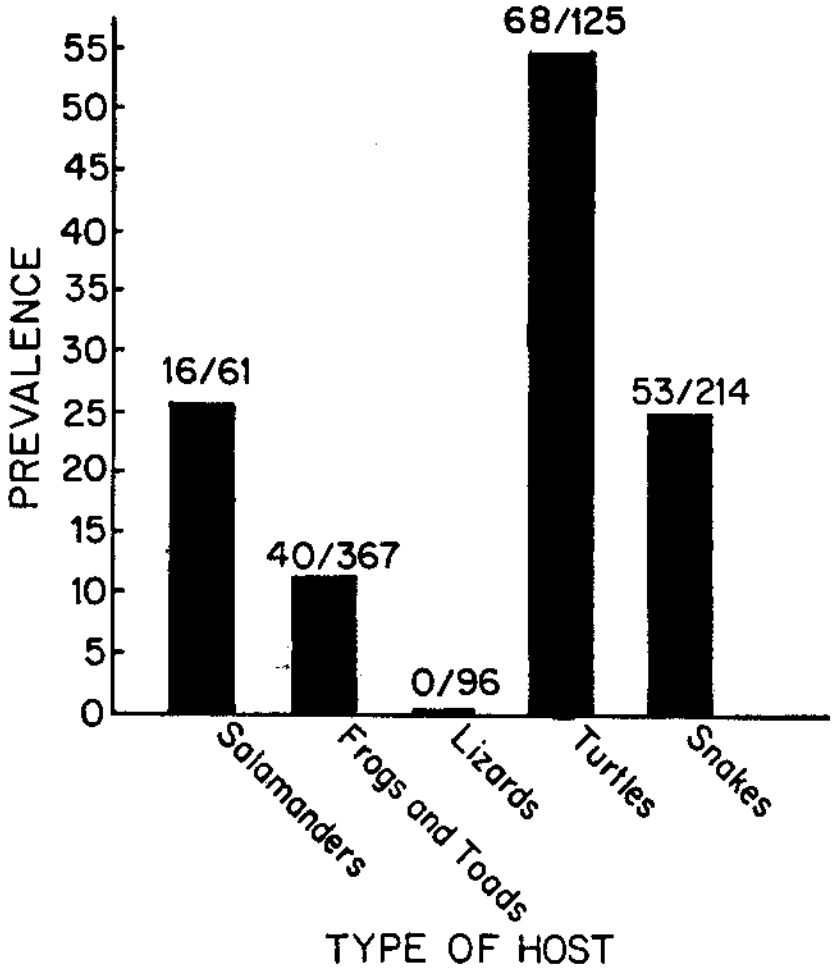

30
25
20
15
10
5
0
PREVALENCE
120/435
56/428
Amphibians
Reptiles
HOST GROUP

FIGURE 5. Prevalence of infection of at least 1 coccidian among 5 host groups of amphibians and reptiles. Numbers above bars are number infected/number examined.


68/125
55
50
45
40
35
30
25
20
15
10
5
0
PREVALENCE
16/61
53/214
40/367
0/96
Salamanders
Frogs and Toads
Lizards
Turtles
Snakes
TYPE OF HOST

Caudata

Sixteen of 61 (26.2%) smallmouth salamanders, Ambystoma texanum (Matthes, 1855) (16/59 Dallas County, 0/2 Somervell County), were infected with Eimeria ambystomae Saxe, 1955 (Fig. 6). These included 3/15 (20%) immature and transforming larvae and 13/46 (28.3%) adults. There was no preference for host sex (X^2 = 0.196, 1 df, $p > 0.7$) as 23.1% of the males and 31.8% of the females were infected with E. ambystomae (Fig. 7).

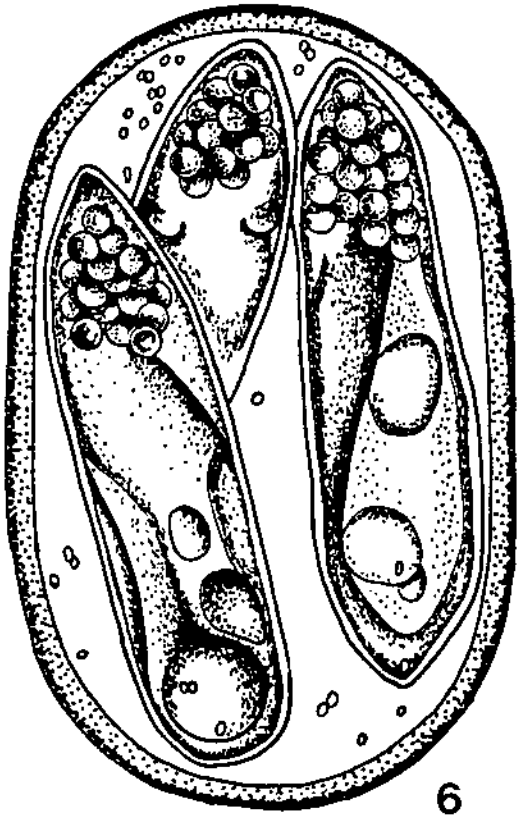
Examination of oocysts from 8 infected adult A. texanum (5 females, 3 males; mean = 72.8 ± 3.4, range = 54-82 mm snout-vent length) that ranged in age from 1 wk to 4 mo, revealed newly sporulated oocysts have a compact residuum whereas older forms had residua that became dispersed throughout the oocyst.

A single adult A. texanum from Somervell County passed an eimerian similar to E. arizonensis Levine, Ivens and Kruidenier, 1957. Because this protozoan is a known coccidium of Peromyscus spp., an abundant rodent in the study area, it was concluded to be pseudoparasite.

Anura

Three of 11 (27.3%) species comprising 2 suborders and 3 families of frogs and toads were found to be passing coccidia (Table II). Combined prevalence of

FIGURE 6. Line drawing of sporulated oocyst of *Eimeria ambystomae* Saxe, 1955 from *Ambystoma texanum*.



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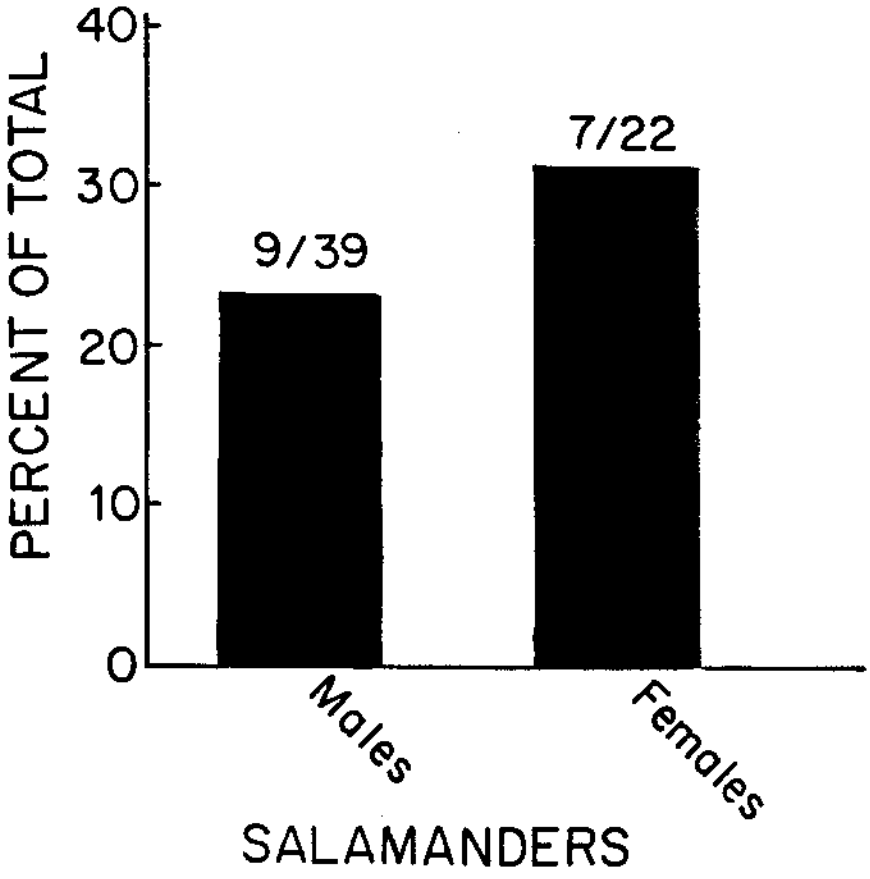
10 µm

FIGURE 7. Preference of Eimeria ambystomae for host sex among 61 Ambystoma texanum. Numbers above bars are number infected/number examined.


PERCENT OF TOTAL
40
30
20
10
0
9/39
7/22
Males
Females
SALAMANDERS

infection was 30/367 (10.9%) anurans.

TABLE II. Species and prevalence data for Anura examined for coccidia.

Host suborder/family/species	Prevalence
Procoela:	
Hylidae:	
Acris crepitans blanchardi	0/43 (0%)
Pseudacris clarkii	0/40 (0%)
Pseudacris streckeri streckeri	18/50 (36%)
Bufonidae:	
Bufo debilis debilis	0/28 (0%)
Bufo valliceps valliceps	3/23 (13%)*
Bufo woodhousii woodhousii	0/20 (0%)
Diplasiocoela:	
Ranidae:	
Rana berlandieri	0/2 (0%)
Rana blairi	0/7 (0%)
Rana catesbeiana	0/15 (0%)
Rana sphenocephala	0/13 (0%)
Microhylidae:	
Gastrophryne olivacea	19/126 (15%)

*A few oocysts were passed by 1 Gulf coast toad which, upon sporulation, were found to represent an *Eimeria* sp.

However, these oocysts had every appearance of a rodent coccidian (see McAllister et al., 1989a). Since the particular toad from which the sample was taken was, at the time, inhabiting an abandoned rodents nest, this coccidian was concluded to be a pseudoparasite. The other 2 hosts were found to be passing what appeared to be adelid sporocysts. Because all known genera in this taxon are found in invertebrates, and because experimental infections into uninfected B. v. valliceps did not result in patent infections (see below), it was concluded that these coccidia were also pseudoparasites.

Two Bufo v. valliceps inoculated with adelid sporocysts did not pass additional sporocysts beyond the initial inoculum. In addition, microscopic examination of the intestinal tract, liver, gall bladder, and kidneys from each of the toads at the end of the 2 wk period revealed no coccidial developmental stages. This supports the contention that these coccidia represented pseudoparasites of B. v. valliceps.

A total of 4 coccidians were recovered from the 2 remaining anuran hosts (Table III). Of these taxa, parasite diversity was highest in Strecker's chorus frog, Pseudacris s. streckeri.

TABLE III. Coccidia recovered from anurans in northcentral Texas.

Host and coccidium	County	Prevalence
Pseudacris s. streckeri:		
Eimeria flexuosa	Dallas	10/50 (20%)
Eimeria streckeri	Dallas	16/50 (32%)
Isospora delicatus	Dallas	5/50 (10%)
Gastrophryne olivacea:		
*Isospora fragosum**	Hood	6/46 (13%)
	Johnson	3/9 (33%)
	Somervell	10/71 (14%)

*Originally reported by McAllister and Upton (1987b) as an *Isospora neos*-like coccidium.

Measurements of oocysts and sporocysts of coccidia recovered were compared with those obtained previously by researchers on other anuran coccidia. Since measurements did not match any of the previously described species, 4 new species of Coccidia were found and described. Below are descriptions of each of these species.

Eimeria flexuosa Upton and McAllister, 1988

(Fig. 8A)

Description: Oocysts irregular in shape, 17.0 (15.2-19.2) (long axis), with a thin, single-layered wall ca. 0.5 thick that encloses the sporocysts tightly. Micropyle and oocyst residuum absent; 1 (rarely more) polar granule(s) present, ca. 1.6-2.5 in diameter. Sporocysts ovoid, 10.3 x 7.3 (9.6-12.0 x 6.4-8.0), with a smooth, thin wall ca. 0.4 thick; shape index (length/width) 1.4 (1.3-1.6). One end of the sporocyst is thickened slightly to form an indistinct Stieda body; substieda body absent. Sporocyst residuum present, 6.6 x 5.1 (4.8-8.0 x 4.0-6.4), composed of numerous coarse granules up to 2.5 in diameter. Occasionally the residuum is diffuse. Sporozoites elongate, 9.4 x 2.4 (8.0-10.4 x 2.0-3.2) *in situ*, each with 2 refractile bodies. Anteriocentral refractile body spherical, rarely subspherical, 2.0 (1.4-3.2) in diameter; posterior refractile body spherical, 1.7 (1.2-2.4) in diameter. An indistinct nucleus is located between the refractile bodies.

Type host: *Pseudacris streckeri streckeri* Wright and Wright, 1933, Strecker's chorus frog (Anura: Hylidae), adult male, ASUMZ 8694.

Type locality: USA, Texas, Dallas County, 2.4 km W DeSoto off FM 1382 on Ellerson Road.

Prevalence: 10/50 (20%) were infected; 0/15 (0%) immatures, 10/35 (28.6%) adults.

Site of infection: Intestine.

Sporulation: Endogenous.

Etymology: The specific epithet reflects the flexibility of the oocyst wall.

Remarks: Only 2 other named species of anuran Eimeria, E. neglecta Nöller, 1920, and E. ranae (Dobell, 1908) Dobell, 1909, are described as having oocyst walls thin enough to adhere to the sporocysts and, thus, produce irregularly shaped oocysts. Eimeria flexuosa is distinguished from E. neglecta by its larger oocysts and sporocysts; those of the latter species measuring 9-10 µm in diameter and 7 x 3.5-4.0 µm, respectively. Although oocysts and sporocysts of E. ranae are similar in size to the form described here, the absence of an oocyst residuum is a distinctive feature that distinguishes E. flexuosa from E. ranae.

Eimeria streckeri Upton and McAllister, 1988

(Fig. 8B)

Description: Oocysts spherical, rarely subspherical, 18.8 x 18.7 (16.8-21.5 x 16.8-20.8), with a smooth, thin, single-layered wall ca. 0.7 thick; shape index 1.0 (1.0-1.1). Micropyle absent; polar granule normally absent, although one may be found rarely.

Spherical oocyst residuum present, 8.0 (6.4-11.2), composed of numerous coarse granules surrounding a large vacuolated or globular area. Sporocysts ovoid, 11.1 x 7.7 (9.6-12.8 x 7.2-8.8), with a smooth, thin wall ca. 0.4 thick; shape index 1.5 (1.2-1.7). One end of the sporocyst is thickened slightly to form an indistinct Stieda body; substieda body absent. Sporocyst residuum present, 6.6 x 5.7 (4.8-8.0 x 4.0-7.2), consisting of an aggregate of granules bound by a limiting membrane. Additional granules are often found scattered free amoung the sporozoites. Sporozoites elongate, 11.0 x 2.6 (9.6-12.8 x 1.8-3.2) in situ, each with two refractile bodies. Spherical or ovoid anterio-central refractile body, 2.2 long x 2.0 wide (1.2-3.2 x 1.2-2.4); posterior refractile body spherical, 1.6 (0.8-2.4). An indistinct nucleus is located between the refractile bodies.

Type host: Pseudacris streckeri streckeri Wright and Wright, 1933, Strecker's chorus frog (Anura: Hylidae), adult male, ASUMZ 8684.

Type locality: USA, Texas, Dallas County, 2.4 km W DeSoto off FM 1382 on Ellerson Road.

Prevalence: 16/50 (32%) were infected; 0/15 (0%) immatures, 16/35 (45.7%) adults.

Site of infection: Intestine.

Sporulation: Endogenous.

Etymology: The specific epithet reflects that of the host species.

Remarks: Over one-half of the species of Eimeria from anurans have spherical or subspherical oocysts (see Upton and McAllister, 1988a). Of these, only 3 species, E. cyanophyctis Chakravarty and Kar, 1944, E. leptodactyli Carini, 1931, and E. prevoti (Laveran and Mesnil, 1902) Doflein, 1909, possess an oocyst residuum. Eimeria streckeri can be distinguished from E. cyanophyctis by its more spherical oocysts and sporocysts and because a sporocyst residuum is present; from E. leptodactyli by its smaller and more spherical oocysts and larger sporocysts; and from E. prevoti by its more spherical shape and much larger oocyst residuum.

