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Coccidia of Gerbils from Mongolia

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COCCIDIA OF GERBILS FROM MONGOLIA

by

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In this study, gerbils collected in the Mongolia over the summers of 2009-2012 were examined for coccidia. In total, 171 gerbils of three species from 22 localities were examined for coccidia. Coccidian oocysts were identified from 21 gerbils, but those found in 1 of those gerbils were probably pseudoparasites of the host from which they were recovered. From the remaining 20 gerbils, 7 morphotypes of *Eimeria* and 1 morphotype of *Isospora* were identified. Four of the 7 morphotypes of *Eimeria* were attributed to new species which were described in this study. In addition, 10 previously described species of *Eimeria* were recommended to be considered junior synonyms or *species inquirendae*. Phylogenetic analyses of the species of *Eimeria* identified in this study based on 9 continuous and 12 categorical morphological characters were then performed. The anaylsis which produced the highest consistency index (CI = 0.6667, excluding uninformative characters) used all data with unweighted character states and produced 3 equally parsimonious trees. However, the tree score distribution for this analysis was only weakly skewed right with a g1 value of −0.25439, indicating a lack of phylogenetic information. The analysis which produced the most strongly right skewed

tree score distribution (g1 = −0.4950) used only categorical data with characters weighted inversely to the number of states and produced seven equally parsimonious trees. In order to predict the spatial distribution of *Eimeria* spp. occurring in gerbils in Mongolia and identify any apparent ecological trends, ecological niche models (ENM's) were produced using both GARP and Maxent, and chi-squared tests were performed to identify correlations between infection with species of *Eimeria* or *Isospora* and host species, sex, infection with helminths, and year and month of capture. ENM's produced with GARP predicted that *Eimeria* spp. occur in 28.63% of Mongolia, while the model produced with Maxent predicted the *Eimeria* spp. occur in 28.70% of Mongolia. The environmental variables with the greatest percent contribution to the ENM predicting the distribution of *Eimeria* spp. created with Maxent were Normalized Differential Vegitative Index (NDVI), mean precipitation of the driest month, and aspect. The only significant (α=0.10) correlation found using a chi-squared test was that between host species and infection by *Eimeria* spp. (p=.07); oocysts of *Eimeria* spp. were recovered from 5% of hosts of *Meriones meridianus* and 14% of hosts of *Meriones unguiculatus*. The additions and revisions to the taxonomy of the coccidia of gerbils in this study contribute to the knowledge base of host-parasite associations which may serve as a foundation for future studies in a wide variety of fields, and while the distributions predicted and phylogenies produced in this study are tentative, they may serve as a starting point for future investigators.

NOMENCLATURAL DISCLAIMER:

This thesis contains species descriptions and taxonomic revisions. However, numerous identical copies of this thesis are not available, nor are electronic copies widely available (Article 8.1.3, International Code of Zoological Nomenclature, ICZN, 1999). Therefore, this thesis is not issued for the purpose of public and permanent scientific record, and remains unpublished for the purposes of zoological nomenclature (Article 8.2). Taxonomic additions and revisions in this thesis will be later made available in widely accessible scientific publications.

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I. INTRODUCTION

Over the summers of 2009-2012, mammals, birds, reptiles and amphibians were collected across Mongolia as part of the Mongolian Vertebrate Parasite Project (MVPP), and their internal and external parasites were documented and preserved. This study presents a survey of the parasites of the family Eimeriidae Minchin, 1903 occurring in gerbil hosts collected as part of the MVPP.

Background

In order to provide a background of knowledge to facilitate the understanding and interpretation of this study, a brief introduction to the parasites (the Eimeriidae), the hosts (the genus *Meriones* Illiger, 1811) and the study location (Mongolia) is provided below.

The Eimeriidae, Minchin 1903

The coccidia are one of the most common and speciose of known parasite groups. Technically, a "coccidian" is any member of the suborder Coccidiasina Leuckart, 1879, however, in the stricter sense of the word, a coccidian is a member of the order Eimeriida Minchin, 1903 or Adeleida Léger, 1911 (Adl et al., 2005). This thesis focuses on the family Eimeriidae, and more specifically, the genus *Eimeria* Schneider, 1875, which are the largest family and genus of coccidia with over 2,000 and 1,300 species described, respectively (Duszynski et al., 2000).

As far as is known, species of the Eimeriidae have a monoxenous (single-host) lifecycle which consists of three phases: merogony, in which asexual reproduction occurs; gamogony, in which sexual reproduction occurs, and sporogony, in which a spore known

as the oocyst is formed. The following description of the lifecycle of *Eimeria nieschulzi* (Fig. 1) Dieben, 1924 is from Levine and Ivens, 1957:

> "The sporulated oocyst is ingested by the host. Chemical and mechanical forces in the host digestive tract stimulate the release of the sporocysts from the oocysts, and the haploid sporozoites from the sporocyst. The sporozoites then penetrate intestinal epithelial cells. Merogony (asexual reproduction) occurs within the host cells which then burst, releasing merozoites. The merozoites then penetrate uninfected epithelial cells, and merogony is repeated. The number or merogony cycles varies between species of *Eimeria*. In gametogony, merozoites penetrate host cells and become either microgametocytes, which burst open releasing microgametes, or macrogametes, which grow until microgametes penetrate the same epithelial cells and fuse to become diploid zygotes. The zygote then secrets granules which coalesce to form a wall and becomes an unsporulated oocyst. Upon being passed in the host's feces, external environmental factors trigger sporogony, in which the unsporulated oocyst undergoes meiosis and forms sporocysts which contain sporozoites.
>
> The oocyst is of particular taxonomic importance, as it is the most readily obtained and observed part of the lifecycle. For these reasons, more than 98% of species in the family Eimeriidae are known by the oocyst, alone (Duszynski et al., 2000). This study focuses on taxonomy, but a variety of sources are available for those interested in other aspects of the biology of the Eimeriidae (e.g., Duszynski et al., 2000; Pellérdy, 1974; Long, 1982; Hammond and Long, 1973).

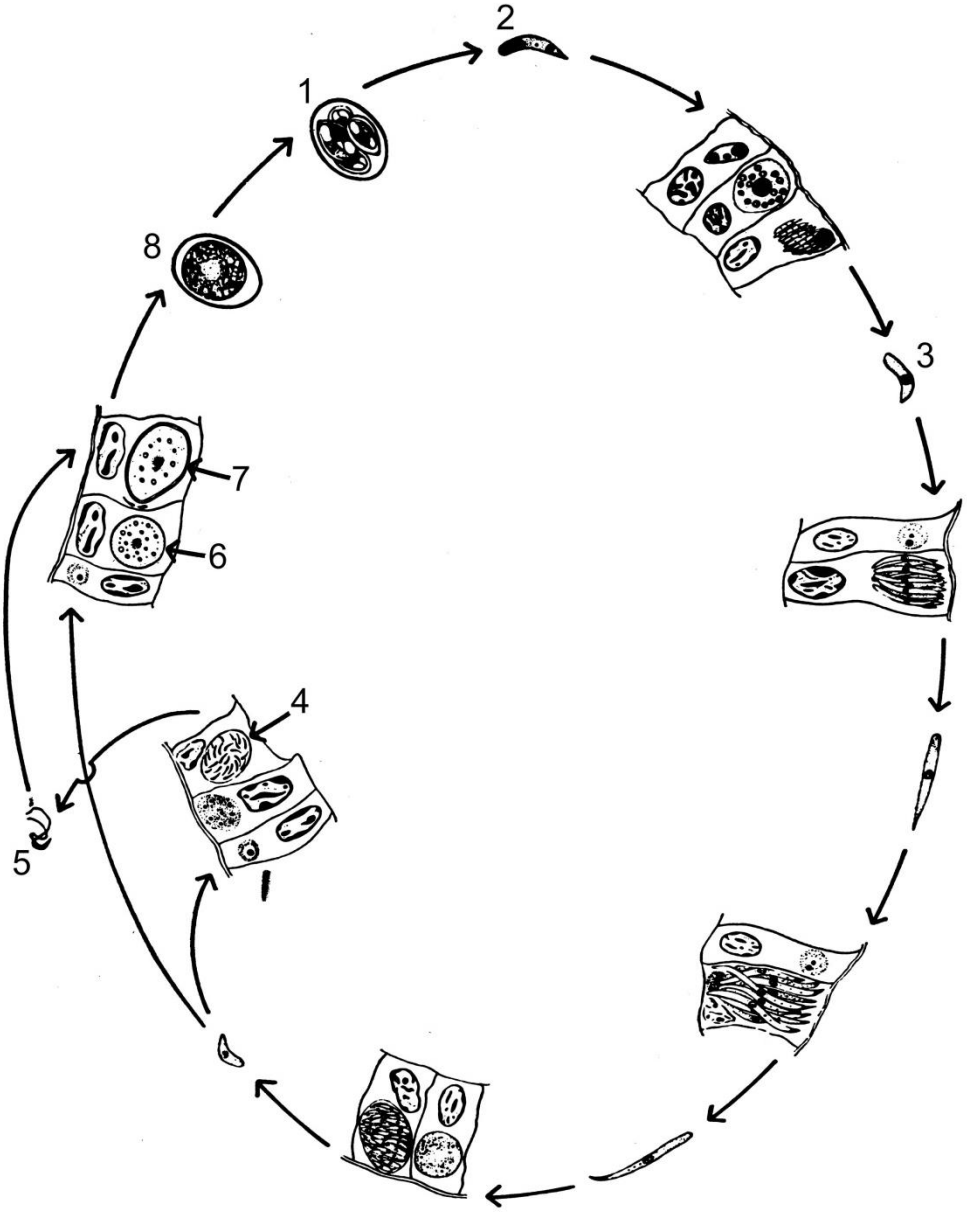


Figure 1: Lifecycle of *Eimeria nieschulzi* from Levine and Ivens, 1957. Labeled stages are sporulated oocyst (1), sporozoite (2), merozoite (3), microgamotocyte (4), microgamete (5), macrogamete (6), zygote (7), and unsporulated oocyst (8). Four generations of merogony are depicted.

The importance of the study of the Eimeriidae is not merely academic; annual global damages caused by these parasites have been estimated at $400 million for the beef industry (Williams, 1998) and $800 million for the poultry industry (Matjila and Penzhorn, 2002). Additionally, species such as *Cyclospora cayetanensis* Ortega, Gilman and Sterling, 1994 are medically important human pathogens (Ortega et al., 1997).

The majority of the Eimeriidae, however, are threats to neither human health nor that of agricultural animals. Due to their occurrence in nearly every vertebrate species (Levine, 1962) and their high host specificity, the Eimeriidae may serve as excellent probes for investigations of historical ecology, epidemiology, immunology, and biogeography (Tenter et al, 2002). As Bandoni and Duszynski (1988) pointed out, however, a "shaky taxonomic foundation" undermines all other investigations involving the Eimeriidae. Among other things, coccidian taxonomy is impaired by a limited sampling of host taxa, which has been heavily though understandably biased towards hosts of medical or economic importance (Morrison, 2009).

As the vast majority of coccidian species are known by the sporulated oocyst alone (Duszynksi et al., 2000), a basic familiarity with the structures of the oocyst (Fig. 2) is a prerequisite to any investigation or discussion of coccidian taxonomy. The walls of oocysts of eimeriid species may be single, double (as in Fig. 2), or triple layerd, and range in texture from completely smooth or slightly dimpled to very rough or mammilated. Oocysts may possess multiple or a single polar granule, which may be spherical or irregular in shape. The oocyst residuum may be composed of a single or several globules, which may be compact or diffuse. Oocysts may possess an opening at

one end known as the micropyle (not shown in Fig. 2), which may or may not be covered with a structure known as the micropyle cap.

Sporocysts may or may not possess a Stieda body, which may range in appreance from inconspicuous and chip-like to rather conspicuous and nipple-like. Sporocysts may or may not possess a substieda body, which is just posterior to the Stieda body, or a parasiteda body, which is at the pole of the sporocyst opposite the Stieda body. Similar to the oocyst residuum, the sporocyst residuum may consist of a single to many globules, and may be compact or diffuse, if it is present at all. The sporozoites may be arranged longitudinally (as in Fig. 2), or at opposite poles of the sporocyst. Finally, the sporozoites may possess a number of refractile bodies, sometimes called refractile globules. The number of refractile bodies is not always apparent, as the cytoplasm of the sporozoites may be coarsely granular, which may obscure other details of sporozoites morphology.

Mongolian biodiversity

Mongolia is a landlocked East Asian country over 1.5 million km^2 in area (USGS, 2008). The combination of desert and semi-desert ecosystems, the range in elevation, and the extreme temperature range support a mammalian fauna more diverse than that of similar North American habitats (Tinnin et al., 2002). These habitats include grasslands, semi-desert shrubland, bare desert, upland tundra, deciduous forests (conifer, broadleaf and mixed) and boreal forests (USGS, 2008). Vertebrate species which occur in Mongolia include 6 amphibians (Terbish et al., 2006), 21 reptiles (Terbish et al., 2006), 427 birds (Lepage, 2013), and at least 136 mammals (Tinnin et al., 2002).

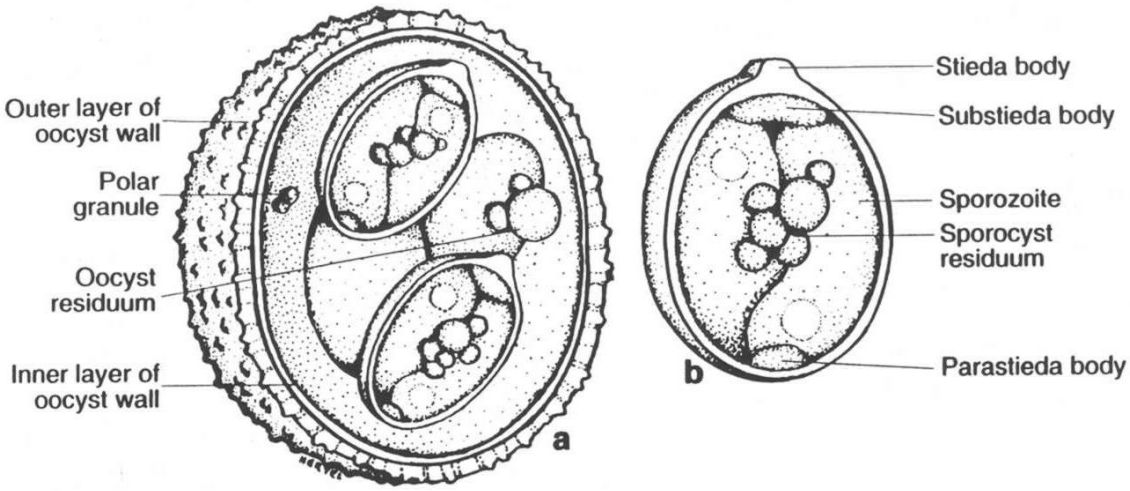


Figure 2: Morphology of sporulated oocyst (a) and sporocyst (b) of *Eimeria* sp. from Duszynski et al., 2000.

The Mongolian Vertebrate Parasite Project (MVPP) is a multinational, multi-university collaboration between Mongolian (University of Mongolia), American (University of Nebraska, University of New Mexico, University of Kansas), Japanese (Hokkaido University) and French (National Natural History Museum) institutions (American Center for Mongolian Studies, 2012). The objectives of the MVPP are to discover, describe, and document the vertebrates of southern Mongolia and their parasites, which are historically understudied (Tinnin, 2008). Field surveys conducted over the summers of 2009-2012 as part of the MVPP provided the specimens examined in this study.

The genus Meriones, *Illiger 1811*

There are four species of gerbil known to occur in Mongolia: *Meriones meridianus* Pallas, 1773, *Meriones tamariscinus*, Pallas, 1773, *Meriones unguiculatus*, Milne-Edwards, 1867, and *Rhombomys opimus*, Lichtenstein, 1823. This study focuses on gerbils of the genus *Meriones*, especially *M. unguiculatus* and *M. meridianus.* The genus

Meriones contains 17 species that are distributed throughout North Africa, the Middle East, and Central and East Asia (Musser and Carleton, 2005). Like other desert mammals such as heteromyids, *Meriones* spp. and other gerbil species are highly adapted to desert life. For instance, when given unlimited access to water in a laboratory setting, individuals of *M. unguiculates* drink only half much as individuals of *Rattus norvegicus* Berkenhout, 1769 (Harriman, 1969).

Given its prevalence as an experimental host in laboratory settings, remarkably little is known about the parasites which infect *M. unguiculatus* in its natural habitat. There are only nine publications which report on helminth parasites occurring in *M. unguiculatus* in the wild (see Tinnin et al., 2011), and one which reports on coccidian parasites (Machul'skii, 1949).

The Eimeriidae of Meriones

Though little is known of the coccidian species which infect *M. unguiculatus*, the Eimeriidae which infect species of the genus *Meriones* are overrepresented in the literature relative to those which infect other genera in the subfamily Gerbillinae Gray, 1825. Though the genus *Meriones* contains only 17 of the 103 species in the subfamily Gerbillinae (Musser and Carleton, 2005), 48 of the 57 species of eimeriid described from gerbils infect hosts of the genus *Meriones* (Levine and Ivens, 1990; Duszynski et al., 2000; Modrý et al., 2008). Of these 48 species infecting *Meriones* spp., 7 are of the genus *Isospora* Schneider, 1881, and 41 are of the genus *Eimeria*. However, only *Eimeria merionis* Machul'skii, 1949 is known to infect individuals of *M. unguiculatus*. *Eimeria merionis* is also the only species reported from what is now the country of Mongolia.

Four species (*Eimeria karschinica* Davronov, 1973, *Eimeria kostencovi* Davronov, 1973, *Eimeria uzbekistanica* Davronov, 1973, *Eimeria meridiana* Veisov, 1964) are reported from *M. meridianus*. Of these five species which infect either *M. unguiculatus* or *M. meridianus*, only *E. merionis* has ever been reported subsequent to its initial discovery (Svanbaev, 1956). Considering the dearth of knowledge regarding the coccidian fauna of gerbils from Mongolia, it is a topic ripe for investigation.

Summary of the present study

Purpose and significance

The goal of this thesis is to contribute to the taxonomy of the Eimeriidae and broaden the knowledge of the associations between these parasites and their gerbil hosts, specifically those occurring in Mongolia. I will accomplish this goal by isolating, identifying, and if necessary, describing species of the family Eimeriidae from gerbils collected in Mongolia over the summers of 2009-2012 as part of the MVPP. In doing this, I seek to expand the knowledge base of the parasite fauna of species of *Meriones* occurring in Mongolia. By documenting what eimeriid species occur in gerbils in Mongolia, I will contribute to the knowledge base of host-parasite associations which may serve as a foundation for future studies in a wide variety of fields, such as ecology, biogeography or epidemiology.

Objectives

The objectives of this study are as follows:

1. To discover and document what species of coccidia occur in hosts of the genus *Meriones* in Mongolia.

2. To contribute to the taxonomy of the Eimeriidae by describing new species and if necessary, identifying previously described species which are likely synonymous or invalid, and designating neotypes for species to which no type material is attributed.
3. To investigate the phylogenetic relationships among these parasites.
4. To predict the spatial distribution of the Eimeriidae occurring in gerbils in Mongolia, and if possible, identify any apparent ecological trends in said distribution.

Overview of methodology

In order to accomplish the aforementioned objectives, a survey of the coccidian parasites infecting gerbils collected in Mongolia as part of the MVPP was conducted. Though I only participated in the collecting and processing of hosts over the summer of 2012, hosts from all four years (2009-2012) were screened for coccidia. Species of Eimeriidae were then identified and described based on the morphology of recovered oocysts. The morphological data gathered in order to describe and identify these species was then used to perform a cladistic analysis using parsimony methods. In addition, the geographic coordinates of localities for infected hosts were used along with a variety of environmental geospatial data from multiple sources in order to predict the distribution of the Eimeriidae infecting gerbils in Mongolia using both the algorithms GARP (Stockwell and Peters, 1999) and MaxEnt (Phillips et al., 2006).

In order to facilitate species identification, I reviewed the existing literature regarding species of the Eimeriidae infecting gerbils and created a dichotomous key to aid in their identification. In the process of constructing this key, I identified multiple species in which the oocysts are morphologically indistinguishable. When factors other than oocyst morphology also failed to distinguish these species, I provided arguments for why said species should be considered synonymous or invalid.

Limitations

The goal of the MVPP is to discover, describe and document the parasite and vertebrate biodiversity of Mongolia (Tinnin, 2010). One result of the breadth of this goal is that investigations in multiple fields including mammalogy, ornithology, helminthology and protozoology occur concurrently as part of the MVPP. Thus, field sampling was not specifically optimized for the investigation of gerbil or coccidian biodiversity. For instance, sampling localities were chosen to maximize the diversity of mammals and birds collected; they were not sampled randomly or with protozoon diversity specifically in mind.

Also, the nature of field work, especially in rural Mongolia, placed constraints on the sample size. While over 400 gerbils were collected, fecal pellets were only preserved for 171 of them. This was partially because when field supplies such as Snap Cap® vials began to run low, only feces from rare host species, such as *Cardiocranius paradoxus* Satunin, 1903 were preserved.

Delimitations

Due to time constraints, the scope of this study is limited in two important aspects. First, while the importance of describing the entire lifecycle of the Eimeriidae has been stressed by some (e.g. Tenter et al., 2002), the species described in this study will be among the >98% of the Eimeriidae (Duszynski et al., 2000) known by the oocyst alone. Additionally, only morphological data will be used for the cladistic analysis. However, because methods for DNA extraction of oocysts and DNA amplification and sequencing are continually being refined, and because the samples of oocysts used in this study are preserved in potassium dichromate solution and their DNA should therefore remain intact until at least the year 2033 (Williams, 2010), I encourage any and all future investigators to obtain molecular data from these oocysts.

Organization of thesis

This chapter (Chapter I) provided a brief overview of the parasites, hosts, and localities with which this study is concerned and identified its purpose, objectives, limitations, and delimitations. Chapter II consists of an in depth review of the literature regarding the taxonomical methodology related to and systematics of the coccidia, as well as the taxonomy and systematics of the host group and a summary of what has been published regarding the Eimeriidae occurring in gerbils. Chapter III details the methods used in this study, and Chapter IV presents the results, which are interpreted and discussed in Chapter V.

II. LITERATURE REVIEW

The coccidia and other apicomplexans present many unique challenges to taxonomists due to their being obligate intracellular parasites. While much progress has been made in overcoming these challenges, many of them persist to this day (Tenter et al., 2002). In this chapter, I present an overview of these challenges and efforts to overcome them, both for historical context and as justification for aspects of this study which would be substandard in the investigation of other parasite taxa (*e.g.* I make no attempts to uncover phylogenetic relationships with previously described species of *Eimeria* occurring in gerbils). Though systematic arrangement and classification should reflect phylogeny (Mayr et al., 1953), the current state of coccidian taxonomy falls short of this ideal in several respects (Tenter et al., 2002; Morrison, 2009). Therefore, I address the history of coccidian taxonomic procedures and the understanding of coccidian systematics separately. Then, in order to provide a background of the host and parasite genera that are the object of this study, I present an overview of the systematics of gerbils before finally reviewing the taxonomy of coccidia which occur in gerbils.

Taxonomic methodology

As coccidiologists are fond pointing out (Levine, 1982; Levine, 1988; Duszynski et al., 2000), oocysts of *Eimeria stiedai* (Lindemann, 1895) Kisskalt and Hartmann, 1907 were among the first protozoons viewed by Antoni van Leeuwenhoek with a microscope in 1674 (Dobel, 1958). However, he did not recognize them as parasitic protozoa, and the genera *Eimeria, Adelina,* and *Klossia* were only erected two centuries later in 1875 by Johann G. T. Schneider. The long history of coccidian taxonomy has been plagued by

many challenges, some of which persist to this day. Chief among these challenges are the lack of a type-material tradition, uncertainties in the interpretation of morphological characters, varying and unknown degrees of host specificity, and a lack of adequate methods for molecular analysis.

Type Material

The oocyst is the most durable, persistent, and readily available stage in the coccidian lifecycle. Because of this, the vast majority (98%) of species of *Eimeria* are known only from their oocysts (Duszynski et al., 2000). For most of the history of coccidian taxonomy, there was no widely accepted method for long-term oocyst preservation. The use of fixatives distorts or destroys oocysts (Duszynski and Gardner, 1991), and type cultures are not a practical alternative because apicomplexans cannot be cultured axenically (Bandoni and Duszynski, 1988).

This lack of a type tradition has been a major hurdle for coccidiologists. A type specimen serves as an indisputable, unaltered point of reference; a real physical entity to which a name is anchored (Mayr et al., 1953). Without it, there is often no way for future investigators to verify the species of their specimens, leading to what Bandoni and Duszynski (1988) described as "an endless series of descriptions and redescriptions, with valueless speculation regarding the significance of real or imagined differences." For instance, when Wilber et al. (1998) reviewed and revised the taxonomy of species of *Eimeria* infecting marmotine rodents, they discovered that various authors had updated incomplete species descriptions with information from specimens they had identified as belonging to said species. However, because there were no type specimens with which to

verify the identity of the species, the descriptions changed over time until they no longer resembled the original descriptions (Wilber et al., 1998). The confusion was so great that Wilber et al. reduced the number of named species from 40 to 26, declaring 35% of the species names to be junior synonyms.

In 1978, Marchiondo and Duszynski documented a method for permanently preserving oocysts in resin on microscope slides. However, this method was not widely enacted. This may be because by the time it could be thoroughly validated (see Marchiondo and Duszynski, 1988), advances in photomicroscopy technology had produced a simpler alternative. In 1988, Bandoni and Duszynski published an article calling for the establishment of a coccidian type tradition. Along with advocating the use of oocysts embedded in resin, Bandoni and Duszynski stressed that illustrations intended to serve as type specimens must be based on a single oocyst instead of being composite drawings. Most importantly, they recommended procedures for the use of a series of photographs, dubbed "photosyntypes", as type materials.

Though the photosyntype concept established a widespread and easily accessible type tradition, the obvious drawback was that it did nothing to preserve DNA. Though oocysts could be rinsed from the coverslip and preserved in ethanol for molecular analysis after being photographed (see Duszynski and Wilber, 1997), the methods of DNA extraction prior to 2001 required that oocysts either be present in large numbers (>1,000), or be alive at the time of extraction (see Zhao et al., 2001). Therefore, situations could have occurred in which coccidiologists, given the known methods at the time, would have had to choose between preserving oocysts in ethanol for later molecular analysis or keeping

them in potassium dichromate solution (PDS) for more immediate morphological studies or life-cycle experiments. This dilemma was based on the assumption that PDS, which had long been used for short term preservation of oocysts, was not suitable for long term preservation of both DNA and morphology. However, in 2010, Williams et al. demonstrated that oocyst morphology and DNA were adequately preserved in oocysts which had been placed in PDS for 25 years. This established the use of oocysts in potassium dichromate solution as viable type specimens, at least relative to DNA extraction.

Interpreting Morphology

As previously mentioned, most coccidian species are known by oocyst morphology and the hosts in which they occur alone (Duszynski et al., 2000). Tenter et al. (2002) stated that the inclusion of data on developmental stages, lifecycle, and identification of the true host confirmed by transmission experiments are "essential" in the description of new coccidian species. However, field conditions and host biology are often not conducive to the gathering of such data. While experimental inoculations may be conducted to remedy this problem, it is in many cases costly or infeasible to obtain individuals of the host species, such as when the host's range is limited and remote, the host has protected status, or the host is difficult to rear in a laboratory setting (Williams, 2010). Therefore, it seems that the careful preservation, documentation, and analysis of oocysts will have to suffice in many cases.

Though this morphology centered approach to taxonomy is adequate for many purposes, it is not without shortcomings. Many problems stem from the fact that there are a small

number of morphological characters which are observable through light microscopy (Long and Joyner, 1984; Morrison, 2009). One of these problems is the difficulty in distinguishing between morphologically similar species and polymorphs of a single species. For instance, Duszynski (1971) documented oocysts of *Eimeria separata* Becker and Hall, 1931 varying in size by as much as 40% throughout patency. Later, Gardner and Duszynski (1990) demonstrated that distinct morphotypes of oocysts of *Eimeria opimi* Lambert, Gardner, and Duszynski, 1988 cannot be diagnosed by oocyst and sporocyst length and width. Duszynski et al. (1992) and Upton et al. (1992) documented that *Eimeria arizonensis* Levine, Ivens and Kruidenier, 1957, a parasite of species in the genera *Peromyscus* Gloger, 1841 and *Reithrodontomys* Giglioli, 1873, varies in a number of morphological features depending on the host species from which it is recovered.

In these studies, what was or might have been presumed to be different species were actually polymorphs of a single species. Conversely, multiple valid species of *Eimeria* may produce oocysts which are morphologically indistinguishable. Upton et al. (1992) and Hnida and Duszynski (1999a) demonstrated the validity of *Eimeria albigulae* Levine, Ivens, and Kruidenier, 1957 and *Eimeria onychomysis* Levine, Ivens and Kruidenier, 1957, species which are sympatric with and occur in the same host family as *E. arizonensis*, through cross-transmission experiments.

Since 1999, molecular methods have allowed for investigations of what morphological traits of the oocyst are phylogenetically informative. Carreno and Barta found that phylogenies derived from 18s sequences suggest that *Isospra* spp. whose sporocysts possess Stieda bodies are in the clade Eimeriidae, whereas those that lack a Stieda body

are of the clade Sarcocystidae Poche, 1913 (see 'Generic and subgeneric systematics' under 'Systematics' below) . Two years later, a cladistic analysis based on morphology, mitochondrial 23s, and nuclear 18s rDNA by Zhao and Duszynski (2001) suggested that the presence or absence of an oocyst residuum can be used to distinguish between two major lineages of the genus *Eimeria* in rodents. However, this was not supported by a cladistic analysis of the coccidia based on 18s rRNA by Morrison et al. (2004).

Host specificity

Another major pitfall in coccidian taxonomy is the unknown or inconsistent extent of host-specificity. Parker and Duszynski (1986) delineated four problem areas which arise from the combination of this uncertainty and the aforementioned uncertainty regarding the interpretation of oocyst morphology. They are as follows:

1: Oocysts thought to represent a single species may be polymorphic within a single or closely related host species. This situation is exemplified by the previously discussed case of *E. arizonensis.*

2: Oocysts thought to represent multiple species may be morphologically similar between closely related host species. This problem is exemplified by the previously mentioned case of *E. albigulae* and *E. onychomysis*.

3: Oocysts thought to represent a single species may be monomorphic in distantly related host groups. This is exemplified *Eimeria chinchillae* De Vos and van der Westhuizen, 1968, which can infect rodents of the families Chinchillidae Bennett, 1833, Muridae Illiger, 1811, and Nesomyidae Major, 1897 (de Vos, 1970).

4: Oocysts thought to represent multiple species may be morphologically distinct between and within host groups.

In 1986, Duszynski stated that "dogma tells us that eimerians, and to a lesser extent isosporans, are highly host specific". Two years later, Levine and Ivens (1988) published a review of all cross-transmission experiments involving eimerians, which revealed that 80% of cross-transmission attempts within host genera were successful, but only 12.5% of transmissions were successful between host genera. Furthermore, of the 14 successful intergeneric transmissions, two were between closely related genera (Todd and Hammond, 1968a; Todd and Hammond, 1968b), one was only possible when the abnormal host was immunocompromised (Todd and Lepp, 1972), one was only successful in certain strains of the abnormal host (Mayberry et al., 1982), and eight (de Vos, 1970) used a single coccidian species, *Eimeria chinchillae*, which is highly exceptional in its broad host range. Despite their own finding that 80% of intrageneric cross-transmissions were successful, Levine and Ivens (1988) stated the assumption that morphologically similar oocysts from two host species represent a single parasite species "can be considered valid only if a cross-infection study proves that the coccidium can be transmitted from one host species to the other." In contrast, Dusznski (1986) stated that if morphologically identical oocysts are found in two congeneric species, "we accept the coccidium as a valid parasite of both".

Another roadblock in the understanding of host-parasite associations may occur when investigators misidentify the species of the host. With no way to assess the accuracy of host identifications, such misidentifications could obscure the true host range into

perpetuity. In order to avoid such issues, Frey et al. (1992) recommended a new taxonomic tradition; the designation of a voucher specimen of the host from which the parasite type specimen was recovered termed the "symbiotype".

In order to consider the extent of host specificity in the coccidia, it is necessary to explore its potential causes. Among others, two explanations have been offered. The more obvious of these two is that host immunity is a heavy selective force on parasites. Thus, coccidia and their hosts exhibit narrow co-accommodation (Brooks, 1979) in that the parasites are highly adapted to evade immunodetection in a specific host group. The species-specific efficacy of anticoccidial vaccines (see Vrba et al. 2011), the ability of immunosuppressants to enable transmission of species of *Eimeria* to novel hosts (Todd and Lepp, 1972), and documented molecular mimicry in other apicomplexans (Blackman et al., 1991) support this explanation of host specificity in the Eimeriidae. The second explanation is that the coccidia manipulate the molecular machinery of host cells to actively nourish the trophic lifecycle stages. This view was championed by Marquardt et al. (1984), who claimed nucleolar hypertrophy as evidence for such phenomena. However, Duszynski (1986) pointed out that nucleolar hypertrophy is not a universal response of host cells to eimeriid parasites and that the genes which the parasite "turns on" could be shared by multiple hosts. Reduker et al. (1986) argued that host speciation does not necessarily incur speciation by parasites, stating "it is theoretically possible that speciation can occur within a host lineage without affecting parameters of the 'internal environment' of the host that are important for the survival and reproduction of the parasite."

Molecular genetic methods

A limited number of readily observable morphologically traits and an even smaller number of those that are phylogenetically informative make traditional phenotype-based taxonomic schemes "complex and unsatisfactory" (Relman et al., 1996).This makes molecular genetic characters particularly important in the study of coccidian systematics. However, extraction of nucleic acids has historically been difficult because coccidia cannot be cultured axenically and the oocyst wall is difficult to break (Zhao et al., 2001). However, in 2001, Zhao et al. published new protocols for extracting nucleic acids from oocysts using lysis buffer, which dramatically lowered the number of oocysts needed to obtain quantities of DNA or RNA necessary for PCR. Then in 2009, Dolnik et al. published methods for obtaining sufficient quantities of both nuclear and plasmid DNA from single oocysts of the genus *Isospora* from avian hosts.

Molecular data have been useful not only as characters for phylogenetic analyses, but also in resolving species boundaries. Hnida and Duszynski (1999b) used ITS1 rDNA sequences to reconfirm the results of their cross-transmission study, namely, that *E. arizonensis*, *E. albigulae*, and *E. onychomysis* represent three valid species. In accordance with the results of this study, they also recommended that 5% genetic distance or greater in ITS1 sequences from two presumed eimerian species be considered a valid species boundary. Recently, Vrba et al. (2011) highlighted the need to include multiple regions in analyses of molecular data when they demonstrated that though previously published 18s sequences for *Eimeria mitis* Tyzzer, 1929 and *Eimeria mivati* Edgar & Seibold, 1964 were significantly different, both sequences were present as different alleles in *E. mitis*.

Hill et al. (2012) also discovered multiple alleles in sequences from *E. macropodis* Wenyon and Scott, 1925 when they used 18s and COI sequences to demonstrate that two morphotypes of *E.macropodis* do not represent distinct species.

Systematics

Historically, the taxonomy of the coccidia and other protists has been based more on utility than phylogenetic accuracy (Tenter et al., 2002; Morrison, 2009). This is problematic because as Bandoni and Duszynski (1988) stated, "all other investigations of eimeriid coccidia… are undermined by a shaky taxonomic foundation." Aside from contributing to a base of information which may be useful in addressing basic questions in parasite evolution and ecology, knowledge of coccidian systematics may also provide immediate utilitarian benefits. As Lee et al. (1985) pointed out, much human suffering could have been avoided had early taxonomists known that *Toxoplasma gondii* Nicolle and Manceaux, 1908 was a coccidian species and knowledge of apicomplexan biochemistry had been used in the development of treatments. In the past half century, great strides have been made in the understanding of coccidian systematics (Tenter et al., 2002). These advances are summarized below.

Suprafamilial systematics

In 1964, an extensive revision of protozoan taxonomy by Honigberg et al. divided the sporozoa into three classes, Teleospora (containing gregarines, eimeriids, adelinids and haemosprinids), Toxoplasmea (containing toxoplasmids), and Haplosporida (containing haplosporids). While this review was a "necessary step" in protozoan taxonomy, it was

soon made obsolete by discoveries made with the advent of electron microscopy (Levine et al., 1980).

The phylum Apicomplexa was first proposed in a revision of protozoan taxonomy by Levine et al. (1980). This revision, constructed using data from more than 65,000 species, split the protozoa into seven phyla. All members of this entirely parasitic phylum at some point in their lifecycle possess at least some of a suite of structures collectively known as the "apical complex." This phylum, by the calculations of Adl et al. (2007) is at least the third most (and likely the absolute most) speciose eukaryotic phylum. What's more, its monophyly has, for the most part, held up despite major discoveries in protist systematics such as the polyphyly of the protozoa (Adl et al., 2005). Unfortunately, for multiple reasons including the inability of apicomplexans to be cultured axenically, Morrison (2009) stated that "the prospects for elucidating their phylogeny might… not be good."