Isospora delicatus Upton and McAllister, 1988

(Fig. 8C)

Description: Oocysts spherical, rarely subspherical, 15.8 x 15.7 (12.8-16.8 x 12.8-16.8), with a smooth, thin, single-layered wall ca. 0.6 thick; shape index 1.0 (1.0-1.1). Micropyle, oocyst residuum, and polar granule absent. Sporocysts ovoid, 13.5 x 8.0 (11.2-14.8 x 7.2-9.6), with a smooth, thin wall ca. 0.4 thick; shape index 1.7 (1.5-1.8). Large Stieda body present at one end of the sporocyst; the opposite end

tapers markedly, often forming a distinct point; substieda body absent. Sporocyst residuum present, composed of numerous coarse granules scattered among the sporozoites. Sporozoites elongate, 11.9 x 2.4 (9.6-13.6 x 2.0-2.8) in situ, each with 2 refractile bodies. Anterior refractile body spherical, 1.8 (1.0-2.4) in diameter; posterior refractile body spherical, 2.0 (0.8-2.8) in diameter. An indistinct nucleus is located between the refractile bodies.

Type host: Pseudacris streckeri streckeri Wright and Wright, 1933, Strecker's chorus frog (Anura: Hylidae), adult male, ASUMZ 8696.

Type locality: USA, Texas, Dallas County, 2.4 km W DeSoto off FM 1382 on Ellerson Road.

Prevalence: 5/50 (10%) were infected; 0/15 (0%) immatures, 5/35 (14.3%) adults.

Site of infection: Intestine.

Sporulation: Endogenous.

Etymology: The specific epithet reflects the thin oocyst wall of this species.

Remarks: Of the species of Isospora infecting anurans, only I. wenyoni has oocysts that are similar in size to I. delicatus n. sp. However, oocysts of the new species are more spherical and the sporocysts larger. In addition, no other species of anuran Isospora is reported to have the large and obvious Stieda body, and

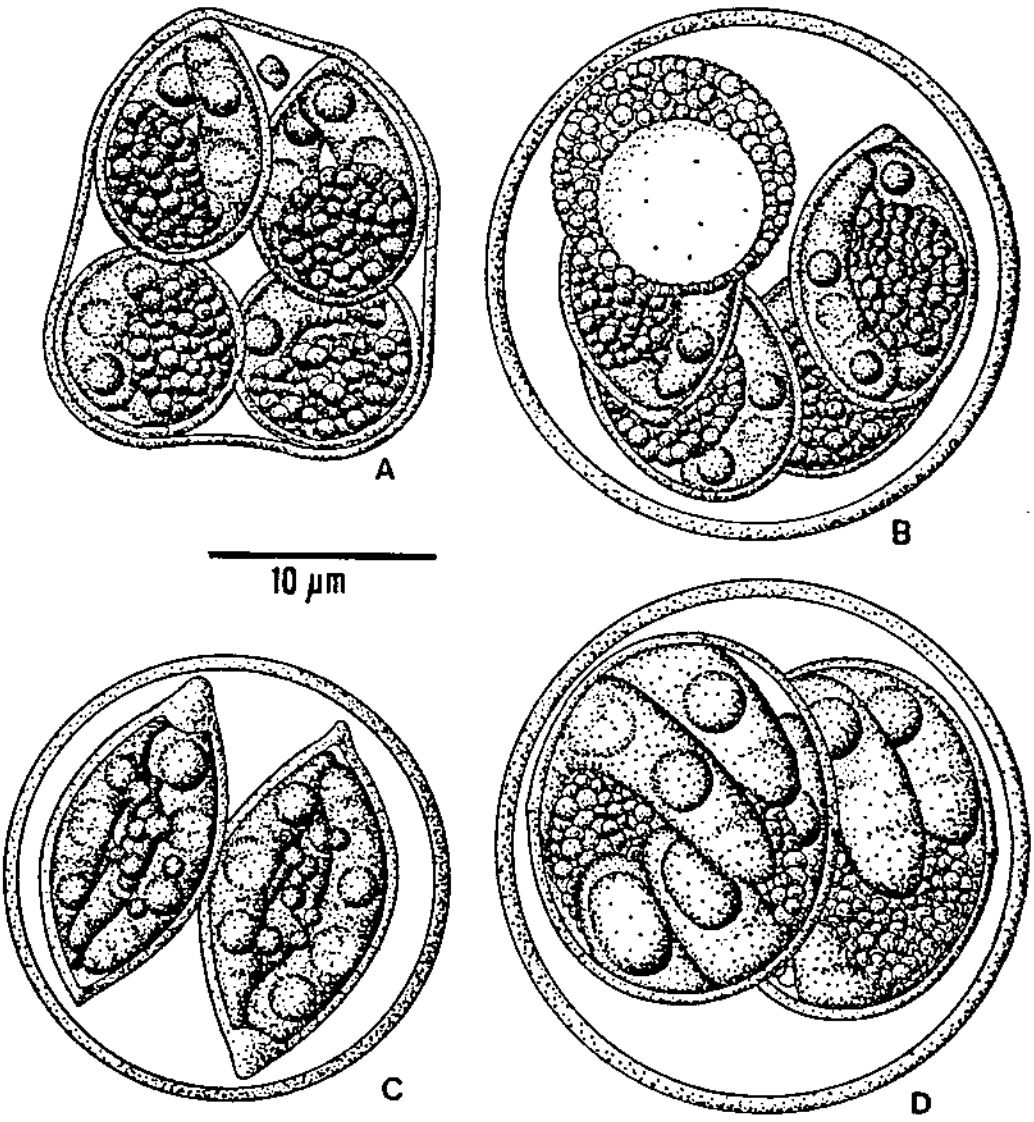
accentuated posterior end of the sporocysts, diagnostic for I. delicatus.

Isospora fragosum Upton and McAllister, 1988

(Fig. 8D)

Description: Oocysts spherical, 18.5 (17.6-20.8), with a smooth, thin, single-layered wall ca. 0.8 thick that ruptures 1-3 days after sporulation releasing free sporocysts. Micropyle, polar granule, and oocyst residuum absent. Sporocysts ovoid, 12.7 x 10.9 (11.2-14.4 x 9.6-12.0), with a smooth, thin wall ca. 0.4 thick; shape index 1.2 (1.1-1.3); Stieda and substieda bodies absent. Rarely, slight thickenings may be observed at opposite ends and at the sides of the sporocysts suggesting presence of sutures. Coarsely granular, spherical or ovoid sporocyst residuum present, 7.9 x 6.9 (4.8-11.2 x 4.8-10.4). Sporozoites elongate, 12.6 x 3.4 (12.0-14.4 x 3.0-4.0) in situ, arranged so that 2 sporozoites lie in one direction while the other 2 lie in the opposite direction. Each sporozoite contains a spherical anterior refractile body, 2.3 (1.2-22.4), and a spherical or ovoid posterior refractile body, 3.0 x 2.3 (2.4-3.6 x 1.6-2.8). The refractile bodies are often obscured in the intact oocyst by the sporocyst residuum. However, they are seen more easily once the sporocysts have been liberated

FIGURES 8A-D. Composite line drawings of sporulated oocysts of 4 new species of Coccidia found in anurans from Texas. Fig. 8A. Eimeria flexuosa Upton and McAllister, 1988 from Pseudacris s. streckeri. Fig. 8B. Eimeria streckeri Upton and McAllister, 1988 from P. s. streckeri. Fig. 8C. Isospora delicatus Upton and McAllister, 1988 from P. s. streckeri. Fig. 8D. Isospora fragosum Upton and McAllister, 1988 from Gastrophryne olivacea.



8

from the oocyst wall. A nucleus is located between the refractile bodies.

Type host: Gastrophryne olivacea (Hallowell, 1856), Great Plains narrowmouth toad (Anura: Microhylidae), adult male, ASUMZ 5900.

Type locality: USA, Texas, Somervell County, 1.6 km SW Nemo off FM 200 on county road 402.

Other localities: USA, Texas, Hood County, 19.3 km SE Granbury off FM 2174 at Russell Ranch; and Johnson County, 1.6 km E junction Somervell County roads 406 and 407 at Ken Fry Ranch.

Prevalence: 19/126 (15.1%) were infected; 0/18 (0%) immatures, 19/108 (17.6%) adults. By month: February (0%), March (57.1%), April (26.7%), May (15.6%), June-July (3.1%), September-October (20.8%) (Fig. 9).

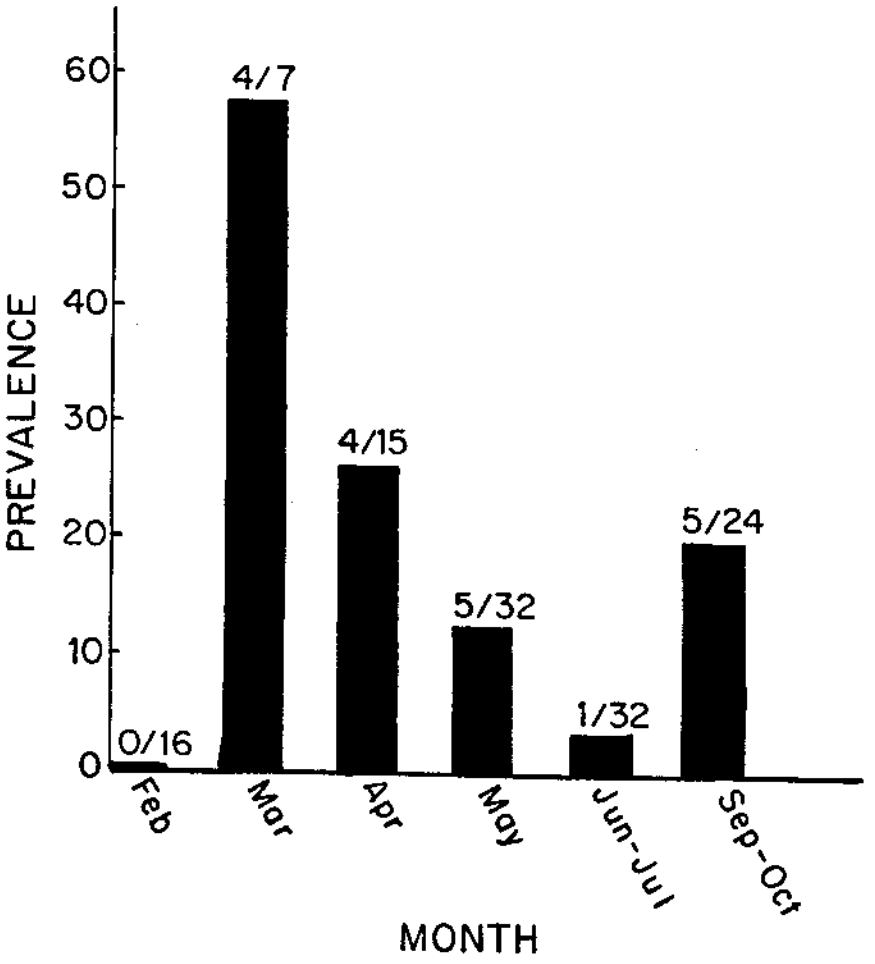
Site of infection: Unknown. Oocysts were recovered from the feces.

Sporulation: Oocysts recovered from the feces were unsporulated, partially sporulated, or (rarely) fully sporulated.

Etymology: The specific epithet reflects the delicate nature of the oocyst wall.

Preference: No preference for host sex was demonstrated for this parasite (X^2 = 0.69, 1 df, $p > 0.99$) as 19.3% of the males and 14.0% of the females

FIGURE 9. Seasonal prevalence of *Isospora fragosum* Upton and McAllister, 1988 in *Gastrophryne olivacea*. Numbers above bars are number infected/number examined.


PREVALENCE
60
50
40
30
20
10
0
4/7
4/15
5/32
1/32
5/24
0/16
Feb
Mar
Apr
May
Jun-Jul
Sep-Oct
MONTH

harbored I. fragosum (Fig. 10).

Remarks: Of the isosporans infecting anurans, I. fragosum n. sp. most closely resembles I. neos Yakimoff and Gousseff, 1936, infecting Rana arvalis in the Soviet Union. However, oocysts of I. fragosum are smaller and a large and highly distinctive sporocyst residuum is present. Kazubski and Grabda-Kazubska (1973) reported an isosporan from R. arvalis in Poland that is slightly larger, although similar to the form described herein; including the presence of a sporocyst residuum. Even though Yakinoff and Gousseff (1936) stated specifically that I. neos lacked a sporocyst residuum, the former authors referred to the form they found as I. neos because, according to Kheysin (1967; from Kazubski and Grabda-Kazubska, 1973, original not seen), the sporocyst residuum is used to provide nutrition to the sporozoites (and, thus, may disappear). Since this hypothesis seems unlikely, it is very possible that the isosporan they reported is also a species separate from I. neos.

Testudines

Five of 7 (71.4%) taxa within 3 families of turtles were infected with 1 or more species of coccidia. Combined prevalence of infection with at least 1 coccidian for all turtles was 68/125 (54.4%) (Table IV).

FIGURE 10. Preference of Isospora fragosum Upton and McAllister, 1988 for host sex among 126 Gastrophryne olivacea. Numbers above bars are number infected/number examined.

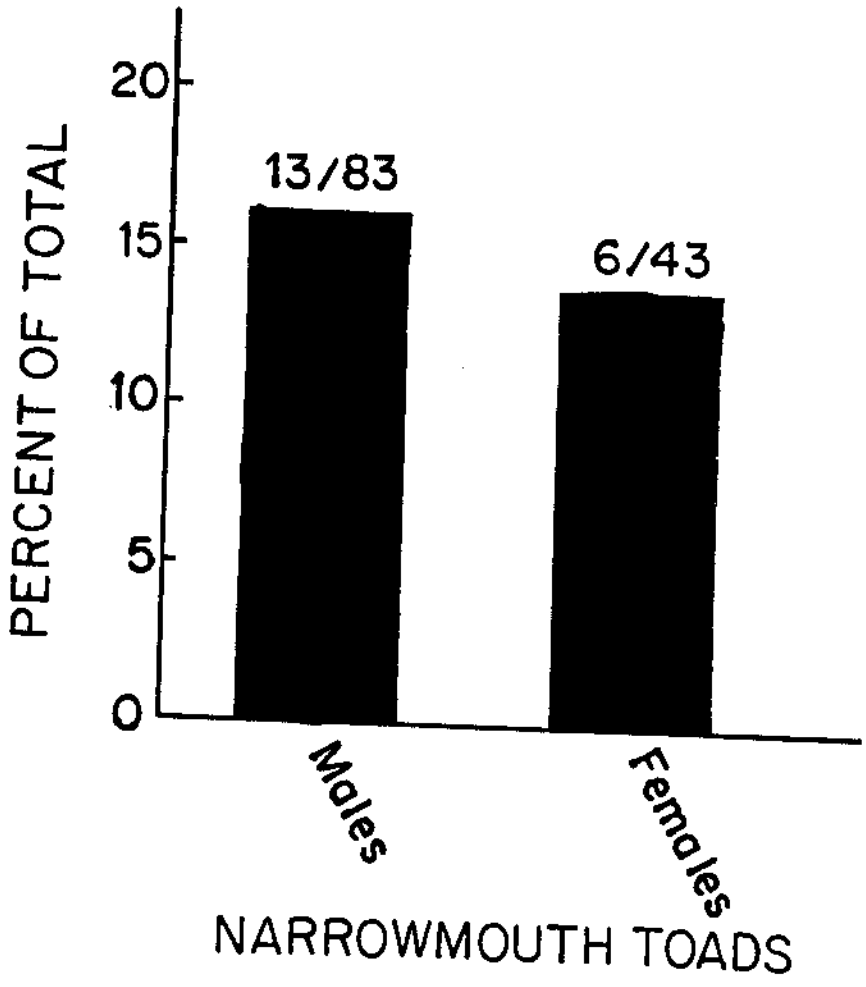

PERCENT OF TOTAL
20
15
10
5
0
13/83
6/43
Males
Females
NARROWMOUTH TOADS

TABLE IV. Species and individual prevalence data for Testudines examined for coccidia (arranged in phylogenetic order).

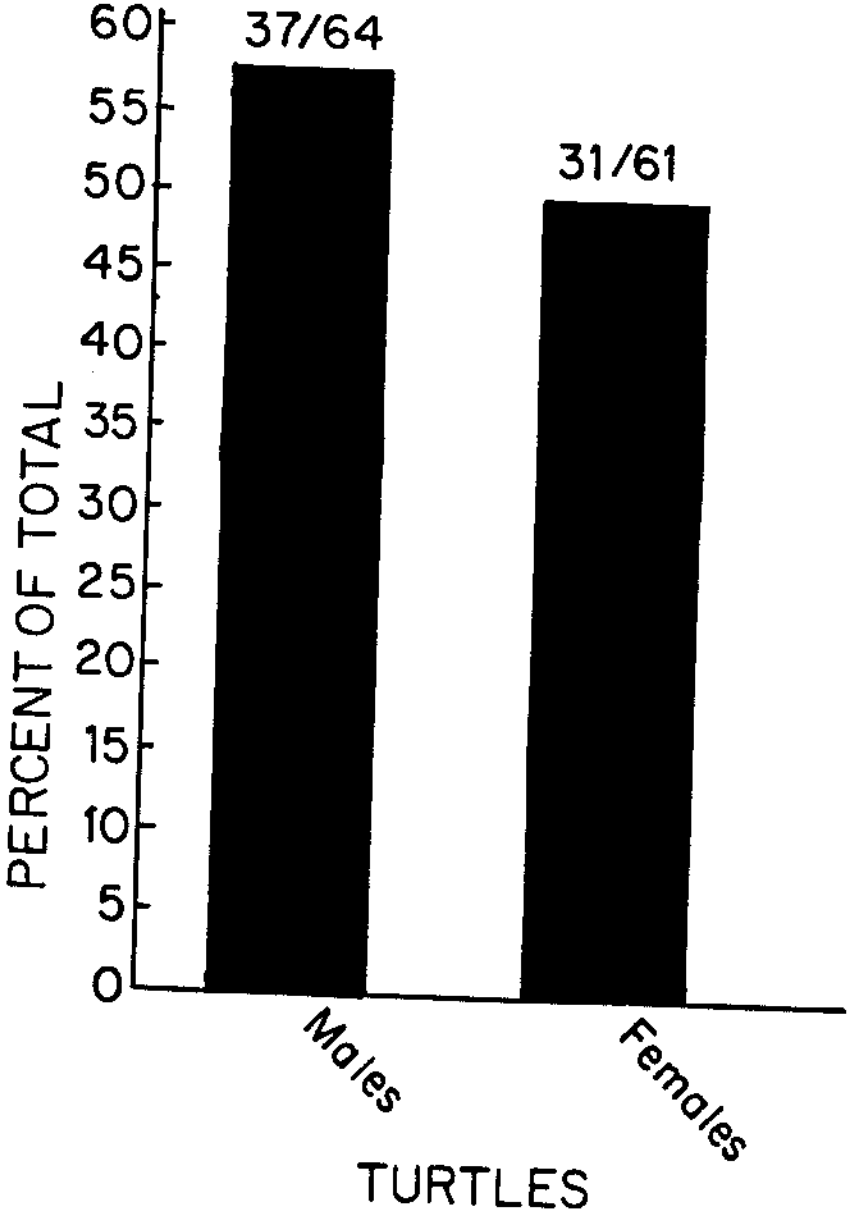
Host family/species	Prevalence
Chelydridae	
Chelydra s. serpentina	3/3 (100%)*
Kinosternidae	
Kinosternon f. flavescens	2/11 (18%)
Emydidae	
Pseudemys texana	4/8 (50%)
Terrapene carolina triunguis	0/1 (0%)
Terrapene o. ornata	6/16 (38%)
Trachemys scripta elegans	53/85 (62%)
Trionychidae	
Apalone spinifera pallidus	0/1 (0%)

*Oocysts were not completely sporulated, therefore, specific identification was impossible.

There was no sexual preference of coccidians among the 5 host turtles (X^2 = 0.37, 1 df, $p > 0.55$) as 57.8% of the males and 50.5% of the females were infected (Fig. 11).

A total of 14 eimerians (2 unknown, 5 new and 7

FIGURE 11. Preference of coccidia for host sex among 125 turtles. Numbers above bars are number infected/number examined.


60
55
50
45
40
35
30
25
20
15
10
5
0
PERCENT OF TOTAL
37/64
31/61
Males
Females
TURTLES

named species) were found in 68 turtles (Table V). Of the 5 turtle taxa, parasite diversity was highest in the red-eared slider, Trachemys scripta elegans. Fifty-three T. s. elegans harbored a total of 11 eimerians, including 9 previously described and 2 new species (Table V).

TABLE V. Eimerians recovered from Testudines in various counties of northcentral Texas*.

Host/Eimeria spp.	County	Prevalence
Chelydra s. serpentina:		
Eimeria sp. A	Johnson	2/3 (67%)
Eimeria sp. B	Johnson	1/3 (33%)
Kinosternon f. flavescens:		
graptemydos	Johnson	2/5 (40%)
lutotestudinis	Johnson	1/5 (20%)
mitraria	Johnson	1/5 (20%)
Pseudemys texana:		
cooteri	Johnson	2/6 (33%)
	Somervell	1/2 (50%)
lutotestudinis	Somervell	1/2 (50%)
mitraria	Johnson	2/6 (33%)
texana	Johnson	1/6 (17%)
	Somervell	1/2 (50%)

Table V (con't)

pseudemydis	Johnson	1/6 (17%)
Terrapene o. ornata:		
ornata	Ellis	2/3 (67%)
	Johnson	3/12 (25%)
	Somervell	1/1 (100%)
Trachemys scripta elegans:		
chrysemydis	Dallas	2/24 (8%)
	Johnson	1/44 (2%)
graptemydos	Dallas	5/24 (21%)
	Hood	3/13 (23%)
	Johnson	15/44 (34%)
lutotestudinis	Dallas	10/24 (42%)
	Denton	1/1 (100%)
	Johnson	14/44 (32%)
marginata	Hood	1/13 (8%)
	Johnson	10/44 (23%)
mitraria	Dallas	5/24 (21%)
	Denton	1/1 (100%)
	Hood	2/13 (15%)
	Johnson	12/44 (28%)
pseudogeographica	Dallas	4/24 (17%)
	Hood	1/13 (8%)
	Johnson	5/44 (11%)
pseudemydis	Dallas	7/24 (29%)
	Johnson	3/44 (7%)

Table V (con't)

scriptae	Dallas	1/24 (4%)
	Johnson	1/44 (2%)
stylosa	Johnson	2/44 (5%)
tetradacrutata	Hood	1/13 (8%)
trachemydis	Dallas	3/24 (13%)
	Johnson	2/44 (5%)
	Somervell	1/3 (33%)

*Counties with hosts not harboring a particular species of coccidia not listed.

Of the 53 infected sliders, 19 (35.8%) harbored a single species, 15 (28.3%) had 2 species, 16 (30.2%) was infected with 3 species, 2 (3.8%) harbored 4 species, and 1 (1.9%) had 6 species. The 3 most common eimerians recovered from infected sliders were Eimeria lutotestudinis (47.2%), E. graptemydos (43.4%), and E. mitraria (37.7%). The least common eimerian was E. tetradacrutata, which was recovered from only 1 (1.9%) infected turtle.

Of the other 4 turtle hosts, 50% of the Texas cooters, Pseudemys texana were infected with 5 species of Eimeria, 2 yellow mud turtles, Kinosternon f. flavescens harbored 3 previously described eimerians, and 6 of the ornate box turtles, Terrapene o. ornata were infected with a single species of Eimeria.

Spherical oocysts of an unknown species of Eimeria (designated sp. A) measuring 12.4 µm were harbored by 2/3 (67%) common snapping turtles, Chelydra s. serpentina from Johnson County. Partially sporulated oocysts did not possess an oocyst residuum; however, a single sporocyst measured 8.8 x 5.6 µm. Oocysts were similar to E. chelydrae Ernst et al., 1969, from C. s. serpentina in Georgia. In addition, a single sporulated oocyst of an unknown eimerian (designated Eimeria sp. B) was found in 2 C. s. serpentina; other oocysts were present but never fully sporulated. The oocyst was ovoid, measured ca. 13 x 9 µm, and did not possess either a polar granule or oocyst residuum. This species may represent the unnamed eimerian of Wacha and Christiansen (1980) from C. s. serpentina in Iowa.

Comparisons were made with measurements of other coccidians previously reported from other turtles. Below are descriptions of the new forms that were observed.

Eimeria texana n. sp. McAllister and Upton, 1989

(Fig. 12A)

Description: Oocyst bent sausage-shaped or elongate, 20.5 x 8.4 (17.6-23.2 x 7.2-9.0) (n=30), with a smooth, thin, single-layered wall, ca. 0.4 thick; when in sucrose solution, often dumb-bell shaped and

concavity exaggerated; shape index (length/width) 2.4 (2.0-3.1). A single ellipsoidal polar granule, 0.8 diameter (0.6-1.2) (n=25) when not fragmented, attached to inner surface of oocyst wall; micropyle absent. An oocyst residuum is present, 4.3 x 3.9 (3.0-6.4 x 3.0-6.4) (n=29), consisting of a thin membrane bound cluster of granules or rarely scattered throughout oocyst; intact residual granules usually enclose a large vacuolated area. Sporocysts ovoid, 8.1 x 4.7 (7.0-8.8 x 4.0-5.4) (n=30), with a smooth, thin, single-layered wall ca. 0.2 thick; shape index 1.7 (1.5-2.0). Stieda body unremarkable, present at 1 end of sporocyst, consisting of region made up by simple point; substieda body absent. Sporocyst residuum present, 1.9 x 1.9 (1.4-2.4 x 1.4-2.4) (n=29), composed of a cluster of small granules, usually not membrane bound. Sporozoites elongate, 7.3 x 2.2 (6.4-8.0 x 1.8-2.4) (n=30) in situ, arranged head-to-tail within the sporocyst. Each sporozoite contains a spherical or ovoid anterior refractile body, 1.8 wide x 1.9 long (1.0-2.2 x 1.0-2.4), and a posterior spherical refractile body, 2.0 wide x 2.5 long (1.8-2.4 x 1.8-3.2). A nucleus lies between the refractile bodies.

Type host: Pseudemys texana Baur, 1893, Texas cooter (Testudines: Emydidae), adult male, ASUMZ 11749.

Type locality: USA, Texas, Johnson County, 19.5 km

SW Cleburne off U.S. 67 on county road 1120 at Georges Creek.

Other localities: USA, Texas, Somervell County, 14.5 km NW Glen Rose off county road 308 at Georges Creek.

Sporulation: Endogenous. Oocysts recovered from feces and intestinal contents were fully sporulated.

Site of infection: Unknown. Oocysts were recovered from fecal and intestinal contents.

Prevalence: 2/8 (25%) of the turtles were infected; 1/6 (16.7%) Johnson County, 1/2 (50%) Somervell County.

Etymology: The specific epithet is derived from the scientific name of the host species.

Remarks: Eimeria texana is most similar to Eimeria pseudogeographica Wacha and Christiansen, 1976, from 3/8 (37.5%) false map turtles, Graptemys pseudogeographica (Gray) and 5/22 (22.7%) western painted turtles, Chrysemys picta bellii (Gray) in Iowa. However, the new form may be distinguished from E. pseudogeographica by having a narrower oocyst, much larger shape index (2.4 vs 1.4), smaller sporocysts, and a smaller sporocyst residuum.

Eimeria cooteri McAllister and Upton, 1989

(Fig. 12B)

Description: Oocyst ellipsoidal top view or bent sausage-shaped side view, 25.9 x 10.9 (thickest width) (22.6-28.0 x 9.6-12.8) (n=30), center width, 10.5 (8.6-12.8), with a smooth, thin, single-layered wall, ca. 0.4 thick; shape index (length/width) 2.4 (1.9-2.9). A single elongate polar granule, 0.9 in diameter (0.6-1.6) (n=24), when not fragmented, attached to inner surface of oocyst wall; micropyle absent. An oocyst residuum is present, 8.6 x 5.8 (5.6-12.0 x 3.2-9.6) (n=29), consisting of a loose aggregate of granules, without membranes or rarely scattered throughout the oocyst; intact residual granules usually enclose a vacuolated area. Sporocysts elongate, 14.9 x 5.3 (12.8-16.0 x 4.8-6.6) (n=30), with a smooth, thin, single-layered wall, ca. 0.2 thick; shape index 2.8 (2.2-3.3). Stieda body elongate, consisting of elongate structures ca. 1.4-2.0 long, with tiny knob-like thickenings at the ends covered by a thin membrane; substieda body absent. Sporocyst residuum present, 2.3 x 2.2 (1.6-4.0 x 1.6-4.0) (n=29), in loose aggregate, not membrane bound. Sporozoites elongate, 11.8 x 2.6 (9.6-14.4 x 2.2-3.2) (n=30) in situ, arranged head-to-tail within the sporocyst. Each sporozoite contains a subspherical or ovoid anterior refractile

body, 2.2 wide x 2.3 long (1.8-2.6 x 1.8-3.2), and a spherical posterior refractile body, 2.4 wide x 3.7 long (2.2-3.0 x 2.6-4.8). A nucleus lies between the refractile bodies.

Type host: Pseudemys texana Baur, 1893, Texas cooter (Testudines: Emydidae) ASUMZ 11749.

Type locality: USA, Texas, Johnson County, 19.5 km SW Cleburne off U.S. 67 on county road 1120 at Georges Creek.

Other localities: USA, Texas, Somervell County, 14.5 km NW Glen Rose off county road 308 at Georges Creek, and 12.5 km SW Cleburne on U.S. 67, Johnson County.

Sporulation: Endogenous. Oocysts recovered from feces and intestinal contents were fully sporulated.

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

Prevalence: 3/8 (37.5%) of the turtles were infected; 2/6 (33.3%) Johnson County, 1/2 (50.0%) Somervell County.

Etymology: The specific epithet is derived from the common name of the host.

Remarks: Eimeria cooteri is most similar to Eimeria trachemydis McAllister and Upton, 1988 from 3/71 (4.2%) red-eared sliders, Trachemys scripta elegans (Wied) in Dallas County, Texas and Eimeria texana

described from P. texana. The new species differs from E. trachemydis by having a narrower oocyst, a longer oocyst residuum, and by not possessing filaments at the ends of the Stieda body, and from E. texana by its larger size, more elongate sporocysts, and lack of Stieda body ornamentation.

Eimeria stylosa McAllister and Upton, 1989

(Fig. 12C)

Description: Oocyst ovoid, composed of a smooth-colorless, single-layered wall ca. 0.8 thick. Each end of the oocyst bears conical projections ca. 4.0 (3.0-5.0) long. Most oocysts possess two projections on one end and three on the opposite end of the oocyst wall; however, 3 specimens with 2 and 2, 2 with 4 and 2, and 1 with 4 and 7 were observed. Oocysts (excluding length of projections) measured 16.5 x 13.1 (14.4-17.6 x 12.0-14.4) (n=25); shape index (length/width) 1.3 (1.2-1.5). Micropyle, oocyst residuum, and polar granule absent. Sporocysts ellipsoid, 11.1 x 5.8 (9.6-14.4 x 5.4-7.2) (n=25), with a smooth, thin, colorless wall ca. 0.2-0.4 thick; shape index highly variable, 1.9 (1.6-2.6); mode=1.9. Small Stieda body present; substieda body absent. Spherical, ovoid, or (rarely) scattered sporocyst residuum present, 4.0 x 3.4 (2.8-6.4 x 2.8-4.8) (n=19). Sporozoites elongate, 9.4 x

2.8 (8.8-10.4 x 2.4-3.2) (n=25), arranged head-to-tail within the sporocyst and reflected along opposite poles. Each sporozoite contains a spherical anterior refractile body, 1.9 (1.8-2.2), and two larger spherical or subspherical, posterior refractile bodies that are similar in size, 2.5 wide x 3.0 long (2.2-3.2 x 2.2-4.0). A nucleus is located between the anterior refractile body and the more centrally located of the posterior refractile bodies.

Type host: Trachemys scripta elegans (Wied, 1838), red-eared slider (Testudines: Emydidae), adult female, ASUMZ 8493.

Type locality: USA, Texas, Johnson County, 13.0 km SSW Cleburne on U.S. 67.

Other locality: USA, Texas, Johnson County, 19.0 km SW Cleburne off U.S. 67 on county road 1120 at Georges Creek.

Sporulation: Endogenous. Oocysts recovered from feces or intestinal contents were fully sporulated.

Site of infection: Unknown. Oocysts were recovered from fecal and intestinal contents.

Prevalence: 2/85 (2.4%) T. s. elegans were infected; 0/1 (0%) Coleman County, 0/24 (0%) Dallas County, 0/1 (0%) Denton County, 0/13 (0%) Hood County, 2/45 (2.4%) Johnson County, 0/3 (0%) Somervell County.

Etymology: The specific epithet reflects the

stylet-like projections on the oocyst.