Since the 1970's, the systematics of the coccidia has been one of the most controversial areas in parasitic protozoology (Cox, 1991). For instance, a major change in the understanding of coccidian systematics began to take shape when a phylogenetic analysis of the "sporozoa" by Barta in 1989 suggested that the genus *Cryptosporidium* Tyzzer, 1907 was not a true coccidian. Later, It was discovered by Bull et al. (1998) that anti-*Cryptosporidium* antibodies are cross reactive with gregarine species. An analysis based on 18s rRNA by Cerreno et al. (1999) added further evidence to the case that *Cryptosporidium* is more closely related to the gregarines than the coccidia. Subsequent studies have done nothing but provide evidence to support this case (see Barta et al., 2006 for a more comprehensive review of this evidence).

Generic and subgeneric systematics

The lower level taxonomy of the coccidia, especially *Eimeria* and *Isospora* can be "economically important" (as the term is commonly used) to agriculture because vaccines are species specific, thus knowledge of patterns of host-specificity and polymorphism in coccidia may be of great aide in maximizing the cost-effectiveness of vaccines for veterinary or agricultural use (Vrba et al., 2011). However, investigations of coccidian biology, including systematics, are disproportionately waited toward those that are economically important (Morrison, 2009). For instance, of the 86 species of *Eimeria* for which sequences were available on Genbank (Benson et al., 2005) as of March 15, 2013, 28 (~33%) occurred in livestock animals. Of the 51 species that were retrieved from wild animals (not counting 6 which were retrieved from *Mus* spp. or *Rattus* spp.), 15 (~29%) were parasites of game species. This bias is to be expected; as Morrison (2009) stated, "trying to get funding for the study of unicellular endoparasites of non-medical and non-veterinary importance, even if they are of phylogenetic importance for the study of biodiversity, might not be too easy."

Nevertheless, much progress has been made in the elucidation of generic and subgeneric relationships of the coccidia in the last three decades. One of the first investigations of these relationships was performed by Reduker, Duszynski and Yates in 1986. In this study, cladistic and phenetic analyses of eimerian species infecting hosts of the genera *Onychomys* Baird, 1857 and *Peromyscus* showed two separate lineages, which were later supported by molecular genetic evidence (Hnida and Dusznski, 1999a; Zhao and Duszynski, 2001).

According to Morrison et al. (2004), who performed a comprehensive phylogenetic analysis based on all available coccidian 18s rRNA sequences at the time, there are "unambiguous patterns" of host-parasite association evident in coccidian systematics. Some traditional views of coccidian systematics were vindicated by the analyses of Morrison et al. (2004), such as the monophyly of the cyst forming coccidia (Sarcocystidae), and the oocyst-forming coccidia (Eimeriidae) with the exception of the genus *Isospora* (Fig. 3). As suggested by Carreno and Barta (1999), the genus *Isospora* is paraphylytic, with the species infecting birds belonging in the family Eimeriidae, and those infecting mammals belonging Sarcocystidae (Fig. 3). This discovery makes sense in light of analyses by Barta et al. (1989), which showed evidence of independent evolution of heteroxenous lifecycles in the 'sporozoa'. This also indicates that the genus *Eimeria* is paraphyletic, as the isosporans which infect birds falls within a clade otherwise compromised of eimerians, as does the genus *Cyclospora* Schneider, 1881, as originally suggested by Relman et al. (1996) (Fig. 3).

Gerbil taxonomy and systematics

The most basic requirement for understanding host-parasite evolutionary relationships is an accurate understanding of both host and parasite systematics. Therefore, a summary of the systematics of the host group, the subfamily Gerbillinae and, more specifically, the genus *Meriones* is presented below.

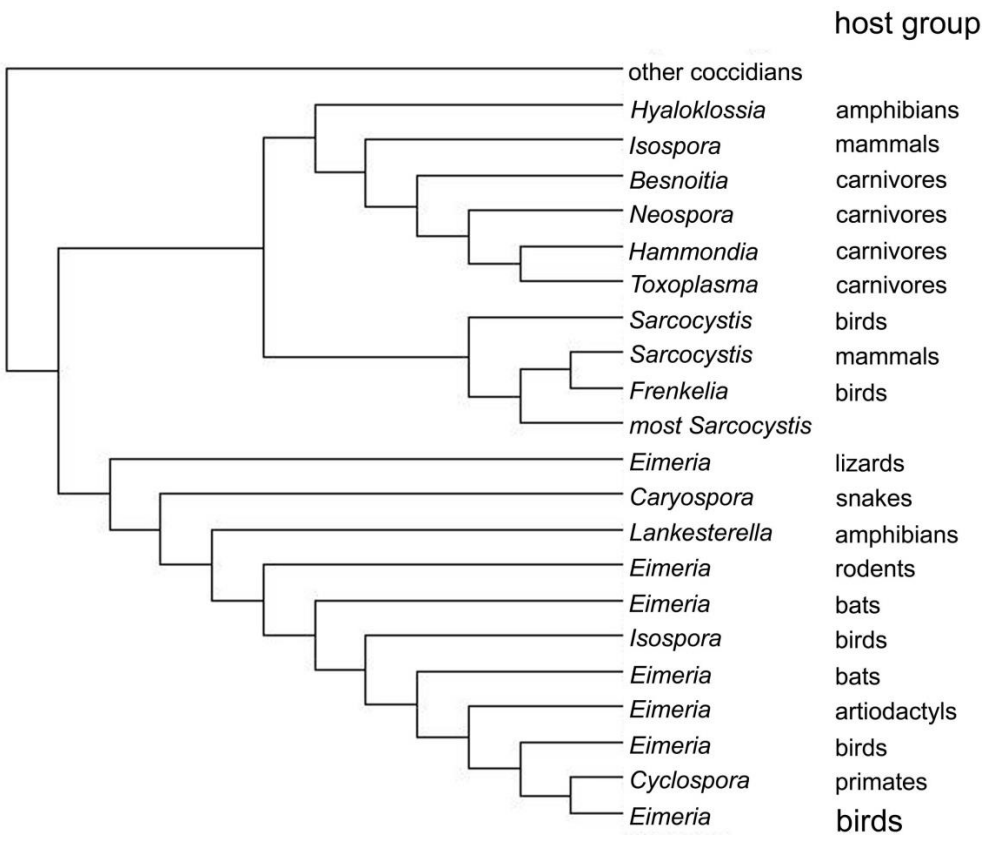


Figure 3: Phylogenetic tree of generic and subgeneric systematics and host associations of the coccidia from Morrison et al. (2009).

Higher taxonomy (family – tribe)

Unlike "rats" or "mice", the mammals which bare the common moniker of "gerbils", or in some cases "jirds", represent a monophyletic clade: the subfamily Gerbillinae. While this subfamily is now generally recognized as belonging in the family Muridae, its taxonomic status was been challenged, revised, and thoroughly debated through the most recent centuries, and dissenters of the *status quo* still remain (Musser and Carleton, 2005). Though the monophyly of gerbils has seldom been contested, the rank of the clade in the taxonomic hierarchy and its placement have been cause for much ado.

In his 1876 revision of the order Glires Linnaeus, 1758, which contained the current orders Lagomorpha Brandt, 1855 and Rodentia Bowdich, 1821, Edward Alston placed Gerbillinae within the family Muridae based principally on mandibular form. This view endured for a century, until in the 1970's and 1980's some hypothesized that the similar dentition of cricetids and gerbils was synapomorphic rather than convergent (Pavlinov, 2001). Along with this controversy regarding gerbil taxonomy was the debate over the proper rank of Gerbillinae. Reig (1980) and Pavlinov (2001) maintained that the clade should be elevated to the rank of a family. However, several works based on multiple gene molecular analyses in the early 2000's (e.g. Michaux et al., 2001; Steppan et al., 2004) showed overwhelming evidence that Gerbillinae is a sister group to Deomyinae Thomas, 1888, and these two groups are in turn a sister group to Murinae Illiger, 1811. Being thusly related to the type subfamily, it is difficult to justify excluding gerbils from the family Muridae. Moreover, due to the "bush-like" radiation of muroid rodents (Michaux et al., 2001), neither could one justify elevating Gerbillinae to the rank of family without doing so for nearly all subfamilies of murid rodents.

Musser and Carleton (2005) defer to Pavlinov on systematics among gerbils with one exception, discounting his recognition of familial status by recognizing the subfamilies and tribes of Gerbillidae described by Pavlinov in 1990 as tribes and subtribes, respectively, of Gerbillinae. This classification contains three tribes, Taterillini Pavlinov, 1982, Ammodillini Pavlinov, 1981, and Gerbillini Pavlinov, 1982 (Fig. 4). Gerbillini is the largest tribe, containing four subtribes and eleven genera, while Taterillini contains two subtribes and five genera. Ammodillini is monotypic, and its phylogenetic placement

remains unresolved (Pavlinov, 2001; Musser and Carleton, 2005). Musser and Carleton (2005) also diverge from Pavlinov's taxonomic recommendations in that Pavlinov places what was thought to be a polymorph of *Gerbillus mauritaniae* Heim de Balsac, 1943 in the monotypic genus *Monodia* Heim de Balsac, 1943, whereas Musser and Carleton do not think the atypical mandible of this morph to be sufficient evidence to split the species, let alone the genus.

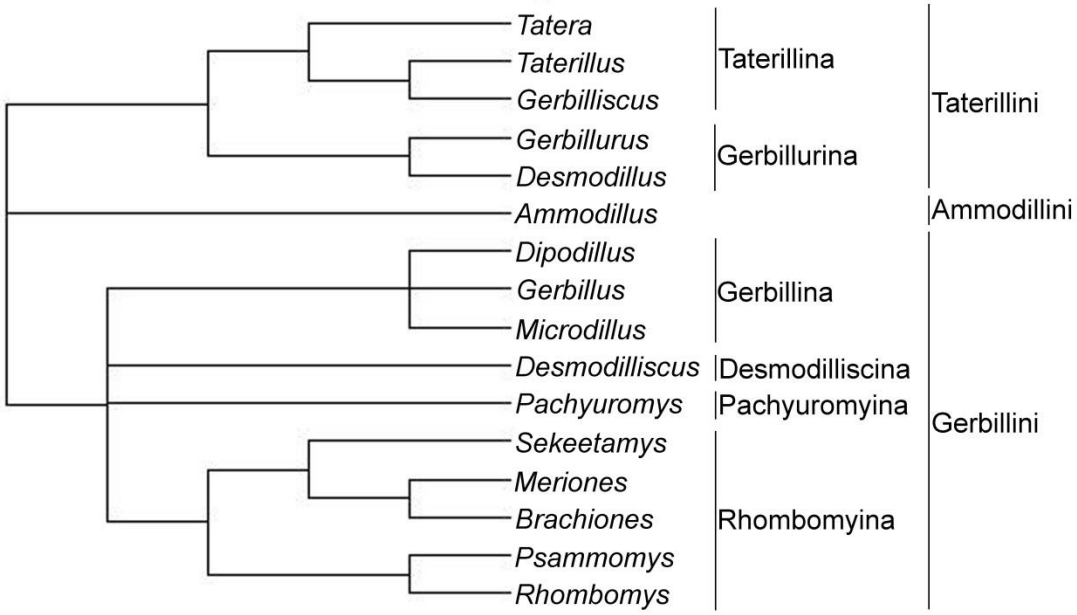


Figure 4: Phylogenetic tree depicting systematic relationships of genera within the subfamily Gerbillinae. Redrawn from Pavlinov, 2001 with names clade rankings from Musser and Carleton (2005).

***The genus* Meriones**

In 1990, Pavlinov et al. proposed four subgenera of the *Meriones*: *Meriones* (*M. tamariscinus* Pallas, 1773); *Parameriones* (*M. persicus* Blanford, 1875, *M. rex* Yerbury and Thomas, 1895); *Pallasiomys* (*M. arimalius* Cheesman and Hinton, 1924, *M. chengi* Wang, 1964, *M. crassus* Sundevall, 1842, *M. dahlia* Shidlovsky, 1962, *M. grandi* Cabrera, 1907, *M. libycus* Lichtenstein, 1823, *M. meridianus, M. sacramenti* Thomas, 1922, *M. shawi* Duvernoy, 1842, *M. tristrami* Thomas, 1892, *M. unguiculatus*, *M. vinogradovi* Heptner, 1931, *M. zarudnyi* Heptner, 1937); and *Cheliones* (*M. hurrianae* Thomas, 1919). However, a molecular phylgenetic analysis of gerbils by Chevret and Dobingy (2005) based on cytochrome *b* (cyt*b*) and 18s rRNA sequences provided strong evidence that *M. crassus* and *M. rex* are sister taxa. An analysis by Ito et al. (2010) based on cyt*b* and cytochrome *c* oxidase subunit II (COII) sequences supported this find. While some relationships such as the relationship between *Meriones* and *Rhombomys* remain unclear, four relationships are strongly supported by Chevret and Dobingy and Ito et al. (Fig. 5):

> 1) *Meriones unguiculatus* and *M. meridianus* are sister taxa, 2) as are *M. rex* and *M. crassus.* 3) *Meriones chengi* falls within the otherwise monophyletic species *M. meridianus*, and thus the former species should be considered a synonym of the later; 4) all other species of *Meriones* besides *M. tamariscinus* share a more recent ancestor with gerbils of other genera than with *M. tamariscinus*. This final relationship is significant to the taxonomy of the genus, as *M. tamariscinus* is the type species.

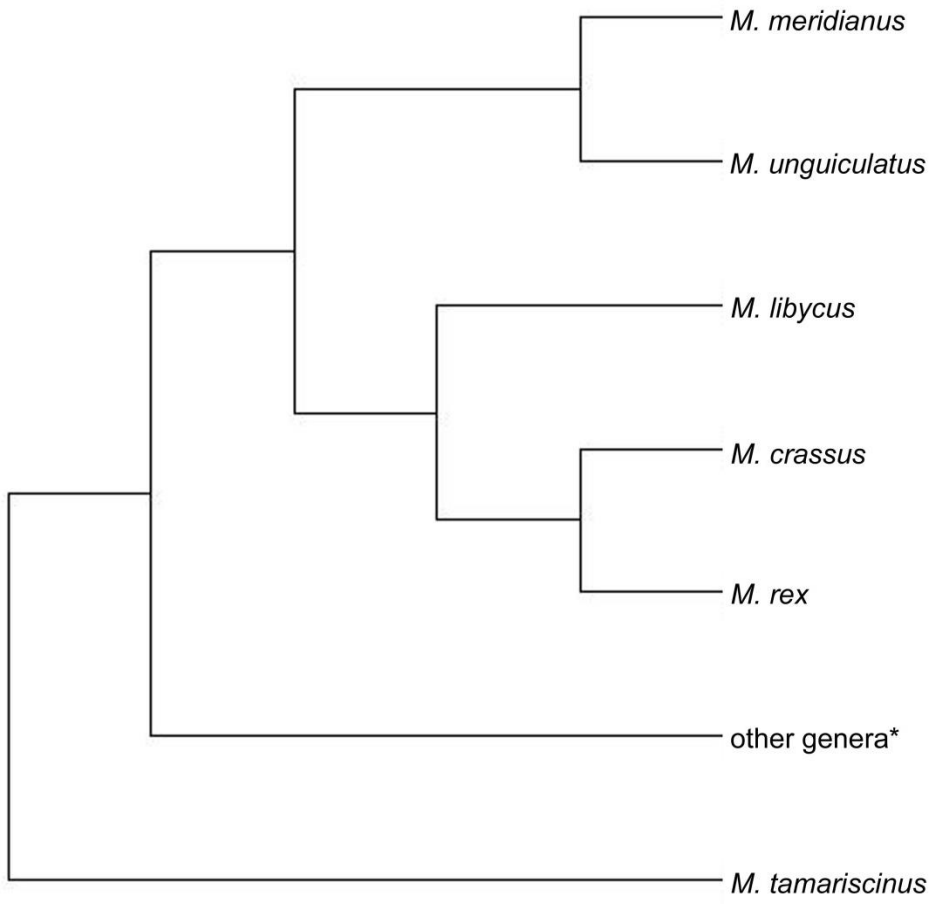


Figure 5: Phylogenetic tree depicting systematic relationships within the genus *Meriones* from Ito et al., 2010. *other genera varied depending on the analysis, but were most often *Rhombomys, Brachiones,* and *Psammomys.*

Eimerians occurring in gerbils

Duszynski et al. (2000) attributed some of the difficulty in coccidian taxonomy to the literature being "vast and widely scattered, much of it appearing in obscure journals that have limited circulation", which seems to be true of the literature concerning the coccidia of gerbils. Levine and Ivens (1965; 1990) Musaev and Veisov (1965) and Pellérdy (1974) published comprehensive syntheses of species descriptions of coccidia of rodents, but as Wilber et al. (1998) point out, these works do not follow the ICZN exactly.

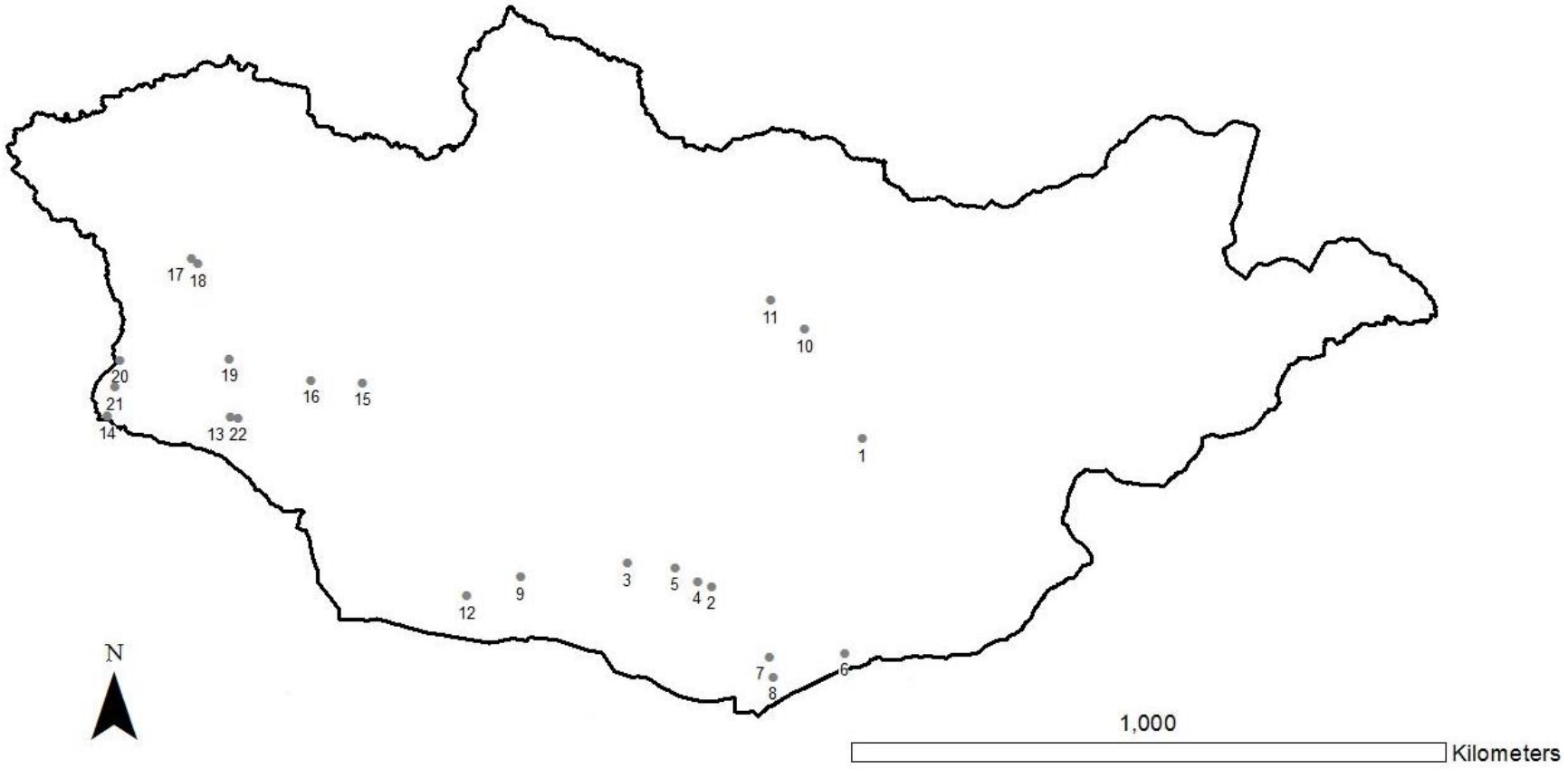
What's more, the species descriptions summarized by Levine and Ivens, Musaev and Veisov and Pellérdy are often unsatisfactory. None of these descriptions contain data on the presence or absence of the substieda or parastieda body. In some cases, host species is the sole character which distinguishes these species from one another. Considering the aforementioned uncertainty regarding host specificity, the validity of such species is questionable. Todd and Hammond (1968a) could not transmit *E. callospermophili* Henry, 1932 from *Urocitellus armatus* Kennicott, 1863 to *M. unguiculatus*. Nor could they (1968b) transmit *E. lateralis* Levine, Ivens, and Kruidenier, 1957 from *U. armatus*, *Otospermophilus variegatus* Erxleben, 1777 or *Callospermophilus lateralis* Say, 1823 to *M. unguiculatus*. However, to the best of my knowledge, no cross-transmissions have ever been attempted between gerbil hosts of the same genus.

III. METHODS AND MATERIALS

Field Collection

Hosts were collected using Sherman® live traps at a variety of trapping localities (Map 1, Table 1). Following retrieval from traps, hosts were euthanized and autopsied as soon as possible following methods outlines by Gardner (1996). Chloroform was useful not only as a humane method of euthanizing the host, but also in killing ectoparasites and thus preventing them from contaminating other specimens or infecting researchers (Gardner, 1996). For this reason, hosts which died before they could be euthanized were also placed in new plastic bags with chloroform in order to kill any ectoparasites which may have outlived their host.

Hosts were shaken in the bags in which they were euthanized to dislodge ectoparasite. Contents of the bags were then rinsed into the bottom of the bag with 70% ethanol and then saved in Whirl-Pak ® bags for later analysis. Standard length measurements (total, tail, hindfoot and ear) and mass were then taken. Host species and sex were identified and age class estimated based on the aforementioned measurements and qualitative characters. Host material saved from hosts included any combination of the following: skins (flat or round), tissue for genomic or virological analysis (liver, spleen, heart, or lung) in liquid nitrogen or in 95% ethanol, skulls, full skeletons or whole animals preserved in 70% ethanol. All host materials, including symbiotype hosts (see Frey, et al. 1992), were submitted to the Mammal Division of the Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico.



Map 1: Collection localities of gerbils examined for coccidia. See p. 34-35 for locality data.

ID	name	state	district	habitat type	hosts collected	lat.	long.	dates collected	elevation
1	NE of Gurvansaikhan	Dundgovi	Shinejiust	semi-desert shrubland	11	45.76123	107.26645	7 June, 2009	1391
2	NW of Yolin Am	Omnogobi	Shinejiust	semi-desert shrubland	3	43.55001	104.03754	10-11 June, 2009	2028
3	Khongorin Els	Omnogobi	Shinejiust	semi-desert shrubland	14	43.87270	102.26508	20-25 June, 2009	1180-1385
4	Tsagaan Ovoo Uul	Omnogobi	Shinejiust	cold grassland/ semi-dessert shrubland	2	43.61792	103.75455	2 July, 2009	2308
5	Baruun Saikhan Uul	Omnogobi	Shinejiust	cold grassland/ montaine	1	43.82028	103.28092	7 July, 2009	2179
6	SW of Bayan Ovoo	Omnogobi	Shinejiust	semi-desert shrubland	19	42.52644	106.79372	23-26 June, 2010	915
7	Borzon Gobi, Byaruuhai Bulag	Omnogobi	Shinejiust	semi-desert shrubland/ bare desert	2	42.48232	105.25375	28-30 June, 2010	1148
8	Borzon Gobi, Halzan Mountain	Omnogobi	Shinejiust	semi-desert shrubland	1	42.18141	105.32956	3 July, 2010	1109
9	Zulganai Gol	Omnogobi	Shinejiust	semi-desert shrubland	3	43.58439	100.06615	9-10 July, 2010	1063
10	Ivgeelt Mountain	Tov	Shinejiust	low, sparse grassland	6	47.43276	106.04160	23-24 July, 2010	1343
11	E of Lun	Tov	Shinejiust	low, sparse grassland	1	47.87735	105.30025	11 July, 2011	1038
12	Ekhiin Gol	Bayankhongor	Shinejiust	semi-desert shrubland/ bare desert	5	43.25015	98.98953	13-15 July, 2011	959
13	Takhi Station	Gobi Altay	Bugat	bare desert	14	45.53862	93.65111	30-31 July, 2011	1684

Table 1: ID (see Map 1), name, state and district, habitat type, # of hosts collected, latitude, longitude, dates for which hosts were collected, and elevation for each locality from which gerbils were collected.

ID	name	state	district	habitat type	hosts collected	lat.	long.	dates collected	elevation
14	Baitag Bogd	Hovd	Altai	semi-desert shrubland	4	45.26446	91.06402	5-7 August, 2011	1895
15	Olon Nuur Valley	Gobi Altay	Zaivar Mod	semi-desert shrubland/ cold grassland	10	46.30659	96.37282	19 June, 2012	2191
16	Rashant Spring Valley	Gobi Altay	Sharga	semi-desert shrubland/ cold grassland	43	46.25144	95.26035	20-25 June, 2012	1013
17	next to lake	Hovd	Manhan	low, sparse grassland next to open water	2	47.79733	92.27154	28 June, 2012	1170
18	Jargalant Khairkhan Mountain	Hovd	Manhan	cold grassland/ montaine	13	47.73328	92.43695	27 June- 3 July, 2012	1294
19	Myangan Ugalzat Mountain	Hovd	Tsetseg	semi-desert shrubland	4	46.40472	93.44452	5 July, 2012	2119
20	Bulgan River Valley	Hovd	Bulgan	semi-desert shrubland/ bare desert	6	46.11908	91.10872	7-9 July, 2012	1146
21	Baruun Huurai, Shagshig	Hovd	Bulgan	bare desert	1	45.71121	91.11048	11 July, 2012	1064
22	Bij River Valley	Gobi Altay	Bugat	bare desert/ semi-desert shrubland	6	45.54286	93.80898	21 July, 2012	1685

Table 1 (cont.): ID (see Map 1), name, state and district, habitat type, # of hosts collected, latitude, longitude, dates for which hosts were collected, and elevation for each locality from which gerbils were collected.

Viscera were examined for metazoan parasites by Dr. Scott L. Gardner, Dr. David Tinnin, Dr. Terry H. Haverkost, Dr. Gabor R. Racz, Dr. Agustin Jiminez-Ruiz, Altangerel Tsogtsaikhan, Kayce Bell, or Ethan T. Jensen, and any metazoans recovered were preserved in either liquid nitrogen, 10% formalin, or 70% or 95% ethanol. Fecal pellets were extracted from the large intestine and preserved in approximately 5 ml of 2% (w/v) potassium dichromate ($K_2Cr_2O_7$) solution (PDS) in 15 ml Wheaton® Snap Cap vials. Upon return to the lab, vials containing fecal pellets in PDS were refrigerated at 2° C until time of analysis.

Processing

Facilitating sporulation

Duszynski and Conder (1977) stated that after being returned to the lab from the field and prior to refrigeration, the fecal pellets should be broken up and the feces/PDS should be placed in a covered petri plate and left at room temperature for seven to ten days to facilitate sporulation. However, this has not been necessary with samples from the MVPP, as ample time for sporulation passed between the collection of the samples and their return to the lab (S.L. Gardner, pers. comm.). Instead, fecal pellets were broken up with wooden applicator sticks just prior to flotation.

Fecal flotation

Oocysts were isolated following coverslip flotation methods as detailed by Duszynski and Wilbur (1997), with few modifications. Other than slight differences in the capacity of the centrifuge tubes, my methods differed from those described by Duszynski and

Wilbur in two ways. First, in order to remove debris with a specific gravity less than that of water from the sample, 1-3 ml of feces/PDS from each sample was first diluted with 9-11 ml of distilled water and centrifuged for 2 minutes at 2,000 RPM. The supernatant was decanted and discarded, and the pellet was resuspended in enough Sheather's solution (Sheather, 1923) to form a slight meniscus extending above the rim of the centrifuge tube, in accordance with Duszynski and Wilbur (1982).

A number 1, 18-mm^2 coverslip was then placed on top of the centrifuge tube and the sample was centrifuged at 2,000 RPM for 4-5 minutes. The coverslip was then carefully removed, placed onto a glass slide, and then systematically scanned for oocysts under 200X total magnification. The second deviation from the methods of Duszynski and Wilbur (1982) is that a thin film of petroleum jelly was deposited along the edges on the underside of the coverslip prior to centrifugation. This was done in order to keep the Sheather's solution within the boundries of the coverslip, both to protect the objective lens and to ensure oocysts remained under the coverslip so that they could be observed and photographed under oil immersion.

Photomicroscopy

Isolated oocysts were photographed using a Zeiss® Axioplan 2 integrated computerized system, which offers many advantages over other photomicroscopic methods. Image files automatically contain a wide array of metadata, such as the data and time, the three dimensional position of the slide, the objective lens used and other microscope settings at

the time the photomicrograph was taken, as well as spatial calibration data relating pixel size to actual size.

In cases where a limited number of oocysts (less than 40) were found on a slide, all oocysts were photographed. If more than 40 oocysts were present, oocysts were photographed until they began to crenate. If found in high concentrations (>100 per slide), all oocysts were photographed under oil immersion (630X or 1000X). Otherwise, oocysts were photographed under 400X until either 40 or all of the oocysts on the slide had been photographed once, at which point oocysts were then photographed or rephotographed under oil immersion until they began to crenate.

Taxonomy

Identification

Oocysts recovered were identified to the genus level. Oocysts of the genus *Eimeria* were grouped into seven morphotypes, while oocysts of the genus *Isospora* which were structurally intact were grouped into a single morphotype. A dichotomous key to all species of *Eimeria* and *Isospora* known to infect any host of the subfamily Gerbillinae based on morphological data reported from Levine and Ivens (1965; 1990) and Pellérdy (1974) was constructed to facilitate species identification of the aforementioned morphotypes. If available, original species descriptions and other sources documenting said species were consulted.

Descriptions

Species which were morphologically distinct from all those previously described which occur in gerbils were described as new species following guidelines set by Wilber et al. (1998). Characters of sporulated oocysts used were length (L), width (W), length to width ration (L/W), wall thickness and texture, micropyle (M), micropyle cap (MC), oocyst residuum (OR), and polar granule (PG). Characters of sporocysts used were length (SL), width (SW), Stieda body (SB), substieda body (SSB), parastieda body (PSB), sporocyst residuum (SR), refractile bodies (RB), and sporozoites (SZ). All phototypes were submitted to the Harold W. Manter Laboratory of Parasitology phototype collection, and feces/PDS were submitted to the Harold W. Manter Laboratory of Parasitology general collection, University of Nebraska-Lincoln, Lincoln, Nebraska.

Taxonomic revisions

Procedures and criteria for identifying synonymous species and *species inquirenda* were based off of those used by Wilber et al. (1998) in their taxonomic revision of the eimerians infecting rodents of the tribe Marmotini. Specifically, a spreadsheet was created containing all known species of *Eimeria* and *Isospora* known to infect gerbils and data from Levine and Ivens (1965; 1990) and Pellérdy (1974). Data filters were used to order species by multiple character states. Species were sorted based on the presence or absence of a micropyle, polar granules, an oocyst residuum, and a sporocyst residuum, as well as the texture and number of layers of the oocyst wall. Original species descriptions were consulted for species which were similar in the aforementioned characters,

overlapping in oocyst and sporocyst length and width, and from congeneric hosts. If the original descriptions also failed to provide sufficient data to distinguish between similar species, it was recommended that said species be considered synonymous. Species which were described using procedures not following the ICZN were recommended to be considered *species inquirendae*.

Cladistic analyses

Characters observed in oocysts of the genus *Eimeria* in this study were used to construct a character matrix for cladistics analysis based on the methods of Reduker et al. (1986). A total of 20 characters were used, 11 categorical and 9 mensural (Tables 2, 3). *Eimeria arizonensis* and *E. tropidura* Aquino-Shuster, Duszynski, and Snell, 1990 were also included using data from their original descriptions. Continuous characters were discretized using MapCode (Archie, 1985). Reduker et al. (1986) did not use continuous traits in their cladistic analysis and instead, superimposed these traits on the tree they built using only categorical data. In the present study, analyses were performed both with and without measurement data, and with characters both unweighted and weighted inversely to the number of character states. The most parsimonious trees were found using PAUP v. 4.0 (Swofford, 2003). Trees were rooted using *E. tropidura* as an outgroup. When multiple equally parsimonious trees were obtained, majority rule consensus trees were built.

Statistical analyses

The variables host species (*M. meridianus* or *M. unguiculatus*), sex, infection with nematodes, infections with cestodes, year of capture, and month of capture were each tested for correlation with infection by *Eimeria* spp. and *Isospora* spp. using a Chi-squared test. Hosts of the species *M. tamariscinus* and hosts for which were not identified to the species level were excluded from this analysis, as their sample size was limited (5 and 15, respectively). In addition, a multi-group discriminant analysis was performed using Statistical Analysis Systems (SAS version 9.2) using log transformed oocyst and sporocyst length and width as well as wall thickness as variables and the 7 morphotypes of *Eimeria* as groups.

Niche modeling

In order to infer the distributions of species of *Eimeria* infecting gerbils in Mongolia and identify ecological trends in the occurrence of eimerian species, ecological niche models (ENM's) were created and evaluated. There were several constraints in the design and execution of these models. First, while the presence of species of *Eimeria* was confirmed by the recovery of oocysts from the feces of infected hosts, the absence of eimerian species could not be confirmed without extensive investigations which are beyond the scope of this study. Second, because most species of *Eimeria* were recovered from a single individual host, sets of models were constructed using occurrence data of all species of *Eimeria*, rather than being constructed using data from each species of *Eimeria*. This use of congeneric species is supported by the findings of Peterson et al.

Taxon	Characters								
	1	2	3	4	5	6	7	8	9
E. salasuzica	2	2	2	2	2	2	3	2	2
E. schachtachtiana	1	1	1	1	1	1	2	1	1
E. tsogoi	2	1	1	2	2	1	2	1	1
E. sarae	5	4	4	4	4	1	2	1	1
E. kostencovi	4	3	3	3	3	1	2	1	1
E. ivgeeltensis	3	2	2	2	2	1	2	1	1
E. briansmithi	1	1	1	2	2	1	2	1	1
E. arizonensis	2	1	1	2	2	1	2	1	1
E. tropidura	4	2	2	1	2	1	1	?	?

Table 2: Character-state data for quantitative characters of species observed and described in this study and *E. arizonensis*, using *E. tropidura* as an outgroup. Characters and character states are defined as follows, with all diminsions in microns: 1] oocyst length (OL): 1= μOL±0.75σ<22.06, 2= 22.66<μOL±0.75σ<25.65, 3= 27.01<μOL±0.75σ<28.45, 4= 32.11<μOL±0.75σ<33.29, 5= μOL±0.75σ>40.78; 2] oocyst width (OW): 1= μOW±1.5σ<22.15, 2= 22.50<μOW±1.5σ<25.61, 3= 27.08<μOW±1.5σ<28.91, 4= μOW±1.5σ>34.47; 3] wall thickness (W): 1= μW±1σ<1.68, 2= 1.68<μW±1σ<2.05, 3= 2.18<μW±1σ<2.58, 4= μW±1σ>3.01; 4] sporocyst length (SL): 1= μSL±1σ<10.69, 2= 11.02<μSL±1σ<12.93, 3= 13.68<μSL±1σ<14.51, 4= μSL±1σ>16.10; 5] sporocyst width (SW): 1= μSW±1σ<7.40, 2= 7.27<μSW±1σ<8.94, 3= 9.27<μSW±1σ<9.83, μSW±1σ>10.52; 6] oocysts length to width ratio (OL:OW): 1= μOL:OW±0.25σ<1.24, 2= μOL:OW±0.25σ<1.24; 7] sporocyst length to width ratio (SL:SW): 1= μSL:SW±0.25σ<1.43, 2= 1.43<μSL:SW±0.25σ<1.58, 3= μSL:SW±0.25σ>1.58; 8] oocyst length to sporocyst length ratio (OL:SL): 1= μOL:SL±0.25σ<1.53, 2= μOL:SL±0.25σ>1.53; 9] oocyst width to sporocyst width ratio (OW:SW): 1= μOW:SW±0.25σ<2.53.

(1999) that models built using occurrence data from one species were able to predict the distributions of closely related species. Finally, because species of *Isospora* were only recovered from three localities, ENM's were constructed only for *Eimeria* spp. and species of *Meriones*. Interestingly, despite the widespread use of GARP and Maxent, only a few studies (e.g., Gonzalez et al., 2011; Haverkost et al., 2010; Chamaillé et al., 2010) have used these methods to predict distributions of mammalian parasites.