Remarks: Eimeria stylosa most closely resembles Eimeria mitraria (Laveran and Mesnil, 1902) Doflein, 1909, because of the ornate projections on the oocyst wall. However, oocysts of E. mitraria are smaller and possess fewer and shorter projections than the form describe herein as new (see Laveran and Mesnil, 1902; Deeds and Jahn, 1939; Wacha and Christiansen, 1976). Wacha and Christiansen (1976) also reported an Eimeria sp. in 1/2 (50%) map turtles, Graptemys geographica (LeSueur, 1817) with similar morphologic characteristics as those reported here. They measured a single oocyst, which was slightly larger than E. stylosa and possessed only 2 projections at either end of the oocyst. The authors also noted a personal communication with Dr. Leon W. Bone, then at the University of Arkansas, who observed oocysts in Barbour's map turtle, Graptemys barbouri Carr and Marchand, 1942 from an unknown locality in the southeastern United States (Bone, pers. comm.) of similar size and shape to the new species. Although only 2 projections are mentioned at either end of the oocyst and sporulation was incomplete, 50 unsporulated oocysts measured 18.6 (17.6-21.1) x 14.4 (14.1-15.7) µm; similar, but larger than E. stylosa.

Eimeria trachemydis McAllister and Upton, 1988

(Fig. 12D)

Oocyst ellipsoid, 25.0 x 13.6 (20.8-30.4 x 12.0-16.0), with a smooth, thin, apparently single-layered wall, ca. 0.6 thick; shape index 1.8 (1.5-2.2). A single ellipsoidal-spherical polar granule (1.6-1.8) is usually present at 1 pole, attached to inner surface of oocyst wall; micropyle absent. An oocyst residuum is present, 6.8 x 6.0 (4.0-10.4 x 3.2-9.6) (n=18), consisting either of a loose cluster of granules or scattered throughout the oocyst; intact residual granules usually enclose a large vacuolated area. Sporocysts elongate, 14.4 x 5.6 (12.8-16.0 x 5.0-6.4), with a smooth, thin, single-layered wall, ca. 0.4 thick; shape index 2.6 (2.3-2.9). Stieda body present at one end of sporocyst, consisting of a slightly flattened region (ca. 1.6 wide) of the wall thickened to 0.6 with stalks bearing 2-5 filaments/sporocyst 6.0-10.0 long; substieda body absent. Sporocyst residuum present, 4.0 x 3.0 (2.4-9.6 x 1.8-4.0) (n=29), in cluster, not membrane bound. Sporozoites elongate, 12.2 x 2.7 (11.2-14.4 x 2.4-3.2) in situ, arranged head-to-tail within the sporocyst. Each sporozoite contains a spherical or ellipsoidal anterior refractile body, 2.4 wide x 2.7 long (1.8-3.0 x 2.4-3.2), and a mid-posterior spherical refractile body,

2.5 wide x 3.5 long (2.0-3.0 x 2.4-5.6). A nucleus lies between the refractile bodies.

Type host: Trachemys scripta elegans (Wied, 1838) Red-eared slider (Testudines: Emydidae), adult male, ASUMZ 8475, adult female, ASUMZ 8493, adult male, ASUMZ 8553).

Type locality: USA, Texas, Dallas County, DeSoto, 1.6 km S I-20 on Bolton Boone Drive at Terrell Pond.

Prevalence: 6/85 (7.1%) of the turtles were infected; 3/24 (12.5%) Dallas County, 0/1 (0%) Denton County, 0/13 (0%) Hood County, 0/44 (0%) Johnson County, 1/3 (33.3%) Somervell County.

Site of infection: Unknown. Oocysts found in feces and intestinal contents.

Sporulation: Endogenous. Oocysts were passed fully sporulated.

Etymology: The specific epithet is derived from the generic name of the host.

Remarks: Eimeria trachemydis most closely resembles E. filamentifera Wacha and Christiansen, 1979, from the common snapping turtle, Chelydra serpentina serpentina (Linnaeus), in Iowa, due to the presence of filaments at the end of the Stieda body. However, oocysts of E. filamentifera are wider and only slightly ovoid to ellipsoid, possess much shorter filaments, and lacks a polar granule. The differences in these characteristics

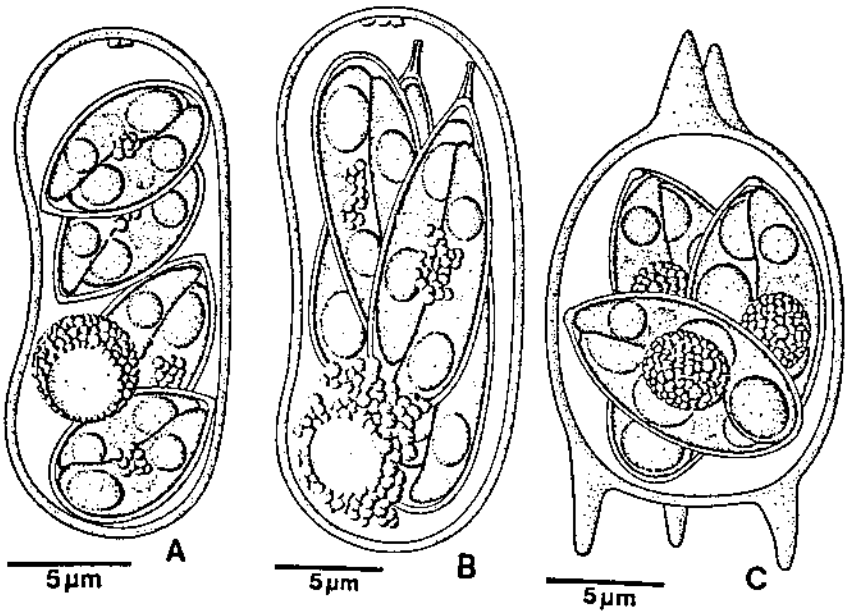
easily distinguishes the form described here as new from E. filamentifera. In addition, the new species does not resemble any of the remaining 30+ eimerians from turtles (see Labbé, 1893; Simond, 1901; Laveran and Mesnil, 1902; Cerruti, 1930; Roudabush, 1937; Das Gupta, 1938; Deeds and Jahn, 1939; Carini, 1942; Chakravarty and Kar, 1943; Kar, 1944; Lainson, 1968; Sampson and Ernst, 1969; Ernst et al., 1969, 1971; Ernst and Forrester, 1973; Wacha and Christiansen, 1974a, 1976, 1977, 1979; Bone, 1975; Pluto and Rothenbacher, 1976; Ovezmukhammedov, 1978; McAllister and Upton, 1989a, c).

Eimeria ornata McAllister and Upton, 1989

(Fig. 12E)

Description: Oocysts ovoid to ellipsoid, 17.9 x 15.7 (16-21 x 14-18), with a thin, single-layered wall about 1.0 thick; shape index (length/width) 1.14 (1.0-1.3). Micropyle absent; polar granule present in 10/30 (33.3%) of the oocysts. Oocyst residuum present, consisting either as an aggregate of numerous small globules and (usually) a large, clear vacuolated area situated along one side of the oocyst or, occasionally, as diffuse granules scattered throughout the oocyst. Sporocysts elongate, 11.1 x 5.4 (9-13 x 5-6), with a smooth, thin wall; shape index 2.1 (1.7-2.3). One pole of the sporocyst tapers gently to form an indistinct

FIGURES 12A-E. Composite line drawings of sporulated oocysts of 5 new species of Eimeria found in Testudines from Texas. Fig. 12A. Eimeria texana McAllister and Upton, 1989 from Pseudemys texana. Fig. 12B. Eimeria cooteri McAllister and Upton, 1989 from P. texana. Fig. 12C. Eimeria styloga McAllister and Upton, 1989 from Trachemys scripta elegans. Fig. 12D. Eimeria trachemydis McAllister and Upton, 1988 from T. s. elegans. Fig. 12E. Eimeria ornata McAllister and Upton, 1989 from Terrapene o. ornata.



12

Stieda body; substieda body absent. Sporocyst residuum present, consisting either as a compact mass of granules, 3.6 x 2.6 (2-6 x 2-4) or as loose granules scattered among the sporozoites. Sporozoites elongate, 9.5 x 2.0 (8-12 x 1.6-2.4), in situ, arranged head-to-tail within the sporocyst. Spherical anterior and posterior refractile bodies present, 1.5 (1-2) and 1.8 (1.6-2.4), respectively. A nucleus is situated between the refractile bodies.

Type host: Terrapene ornata ornata (Agassiz, 1857), Ornate box turtle (Testudines: Emydidae), ASUMZ 8490, 8600.

Site of infection: Unknown. Oocysts found in feces.

Sporulation: Endogenous. Oocysts passed fully sporulated.

Type locality: USA, Texas, Ellis County, 6.4 km SW Midlothian at Ward Spur along Soap Creek.

Prevalence: 6/16 (37.5%) of the turtles from northcentral Texas were passing oocysts; 2/3 (66.7%) Ellis County, 3/12 (25%) Johnson County, and 1/1 (100%) Somervell County.

Etymology: The specific epithet is derived from the specific name of the host.

Remarks: Oocysts of Eimeria ornata n. sp. are similar to several eimerians known to infect turtles.

These species include: E. amydae Roudabush, 1937, from the western spiny softshell, Apalone (=Trionyx) spiniferus hartwegi (Conant and Goin, 1948) in Iowa; E. pseudemydis Lainson, 1968, from the beautiful turtle, Pseudemys ornata (Gray, 1845) in Belize and red-eared slider, Pseudemys (=Trachemys) scripta elegans (Wied, 1838) in Arkansas; E. pseudogeographica Wacha and Christiansen, 1976, from the false map turtle, Graptemys pseudogeographica (Gray, 1831) and western painted turtle, Chrysemys picta bellii (Gray, 1831) in Iowa; E. vesicostieda Wacha and Christiansen, 1977, from A. s. hartwegi in Iowa; and E. carri Ernst and Forrester, 1973, from the eastern box turtle, Terrapene carolina (Linnaeus, 1758) in Alabama and Florida. The new species differs from E. amydae because the latter has smaller and considerably more elongate oocysts (Roudabush, 1937). Eimeria pseudemydis oocysts are smaller, the sporocysts smaller and less elongate, and the Stieda body is more pointed than for E. ornata (Lainson, 1968; Bone, 1975). Eimeria pseudogeographica has smaller and considerably more elongate oocysts and shorter sporocysts (Wacha and Christiansen, 1976). Eimeria vesicostieda has more elongate oocysts, no oocyst residuum, and stouter sporocysts (Wacha and Christiansen, 1977). The most similar species is E. carri, described by Ernst and Forrester (1973) from 2/7

(29%) T. carolina in Alabama and Florida. Oocysts and sporocysts of this eimerian are somewhat smaller than those of E. ornata; however, a vacuolated area was not reported to be present within the oocyst residuum, and a polar granule is never present. In addition, and most importantly, none of the species listed above, including E. carri, sporulate endogenously. Oocysts of E. carri was reported by Ernst and Forrester (1973) to sporulate exogenously during 1 week at room temperature (20-24 C).

Sauria

All 96 lizard specimens, representing 7 species within 3 families, were not found to be passing coccidia, including 77 iguanids, 5 scincids, and 14 teiids. Individual taxa examined are listed in Table VI.

TABLE VI. Families, species and numbers of Sauria examined for coccidia (arranged phylogenetically).

Host family and species	Number examined
Iguanidae:	
Cophosaurus t. texanus	48
Crotaphytus c. collaris	14
Phrynosoma cornutum	3

Table VI (con't)

Sceloporus olivaceus	12
Scincidae:	
Eumeces septentrionalis obtusirostris	3
Scincella lateralis	2
Teiidae:	
Cnemidophorus g. gularis	14

Serpentes

Twelve of 24 (50%) taxa within 2 families of snakes were found to be passing coccidian oocysts at the time they were examined (Table VII). Overall prevalence of

TABLE VII. Species and individual prevalence data for Serpentes examined for coccidia (arranged phylogenetically).

Host family/species	Prevalence
Leptotyphlopidae	
Leptotyphlops d. dulcis	0/4 (0%)
Colubridae	
Coluber constrictor flaviventris	0/9 (0%)
Elaphe guttata emoryi	1/9 (11%)

Table VII (con't)

Elaphe obsoleta lindheimeri	1/6 (17%)
Heterodon platyrhinos	0/1 (0%)
Hypsiglena torquata jani	0/1 (0%)
Lampropeltis c. calligaster	0/2 (0%)
Lampropeltis getulus splendida	0/1 (0%)
Masticophis flagellum testaceus	2/12 (17%)
Nerodia erythrogaster transversa	9/23 (39%)
Nerodia h. harteri	8/10 (80%)
Nerodia r. rhombifera	12/19 (63%)
Opheodrys aestivus	0/2 (0%)
Pituophis melanoleucus sayi	1/4 (25%)*
Salvadora grahamiae lineata	1/5 (20%)
Sonora s. semiannulata	0/40 (0%)
Storeria dekayi texana	0/1 (0%)
Thamnophis proximus orarius	0/1 (0%)
Thamnophis p. proximus	1/4 (25%)
Thamnophis p. rubrilineatus	4/14 (29%)
Thamnophis sirtalis annectans	0/2 (0%)
Tropidoclonion lineatum texanum	0/12 (0%)
Virginia striatula	3/13 (23%)
Viperidae	
Crotalus atrox	10/18 (56%)*
Sistrurus catenatus tergiminus	0/1 (0%)

*The single P. m. sayi and 2 C. atrox were found to be

passing oocysts of a non-reptile eimerian (see Table VIII).

with at least 1 coccidian was 53/214 (24.8%). There was no sexual preference of coccidians among all host snakes (X^2 = 0.17, 1 df, p > 0.68) as 22.7% of the males and 26.2% of the females were infected (Fig. 13)

Of the 12 infected taxa, prevalence and parasite diversity was highest in 3 species of North American water snakes, genus Nerodia. Twenty-nine of 52 (55.8%) Nerodia spp., including 9 blotched water snakes, N. erythrogaster transversa, 8 Brazos water snakes, N. harteri harteri and 12 diamondback water snakes, N. rhombifera rhombifera harbored a total of 8 (4 new and 4 previously described) eimerians and an unknown species of Cryptosporidium (Table VIII).

TABLE VIII. Coccidians recovered from Serpentes in various counties of northcentral Texas.

Host/coccidian	County	Prevalence
Elaphe guttata emoryi:		
Caryospora duszynskii	Hood	1/7 (14%)
Elaphe obsoleta lindheimeri:		
Caryospora duszynskii	Johnson	1/4 (25%)

Table VIII (con't)

Masticophis flagellum testaceus:		
Eimeria zamenis	Palo Pinto	1/1 (100%)
Sarcocystis sp. 2	Somervell	1/3 (33%)
Nerodia erythrogaster transversa:		
Eimeria attenuata	Johnson	2/16 (13%)
Eimeria conanti	Hood	1/4 (25%)
	Somervell	1/2 (50%)
Eimeria helmisophis	Hood	1/4 (25%)
	Johnson	2/16 (13%)
Eimeria hydrophis	Johnson	2/16 (13%)
Eimeria sipedon	Johnson	3/16 (19%)
Nerodia h. harteri:		
Cryptosporidium sp.	Palo Pinto	1/2 (50%)
	Somervell	3/8 (38%)
Eimeria conanti	Somervell	1/8 (13%)
Eimeria helmisophis	Palo Pinto	1/2 (50%)
	Somervell	5/8 (63%)
Eimeria hydrophis	Somervell	1/8 (13%)
Nerodia r. rhombifera:		
Cryptosporidium sp.	Denton	1/5 (20%)
Eimeria helmisophis	Johnson	1/8 (13%)
Eimeria infirmus	Denton	1/5 (20%)
	Hood	2/4 (50%)
Eimeria rhombifera	Denton	1/5 (20%)
	Hood	1/4 (25%)
	Johnson	1/8 (13%)

Table VIII (con't)

	Somervell	2/2 (100%)
Eimeria tenuis	Denton	2/5 (40%)
	Hood	3/4 (75%)
	Johnson	3/8 (38%)
	Somervell	1/2 (50%)
Pituophis melanoleucus sayi:		
Eimeria sp.*	Johnson	1/2 (50%)
Salvadora grahamiae lineata:		
Eimeria papillosum	Hood	1/2 (50%)
Thamnophis p. proximus:		
Eimeria attenuata	Palo Pinto	1/2 (50%)
Thamnophis p. rubrilineatus:		
Eimeria attenuata	Hood	1/4 (25%)
	Johnson	1/6 (17%)
	Somervell	1/3 (33%)
Eimeria serpenticola	Hood	1/4 (25%)
	Somervell	1/3 (33%)
Virginia striatula:		
Eimeria striatula	Hood	2/6 (33%)
Eimeria sp. C	Dallas	1/5(20%)
	Hood	2/6 (33%)
Crotalus atrox:		
Eimeria sp.*	Johnson	1/5 (20%)
	Somervell	1/5 (20%)
Sarcocystis sp. 1	Hood	4/8 (50%)

Table VIII (con't)

	Johnson	1/5 (20%)
	Somervell	3/5 (60%)

*Oocysts were of the "type A" morphology (see Reduker et al., 1987), characteristic of rodent eimerians. Thus, they were judged to be pseudoparasites of these 3 hosts.