Modeling methods

The two methods used to create ENM's in this study were Maximum Entropy (Maxent), and Genetic Algorithm for Rule set Prediction (GARP). These methods were chosen

	Characters											
Taxon	1	2	3	4	5	6	7	8	9	10	11	12
E. salasuzica	1	3	1	1	1	1	1	2	2	0	2	1
E. schachtachtiana	0	2	1	1	1	1	1	2	1	0	2	1
E. tsogoi	1	3	2	2	1	1	1	1	2	1	1	1
E. sarae	1	4	2	2	0	0	1	3	2	1	0	2
E. kostencovi	2	4	3	1	1	1	1	3	2	1	1	2
E. ivgeeltensis	0	2	3	2	1	1	1	2	2	1	1	1
E. briansmithi	0	1	1	2	2	2	1	1	2	0	1	2
E. arizonensis	1	4	1	2	2	2	2	2	2	2	1	1
E. tropidura	0	1	1	0	0	0	2	1	2	1	0	2

Table 3: Character-state data for categorical characters of species observed and described in this study and *E. arizonensis*, using *E. tropidura* as an outgroup. Characters and character states are defined as follows: 1] oocyst residuum morphology: 0= residuum absent,1= one globule,2= several globules; 2] # of bodies in sporocyst residuum: 1= 1 , 2= 2-6, 3= 6-12, 4= 12+; 3] arrangement of sporocyst residuum: 1=bodies "clumped" in single mass , 2= bodies "clumped" and in a line, 3= bodies arranged in a line; 4] shape of Stieda body: 0= Stieda body absent, 1= not elevated, 2= elevated and nipple-like; 5] most common # of polar granules: 0=0, 1=1, 2=2, 6] maximum # of polar granules: 0=0, 1=1, 2=2; 7] number of layers in wall: 1=1, 2=2; 8] wall texture: 1= smooth or lightly pitted, 2= smooth (rare) to rough (common) , 3= always rough; 9] sporozoites arrangement: 1= at opposite poles, 2= longitudinal; 10] number of visible refractile bodies: 0=0, 1=1, 2=2; 11] polar granule shape: 0= absent, 1= spherical, 2= ovoid, ellipsoid, or irregular; 12] appearance of cytoplasm in sporozoites: 1= finely granular, 2= coarsely granular.

because they are 'presence only' methods which are reliable for sample sizes as small as 5 for Maxent and 10 for GARP (Pearson et al., 2007).

Maximum entropy is a machine learning method which fits the distribution of probabilities of a species occurring in covariate space to whatever statistical distribution is most similar to a uniform distribution, subject to constraints from the data (Phillips et al., 2006). This general method, which has been used in fields such as astronomy, image reconstruction, and statistical physics, was adapted for use in ecological niche modeling by Phillips et al. in 2006. Since then, ENM's constructed with Maxent have been used in the study of a wide variety of topics (see Franklin, 2009).

GARP utilizes four types of niche modeling rule types: atomic rules, boxcar rules, range rules, and logit rules. For this reason, GARP is referred to as a "super-algorithm" by Franklin (2009). Which of the four rule types is most appropriate depends greatly on many factors such as characteristics of the taxon whose distribution is being modeled; GARP overcomes this obstacle by using the rule type which yields the greatest predictive accuracy and significance in a given situation (Stockwell and Peters, 1999). As the name implies, GARP is a genetic algorithm. Genetic algorithms are a class of machine learning methods first developed by Holland in 1975 which mimic chromosomal evolution and use stochastic processes analogous to mutation and crossing over. This stochasticity causes GARP to exhibit 'random walk' behavior, such that identical experiments produce varying results. To overcome this issue, Anderson et al. (2003) proposed creating numerous models with GARP and filtering the results based on omission and commission error characteristics to obtain a best subset model. Though GARP has not fared well against Maxent in several studies (*e.g.*, Elith et al., 2006; Hernandez et al., 2006; Phillips et al., 2006), most of these studies evaluate models using the full area under the curve (AUC) of the receiver operating characteristic (ROC) curve, which Peterson et al. (2008) argue is unsatisfactory for multiple reasons.

Environmental layers and occurrence data

For both methods (GARP and Maxent), the analyses used identical species occurrence data and environmental layers. Species occurrence data consisted of the longitude and latitude of traplines from which hosts were retrieved measured with handheld GPS

devices accurate to within 1,000 m. For each method, ENM's were produced for both the host and parasite genera (*Meriones* and *Eimeria*, respectively).

The following environmental data layers were downloaded from the WorldClim website (http://www.worldclim.org/bioclim): elevation, annual average temperature, total annual precipitiation, mean precipitation of the driest month, mean precipitation of the wettest month, mean annual temperature, mean temperature of the coldest month, and mean temperature of the hottest month. These layers were derived from data collected from the years 1950-2000. The following environmental data layers were downloaded from the NASA website (http://reverb.echo.nasa.gov/): mean temperatures and Normalized Difference Vegetation Index (NDVI) for summer months of 2009 and 2010. Tools from ArcGIS© 10.1 were used to create slope and aspect layers from elevation data, create single averaged NDVI and summer temperature layers from 2009 and 2010 data, and resample all layers to 30 arc second resolution. In total, 11 layers were used.

Implementation and evaluation

For each taxon whose distribution was being modeled, Maxent v. 3.3 software (available at http://www.cs.princeton.edu/~schapire/maxent/) was used to construct an ENM. This software was also used to perform analyses of variable contributions, and marginal response curves were obtained for the three variables with the largest percent contributions. Because Maxent produces continuous values of the probability of a species occurring in each cell, while GARP produces binary presence/absence predictions in each cell, the output layer was reclassified in ArcMap such that cells with values ≥0.5 were

classified as present, and those with values <0.5 were classified as absent to facilitate comparison with results from GARP.

DesktopGARP© 1.1.6 software (available at http://www.nhm.ku.edu/desktopgarp/) was used to construct ENM's using GARP. One thousand random replicate models were constructed using 75% of the data points for training and 25% for testing of the distribution of each taxon. The first 20 models produced with no omission error were selected; from each of those groups, the 10 models which deviated the least from the median commission index were selected. All 10 of these models were then summed, such that cells in which all models predicted presence have a value of 10, cells in which half of the models predict presence have a value of 5, and so forth. *Meriones* spp. or *Eimeria* spp. were predicted as present in cells with values of 5 or higher.

In order to evaluate the performance of Maxent versus that of GARP, the raster calculator tool in ArcMap was used to calculate the percentage of the cells in which *Eimeria* spp. are predicted to occur and *Meriones* spp. are not out of all the cells in which *Eimeria* spp. are predicted to occur. Because the parasites cannot occur in areas where their hosts does not, the method which produces the smallest percentage of the parasite distribution falling outside its host distribution was assumed to be superior in this respect. In addition, ROC curves were created, and both traditional AUC values and partial AUC with an error tolerance (*E)* value of 0.9 values (Peterson et al., 2008) were obtained. In order to facilitate comparison, the analyses were repeated and ROC curves obtained using the software openModeller (available at http://openmodeller.sourceforge.net/). All

parameters used to obtain ROC curves were the same as those used in the initial analyses. Finally, distributions predicted using both Maxent and GARP were superimposed on the same map for each genus, and percentages of overlapping area were calculated.

IV. RESULTS

Out of 495 gerbils collected (5 *M. sp.*, 294 *M. meridianus*, 15 *M. tamariscinus*, 168 *M. unguiculatus*, 9 *R. opimus*), fecal pellets were recovered and preserved from 171 (5 *M. sp*, 105 *M. meridianus*, 6 *M. tamariscinus*, 55 *M. unguiculatus*). Coccidian oocysts were found in 21 of these fecal samples (13 *Eimeria*, 8 *Isospora* [1 produced both *Eimeria* and *Isospora*], 1 *Klossia*). However, the ability of *Klossia* spp. to infect vertebrates has not been demonstrated (see Levine et al., 1955), and it is therefore likely a parasite of an invertebrate eaten by the gerbil in which it was found. With the exception of one host which was infected with both oocysts of both *Eimeria* and *Isospora* and one host which was infected with two species of *Eimeria*, only a single coccidian species was present in each infected host.

Taxonomy

Descriptions

Isospora merionis Veisov, 1964 (Figs. 6, 14)

Diagnosis: Oocyst shape: ellipsoidal or occasionally ovoidal; L x W: (n = 59) 23.79 x 20.33 (SD = 1.23 x 1.78) (21.49-27.27 X 17.13-25.81); L/W ratio: 1.18 (SD = .10) (1.01-1.42); wall (n=58) 1.53 (SD = .19) (1.20-2.00) of even thickness is doubled-layered, with moderately rough outer layer and smooth inner layer, though outer layer is frequently missing; M and OR absent, but PG sometimes present. Single PG is 2.07 (SD = 1.21) (1.00 - 4.00). Sporocysts (n = 107) ellipsoid, SL x SW: 15.09 x 10.43 (SD = 1.25 X 1.04)

(11.18-17.77 X 8.06-13.45); SR consists of many spherical globules ~1.5 in diameter scattered throughout the sporocyst but concentrated near posterior pole; SB present, but coarsely granular material obscures internal structures of sporocysts such that the presence or absence of a SSB, PSB, or RB could not be determined. 154, 157, 159, 203, 206, 207, 440, and 552 days elapsed between the collection of the hosts and the isolation of the oocysts.

Hosts: Meriones unguiculates Milne-Edwards, 1867 and *Meriones meridianus* Pallas, 1773.

Localities: Takhi Station, Baruun Huurai, Shagshig, and Near Rashant Spring Valley (Map 1, Table 1).

Prevalence: Oocysts were found in 1 of 55 (1.8%) *Meriones unguiculatus* and 6 of 105 (5.7%) *Meriones meridianus* (8 of 171 [4.7%] *Meriones* spp.).

Material deposited: Neophotosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68478, and oocysts preserved in potassium dichromate, HWML Coll. No. 68486 (see Williams et al., 2010).

Remarks

Oocysts were identified as *I. meriones* because they lack a M and OR, possess PG, SR, and SB. The outer wall layer in these oocysts was often not present, and was inconspicuous when present.

***Eimeria salasuzica* Musaev and Veisov, 1960 (Figs. 7, 15)**

Diagnosis: Oocyst shape: ellipsoidal or occasionally subspheroidal; L x W: (n = 67) 24.44 x 22.46 (SD = 1.56 x 1.53) (19.70-27.45 X 16.82-26.52); L/W ratio: 1.09 (SD = .05) (1.00-1.30); wall (n=67) 1.81 (SD = .27) (1.00-2.47) of even thickness is single-layered and variable in texture but usually rough; M absent; OR and PG present. The OR consist of a single, clear, spherical globule 6.32 (SD = .91) (4.32 – 8.67) in the center of oocyst. Single PG is 1.71 (SD = .27) (1.15 - 2.26) and located in center of oocyst. Sporocysts (n = 190) ellipsoid, SL x SW: 11.58 x 7.57 (SD = .91 X .61) (8.85-13.92 X 5.44-9.07); SR consists of ~8 spherical globules ~1.5 in diameter aggregated in the center of the sporocyst; SB conspicuous along with SSB and PSB; SZ lacks apparent RB. 154, 156, 157, 157 and 1,226 days elapsed between the collection of the hosts and the isolation of the oocysts.

Hosts: Meriones unguiculates Milne-Edwards, 1867 and *Meriones meridianus* Pallas, 1773.

Localities: Khongorin Els, Olon Nuur Valley, and Near Rashant Spring Valley (Map 1, Table 1).

Prevalence: Oocysts were found in 3 of 55 (5.5%) *Meriones unguiculatus* and 3 of 105 (2.9%) *Meriones meridianus* (6 of 171 [3.5%] *Meriones* spp.).

Material deposited: Neophotosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68479, and oocysts preserved in potassium dichromate, HWML Coll. No. 68487 (see Williams et al., 2010).

Remarks

Oocysts were identified as *E. salasuzica* because they lack a M, but possess a rough single-layered wall, OR, PG, and SR, and are shorter than 26 on average. Furthermore, if *E. tasakendica* Veisov, 1961 and *E. salasuzica* are indeed distinct species (see 'Taxonomic revisions', below), recovered oocysts are more similar to *E. salasuzica* in that its oocyst walls are on average 1.81, while the maximum wall thickness of *E. tasakendica* was reported as 1.4. The only previously reported host for *E. salasuzica* is *M. persicus*, and the only reported host for *E. tasakendica* is *M. vinogradovi*.

***Eimeria kostencovi* Davronov, 1973 (Figs. 8, 16)**

Diagnosis: Oocyst shape: ellipsoidal; L x W: (n = 42) 32.70 x 27.99 (SD = 1.58 x 1.22) (28.33-35.23 X 24.58-30.17); L/W ratio: 1.17 (SD = .05) (1.07-1.28); wall (n=42) 2.38 (SD = .40) (1.87-3.63) of even thickness is rough in texture; OR and PG present, but M absent. OR consists of roughly spherical granular mass 3.59 (SD = 1.16) (2.60 – 9.59) in diameter and located near the wall near the longitudinal center oocyst. PG is a single granule near center 1.86 (SD = .34) (1.15-2.57) in diameter. Sporocysts (n = 107) navicular, SL x SW: 14.09 x 9.55 (SD = .83 X .56) (12.48-16.25 X 7.78-10.51); SR consists of about 18 spherical globules ~1.5 in diameter, with about 6 in a row running longitudinally along the confluence of the SZ's, and 6 in a row on opposing sides near the poles; SB and SSB present but PSB absent. SZ along the longitudinal axis with anterior ends on opposite poles; SZ each possess a conspicuous anterior RB ~ 4 in diameter. 818 days elapsed between the collection of the hosts and the isolation of the oocysts.

Host: Meriones unguiculates Milne-Edwards, 1867.

Locality: Ivgeelt Mountain (Map 1, Table 1).

Prevalence: Oocysts were found in 1 of 55 (1.8%) *Meriones unguiculatus*, (1 of 171 [0.6%] *Meriones* spp.).

Material deposited: Neophotosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68483, and oocysts preserved in potassium dichromate, HWML Coll. No. 68514 (see Williams et al., 2010).

Remarks

Recovered oocysts are most similar in structure to *E. conveni* Glebezdin, 1969 and *E. kostencovi* Davronov, 1973 in that they lack a micropyle but possess an OR, PG, SR and OR, the oocyst walls are single layered and rough in texture, and that the maximum OL exceeds 32. As the range of wall thickness (1.87-3.63) of these oocysts overlaps with that for *E. kostencovi* (1.7-1.2) but not with that for *E. conveni* (1.5-1.7), and because *E. kostencovi* also occurs in *M. meridianus*, whereas *E. conveni* has only been documented as occurring in *Rhombomys opimus*, it is most likely that the recovered oocysts are of the species *E. kostencovi*.

***Eimeria schachtachtiana* Musaev and Veisov, 1960 (Figs. 9, 17)**

Diagnosis: Oocyst shape: ellipsoidal or occasionally spheroidal; L x W: (n = 48) 21.65 x 19.46 (SD = 1.09 x 1.23) (19.03-24.65 X 16.05-22.12); L/W ratio: 1.12 (SD = .06) (1.00-1.24); wall (n=51) 1.48 (SD = .39) (1.15-4.00) of even thickness is single-layered and variable in texture but usually smooth with moderate pitting; M and OR absent, but PG present. Single PG is 1.90 (SD = .37) (0.98 - 1.24) and located in center of oocyst. Sporocysts (n = 80) ellipsoid, SL x SW: 10.28 x 7.07 (SD = .81 X .66) (8.84-12.33 X 5.27-8.25); SR consists of 2-4 spherical globules ~1.5 in diameter near the center of the

sporocyst; SB present but SSB absent. An observed thickening of the sporocyst wall slightly off-center from posterior pole may be PSB; SZ lie near opposite poles rather than along the longitudinal axis; SZ lacks apparent RB. 454 and 1,226 days elapsed between the collection of the hosts and the isolation of the oocysts.

Host: Meriones unguiculates Milne-Edwards, 1867.

Locality: East of Lun (Map 1, Table 1).

Prevalence: Oocysts were found in 2 of 55 (3.6%) *Meriones unguiculatus* (2 of 171 [1.2%] *Meriones* spp.).

Material deposited: Neophotosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68480, and oocysts preserved in potassium dichromate, HWML Coll. No. 68488 (see Williams et al., 2010).

Remarks

Recovered oocysts are most similar to those of *E. erythrourica* Musaev and Alieva, 1961, *E. schachtachtiana* and *E. vinogradovi* Veisov, 1961 in that they lack a M, possess a single-layered wall, lack an OR, possess a PG and a SR, and typically possess smooth walls. However, while sporozoites are positioned along the longitudinal axis of the sporocyst in *E. erythrourica* and *E. vinogradovi*, sporozoites of this species are located at opposite poles of the sporocyst, like those of *E. schachtachtiana*. For these reasons, it is most likely that these oocysts are of the species *E. schachtachtiana*

***Eimeria tsogoi* n. sp. (Figs. 10, 18)**

Diagnosis: Oocyst shape: piriform or ellipsoidal; L x W: (n = 15) 25.18 x 20.43 (SD = 1.25 x 1.26) (22.91-26.80 X 18.29-22.83); L/W ratio: 1.23 (SD = .10) (1.09-1.40); wall

(n=15) 1.48 (SD = .16) (1.17-1.85) of even thickness is pitted and golf-ball like in texture; M and PG present, but OR and MC absent. M (n = 8) is often very inconspicuous, but can be up to 2.69 (SD = 1.44) (2.86 – 5.73) wide, and is located at narrow pole of piriform oocysts. Single PG is 1.94 (SD = .33) (1.56 - 1.85) and located in center of oocyst. Sporocysts (n = 26) ellipsoid, SL x SW: 11.68 x 7.75 (SD = 1.09 X .97) (7.57-13.11 X 6.69-11.58); SR consists of 6 to 12 spherical globules ~1.5 in diameter, either aggregated in the center or in a single row along wall near anterior end of sporocyst; SB present but SSB and PSB absent. SZ along the longitudinal axis with anterior ends on opposite poles; SZ each possess a single anterior RB ~ 1.6 in diameter. 863 days elapsed between the collection of the hosts and the isolation of the oocysts.

Taxonomic summary

Symbiotype host: Meriones meridianus Pallas, 1773, Museum of Southwestern Biology, division of Mammals, MSB 227234, NK 192164 (adult, female) (see Frey et al., 1992).

Type locality: SW of Bayan Ovoo (Map 1, Table 1), Omnogobi, Mongolia, 915 m elevation (42° 31' 35.184" N, 106° 47' 37.3914" E)

Prevalence: Oocysts were found in 1 of 105 (1.0%) *Meriones meridianus* (1 of 171 [.6%] *Meriones* spp.).

Site of infection: Unknown; recovered from feces.

Material deposited: Photosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68481, and oocysts preserved in potassium dichromate, HWML Coll. No. 68489 (see Williams et al., 2010).

Etymology: This species is named in honor of Tsogo, whose skills as a driver, mechanic, chef, and singer were greatly appreciated during fieldwork for the MVPP.

Remarks

Oocysts of *E. tsogoi* are most similar to those of *E. sadarktica* Veisov, 1961and *E. achburunica* Ismailov and Gaibova, 1981 in that they possess a M, a single-layered wall, and a PG, but lack an OR. Of those two species, *E. tsogoi* is more similar to *E. sadarktica* in that the average OL for *E. sadarktica* is 23, while that of *E. achburunica* is only 19.8. Though *E. three* is more similar to *E. sadarktica* in this respect, *E. sadarktica* is likewise more similar to *E. achburunica* than to *E. tsogoi*, as the ranges for *E. sadarktica* and *E. achburunica* (18-24 and 14-24) overlap greatly, whereas the average OL of *E. tsogoi* exceeds the maximum OL of the other two species. Finally, sporocysts of *E. tsogoi* possess a SB, while those of *E. sadarktica* and *E. achburunica* do not.

***Eimeria sarae* n. sp. 4 (Figs. 11, 19)**

Diagnosis: Oocyst shape: ellipsoidal; L x W: (n = 52) 41.30 x 35.23 (SD = 1.40 x 1.01) (37.64-46.12 X 32.44-37.22); L/W ratio: 1.17 (SD = .05) (1.07-1.30); wall (n=52) 3.14 (SD = .27) (2.17-3.63) of even thickness is rough with a deeply dimpled texture; OR present, but PG and M absent. OR consists of single sphere 8.63 (SD = .93) (6.62 - 11.35) in diameter and located slightly off-center of both the longitudinal and radial axis of oocyst. Sporocysts (n = 95) ellipsoidal, SL x SW: 16.50 x 10.82 (SD = .80 X .61) (14.57-18.98 X 9.71-12.69); SR consists of about two dozen spherical globules ~1.5 in diameter, with about 12 in the center of the SP and 12 on opposing sides near the poles; SB and SSB present but PSB absent. SZ along the longitudinal axis with anterior ends on

opposite poles; SZ each possess a central RB ~ 2.6 in diameter. 828 days elapsed between the collection of the hosts and the isolation of the oocysts.

Taxonomic summary

Symbiotype host: Meriones meridianus Pallas, 1773, Museum of Southwestern Biology, division of Mammals, MSB 227423, NK 192240 (adult, male) (see Frey et al., 1992).

Type locality: Borzon Gobi, Byaruuhai Bulag (Map 1, Table 1), Omnogovi, Mongolia, 1148 m elevation (42° 28' 56.352" N, 105° 15' 13.4994" E)

Prevalence: Oocysts were found in 1 of 105 (1.0%) *Meriones meridianus* (1 of 171 [.6%] *Meriones* spp.).

Site of infection: Unknown; recovered from feces.

Material deposited: Photosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68482, and oocysts preserved in potassium dichromate, HWML Coll. No. 68490 (see Williams et al., 2010).

Etymology: This species in named in honor of my wife, Sara Kvien-Jensen, for tolerating my missing our first wedding anniversary due to field work and for putting up with all the other challenges of being married to a graduate student.

Remarks

Oocysts of *E. sarae* are by far the largest of any species known to infect gerbils, with the next largest being *E. krivoli* Glebezdin, 1974 whose largest oocysts (max. = 40) are smaller in length then the average of *E. sarae*. Structurally, *E. sarae* is similar to *E. jurschuensis* Veisov, 1961, *E. musajevi* Veisov, 1961,and *E. ordubadica* Musaev and Veisov, 1965 in that lacks a micropyle, possesses a single layered wall and an OR and

lacks a PG. However, sporocysts of *E. jurschuensis* and *E. musajevi* both lack an apparent SB, and the maximum OL of *E. ordubadica* is more than 5 microns less than the minimum OL of *E. four*.

***Eimeria ivgeeltensis* n. sp. (Figs. 12, 20)**

Diagnosis: Oocyst shape: ellipsoidal; L x W: (n = 35) 27.73 x 23.44 (SD = 1.93 x 1.26) (23.71-33.12 X 21.18-27.15); L/W ratio: 1.18 (SD = .06) (1.07-1.34); wall (n=36) 1.94 (SD = .21) (1.53-2.37) of even thickness is lightly pitted and ranges from smooth to rough; PG present, but M and OR absent. PG is a single granule near one pole 2.20 (SD = .47) (1.38-3.29) in diameter. Sporocysts (n = 96) ellipsoidal, SL x SW: 12.50 x 8.64 (SD = .85 X .60) (10.49-14.53 X 7.61-10.62); SR either absent or consists of about 4 spherical globules ~1.5 in diameter along the sporocyst wall; SB and SSB present but PSB absent. SZ along the longitudinal axis with anterior ends on opposite poles; SZ each possess a very conspicuous anterior RB ~ 3.2 in diameter. 818 days elapsed between the collection of the hosts and the isolation of the oocysts.

Taxonomic summary

Symbiotype host: Meriones unguiculates Milne-Edwards, 1867, Museum of Southwestern Biology, division of Mammals, MSB 230896, NK 192467 (adult, female) (see Frey et al., 1992).

Type locality: Ivgeelt Mountain (Map 1, Table 1), Omnogovi, Mongolia, 1343 m elevation (47° 25' 57.936" N, 106° 2' 29.760" E).

Prevalence: Oocysts were found in 1 of 55 (1.8%) *Meriones unguiculatus*, (1 of 171 [0.6%] *Meriones* spp.).

Site of infection: Unknown; recovered from feces.

Material deposited: Photosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68484, and oocysts preserved in potassium dichromate, HWML Coll. No. 68491 (see Williams et al., 2010).

Etymology: This species is named for the Ivgeelt Mountain, on which the type locality is found.

Remarks

Oocysts of *E. ivgeeltensis* are most similar in structure to *E. erythrourica*, *E. schachtachtiana*, *E. vinogradovi* and *E. peschankae* Levine and Ivens, 1965 in that they lack a M and OR, possess a PG, and have a single-layered wall. However, of these previously reported species, all but *E. peschankae* lack an apparent SB, and the presence or absence of a SB is not documented for *E. peschankae*. Oocysts of *E. ingeeltensis* can then be differentiated between those of *E. peschankae* by their size; while there is some overlap in the OL ranges of the two species (24.85-30.46 and 19-27, respectively), the average OL (27.77 and 22, respectively) for each species falls outside the reported range of the other.

***Eimeria briansmithi* n. sp. (Figs. 13, 21)**

Diagnosis: Oocyst shape: ellipsoidal; L x W: (n = 49) 21.06 x 20.33 (SD = .77 x .84) (19.43-22.65 x 17.00-20.43); L/W ratio: 1.10 (1.05-1.18); wall (n=49) 1.45 (SD = .11) (1.22-1.66) of even thickness is single-layered and smooth; M and OR absent; 3-4 PG present, 1-2 solid granules near center 1.89 (SD = .35) (1.34-1.82) in diameter, and one diffuse granule near each end of the oocyst; sporocysts (n = 103) ellipsoid, SL x SW:

11.40 x 8.27 (SD = .76 X .54) (9.00-12.84 X 5.88-8.31); SR consists of single spheroid ~4 in diameter near center of SP; nipple-like SB present but SSB and PSB are absent; SZ lacks apparent RB. 144 days elapsed between the collection of the host and the isolation of the oocysts.

Taxonomic summary

Symbiotype host: Meriones unguiculates Milne-Edwards, 1867, Museum of Southwestern Biology, division of Mammals, NK 223915 (adult female) (see Frey et al., 1992).

Type locality: Near Myangan Ugalzat Mountain, Mongolia, 2119 m elevation (46° 24' 16" N, 93° 26' 40" E)

Prevalence: Oocysts were found in 1 of 55 (1.8%) *Meriones unguiculatus*, (1 of 171 [0.6%] *Meriones* spp.).

Site of infection: Unknown; recovered from feces.

Material deposited: Photosyntypes (see Bandoni and Duszynski, 1988) of sporulated oocysts, HWML Coll. No. 68485, and oocysts preserved in potassium dichromate, HWML Coll. No. 68492 (see Williams et al., 2010).

Etymology: This species is named in memory of my friend and colleague Brian Smith, whose love of nature, enthusiasm for biology, and kindness were an inspiration to all who knew him.

Remarks

Oocysts of *E. briansmithi* are most similar to those of *E. schachtachtiana* and *E. vinogradovi* in that they lack a M and an OR, possess a single-layered wall, PG, and SR, and their maximum wall thickness does not exceed 1.75 microns. However, while *E.*

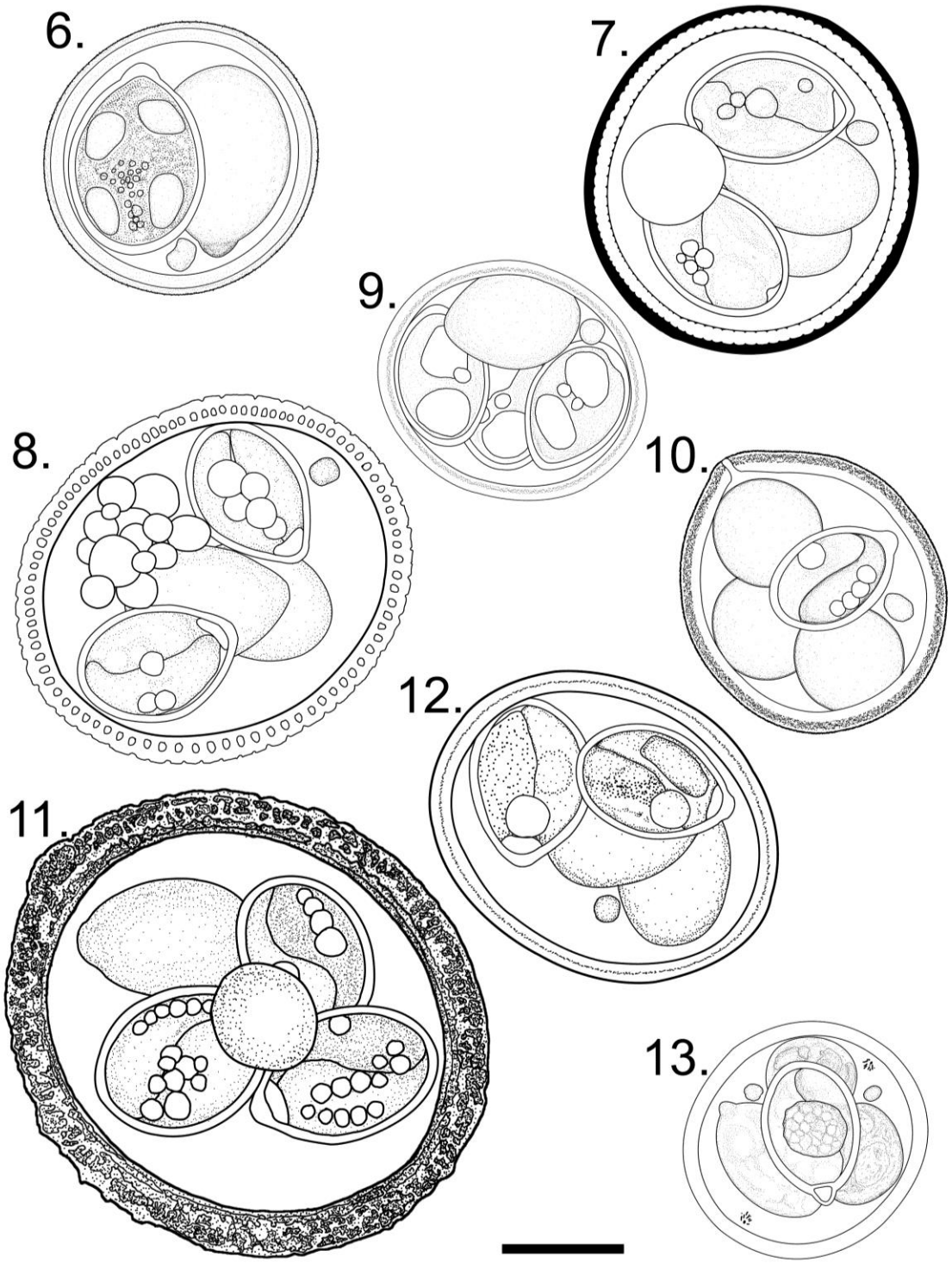
schachtachtiana and *E. vinogradovi* lack an apparent SB, *E. briansmithi* possesses a prominent, nipple-like SB. Oocysts of *E. briansmithi* can also be differentiated from those of *E. schachtachtiana* in that while sporozoites are positioned along the longitudinal axis of sporocysts in *E. schachtachtiana*, they are positioned at opposite poles of the sporocysts in *E. briansmithi*.

Taxonomic revisions

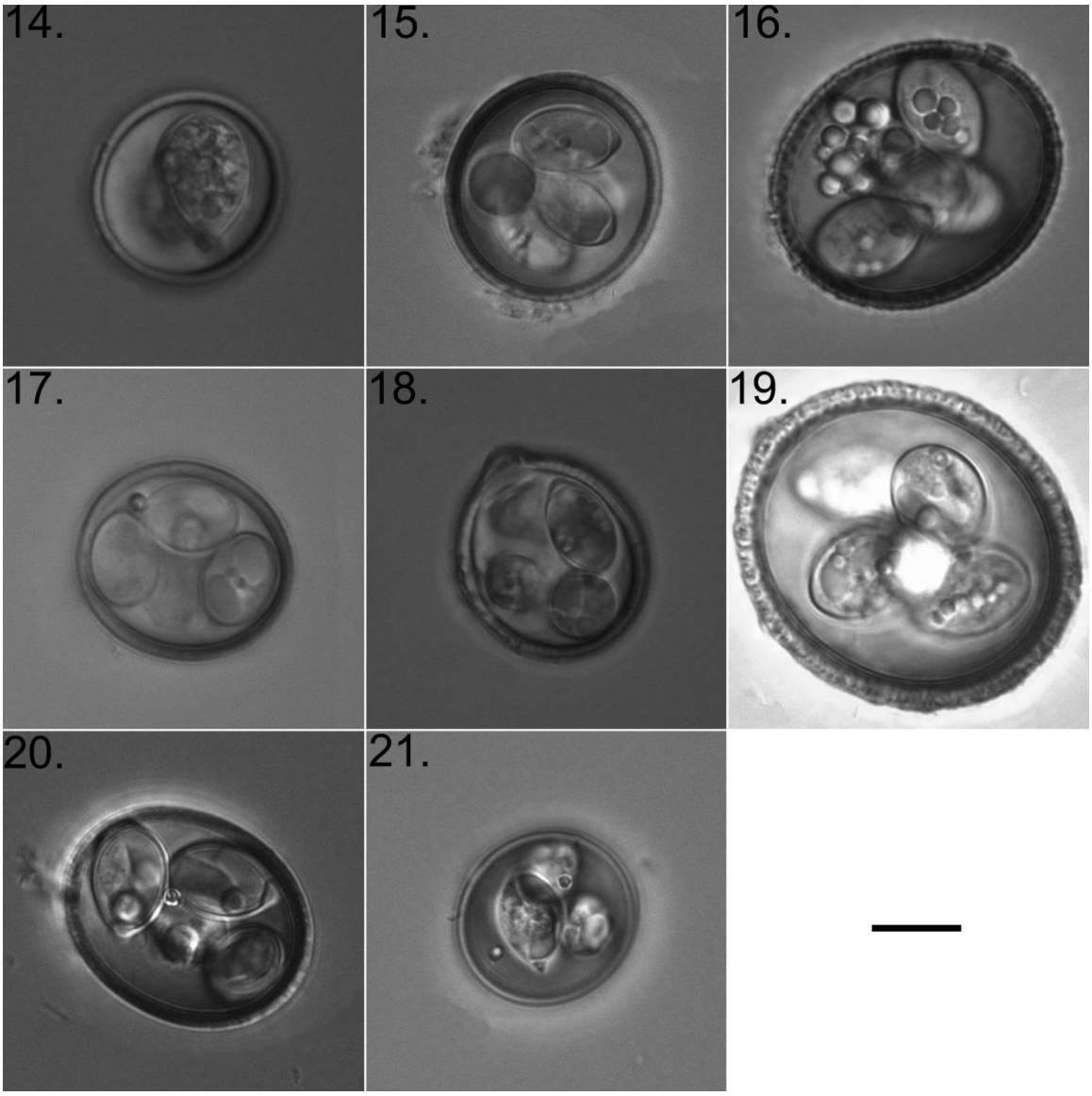
Species which were deemed synonymous or otherwise inadequate are listed below. Unless otherwise indicated, all data used in these revisions is from the original descriptions.

Eimeria astrachanbazarica Musaev and Veisov, 1960 and _Eimeria sumgaitica_ Musaev and Alieva, 1961 (Figs. 22, 23)

These two species overlap in most of their mensural characters (Fig. 33). The only difference is that *E. atrachanbazarica* has 'comma shaped, rarely pear-shaped' sporozoites and was reported from hosts of *Meriones tristrami* (Musaev and Veisov, 1960), whereas *E. sumgaitica* has 'pear-shaped' sporozoites and occurs in *Meriones libycus*. Both species have similar sporulation times (3-3.5 and 3-4 days for *E. atrachanbazarica* and *E. sumgaitica*, respectively), occur in the large intestine, and are reported from Azerbaidzhan. Considering the morphological similarity of these two species and their occurrence in the same host genus and geographical region, I believe that *E. sumgaitica* should be regarded as a junior synonym of *E. astrachanbazarica*.



Figures 6-13: Line drawings of sporulated oocysts. 6. *Isospora merionis.*7. *Eimeria salasuzica.* 8. *E. kostencovi.* 9. *E. schachtachtiana*. 10. *E. tsogoi.* 11. *E. sarae.* 12. *E. ivgeeltensis*. 13. *E. briansmithi.* Scalebar = 10 µm.



Figures 14-21: Photomicrographs of sporulated oocysts. Scalebar = 10 µm. 14. *Isospora merionis.* 15. *Eimeria salasuzica.* 16. *E. kostencovi.* 17. *E. schachtachtiana.* 18. *E. tsogoi.* 19. *E. sarae.* 20. *E. ivgeeltensis*. 21. *E. briansmithi.* Images 18 and 20 are edited to show features from multiple planes of focus.