Of the infected water snakes, 16 (55%) were infected with only 1 species, 12 (41%) harbored 2 species, and 1 (3%) was multiply infected with 3 species of coccidia. The 3 most common coccidians among infected Nerodia spp., were Eimeria helmisophis (35%), E. tenuis (31%) and E. rhombifera (17%). The least common eimerian in water snakes was E. attenuata, which was found in only 2 of the 29 (7%) infected individuals; however, it was harbored by 4 of the 5 (80%) infected semiaquatic ribbon snakes, Thamnophis proximus.

When Nerodia and Thamnophis spp. are combined and tested for coccidian preference among the sexes, no sexual preference was evident (X^2=0.17, 1 df, P > 0.68) as 54.2% of the males and 45.8% of the females were infected (Fig. 14).

Comparisons were made with measurements of other coccidians previously reported from other snakes. Below are descriptions of the new species that were observed.

FIGURE 13. Preference of coccidia for host sex among 214 snakes. Numbers above bars are number infected/number examined.

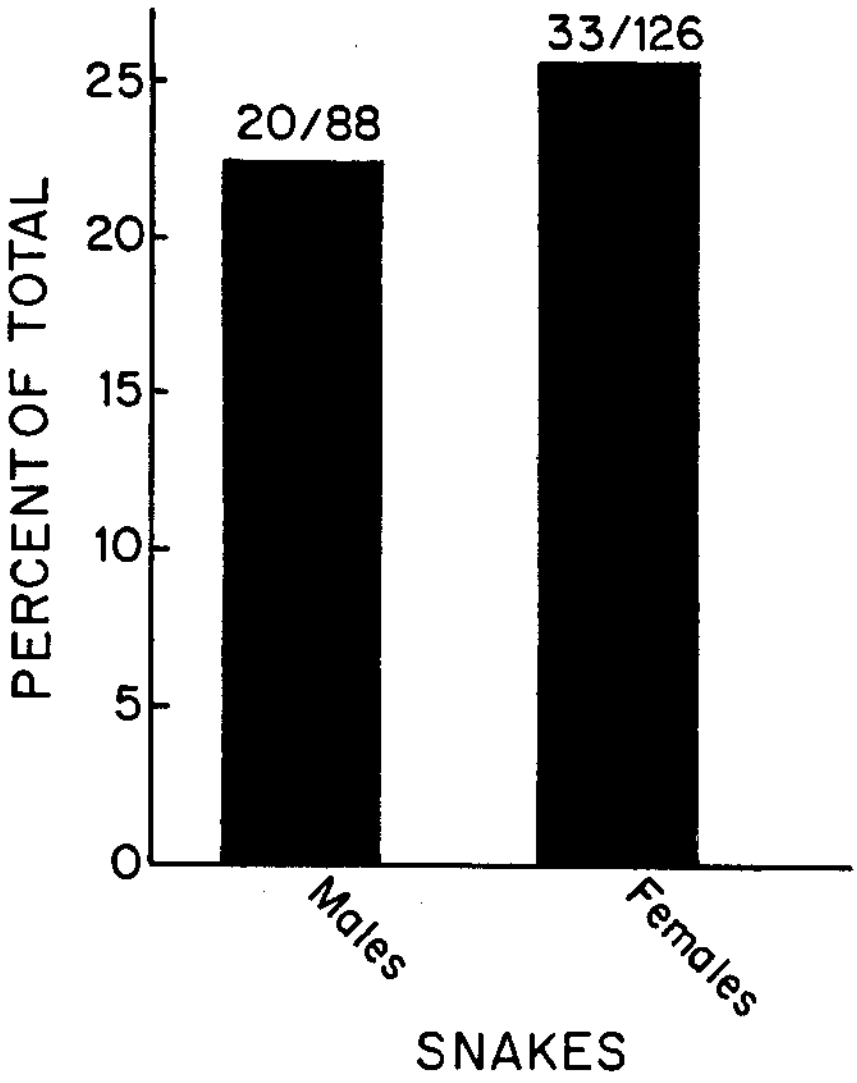
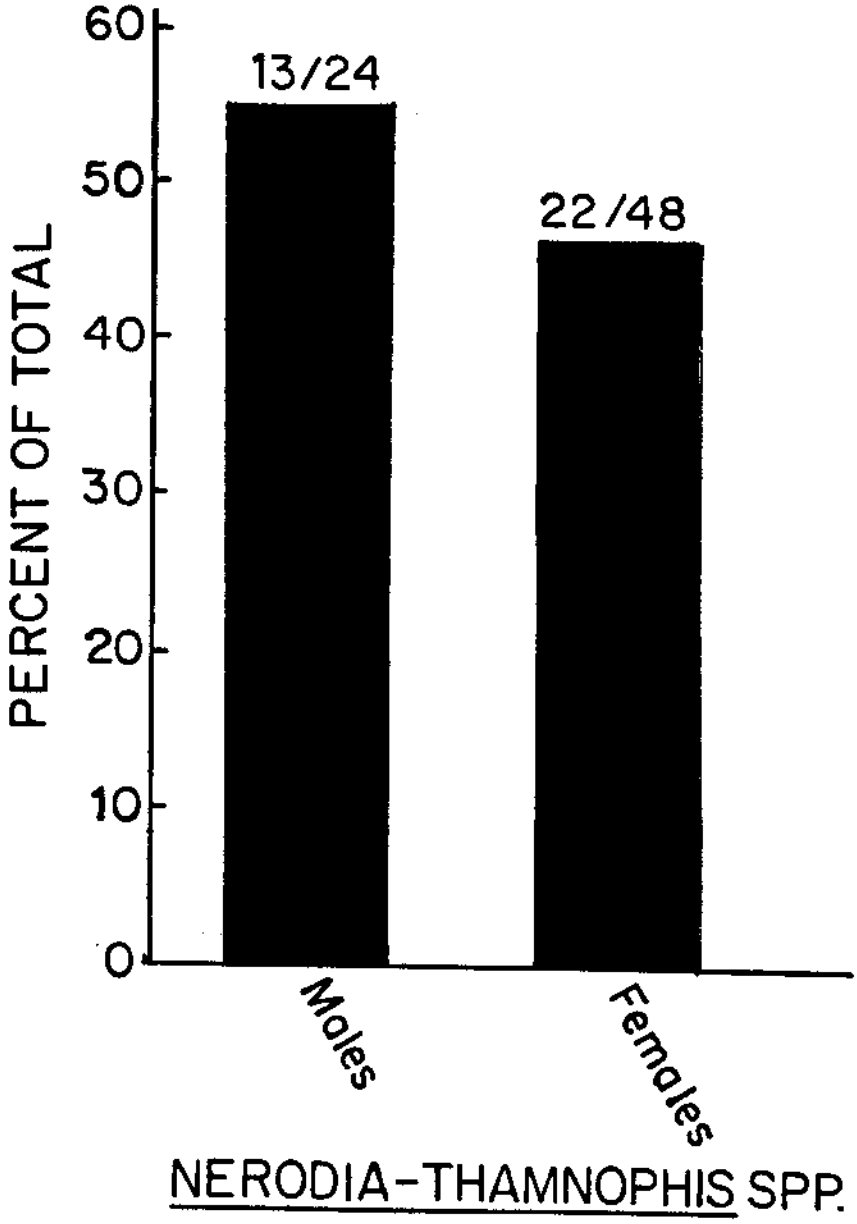

33/126
20/88
25
20
15
10
5
0
PERCENT OF TOTAL
Males
Females
SNAKES

FIGURE 14. Preference of coccidia for host sex among 72 aquatic snakes, Nerodia and Thamnophis spp. Numbers above bars are number infected/number examined.


60
50
40
30
20
10
0
PERCENT OF TOTAL
13/24
22/48
Males
Females
NERODIA-THAMNOPHIS SPP.

Eimeria infirmus Upton and McAllister, 1988

(Fig. 15A)

Description: Oocysts irregular in shape, 11.6 (8.8-14.4) in diameter, with a smooth, thin, membranous wall that encloses the sporocysts tightly. The wall is so frail that it ruptures frequently, releasing free sporocysts. A small, often obscure polar granule is located among the sporocysts, which occasionally fragments into several smaller granules. Micropyle and oocyst residuum are absent. Sporocysts are bean-shaped, with 1 side flattened slightly, 9.1 x 5.0 (7.2-10.4 x 4.4-5.8); shape index (length/width) 1.8 (1.6-2.1). Sporocyst wall thin, single-layered, ca. 0.4 thick, and often thickened slightly at 1 end forming what may be a thin Stieda body; substieda body absent. Spherical or ovoid sporocyst residuum present, 2.8 x 3.8 (2.0-4.8 x 2.4-6.4), consisting of numerous granules usually arranged as a compact mass. Sporozoites elongate, 8.1 x 2.1 (6.6-9.0 x 1.8-2.4), in situ, arranged head-to-tail within the sporocyst. Each sporozoite contains a single nucleus and a spherical or ovoid posterior refractile body, 1.9 wide x 2.3 long (1.6-2.2 x 1.8-3.2).

Type host: Nerodia rhombifera rhombifera (Hallowell, 1852), diamondback water snake (Serpentes: Colubridae), adult male, ASUMZ 8513.

Type locality: USA, Texas, Hood County, 18.5 km SE

Granbury off FM 2174 at Taylor Branch.

Other locality: USA, Texas, Denton County, Denton city limits off I-35 and Augusta Drive.

Prevalence: 3/19 (16%) of the N. r. rhombifera were infected; 1/5 (20%) Denton County, 2/4 (50%) Hood County, 0/8 (0%) Johnson County, 0/2 (0%) Somervell County.

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

Sporulation: Endogenous. Oocysts were passed fully sporulated.

Etymology: The specific epithet reflects the feeble nature of the oocyst wall.

Remarks: The frail oocyst wall of E. infirmus is unlike that reported for any of the 44 named and 4 unnamed species of snake coccidia thus far reported. In addition, only E. helmisophis Wacha and Christiansen, 1974 from Carphophis amoenus vermis (Kennicott), Eimeria sp. of Van Peenen and Birdwell, 1968 from Lampropeltis getulus californiae (Blainville), and E. zamenis Phisalix, 1921 from various colubrids have been reported to have polar granules (see Van Peenen and Birdwell, 1968; Wacha and Christiansen, 1974b). However, these species are larger than the form reported herein.

Eimeria rhombifera Upton and McAllister, 1988

(Fig. 15B)

Description: Unsporulated oocysts spherical or subspherical; sporulated oocysts similar in shape but somewhat irregular, 13.1 x 12.6 (12.0-14.4 x 11.2-14.4), with smooth thin, single-layered wall ca. 0.4 thick that collapses readily around the sporocysts, even in wet mounts; shape index 1.6 (1.3-1.8). Polar granule present but micropyle and oocyst residuum are absent. Sporocysts ovoid, 8.8 x 5.5 (8.0-9.6 x 5.0-6.0), with smooth thin, single-layered wall ca. 0.3 thick; shape index 1.6 (1.3-1.8). One end of sporocyst thickened slightly to form Stieda body; substieda body absent. Spherical or subspherical sporocyst residuum present, 2.4 x 2.5 (1.8-4.0 x 1.8-3.2), consisting of compact mass of coarse, spherical granules. Sporozoites elongate, 8.1 x 2.4 (7.2-10.0 x 2.2-2.6) in situ, arranged head-to-tail. Each sporozoite with single nucleus and a spherical or subspherical posterior refractile body, 2.1 wide x 2.3 long (1.6-2.4 x 1.6-4.0).

Type host: Nerodia rhombifera rhombifera (Hallowell, 1852), diamondback water snake (Serpentes: Colubridae), adult females, ASUMZ 11734, 11737.

Type locality: USA, Texas, Hood County, 18.5 km SE Granbury off FM 2174 at Taylor Branch.

Other localities: USA, Texas, Denton County, Denton city limits off I-35 and Augusta Drive; Johnson County, 17.5 km SW Cleburne off US 67 on county rd. 1120 at Georges Creek Ranch; Somervell County, 8.0 km NE Glen Rose off FM 200 at Brazos River.

Prevalence: 5/19 (26%) of the N. r. rhombifera were infected; 1/5 (20%) Denton County, 1/4 (25%) Hood County, 1/8 (13%) Johnson County, 2/2 (100%) Somervell County.

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

Sporulation: Only a few of the oocysts recovered from feces were sporulated. Most were partially sporulated and became fully sporulated within 5 days in tap water supplemented with antibiotic at 23 C.

Etymology: The specific epithet reflects that of the host species.

Remarks: Only 7 named and 1 unnamed species of snake Coccidia have been reported to be spherical or subspherical. Of these species, only E. liophi Lainson and Shaw, 1973 from Liophis cobella (Linnaeus) and E. poecilogyrus Carini, 1933 from Leimadophis poecilogyrus (Wied) (syn. Liophis poecilogyrus) are similar enough in size to be confused with the species reported herein (see Carini, 1933; Lainson and Shaw, 1973). Eimeria rhombifera can be distinguished from both of these

species by the presence of a polar granule, smaller sporocysts, and compact sporocyst residuum.

Eimeria tenuis Upton and McAllister, 1988

(Fig. 15C)

Description: Oocysts ellipsoid, 17.2 x 10.8 (15.2-20.8 x 9.6-12.0), with smooth, thin, single-layered wall ca. 0.4 thick; shape index 1.6 (1.3-1.9). One, occasionally 2, polar granule(s) present; micropyle absent. Oocyst residuum present, 3.4 x 3.7 (1.6-5.0 x 1.6-7.0) (n = 12), consisting of numerous granules enclosing a clear area. The residuum falls apart soon after sporulation and the granules become scattered throughout the oocyst. Sporocysts elongate, 13.2 x 4.9 (11.2-15.2 x 4.4-5.6), with thin, smooth, single-layered wall; shape index 2.7 (2.3-3.2). Stieda body at 1 end of sporocyst, consisting only of a thickened area of sporocyst wall; substieda body absent. Spherical, subspherical, or ovoid sporocyst residuum present, 2.2 x 2.6 (0.8-3.2 x 1.0-5.0) (n = 26). Sporozoites elongate, 11.6 x 2.4 (10.0-13.6 x 2.2-3.0) in situ, arranged head-to-tail within sporocyst. Each sporozoite contains a spherical or subspherical anterior refractile body, 2.0 wide x 2.1 long (1.0-2.4 x 1.0-3.2), and a spherical to ellipsoid posterior refractile body, 2.2 wide x 2.7 long (1.8-2.8 x

1.8-4.0). The nucleus lies between the refractile bodies.

Type host: Nerodia rhombifera rhombifera (Hallowell, 1852), diamondback water snake, adult male, ASUMZ 8513.

Type locality: USA, Texas, Hood County, 18.5 km SE Granbury off FM 2174 at Taylor Branch.

Other localities: USA, Texas, Denton County, Denton city limits off I-35 and Augusta Drive; Johnson County, 17.5 km SW Cleburne off US 67 on county rd. 1120 at Georges Creek Ranch; Somervell County, 8.0 km NE Glen Rose off FM 200 at Brazos River.

Prevalence: 9/19 (47%) of the N. r. rhombifera were infected; 2/5 (40%) Denton County, 3/4 (75%) Hood County, 3/8 (38%) Johnson County, 1/2 (50%) Somervell County.

Site of infection: Unknown. Oocysts found in feces and intestinal contents.

Sporulation: Endogenous. Oocysts were passed fully sporulated.

Etymology: The specific epithet reflects the thin nature of the oocyst wall.

Remarks: Oocysts of E. tenuis are somewhat similar to those of E. attenuata Wacha and Christiansen, 1974 from Nerodia sipedon sipedon (Linnaeus) in Iowa and also to E. natricis Wacha and Christiansen, 1975 (also from

N. s. sipedon) in Iowa, and E. iowaensis Wacha and Christiansen, 1974 from Thamnophis sirtalis parietalis (Say) in Iowa (see Wacha and Christiansen, 1974b, 1975). Eimeria tenuis differs from E. attenuata by its less elongate untapered oocysts, more elongate sporocysts, and presence of an oocyst residuum; from E. natricis by its smaller oocysts, presence of an oocyst residuum, and more elongate sporocysts; and from E. iowaensis by its more elongate shape, presence of an oocyst residuum, and more elongate sporocysts.