***Eimeria jersenica* Davronov, 1973 and *Eimeria karschinica* Davronov, 1973 (Figs. 24, 25)**

These two species overlap in most mensural characters (Fig. 34) (Davronov, 1973). However, the maximum wall thickness reported for *E. jersenica* is equal to the minimum of that reported from *E. karschinica*. *E. jersenica* is reported to occur in *M. libycus*, while *E. karschinica* is reported to occur in *M. meridianus.* In the line drawings (Figs. 24, 25), it appears that the oocyst residuum of *E. jersenica* is a solid mass, while that of *E. karschinica* is an aggregate of a single large globule and several smaller granules. However, considering that these line drawings were not drawn to scale, their accuracy is somewhat dubious. Even if the drawings are accurate in this respect, a slight difference in the quality of the oocyst residuum could easily be attributed to polymorphism of a single species. These two species were not directly compared in the document in Davronov, 1973. In light of their similar morphology, and their occurrence in the same host genus and geographical region (Uzbekistan), I believe these two species are synonymous. As they are described in the same document, *E. karschinica* should be considered a junior synonym of *E. jersenica*, which is described first in the document (Davronov, 1973).

***Eimeria martunica* Musaev and Alieva, 1961, *Eimeria meridiana* Veisov, 1964 and *Eimeria tristrami* Musaev and Veisov, 1965 (Figs. 26, 27, 28)**

These three species overlap in most of their mensural characters (Fig. 35). However, wall thicknesses may or may not overlap; they are described with single measures of 2 μm and 3 μm for *E. martunica* and *E. tristrami*, respectively, and as a range between 2 μm and 2.5 μm for *E. meridiana*. All three species have a granular sporocyst residuum, and the

sporozoites are described as ‘pear or bean-shaped’, ‘comma-shaped’ and ‘comma-shaped or bean-shaped’ for *E. martunica, E. meridiana* and *E. tristrami*, respectively. There is a slight difference in the descriptions regarding refractile globules. No details regarding the presence or absence of refractile bodies are offered in the text of the descriptions. However, in the illustrations, it appears that *E. martunica* and *E. tristrami* are without refractile bodies, while there is apparently a refractile body located in the anterior of each sporozoite in *M. meridianus*. *Eimeria martunica, E. meridiana* and *E. tristrami* are reported as infecting *Meriones libycus, Meriones meridianus* and *Meriones tristrami*, respectively.

Despite the fact that it is the last species described of the three, *E. tristrami* is only compared with other species of *Eimeria* which were known to infect *M. tristrami* in Musaev and Veisov, 1965. Veisov (1964) failed to compare oocysts of *E. meridian* with those of any other species of *Eimeria*. The type localities for *E. tristrami* and *E. martunica* are both in the Caucasus (Armenia and Azerbaijan, respectively), while that of *E. meridiana* is in Central Asia (Tajikistan). Considering the morphological similarities of these three species, and their occurrence in the same host genus and neighboring geographical regions, I believe they are synonymous. I therefore recommend that *E. meridiana* and *E. tristrami* be considered junior synonyms of *E. martunica*.

***Eimeria salasuzica* Musaev and Veisov, 1960b and *Eimeria tasakendica* Veisov, 1961**

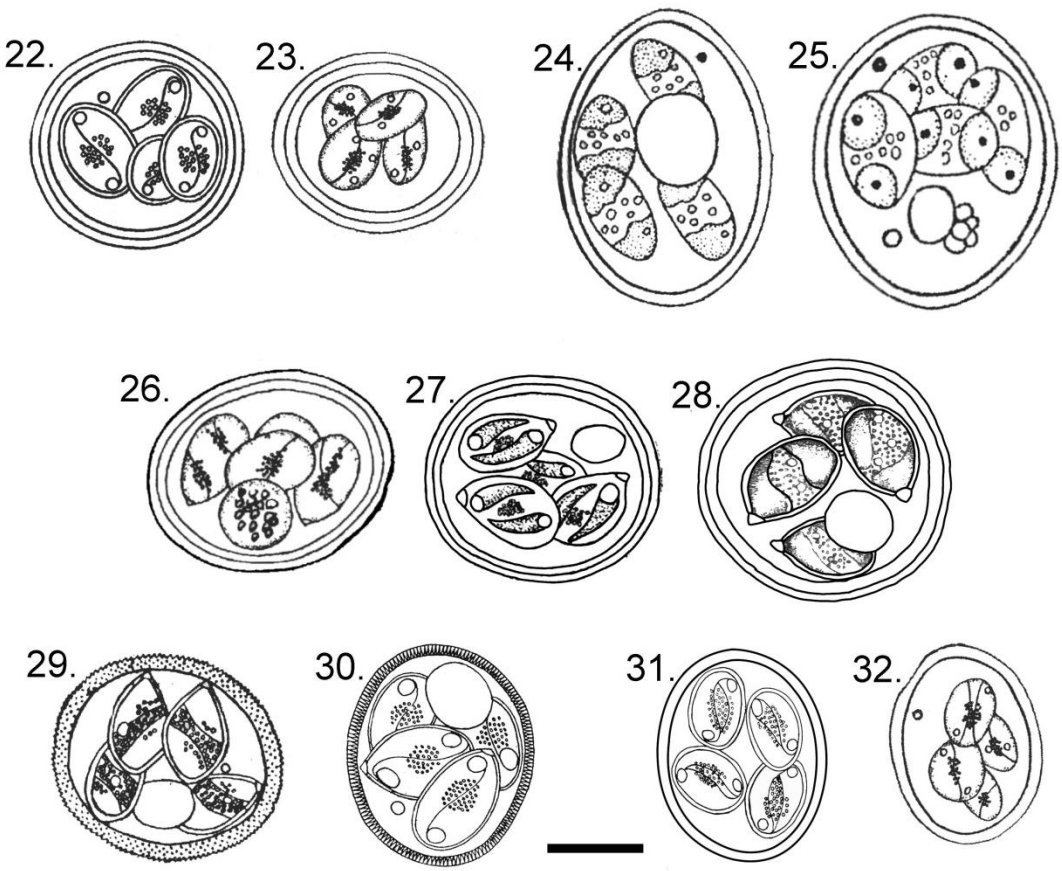
(Figs. 29, 30)

These two species overlap in most mensural characters (Fig. 36). However, while the wall thickness of *E. salasuzica* is listed as 1.5 μm on average, that of *E. tasakendica* islisted as 1.2 to 1.4 μm, with no average given. Even though there is no refractile body visible in the line drawing of *E. salasuzica*, the text states that it is present. *E. salasuzica* is reported from *M. persicus*, while *E. tasakendica* is reported from *M. vinogradovi*. In light of these two species morphological similarities and their occurrence in the same host genus and geographical region (Azerbaijan), I believe them to be synonymous. Therefore, I recommend that *E. tasakendica* be considered a junior synonym of *E. salasuzica*.

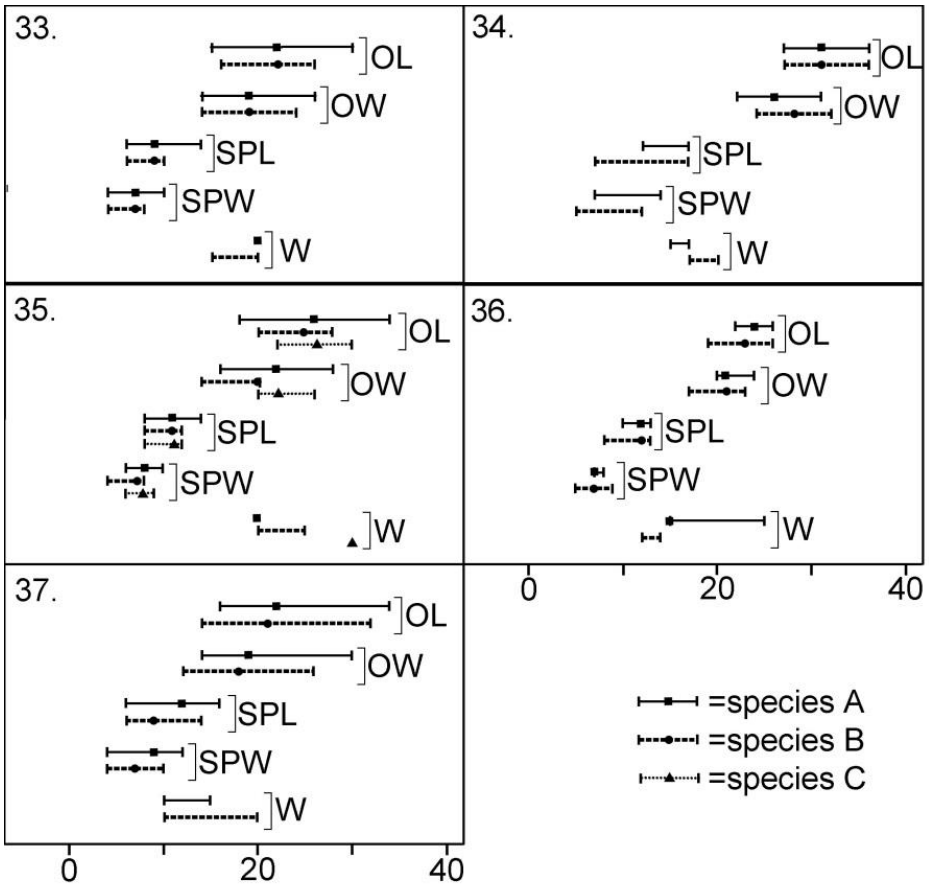
***Eimeria vinogradovi* Veisov, 1961 and *Eimeria erythrourica* Musaev and Alieva, 1961**

(Figs. 31, 32)

These two species overlap in all mensural characters (Fig. 37). There is also no discernible difference in qualitative characters. *Eimeria schachtachtiana* is reported as infecting *Meriones shawi*, whereas *E. vinogradovi* is reported as infecting *Meriones vinogradovi*. In light of these two species morphological similarities and their occurrence in the same host genus and geographical region (Azerbaijan), I believe them to be synonymous. The description of *E. vinogradovi* was published in the 4th issue of the 1961 volume of the *Academy of Sciences of Azerbaijan, Biology and Medicine Series*, while that of *E. erythrourica* was published in the 5th issue of the same journal. Therefore, I recommend that *E. erythrourica* be considered a junior synonym of *E. vinogradovi*.



Figures 22-32: Line drawings of sporulated oocysts. Scalebar = 10 µm. 22. *Eimeria astrachanbazarica*, scanned from Musaev and Veisov, 1960a. 23. *E. sumgaitica*, scanned from Musaev and Alieva, 1961. 24. *E. jersenica*, scanned from Davronov, 1973. 25. *E. karschinica*, scanned from Davronov, 1973. 26. *E. martunica*, scanned from Musaev and Alieva, 1961. 27. *E. meridiana*, scanned from Veisov, 1964. 28. *E. tristrami*, scanned from Musaev and Veisov, 1965. 29. *E. salasuzica*, scanned from Musaev and Veisov, 1960b. 30. *E. tasakendica*, scanned from Veisov, 1961. 31. *E. vinogradovi*, scanned from Veisov, 1961. 32. *E. erythrourica*, scanned from Musaev and Alieva, 1961.



Figures 33-37: Comparison of oocyst length (OL), oocyst width (OW), sporocyst length (SL), sporocyst width (SW), and wall thickness (W) for likely synonymous species. Wall thickness presented at 10 X reported thickness for comparison. 33. *Eimeria astrachanbazarica* (A) and *E. sumgaitica* (B). 34. *E. jersenica* (A) and *E. karschinica* (B). 35. *E. martunica* (A), *E. meridiana* (B), and *E. tristrami* (C). 36. *E. salasuzica* (A) and *E. tasakendica* (B). 37. *E. vinogradovi* (A) and *E. erythrourica* (B).

Eimeria akeriana Ismailov and Gaibova, 1983

No descriptions or line drawings of the oocysts of this species are offered in the original description, a previous study by Musaev et al. (1982), or in Levine and Ivens (1990). Though Musaev et al. (1982) must have observed these oocysts, given that they used them to inoculate gerbils in order to observe the lifecycle, they apparently never saw fit to

provide details on its morphology. Because the majority of coccidia from hosts of the genus *Meriones* are known by the oocyst alone, there is no way to verify that the meronts described by Ismailov and Gaibova represent a previously undescribed species. Therefore, *Eimeria akeriana* is not a valid species name.

Eimeria assaensis **Levine and Ivens, 1965, *Eimeria peschankae*** **Levine and Ivens, 1965, and *Eimeria tamariscini*** **Levine and Ivens, 1965**

These three species were all named by Levine and Ivens in their 1965 synthesis of the taxonomy of the coccidia of rodents. These species were not actually observed by Levine and Ivens. Instead, they represent species records that occurred in hosts distantly related to the original host of a previously described species. Oocysts originally thought to be *E. callospermophili* (host: *C. lateralis*) by Svanbaev (1962 *non vida*) were named *Eimeria assaensis;* oocysts thought to be *Eimeria krijgsmanni* Yakimoff and Gousseff, 1938 (host: *Mus musculus* Linnaeus, 1758) by Svanbaev (1956; 1962 *non vida*) were named *Eimeria peschankae*; oocysts thought to be *Eimeria musculi* Yakimoff and Gousseff, 1938 (host: *M. musculus*) by Svanbaev (1956) were named *Eimeria tamariscini*.

The argument presented by Levine and Ivens (1965) that *E. assaensis*, *E. peschankae*, and *E. tamariscini* are distinct from *E. callospermophili*, *E. krijgsmanni*¸ and *E. musculi*, respectively, may have been valid in some cases. In fact, Todd and Hammond (1968b) experimentally demonstrated that *E. callospermophili* from *U. armatus* could not be transmitted to *M. unguiculatus*. However, because Levine and Ivens provided no photographs, illustrations, or any other type materials for the three species they named,

the species are not in compliance with the ICZN (Ride et al., 1999). Therefore, I recommend that *E. assaensis, E. peshankae,* and *E. tamariscini* be considered *species inquirendae.*

Cladistic analyses

Tree score distributions from all 4 analyses were weakly skewed right, with g1 values ranging from -0.25439 (all data, unweighted characters) to -0.494937 (categorical data only, characters weighted inversely to the number of character states) (Table 4). Using all data, 3 and 8 equally parsimonious trees were found using unweighted characters and characters weighted inversely to the number of character states, respectively (Table 4). Using only categorical data, 10 and 7 equally parsimonious trees were found using unweighted characters and characters weighted inversely to the number of character states, respectively (Table 4). Majorityrule consensus trees built from the four analyses differ only in their placement of *E. ivgeeltensis* and *E. briansmithi* (Figs. 37, 38).

The trees found using all data and unweighted character states had the highest consistency index (CI) excluding uninformative characters with a value of 0.6667 (Table 4). However, the highest retention index (RI) and rescaled consistency index (RC) values belonged to trees found using only categorical data, weighted inversely to the number of character states, with values of 0.358 and 0.548, respectively (Table 4). Characters 5, 6, 7, 8, 9 and 18 were found to be parsimony uninformative (Table 5).

	all data		categorical only	
	unweighted	weights = scale^{-1}	unweighted	weights = scale^{-1}
# best trees	3	8	10	7
g1	-0.254	-0.431	-0.469	-0.495
CI	0.6667 (0.7167)	0.6452 (0.7180)	0.6364 (0.6471)	0.6346 (0.655)
HI	0.3333 (0.2833)	0.3548 (0.2820)	0.3636 (0.3529)	0.3654 (0.345)
RI	0.469	0.490	0.520	0.548
RC	0.336	0.352	0.337	0.358
Rohlf's CI	0.889	0.821	0.821	0.821
Mickevich's CI	0.750	0.688	0.688	0.688

Table 4: Number of equally parsimonious trees, g1 value of tree scores distribution, CI, HI, RI and RC of best trees (CI and HI excluding uninformative characters listed with raw CI and HI in parentheses), and Rohlf's CI and Mickevich's consensus information for majority rule consensus trees for each analysis.

character	range	min	tree	max	CI	RI	RC	HI	G-fit
1	4	4	5	6	0.80	0.50	0.40	0.20	0.75
2	3	3	5	5	0.60	0.00	0.00	0.40	0.60
3	3	3	5	5	0.60	0.00	0.00	0.40	0.60
4	3	3	4	4	0.75	0.00	0.00	0.25	0.75
5	3	3	3	3	1.00	0/0	0/0	0.00	1.00
6	1	1	1	1	1.00	0/0	0/0	0.00	1.00
7	2	2	2	2	1.00	0/0	0/0	0.00	1.00
8	1	1	1	1	1.00	0/0	0/0	0.00	1.00
9	1	1	1	1	1.00	0/0	0/0	0.00	1.00
10	2	2	4	5	0.50	0.33	0.17	0.50	0.60
11	3	3	4	6	0.75	0.67	0.50	0.25	0.75
12	2	2	4	4	0.50	0.00	0.00	0.50	0.60
13	2	2	3	4	0.67	0.50	0.33	0.33	0.75
14	2	2	3	4	0.67	0.50	0.33	0.33	0.75
15	2	2	3	4	0.67	0.50	0.33	0.33	0.75
16	1	1	2	2	0.50	0.00	0.00	0.50	0.75
17	2	2	3	5	0.67	0.67	0.44	0.33	0.75
18	1	1	1	1	1.00	0/0	0/0	0.00	1.00
19	2	2	3	4	0.67	0.50	0.33	0.33	0.75
20	2	2	3	4	0.67	0.50	0.33	0.33	0.75
21	1	1	1	4	1.00	1.00	1.00	0.00	1.00

Table 5: Character diagnostics from cladistic analysis using all data and characters weighted inversely to the number of character states.

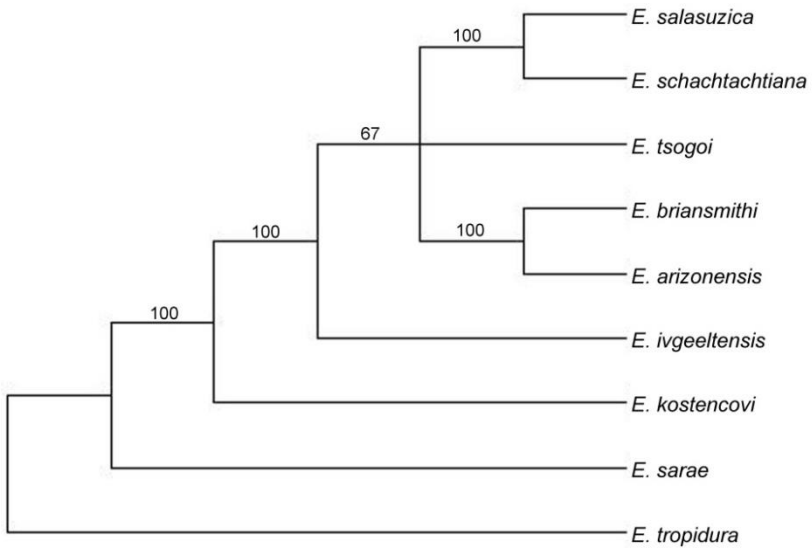


Figure 38: Majority-rule consensus tree for cladistic analysis using all data and unweighted characters. Nodes labeled with node support.