Eimeria conanti McAllister and Upton, 1989

(Fig. 15D)

Oocysts ellipsoid, 17.9 x 13.0 (15-21 x 12-15), with a smooth, thin, single-layered wall ca. 0.5 thick; shape index 1.4 (1.2-1.5). One to several (usually two) polar granule(s) present, ca. 1.6 long; micropyle absent. Oocyst residuum present, 5.7 x 5.5 (4-9 x 4-8) (n = 29), consisting of a vacuole surrounded by homogeneous globules, not membrane bound. Sporocysts elongate, 13.9 x 5.2 (13-15 x 5-6), with a smooth, thin, single-layered wall ca. 0.2 thick; shape index 2.7 (2.3-3.3). No true Stieda body structure evident, however, the sporocysts taper to a point that may represent a Stieda body; substieda body absent. Ellipsoid sporocyst residuum present, 3.9 x 3.2 (3-6 x

2-4). Sporozoites elongate, 11.4 x 2.5 (10-14 x 2-3) *in situ*, sometimes, with transverse striations anteriorly and usually arranged in opposite directions in sporocyst, rarely in same direction. Each sporozoite contains a spherical or subspherical anterior refractile body, 2.1 wide x 2.4 long (1.8-2.4 x 1.8-3.2), and a spherical to ellipsoid posterior refractile body, 2.2 wide x 2.9 long (1.8-2.6 x 2.0-4.8). A nucleus lies between the refractile bodies.

Type host: *Nerodia erythrogaster transversa* (Hallowell, 1852), blotched water snake (Serpentes: Colubridae), juvenile female, ASUMZ 11731.

Type specimens: Syntypes (oocysts in 10% formalin) are deposited in the U.S. National Museum, Beltsville, Maryland as USNM 80556.

Type locality: USA, Texas, Hood County, 18.5 km SE Granbury off FM 2174 at Taylor Branch.

Other host. *Nerodia harteri harteri* (Trapido, 1941), Brazos water snake (Serpentes: Colubridae), adult female, ASUMZ 11765.

Other locality: USA, Texas, Somervell County, 8.0 km NE Glen Rose off FM 200 at Brazos River.

Prevalence. 2/23 (9%) of the *N. e. transversa* were infected; 0/1 (0%) Dallas County, 1/4 (25%) Hood County, 0/16 (0%) Johnson County, 1/2 (50%) Somervell County. 1/9 (11%) of the *N. h. harteri* were infected; 0/1 Palo

Pinto County, 1/8 (13%) Somervell County.

Site of infection: Unknown. Oocysts found in feces and intestinal contents.

Sporulation: Exogenous. Oocysts were unsporulated or only partially sporulated and became fully sporulated within 3 to 5 days at ca. 23 C in 2.5% (w/v) potassium dichromate solution.

Etymology: Named in honor of Dr. Roger Conant, Director Emeritus, Philadelphia Zoological Gardens and Adjunct Professor, University of New Mexico, in recognition of his work on natricine snakes and lifelong contributions to herpetology.

Remarks: Oocysts of Eimeria conanti most closely resemble Eimeria tenuis Upton and McAllister, 1988, from Nerodia r. rhombifera in northcentral Texas. However, the new form described here can easily be differentiated from E. tenuis using any of the following characteristics: by having less elongate oocysts, a smaller shape index (1.4 vs 1.6), a larger oocyst residuum, sporocysts that are tapered at both ends rather than bluntly rounded at the posterior end, and sporozoites with anterior ends that extend well beyond the posterior ends of the other sporozoite within the same sporocyst.

Eimeria papillosum Upton and McAllister, 1990

(Fig. 15E)

Description: Oocysts cylindrical, 32.0 x 18.0 (28.8-35.2 x 16.0-20.4); shape index 1.8 (1.7-2.0). Wall bilayered, ca. 1.6 thick, the inner layer being 0.6 thick and the outer layer ca. 1.0 thick. The outer surface is covered by numerous papules that tend to be lost as oocysts age over many days or weeks. Micropyle and oocyst residuum absent; polar granule present. Sporocysts ellipsoid, 11.2 x 8.8 (10.4-12.8 x 8.2-11.2), with thin, smooth single-layered wall, ca. 0.5; shape index 1.3 (1.1-1.5). Stieda and substieda bodies absent. Sporocyst residuum present, spherical or subspherical, 5.8 (4.4-8.0) in diameter (n=24). Sporozoites elongate, 13.0 x 2.9 (11.2-14.4 x 2.6-3.2) *in situ*, arranged head-to-tail within the sporocyst. Each sporozoite contains a spherical or subspherical posterior refractile body, 3.2 long x 2.7 wide (2.4-4.0 x 2.4-3.0), and a centrally located nucleus.

Type host: *Salvadora grahamiae lineata* Schmidt, 1940, Texas patchnose snake (Serpentes: Colubridae), gravid adult female, ASUMZ 8532.

Type locality: USA, Texas, Hood County, 18.5 km SE Granbury off FM 2174 at Hinton-Parker Ranch.

Prevalence: 1/5 (20%) of the *S. g. lineata* from northcentral Texas were infected; 1/2 (50%) Hood County,

0/3 (0%) Somervell County.

Site of infection: Unknown. Oocysts found in feces and intestinal contents.

Sporulation: Exogenous. Oocysts were passed unsporulated and sporulated within 1 week at 23 C in 2.5% (w/v) potassium dichromate.

Remarks: Oocysts of this form are most similar in size and shape to several other elongate snake Eimeria, including E. collanuli Wacha and Christiansen, 1974 from Diadophis punctatus arnyi in Iowa, E. cystisfellae Debaisieux, 1914 from Natrix natrix in Germany, E. lampropeltis Anderson, Duszynski, and Marquardt, 1968 from Lampropeltis c. calligaster in Illinois, E. natricis Wacha and Christiansen, 1975 from Nerodia s. sipedon in Iowa, and E. zamenis Phisalix, 1921 from various Coluber spp. and Lampropeltis spp. in North America. However, none of these other species of snake Eimeria have been reported to possess the papillated wall distinctive of the species described herein.

Eimeria serpenticola Upton and McAllister, 1990

(Fig. 15F)

Description: Oocysts ellipsoid, 20.3 x 17.5 (17.2-22.4 x 15.8-19.8), with a smooth, thin, colorless single-layered wall ca. 0.6 thick; shape index 1.2 (1.1-1.3). Micropyle and oocyst residuum absent; a

polar granule is present in about 50% oocysts whereas in other oocysts the structure appears to have fragmented. Sporocysts elongate, 14.7 x 7.0 (12.8-18.0 x 6.4-7.4), with a smooth, thin, single-layered wall ca. 0.5 thick; shape index 2.1 (1.9-2.6). Stieda body present, consisting only of thickened portion of the sporocyst wall; substieda body absent. Spherical to ellipsoid sporocyst residuum present, 3.4 x 3.1 (2.6-4.8 x 2.4-4.0). Sporozoites elongate, 12.2 x 3.0 (9.6-14.4 x 2.6-3.8) in situ, twisted within the sporocyst and with transverse striations anteriorly. Each sporozoite contains a spherical anterior refractile body 2.4 (1.6-3.4), a spherical or ellipsoid median refractile body 3.1 x 2.7 (2.4-4.0 x 2.2-3.5) and an elongate posterior refractile body 3.8 x 2.6 (2.6-6.4 x 2.4-3.2). The nucleus is situated between the anterior and second refractile bodies.

Type host: Thamnophis proximus rubrilineatus Rossman, 1963, redstripe ribbon snake (Serpentes: Colubridae), adult female, ASUMZ 8580.

Type locality: USA, Texas, Hood County, 19.5 km SE Granbury off FM 2174 at Russell Ranch.

Other locality: USA, Texas, Somervell County, 12.9 km NW Glen Rose off US 67 on county road 406.

Prevalence: 2/14 (14.3%) of the T. p. rubrilineatus from northcentral Texas were infected; 1/4

(20%) Hood County; 0/6 (0%) Johnson County; 1/4 (20%) Somervell County.

Site of infection: Unknown. Oocysts found in feces and intestinal contents.

Sporulation: Exogenous. Oocysts were passed unsporulated and sporulated within 1 week at 23 C in 2.5% potassium dichromate.

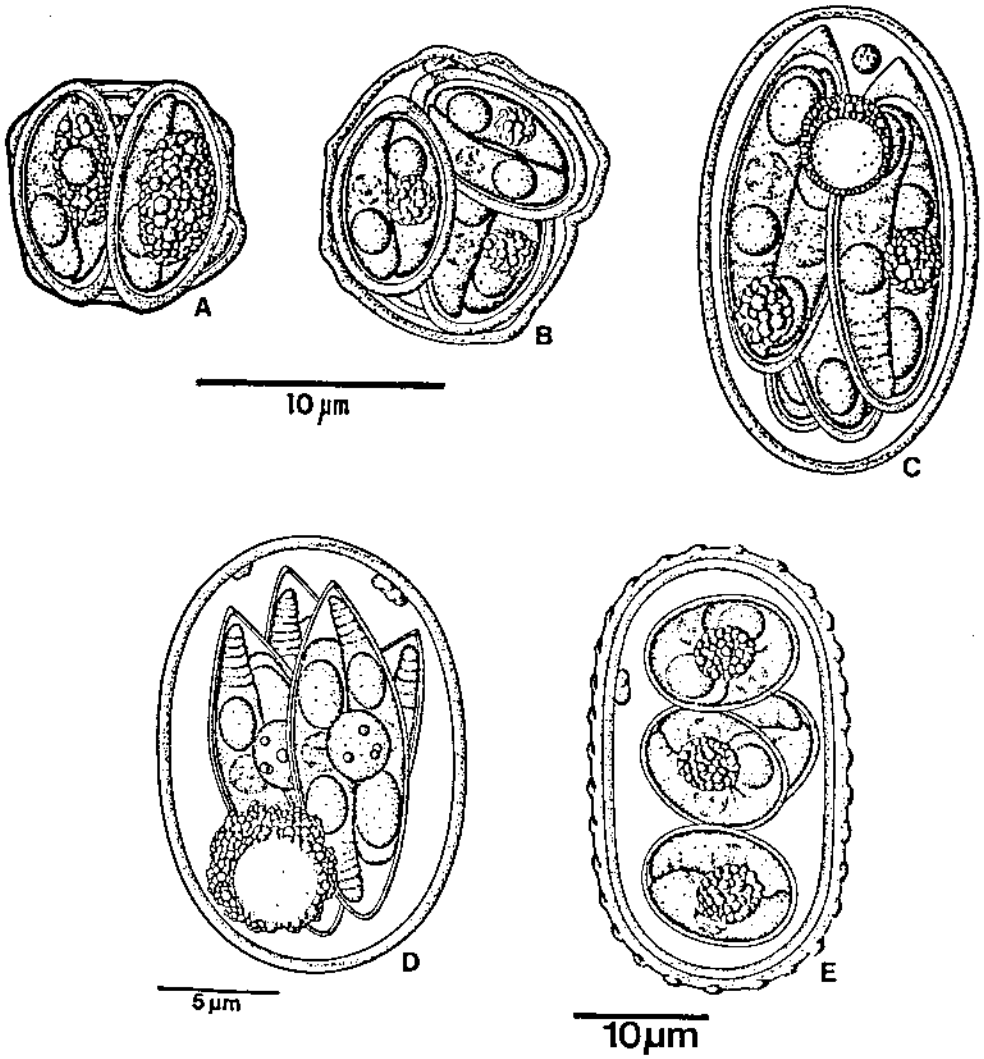
Remarks: Oocysts of Eimeria serpenticola are most similar to Eimeria conanti McAllister and Upton, 1989 from Nerodia e. transversa and N. harteri harteri from northcentral Texas and also to Eimeria cyclopion McAllister, Upton and Trauth, 1990 from Nerodia c. cyclopion from Arkansas (McAllister et al., 1990a). However, the new form can be distinguished from these similar species by having much wider oocysts, not possessing an oocyst residuum, and possessing 3 refractile rather than 2 sporozoite refractile bodies.

Eimeria striatula Upton and McAllister, 1990

(Fig. 15G)

Description: Oocysts spherical, 12.5 (11.2-15.2) in diameter, with a smooth, thin, single-layered wall ca. 0.4 thick that collapses readily. Micropyle and oocyst residuum absent; polar granule present. Sporocysts elongate, 9.9 x 5.1 (8.0-11.2 x 4.4-6.0), with smooth, thin, single-layered wall, $\leq$ 0.4 thick;

FIGURES 15A-G. Composite line drawings of sporulated oocysts of 7 new species of Eimeria found in Serpentes from Texas. Fig. 15A. Eimeria infirmus Upton and McAllister, 1988 from Nerodia r. rhombifera. Fig. 15B. Eimeria rhombifera Upton and McAllister, 1988 from N. r. rhombifera. Fig. 15C. Eimeria tenuis Upton and McAllister, 1988 from N. r. rhombifera. Fig. 15D. Eimeria conanti McAllister and Upton, 1989 from N. erythrogaster transversa. Fig. 15E. Eimeria papillosum Upton and McAllister, 1990 from Salvadora grahamiae lineata. Fig. 15F. Eimeria serpenticola Upton and McAllister, 1990 from Thamnophis proximus rubrilineatus. Fig. 15G. Eimeria striatula Upton and McAllister, 1990 from Virginia striatula.



15

shape index 2.0 (1.6-2.2). Stieda body present, consisting only of thickened area of the sporocyst wall; substieda body absent. Sporocyst residuum present, consisting usually of a few scattered granules but sometimes as a small compact mass. Sporozoites elongate, 8.1 x 2.3 (6.4-10.4 x 2.0-2.8) in situ, arranged head-to-tail within sporocyst. Each sporocyst contains a spherical anterior refractile body, 1.7 (1.2-2.4) and a spherical or subspherical posterior refractile body, 2.2 long x 2.0 wide (1.8-3.2 x 1.8-2.4). The nucleus lies between the refractile bodies.

Type host: Virginia striatula Linnaeus, 1766, rough earth snake (Serpentes: Colubridae), adult male, ASUMZ 8563.

Type locality: USA, Texas, Hood County, 18.5 km SE Granbury off FM 2174 at Hinton-Parker Ranch.

Other locality: USA, Texas, Hood County, 19.3 km SE Granbury off 2174 at Russell Ranch.

Prevalence: 2/13 (15.4%) of the V. striatula from northcentral Texas were infected; 0/5 (0%) Dallas County; 2/6 (33%) Hood County; 0/2 (0%) Somervell County.

Site of infection: Unknown. Oocysts found in feces and intestinal contents.

Sporulation: Exogenous. Oocysts were passed

unsporulated and sporulated within 1 week at 23 C in 2.5% (w/v) potassium dichromate.

Remarks: Oocysts of this species are similar to E. liophi Lainson and Shaw, 1973, from Liophis cobella in Brazil and E. poecilogyri Carini, 1933, from Leimadophis poecilogyrus in Brazil. However, it may be distinguished from E. liophi by possessing a polar granule and sporozoites without recurved ends and from E. poecilogyri by the smaller oocysts and presence of a polar granule.

Sarcocystis sp. 1

Remarks and Description: Sporocysts of a Sarcocystis sp. were commonly collected from western diamondback rattlesnakes, Crotalus atrox. However, 20 sporocysts measured 11.2 x 9.7 (10.4-12.0 x 9.2-10.0); shape index 1.15 (1.1-1.2). These measurements are somewhat larger than those reported for S. crotali Enzeroth, Chobotar, and Scholtyseck, 1985, a Sarcocystis sp. described from the Mojave rattlesnake, Crotalus s. scutulatus, from California (Enzeroth et al., 1985).

Experimental Infections: Sarcocysts were not found in mice inoculated with sporocysts and killed 97 DPI. Using wet mounts and NIC microscopy, no micro- or macroscopic cysts were present either in tongue or diaphragm tissues. This suggests that this form is

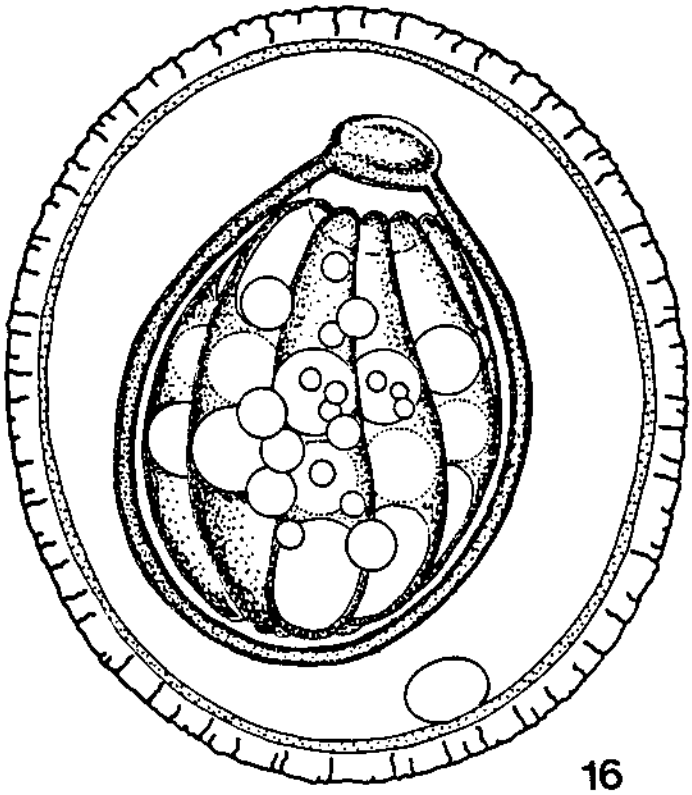
probably a species distinct from S. crotali since the latter species has been shown to infect Mus musculus experimentally. However, failure to establish experimental infections may also mean that sporocysts failed to retain viability after storage for 18 days in 2.5% potassium dichromate. Therefore, description of a new species will have to await successful experimental transmissions.

Caryospora duszynskii Upton, Current, and Barnard, 1984

(Fig. 16)

Remarks and Description: Oocysts of a species of coccidian virtually indistinguishable from those described by Upton et al. (1984) from the corn snake, Elaphe g. guttata in Georgia and the black rat snake, E. o. obsoleta in Missouri were found in a Great Plains rat snake, E. g. emoryi and a Texas rat snake, E. o. lindheimeri. Most oocysts collected from the latter host failed to possess a polar granule, however, unlike specimens described in the original description. Thirty oocysts from E. o. lindheimeri measured 27.7 x 26.0 (25.6-29.6 x 24.8-28.0) and 30 sporocysts 19.3 x 14.3 (18.4-20.8 x 13.6-15.0). The original description of C. duszynskii list oocyst and sporocyst measurements as 25.7 x 24.3 (23.0-28.5 x 22.0-28.0) and 18.3 x 14.8 (17.0-21.5 x 13.5-16.5), respectively. Although

FIGURE 16. Line drawing of Caryospora duszynskii Upton, Current and Barnard, 1984 from Elaphe spp. (Redrawn from Upton et al., 1984).



16

10µm

slightly larger, this represents an insignificant size difference and that the oocysts found in Texas colubrids represent C. duszynskii.

Cryptosporidium spp.

Of 428 amphibians and 435 reptiles examined for cryptosporidiosis, only 5 (1.1%) reptiles representing a single genus and 2 species were found to be infected: 4 (44.4%) Brazos water snakes, Nerodia h. harteri and 1 (5.3%) diamondback water snake, N. r. rhombifera.

Measurements on the 2 isolates are shown in Table IX.. Although visual evidence may not support separate

TABLE IX. Measurements of oocysts of Cryptosporidium spp. isolated from Nerodia spp.

Nerodia spp.	Oocyst length (µm) ($\bar{X}$ ± SD) (range)	Oocyst width(µm) ($\bar{X}$ ± SD) (range)
harteri*	6.7 (0.31) (6.4-7.2)	5.6 (0.23) (5-6)
rhombifera	6.5 (0.23) (5.8-7.0)	5.6 (0.20) (5-6)

*For lengths, $P < 0.025$ from N. r. rhombifera; for widths, $P > 0.05$ from N. r. rhombifera (Wilcoxon Mann-Whitney U-test).

morphologic types, statistical evaluation of the measurements suggests that oocysts could be placed into 2 separate groups. When compared to data presented by Upton et al. (1989) for other isolates from reptiles, the following may be concluded. Oocysts in group IV of Upton et al. (1989) were found only in Nerodia spp. and are the second largest of the isolates. Although oocysts from N. h. harteri were noted to be somewhat more elongate, both visually and statistically, than those of N. r. rhombifera, taxonomic separation of the 2 isolates is pending cross transmission studies.

Oocysts from N. h. harteri were affected by prolonged exposure to Sheather's sucrose solution. Oocysts exposed only to 2.5% potassium dichromate solution measured 6.8 ± 0.35 x 5.8 ± 0.30 (6.4-7.2 x 5.6-6.6) µm; those immediately after flotation 6.7 ± 0.31 x 5.6 ± 0.23 (6.4-7.2 x 5.0-6.0) µm; and those after remaining in Sheather's for 1 hr 6.5 ± 0.19 x 5.5 ± 0.21 (5.6-7.2 x 4.8-5.8) µm. While treatments 1 and 3 were not significantly different from oocysts measured immediately after flotation, a comparison of treatment 1 and 3 to each other revealed both lengths and widths to vary at $P < 0.05$ (Wilcoxon Mann-Whitney U-test).

Host phylogeny of Thamnophiine snakes

In addition to the 5 eimerians described herein from Nerodia spp. and Thamnophis proximus, several other

coccidians were found in these hosts (see also Table VIII). Oocysts of Eimeria attenuata Wacha and Christiansen, 1974, known previously from 1/25 (4%) red-sided garter snakes, Thamnophis sirtalis parietalis (Say) and 1/4 (25%) northern water snakes, Nerodia sipedon sipedon (Linnaeus) in Iowa (Wacha and Christiansen, 1974) were found only in N. e. transversa and T. p. rubrilineatus. However, oocysts of Eimeria helmisophis Wacha and Christiansen, 1974 were recovered from N. e. transversa, N. h. harteri and N. r. rhombifera. This coccidium was reported previously in Iowa from 1/5 (20%) western worm snakes, Carphophis amoenus vermis (Kennicott) (Wacha and Christiansen, 1974). Oocysts of Eimeria hydrophis Wacha & Christiansen, 1974, previously reported from 1/1 (100%) N. r. rhombifera and 5/14 (36%) N. s. sipedon in Iowa (Wacha and Christiansen, 1974) were found in N. e. transversa and N. h. harteri, but not in 19 N. r. rhombifera. Eimeria sipedon Wacha and Christiansen, 1974, originally described from 2/2 (100%) N. s. sipedon in Iowa (Wacha and Christiansen, 1975) was harbored only by N. e. transversa.

CHAPTER VI

DISCUSSION

Systematics and prevalence

Coccidian parasites were found in all host groups except Sauria. When lizards are excluded from the prevalence data, 23% of the remaining 767 specimens were infected. The highest prevalence occurred in the group Testudines, where over one-half of the turtles harbored at least 1 species of coccidian. In addition, reptiles were infected at a rate 2 times higher than amphibians. These data were not expected because coccidia had been hypothesized to be more prevalent in aquatic/semiaquatic hosts. However, along with the majority of turtles, many of the infected snakes were aquatic or semiaquatic, which may help explain this disparity.

Individual group taxa

Caudata

The only coccidian found in salamanders, Eimeria ambystomae, was described originally by Saxe (1955) from 13/56 (23%) eastern tiger salamanders, Ambystoma tigrinum tigrinum from Iowa, and 1/8 (13%) seal salamanders, Desmognathus monticola and 1/2 (50%)

blackbelly salamanders, D. quadramaculatus, both obtained from commercial sources but apparently originated from an unknown locality in the Appalachians. Duszynski et al. (1972) provided new distributional records for the coccidium when they reported 17/17 (100%) barred tiger salamanders, A. t. mavortium from Colorado and New Mexico to be infected.

Smallmouth salamanders harboring E. ambystomae were abundant only during the breeding season from December 1986 to March 1987 when the pond they inhabited contained an adequate supply of standing water. Between December 1987 and 1988 when drought conditions predominated (see Table 1) and the pond completely dried, the majority of salamanders presumably remained inactive underground. This pond population was apparently unable to take part in above-ground activities including spring breeding when precipitation is normally higher. On 2 occasions during the drought, once in December 1987 and again in February 1988, the same 3 A. texanum were collected under a piece of damp sheet metal following a brief rainfall. Each time 2 of the marked salamanders were found to be harboring E. ambystomae whereas the third was not. In March 1988, these same hosts were negative for coccidia. These short-term observations suggest that the parasite may be able to remain dormant in host epithelial cells while

the infected host is inactive during unfavorable conditions in subterranean habitat. During December 1988, following more than a year of drought, 4 A. texanum were collected at the same locale but none were infected with E. ambystomae. This may also explain why some of these same salamanders were free of trematodes and nematodes that rely on molluscan intermediate hosts in their life cycle (McAllister and Upton, 1987a). Additional studies designed to examine mechanisms by which E. ambystomae can be transmitted in salamanders even during short-term drought conditions is warranted.

Based solely on morphologic identification of the parasite, it appears E. ambystomae has little host specificity. The coccidium has now been reported from 2 host families, including 2 lungless salamanders (Family Plethodontidae) and 2 mole salamanders (Family Ambystomatidae) from widely separated geographic localities in North America.

Anura

Species of coccidia in anurans appear to be similar to those in fish because they often have a delicate oocyst wall which rapidly distorts in flotation solutions. For example, E. streckeri and I. fragosum could be identified in Sheather's sugar solution; however, the other 2 species from anurans (E. flexuosa

and I. delicatus) described herein collapsed rapidly and internal details were obscured. Therefore, wet mounts should be the method of choice when examining anuran hosts for coccidia.

Of the 11 host taxa examined for coccidia, only 2 (18%) harbored true species of anuran coccidia and 4 previously undescribed species were found. Therefore, the number of species of coccidia infecting anurans is probably much higher than the figure of 31 reported in a worldwide summary by Upton and McAllister (1988a). The difficulty in working with frail coccidia often prevents new species descriptions, however, and the present report contains the first new species of anuran coccidia described since 1944. The last new species of coccidia reported from amphibians were Eimeria microcapi and E. urodela from the salamander, A. tigrinum (see Duszynski et al., 1972).

Adult anurans harbored coccidia whereas tadpoles and juveniles did not. It is unknown if the prevalence observed herein was due to dietary habits of the host, unusually long prepatent and patent periods, differences in physiology, or even other factors. However, E. neglecta has been reported in tadpoles of European Rana spp. by Nöller (1920) and an Isospora sp. was found in a "young" R. arvalis by Kazubski and Grabda-Kazubska (1973). Thus, it appears that immature animals are at

least capable of being infected.

The data presented in Tables II and III provides fairly convincing evidence that anuran coccidia found during this study are host specific. Often, several species were collected from the same locality and none of the coccidia were observed to cross species boundaries. For example, many of the Pseudacris clarkii and P. s. streckeri were collected from the same site in Dallas County but only the latter species harbored coccidia. Interestingly, P. clarkii was collected at various times throughout the study while P. s. streckeri was taken only during a 2-month period in January and February 1987. However, Chen and Desser (1989) provided contrasting results when they reported that both E. algonquini and E. kermiti were capable of infecting 4 different Rana spp. collected during June and July in Ontario, Canada.

Although large sample sizes were not obtained during all months, enough G. olivacea were examined to draw some preliminary conclusions about seasonality. Prevalence varied monthly among adult toads infected with I. fragosum (see Fig. 9) and, in general, it appears that a higher prevalence follows emergence of toads from winter dormancy in the spring and prior to fall inactivity. In Texas, these seasons are typically characterized by an increase in humidity and rainfall,

which initiates migration to temporary pools for courtship and breeding activities. Resumption of feeding and congregation of toads at breeding sites probably increases the probability of infection. The lower prevalence in June and July, and lack of available toads during August, may result from generally hotter and dryer weather. Drying up of seasonal ponds, coupled with the frail nature of the oocyst wall of I. fragosum, may also serve to limit viability of exogenous oocysts.

Of the anurans examined, only 2 species (G. olivacea and B. debilis) are considered fossorial. These toads are typically burrowing anurans that have very limited exposure to aquatic habitats. However, only G. olivacea was infected with coccidia. Narrowmouth toads often preferred moist areas under limestone rocks in cedar glade habitat and even frequented abandoned rodent burrows. It is possible that the burrow microhabitat frequented by G. olivacea retains enough moisture for oocyst viability and is apparently conducive to the life cycle of I. fragosum. Conversely, more terrestrial anurans such as B. valliceps and B. woodhousii, also burrow but do not have a relatively long exposure to aqueous environments during breeding. As with B. debilis, neither of these toads served as hosts for coccidian parasites. Coccidia have been reported from various bufonids from the

Eastern Hemisphere (Upton and McAllister, 1988a), but have yet to be found in North American toads.

The true frogs, Rana spp., can be considered either semiaquatic or aquatic since they spend most of their time near or in an aquatic habitat. Coccidia were not found in any of the 4 congeners examined (R. berlandieri, R. blairi, R. catesbeiana and R. sphenocephala). At the primary study area, these frogs preferred shallow water sites along the edge of creeks and cattle tanks but a few were collected some distance from water where dense vegetation was present. It is surprising that none of these 37 ranid frogs were infected since 5 North American ranids (R. catesbeiana, R. clamitans, R. pipiens, R. septentrionalis and R. sylvatica), all from northern latitudes, have been reported previously to harbor coccidia and many other ranids from other continents are known to serve as hosts for various coccidians (see Levine and Nye, 1977; Upton and McAllister, 1988a; Chen and Desser, 1989). Indeed, this disparity probably is related to the general lack of surveys for coccidia from North American amphibians.

As a group, coccidia of Anura consist of numerous poorly described species, many of whose taxonomic affinities can only be postulated. For instance, reports by Hegner and Chu (1930), Griner (1983) and Valentine and Stoskopf (1984) of unidentified coccidians

in Asiatic horned frogs, R. vittigera from the Philippines and neotropical marine toads, B. marinus, respectively, are not complete enough to even place the coccidia in the proper genus. In addition, Yakimoff and Gousseff (1936) described a new species of eimerian, E. transcaucasica, from the intestinal tract of B. bufo. Except that the article is in Russian and has a different specific epithet, it is virtually identical (including format, tables, measurements, geographic and host data) to the description of E. mazzai, written in German by Yakimoff and Gousseff (1934). It is apparent that an error occurred, which Pellérdy (1974), Saxe (1955) and Walton (1964b) all eluded to when they reported the validity of the former species was questionable. Perhaps the first article was delayed in press, or the manuscript lost in transit, long enough so that the authors thought it would not be published. Resubmitting the manuscript elsewhere, they used a different specific epithet. Whatever the cause, it is obvious the 2 articles are duplicates.

Numerous host/parasite lists and indexes were published throughout the middle part of the century by A. C. Walton, eventually summarized in a series of monographs (Walton 1964a, 1964b, 1966, 1967). Although containing a considerable amount of taxonomic information, numerous errors and unsubstantiated data

are reported in these compilations. For instance, Walton (1949) reported the nomem nudum Eimeria pylori (Gebhardt, 1897) Levine and Becker, 1933 from North America, despite the lack of morphologic data. In addition, Walton (1941) reported that this species may actually represent eggs of the helminth parasite, Distomum turgidum. Walton (1941, 1961) reinterates Rankin (1937) that 2 salamanders are hosts of Eimeria ranarum, although these data seem unlikely because this coccidium is reported from frogs. Finally, Walton (1941) lists the poorly described coccidium reported by Rivolta (1878) as Isospora ranae (Rivolta, 1878) Dobell, 1909; however, Dobell (1909) never mentions this coccidium.

Sauria

I cannot explain why coccidians were not recovered from any of the 96 lizards examined in this study; however, the number of previous reports of coccidia from saurian hosts in North America suggests a low prevalence of infection. Indeed, Matuschka and Bannert (1987) and Matuschka (1989) collectively list 30 species of Eimeria and 19 species of Isospora from lacertilian (saurian) hosts, excluding gekkonids. Of the species listed, only 20% of the eimerians and 11% of the isosporans are known from North America (6 from iguanids, 2 from xantusids

and 1 from a scincid). In addition, all of the lizards that have been reported to serve as hosts for coccidia were collected from humid regions of the extreme western or Gulf Coastal area of the U. S. in the states of California, Washington and Louisiana (Bovee and Telford, 1965a, b; Bovee, 1966, 1969; Clark, 1970; Pellerdy, 1974; Atkinson and Ayala, 1987).

It is possible that lizards from the study area did not serve as suitable hosts for coccidia because of habits of defecation. Many of the lizards were observed to bask upon limestone outcroppings, logs and miscellaneous debris. As soon as lizards deposited feces on the substrate, the pellet was dessicated within minutes. During periods of increased lizard activity, typical substrate temperatures can range from 35-45 C. If these conditions predominated (as they did during lizard activity seasons at the study areas described herein), the upper high temperatures would not represent ideal conditions for coccidia to develop or even remain viable. Indeed, the process of sporulation is clearly temperature dependent (Long and Joyner, 1984). For example, Lindsey et al. (1982) reported that oocysts of I. suis were unable to sporulate at temperatures above 37 C. Further, except for 5 skinks and 3 horned lizards collected during this study, all of the remaining lizards were observed to be most active during warmer

periods of the day. If lizards defecated at these times, it would serve to limit viability of oocysts that have exogenous sporulation.

Testudines

The Testudines were the most commonly infected host group examined in this study. Seventy-one percent of this group were infected with at least 1 coccidian. Since the majority (79%) of turtles examined were aquatic, perhaps coccidian oocysts persisted longer in an aqueous environment and became more accessible to suitable hosts. However, even terrestrial box turtles, T. o. ornata, which inhabits more arid regions of the study area had prevalence of infection of 38%.

The information in Table V, as well as data presented in previous turtle surveys (see McAllister and Upton, 1989c for summary), support the contention that most species of coccidia from turtles in aqueous environments in North America are not particularly species specific. For example, 3 turtle hosts (T. s. elegans, P. texana, and K. f. flavescens) were sometimes collected from the same locale and, except for apparent host specificity among a few of the species reported herein, some species of Coccidia were found to be shared among members of different turtle families (see Table V). However, the majority of species of coccidia in the

Testudines do appear to be specific at the family level. For instance, the painted turtles (Chrysemys), cooters (Pseudemys), map turtles (Graptemys), and sliders (Trachemys) are all included within the family Emydidae and share several Eimeria spp. A few coccidia also appear unique to their respective genera, for example, E. trachemydis in T. s. elegans, several Eimeria spp. in P. texana, and E. carri and E. ornata in Terrapene spp., the box turtles. Although a few coccidia also appear to be shared with mud turtles (Kinosternon spp.), this might be expected since the Kinosternidae are considered the closest living relatives of the Emydidae. Sympatric Chelydra (Chelydridae) and Apalone (Trionychidae), which are considerably more primitive and advanced, respectively, were never found to possess any of the species of coccidia found within the former 2 families. This rule applied even when hosts from various families were sampled from the same ponds. The only exception to this hypothesis is E. mitraria, a coccidian reported not only from Emydidae and Kinosternidae, but also Chelydridae (Wacha and Christiansen, 1980). However, further studies do not support the contention that Chelydra serpentina is a host for this coccidian. Indeed, even when the parasite is prevalent in Emydidae from a single locale, snapping turtles collected from this same pond were never found to be infected with this

parasite (McAllister et al., 1990b). Rather, a morphologically similar coccidian, Isospora chelydrae McAllister, Upton, and Trauth, 1990, occurs in C. serpentina and these authors hypothesized that this may actually have been the coccidian seen by Wacha and Christiansen (1980). Another plausible explanation is that the report of E. mitraria from C. serpentina actually represents a pseudoparasite. Snapping turtles readily eat small members of the Emydidae and, considering the high prevalence of the parasite within the latter family, oocysts would probably be detected periodically in the feces of C. serpentina.

Coccidia of Testudines are largely comprised of adequately described species that appear to be true endoparasites of turtles. With the exception of an apparent pseudoparasite, Mantonella hammondi from a single Illinois mud turtle, K. f. spooneri, in Iowa (see Wacha and Christiansen, 1976), all of the remaining 39 coccidians from turtles appear to have sound descriptions (McAllister and Upton, 1989c).

Although some size differences occur between the box turtle coccidians E. ornata and E. carri, a description of the former coccidian is provided herein based primarily on marked differences in sporulation. Except for the presence or absence of a polar granule, a vacuole in the oocyst residuum and slight differences in

oocyst size, the oocysts of the 2 species appear similar. However, by examining the historical range and ecological and habitat requirements of the 2 host species in question, an adaptive explanation for differences in sporulation can be found. As previously noted, T. ornata inhabits xeric areas of the south and midwest unlike its eastern relative T. carolina, which prefers more humid woodland habitats. In order to coevolve with its host and persist in a harsher environment, E. ornata is likely to be passed in the feces fully sporulated and therefore capable of immediately infecting another turtle. Eimeria carri sporulates exogenously and this sporulation pattern is possibly related to a higher humidity and more precipitation in its environment.

Serpentes

The second most commonly infected host group were the snakes. Twenty-five percent of 24 snake taxa were infected with at least 1 species of coccidian. However, if terrestrial snakes are excluded from the prevalence data, almost one-half (47%) of all aquatic snake taxa (3 species of Nerodia and 2 species of Thamnophis) were infected and only 14% of the true terrestrial snakes harbored coccidia. These data suggest a positive correlation between prevalence and snakes that inhabit

aqueous environments.

In addition to the forms described herein as new, several other species of coccidia were observed in some of the snakes collected. Eimeria attenuata Wacha and Christiansen, 1974 was found in T. p. rubrilineatus. It infects several species of thamnophiine colubrids (see Upton and McAllister, 1990; table II), and most likely will be found in additional semiaquatic hosts in the future. A second eimerian, also found in Virginia striatula, cannot be named at this time because only a few oocysts were found to sporulate within the samples. However, unlike E. striatula Upton and McAllister, 1990, oocysts of this coccidian were found to have stouter sporocysts and possess a distinct oocyst residuum. Further studies in the future, perhaps using tap water or saline solution and antibiotics as a collection medium, may eventually allow enough specimens to complete development so that an adequate description can be obtained.

Sarcocystis spp. were found in the feces of 8 C. atrox and in a single M. f. testaceus. Since the life cycle is obligatory heteroxenous, that is, asexual development occurs in carrion and prey species (rodents) and sexual development takes place in predators (snakes) or scavengers (Markus, 1978), experimental transmissions were attempted in mice. The negative results strongly

suggested that this coccidian may be a species distinct from S. crotali and S. muriviperae, which are both capable of infecting Mus musculus and are the only other known species of Sarcocystis from viperid snakes (see Matuschka, 1987 for review). Because no positive controls were used to measure sporocyst viability, however, caution must be used when interpreting the data. If this coccidian is found to be a valid species of Sarcocystis, the probable host could be Peromyscus spp. These rodents were the most common food items that were encountered during this study in stomach contents of C. atrox. Sarcocystis peromysci Dubey, 1983 has been reported from deer mice, P. maniculatus and the definitive host is unknown (Dubey, 1983). Another possibility is S. sigmodontis Dubey and Sheffield. 1988, a sarcosporidian described from the cotton rat, Sigmodon hispidis, a common rodent in the study area but also with an unknown definitive host (Dubey and Sheffield, 1988). Numerous other rodents, including voles, squirrels, and chipmunks, are also potential intermediate hosts (see Dubey et al., 1989 for review) as well as common rodents of the study area (pygmy mice, harvest mice, pocket mice and woodrats). Further investigation utilizing native rodents from the study area in experimental transmission studies will likely confirm that this coccidian is indeed a new species of

Sarcocystis.

The recovery of oocysts of Caryospora duszynskii Upton et al. (1984) from E. g. emoryi and E. o. lindheimeri in northcentral Texas represents new host and locality records for the parasite. This coccidium was reported previously from the related corn snake, E. g. guttata in Georgia and black rat snake, E. o. obsoleta in Missouri (Upton et al., 1984). Forty species of Caryospora have been reported from hosts worldwide, mostly in snakes (Upton et al., 1986; Upton and Sundermann, 1990). Several studies (Stockdale and Cawthorn, 1981; Cawthorn and Stockdale, 1982; Wacha and Christiansen, 1982; Upton et al., 1983) have demonstrated heteroxenous life cycles for Caryospora spp., although Upton et al. (1984) failed to infect laboratory mice with C. duszynskii using 10,000 oocysts and speculated that not all Caryospora spp. may be heteroxenous.

My interpretation of the statistical and visual results and data from Upton et al. (1989) suggests that more than 1 species of Cryptosporidium exists in reptiles. However, until additional isolates can be examined, and sites of infection and life cycles be established, it would be premature to name any new species at this time. One reason is that several investigators have shown that oocyst size (but usually

not shape index) may fluctuate significantly depending upon the time of patency (reviewed by Duszynski, 1971). It should be noted, however, that oocysts of Cryptosporidium spp. can be shed over many months by some reptiles and it is possible that significant changes in oocyst size may not occur with Cryptosporidium spp. (Upton et al., 1989). Continual or prolonged shedding of Cryptosporidium spp. by snakes also has been observed previously by others (Boylan et al., 1985; Brownstein et al., 1977). Another reason for not naming new species of Cryptosporidium is that although the wavelength of light allows for a 0.2 µm resolution, it is improbable that this resolution is actually achieved by most conventional light microscopy optics. Therefore, a certain amount of inherent variability exists in the study of Upton et al. (1989) that prompts caution when interpreting the data.

It appears important to measure oocysts of Cryptosporidium spp. from aquatic snakes relatively quickly following flotation. Although Sheather's sugar solution did not significantly affect oocyst measurements immediately after flotation, prolonged exposure would probably have resulted in significant changes among some isolates. Therefore, measurements presented in Table IX were based on $\leq$ 30 min exposure to the flotation medium.

Host phylogeny of Thamnophiine snakes

Recent molecular evidence (Lawson, 1987) suggests that the New World natricine snakes are composed of 3 distinct lineages, viz. the taxispilota group, the cyclopion group, and the sipedon group (the latter including the garter and ribbon snakes, genus Thamnophis). It is noteworthy that some coccidians are shared among 3 species of sympatric Nerodia and/or Thamnophis spp. (see Table VIII). For example, E. attenuata was found only in N. e. transversa and T. p. rubrilineatus and is corroborated by molecular data that suggests the genus Thamnophis to be phylogenetically closer to N. erythrogaster (Lawson, 1987). In addition, Wacha and Christiansen (1974) reported that E. attenuata appeared to be shared by T. sirtalis and N. sipedon. The molecular approach again supports these organismal data because Thamnophis has been noted to be associated with the sipedon group leading to N. erythrogaster, N. harteri, Regina sp., and other Nerodia spp. (Lawson, 1987).

Based on the above information and that of Wacha and Christiansen (1974, 1975), the following may be summarized about eimerian coccidia in thamnophiine snakes: (1) E. attenuata is shared by N. e. transversa, N. sipedon, and some Thamnophis spp., (2) E. sipedon by N. sipedon and N. e. transversa, (3) E. hydrophis by N.

r. rhombifera, N. sipedon, N. h. harteri, and N. e. transversa, (4) E. helmisophis by C. a. vermis, N. r. rhombifera, N. h. harteri and N. e. transversa, (5) E. conanti by N. e. transversa and N. h. harteri, and (6) E. infirmus, E. rhombifera, and E. tenuis are not shared by other sympatric Nerodia spp. examined and have only been found in N. r. rhombifera. Thus, it appears that these preliminary organismal-level data where sharing of parasite species was noted supports the contention of Lawson (1987) that Thamnophis is more closely related to N. erythrogaster and other species within the sipedon group (N. clarkii, N. fasciata, N. harteri and N. sipedon) than to N. rhombifera or N. taxispilota of the taxispilota group of North American water snakes. However, the relationship is unclear as to why N. e. transversa and N. h. harteri share E. helmisophis with N. r. rhombifera but apparently are more host specific for E. conanti. These data are similar to that reported herein for the turtle, Trachemys scripta elegans, where there appears to be a differential host specificity to the various species of coccidia.

Multiple hypotheses are possible for the data on host phylogeny of thamnophiine snakes. For instance, if geographic ranges of potential host species come into contact after reproductive isolation, it is possible that only some species of coccidia become biologically

accessible to other potential hosts that share niche overlap. Alternatively, a certain coccidium could become isolated from conspecifics due to behavioral differences of the host. Some coccidia, may have more intermittent exposure than others due to host behavior and, thus, be more tolerant to the intestinal physiology of "occasional" hosts (Price, et al., 1988). Thus, strict coevolution of host and parasite may not completely explain patterns of infection. Further investigations that involve examining additional species of Nerodia and those which include conducting cross transmission and life cycle studies may be necessary to clarify this question.

CHAPTER VII

SUMMARY

Several new and previously described coccidians were recovered from amphibians and reptiles in northcentral Texas. Of 863 individual herptiles examined, coccidians were found in 176 (20%) hosts; 13% were amphibians and 28% were reptiles. When hosts are broken down into 5 groups, 26% of the salamanders, 11% of the frogs and toads, 0% of the lizards, 54% of the turtles, and 25% of the snakes harbored 1 or more species of coccidian parasites. In addition, 20 previously described coccidians, including 1 in salamanders, 13 in turtles and 6 from snakes were found whereas 16 new species, including 4 from anurans, 5 from turtles and 7 from snakes were recovered.

No preference for coccidia was found between host sexes. Furthermore, no difference was found either when host sexes were examined for 4 individual groups (see Figs. 7, 10, 11, 13) or when these groups were combined (n = 526 individuals; 274 males, 252 females), as 29% of the males and 31% of the females harbored Coccidia (X^2 = .74, 1 df, $p > .11$).

Only enough data was collected from a single host

(G. olivacea) to determine whether prevalence of coccidia was higher in wetter months of spring than in the hot, dry summer. A large sample (n = 126) of narrowmouth toads collected from February to October revealed that prevalence of I. fragosum was two-fold higher in spring months (March-May, 13/54, 24%) when precipitation was highest than in summer (June-September, 6/51, 12%). However, this prediction could not be tested in other hosts because not enough animals were collected throughout the year to allow for comparison.

Overall prevalence of infection with coccidia was higher in aquatic/semiaquatic hosts than in strictly terrestrial species. When the 2 host groups are examined, 153/608 or 25% of the aquatic/semiaquatic hosts were infected compared to only 24/255 or 9% of the terrestrial hosts (X^2 = 26.39, 1 df, $p < 0.0001$). However, the analysis appears to be biased due to variability in samples sizes among the groups. For example, all of the salamanders, many of the anurans and most of the turtles were aquatic/semiaquatic while all of the lizards, which were not infected, were terrestrial. Therefore, the only group data which can truly examine this is from the Serpentes. Of 75 aquatic/semiaquatic snakes, 34 or 45% harbored coccidia

while only 18 (13%) of the 142 terrestrial snakes were infected ($X^2 = 26.96$, 1 df, $p < 0.0001$).

Depending on whether there is actually true host specificity of coccidia, perhaps coevolutionary relationships could be inferred using organismal data supplemented by previously published molecular approaches. Although this could only be used with 2 groups, the Testudines and thamnophiine snakes, preliminary information from the both groups suggested that this may be an alternative method of studying host phylogeny. However, as noted previously, true host specificity would have to be proven utilizing cross-transmission and life cycle studies before information derived from the study of coccidian parasites could be used to supplement genetic data on host phylogeny.

The preliminary information presented herein will hopefully provide foundation for future studies and lead to better understanding the role that coccidian parasites play in natural populations of amphibians and reptiles. As far as I know, the present work represents the first attempt to survey a large sample of herpetofauna from a defined geographic area for coccidial parasites. Thus, being able to relate these results with previously published anectodal information

on coccidia of amphibians and reptiles is a major step towards filling a void and bring about an interest equal to that seen in coccidia of birds and mammals.

APPENDIX

Sixteen new species of coccidia found in amphibians and reptiles from northcentral Texas during this study which were formally published in the scientific literature prior to the completion of the dissertation.

NEW SPECIES	REFERENCE
Isospora fragosum	Upton and McAllister, 1988a
I. delicatus	Upton and McAllister, 1988a
Eimeria conanti	McAllister and Upton, 1989b
E. cooteri	McAllister and Upton, 1989c
E. flexuosa	Upton and McAllister, 1988a
E. infirmus	Upton and McAllister, 1988b
E. ornata	McAllister and Upton, 1989a
E. papillosum	Upton and McAllister, 1990
E. rhombifera	Upton and McAllister, 1988b
E. serpenticola	Upton and McAllister, 1990
E. streckeri	Upton and McAllister, 1988a
E. striatula	Upton and McAllister, 1990
E. stylosa	McAllister and Upton, 1989c
E. tenuis	Upton and McAllister, 1988b
E. texana	McAllister and Upton, 1989c
E. trachemydis	McAllister and Upton, 1988

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