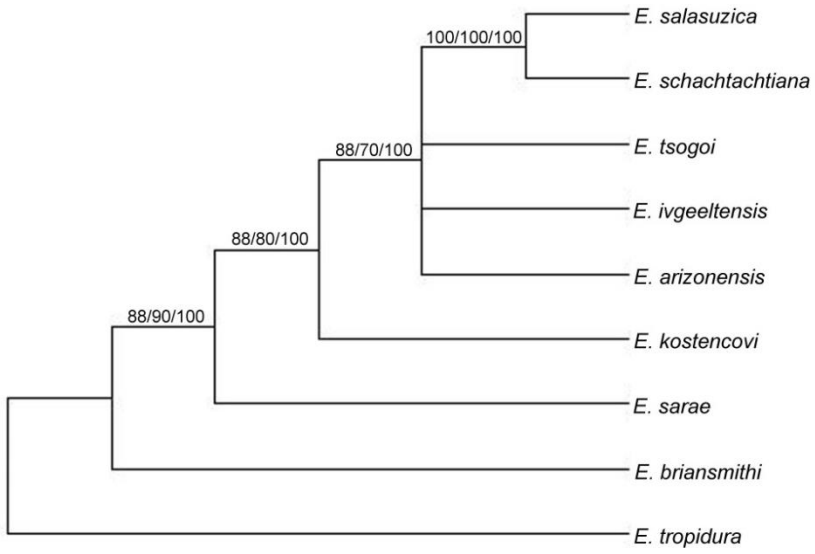


Figure 39: Majority-rule consensus tree for cladistic analyses using all data and characters weighted inversely to the number of states, and using only categorical data with both unweighted characters and characters weighted inversely to the number of states. Nodes labeled with node support for all three analyses, respectively.

Statistical analyses

The most significant correlation between a host variable and coccidian infections was between host species and infection by *Eimeria* spp., with a p-value of .07 (Table 6). This was followed by year of capture and infection by *Isospora* spp. (p=.14), sex and infection by *Eimeria* spp. (p=.27), and infection by cestodes and infection by *Eimeria* spp. (p=.28) (Table 6).

According to the multigroup discriminant analysis, 98.99% of the variation is accounted for in the first 2 canonical variates. The squared distances between all pairs of species were significant (Table 7). However, the squared distance between *E. schachtachtiana* and *E.briansmithi* was much less than that between any other pair of species (Fig. 40, Table 7). The greatest squared distance between any two species was between *Eimeria sarae* and *E. schachtachtiana*. *Eimeria sarae* was also the only species whose minimum area enclosing polygon did not overlap with that of any other species (Fig. 40).

Niche modeling

The ENM's created using Maxent predicted that *Eimeria* spp. occur in 28.70% and *Meriones* spp. occur in 11.03% of the total area of Mongolia (Table 8, Maps 2, 4, 6). Of the total distribution of *Meriones* spp., *Eimeria* spp. were predicted to occur in 54.34% (Table 8). The three data layers which had the greatest percent contribution to the models were NDVI, mean precipitation of the driest month, and aspect for *Eimeria* spp., and total annual precipitation, slope, and NDVI for species of *Meriones* (Table 9, Fig. 41).

The best subset model created using GARP predicted that *Eimeria* spp. occur in 28.63% and *Meriones* spp. occur in 55.78% of the total area of Mongolia (Table 8, Maps 3, 5, 7). Of the total distribution of *Meriones* spp., *Eimeria* spp. were predicted to occur in 47.28% (Table 8). All data layers were used in all 10 'best' models for both *Eimeria* spp. and *Meriones* spp., as were all four rule types.

When compared against random chance using a chi-squared test with one degree of freedom, the ten best models predicting the distribution of *Eimeria* spp. had *p*-values ranging from 0.05 to 0.09, while the ten best models predicting the distribution of *Meriones* spp. were all highly significant ($p < .001$) (Table C).

For models built using GARP, 7.88% of the predicted distribution of *Eimeria* spp. did not coincide with that of species of *Meriones* (Table 8). For models built using Maxent, 79.12% of the predicted distribution of *Eimeria* spp. did not coincide with that of species of *Meriones* (Table 8). The full AUC values for models of the distribution of *Eimeria* spp. were 0.72 and 0.87 for models made with Maxent and GARP, respectively (Fig. 42). The full AUC values for models of the distribution of *Meriones* spp. were 0.80 and 0.79, likewise (Fig. 43). For each taxon, the method which produced the greater full AUC also produced the greater partial AUC with a user-defined error level of 0.2 (Figs. 42, 43). For *Eimeria* spp., presence area predicted only by Maxent, presence area predicted only by GARP, and presence area predicted by both methods occurred in approximately equal proportions (Table 10). For *Meriones* spp., proportion of presence area predicted by Maxent only was much smaller than that predicted by GARP only, and the presence area predicted by both methods was about half of the total area of Mongolia (Table 10).

	Eimeria		*Isospora*		
host variable	negative (n=158)	positive (n=13)	negative (n=163)	positive (n=8)	total*
species					
M. meridianus	99 (95%)	5 (5%)	98 (95%)	6 (5%)	104
M. unguiculatus	48 (86%)	8 (14%)	55 (98%)	1 (2%)	56
	X^2=3.20 (df=1, p=.07)		X^2=.59 (df=1, p=.44)		
sex					
male	79 (95%)	4 (5%)	79 (95%)	4 (5%)	83
female	76 (92%)	9 (8%)	81 (95%)	4 (5%)	85
	X^2=1.23 (df=1, p=.27)		X^2=0.11 (df=1, p=.74)		
infection with nematodes					
positive	59 (94%)	4 (6%)	59 (94%)	4 (6%)	63
negative	91 (93%)	7 (7%)	94 (96%)	4 (4%)	98
	X^2=.02 (df=1, p=.90)		X^2=.08 (df=1, p=.78)		
infection with cestodes*					
positive	7 (78%)	2 (22%)	8 (89%)	0 (0%)	9
negative	143 (93%)	10 (7%)	145 (94%)	9 (6%)	154
	X^2=1.19 (df=1, p=.28)		X^2=.01 (df=1, p=.93)		
month of capture					
June	103 (92%)	9 (8%)	106 (95%)	6 (5%)	112
July	51 (93%)	4 (7%)	53 (96%)	2 (4%)	55
August	4 (100%)	0 (0%)	4 (100%)	0 (0%)	4
	X^2=.37 (df=2, p=.83)		X^2=.44 (df=2, p=.80)		
year of capture					
2009	29 (94%)	2 (6%)	31(100%)	0 (0%)	31
2010	27 (87%)	4 (13%)	31(100%)	0 (0%)	31
2011	23 (96%)	1 (4%)	23 (96%)	1 (4%)	24
2012	79 (93%)	6 (7%)	78 (92%)	7 (8%)	85
	X^2=1.74 (df=3, p=.63)		X^2=5.47 (df=3, p=.14)		

Table 6: Chi-squared and *p* values of correlations between host variables and infection by *Eimeria* sp. and *Isospora* sp.. *Some data are omitted from analyses due to unknown values.

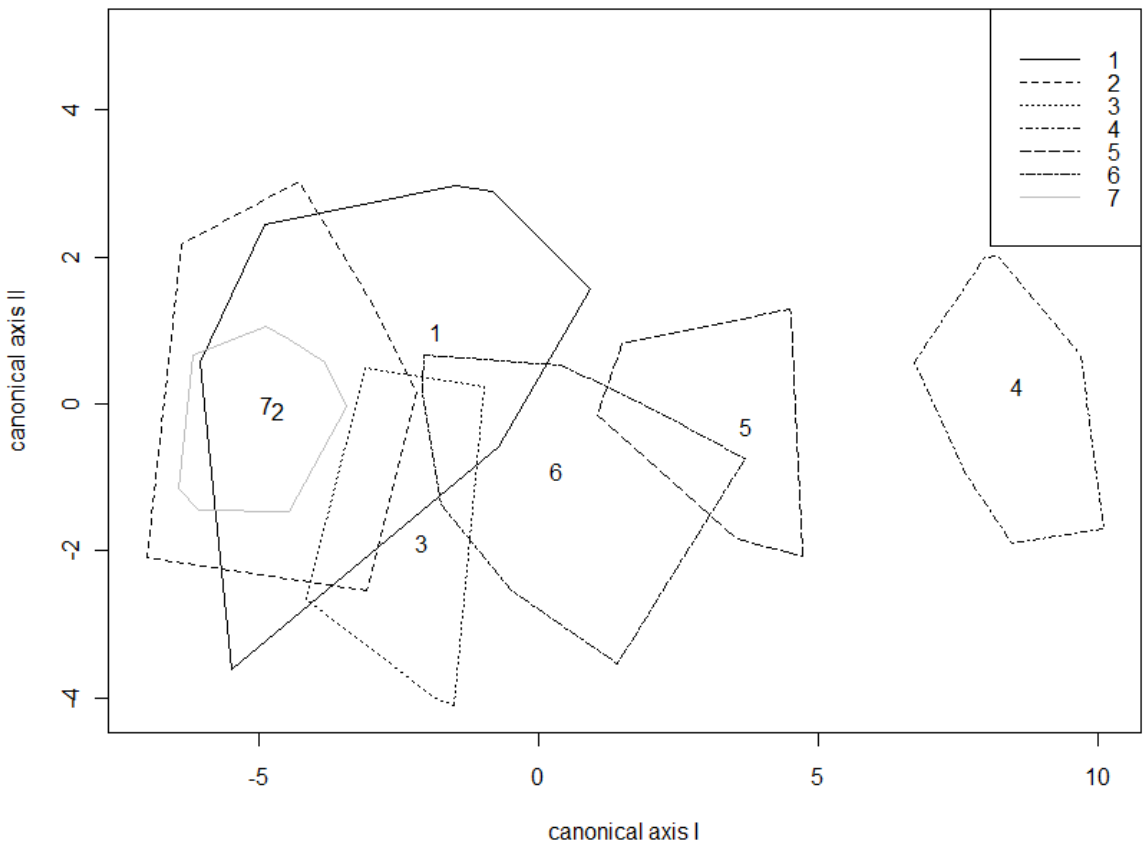


Figure 40: Minimum area enclosing polygons of discriminant scores of log-10 transformed measurements for the seven species of *Eimeria* found in this study: 1. *E. salasuzica*. 2. *E. schachtachtiana*. 3. *E. tsogoi*. 4. *E. sarae*. 5. *E. kostencovi*. 6. *E. ivgeeltensis*. 7. *E. briansmithi*.

	squared distances between species						
	E. salasuzica	*E. schachtachtiana*	*E. tsogoi*	*E. sarae*	*E. kostencovi*	*E. ivgeeltensis*	*E. briansmithi*
E. salasuzica	-	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
E. schachtachtiana	9.43	-	<.0001	<.0001	<.0001	<.0001	0.0003
E. tsogoi	9.13	11.82	-	<.0001	<.0001	<.0001	<.0001
E. sarae	108.32	174.31	118.89	-	<.0001	<.0001	<.0001
E. kostencovi	32.73	70.35	37.62	23.77	-	<.0001	<.0001
E. ivgeeltensis	8.71	25.61	9.39	69.32	12.57	-	<.0001
E. briansmithi	10.61	1.17	12.88	180.06	74.02	28.24	-

Table 7: Squared distances between species multivariate means listed in lower cells and probability that distances exceed Mahalanobis distances in upper cell.

	Maxent	GARP
% of presence area for *Eimeria* spp.	28.70%	28.63%
% of presence area for *Meriones* spp.	11.03%	55.78%
% of *Meriones* presence area coinciding with *Eimeria* presence area	54.34%	47.28%
% of *Eimeria* presence area no coinciding with *Meriones* presence area	79.12%	7.88%
full AUC (*Eimeria)*	0.72	0.87
full AUC (*Meriones*)	0.80	0.79
partial AUC (*E* = 0.9) (*Eimeria*)	0.43	0.74
partial AUC (*E* = 0.9) (*Meriones*)	0.57	0.52

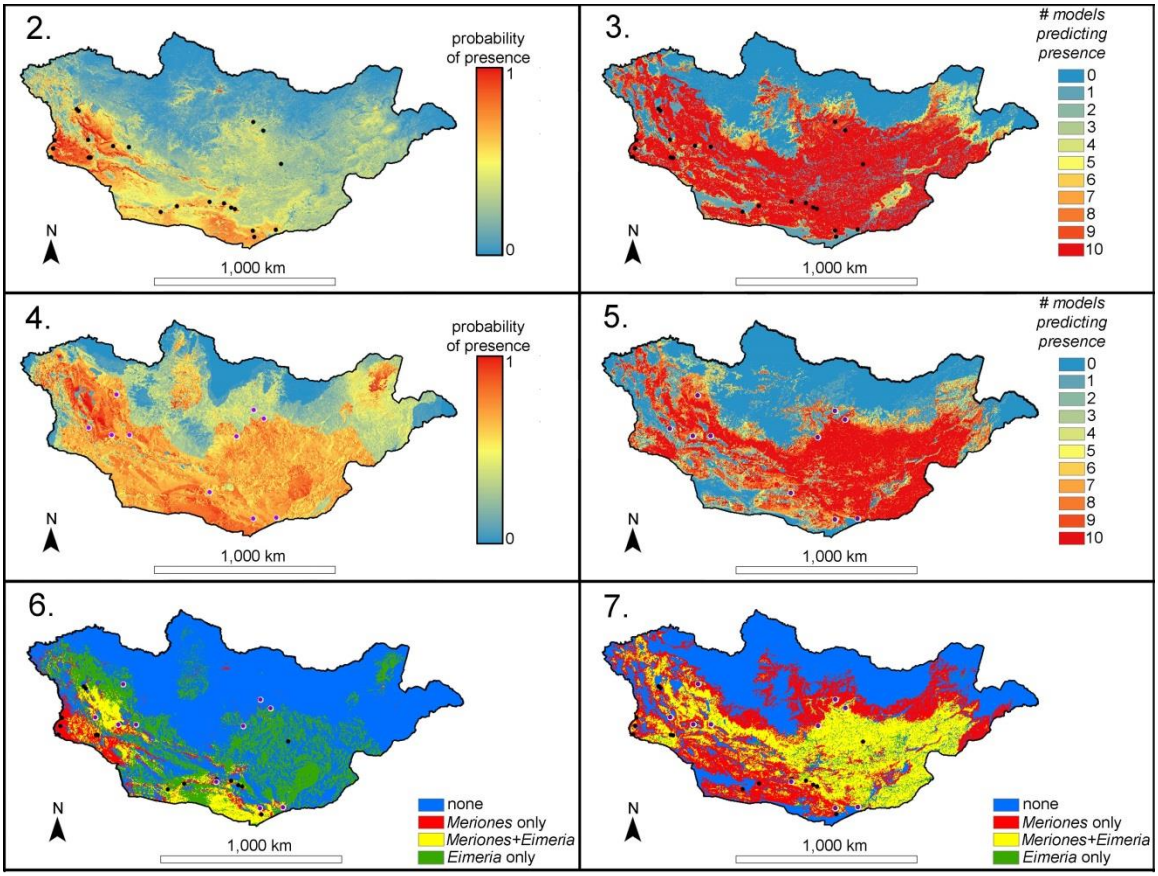
Table 8: Percentage of total area predicted present, percentage of host presence area coinciding with parasite presence area, percentage of parasite presence area not coinciding with host presence area, and full and partial AUC values for models made with Maxent and GARP.

Variable	*Eimeria* percent contribution	*Meriones* percent contribution
NDVI	45.20%	22.20%
min. precipitation	36.40%	0.10%
aspect	11.30%	2.10%
slope	3.50%	11.40%
mean annual temp.	3.20%	7.60%
max. precipitation	0.40%	49.90%
min.temp.	0.00%	0.80%
max. temp.	0.00%	0.60%
total annual precip.	0.00%	2.20%
mean summer temp.	0.00%	0.90%
elevation	0.00%	2.10%

Table 9: Percent relative contribution of environmental layers to Maxent models.

	Eimeria spp.		*Meriones* spp.	
	presence area (GARP)	absence area (GARP)	presence area (GARP)	absence area (GARP)
presence area (Maxent)	14.34%	14.37%	49.57%	1.15%
absence area (Maxent)	14.31%	56.99%	25.95%	23.32%

Table 10: Coincidence of presence and absence area for distributions of *Eimeria* spp. and *Meriones* spp. predicted with Maxent and GARP.



Maps 2-7: Distributions for *Meriones* spp. (2,3,6,7) and *Eimeria* spp. (4,5,6,7) predicted by Maxent (2,4,6) and GARP (3,5,7).

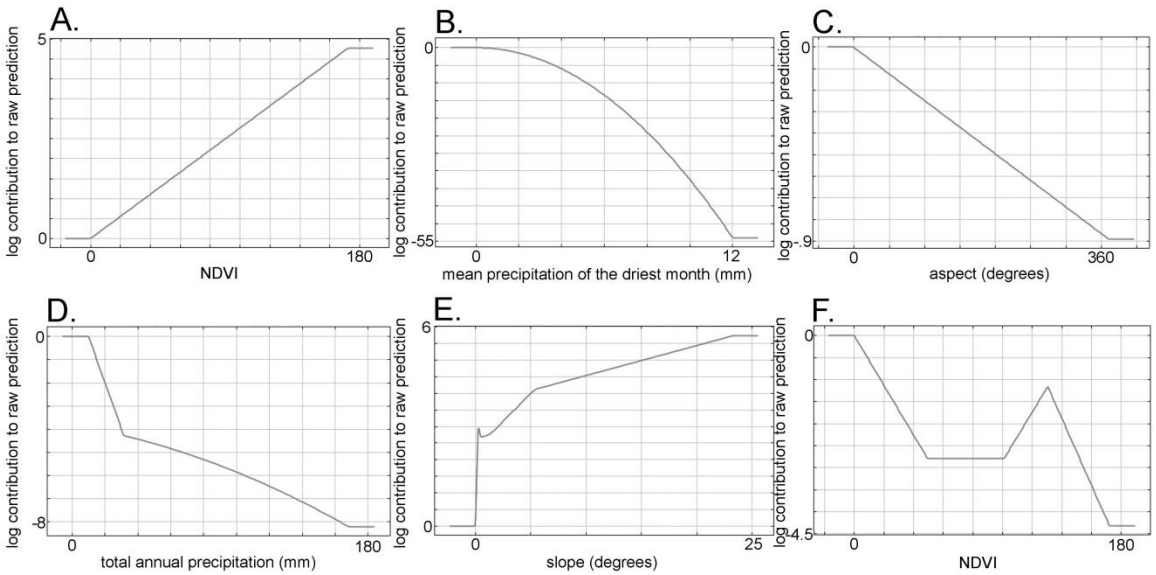
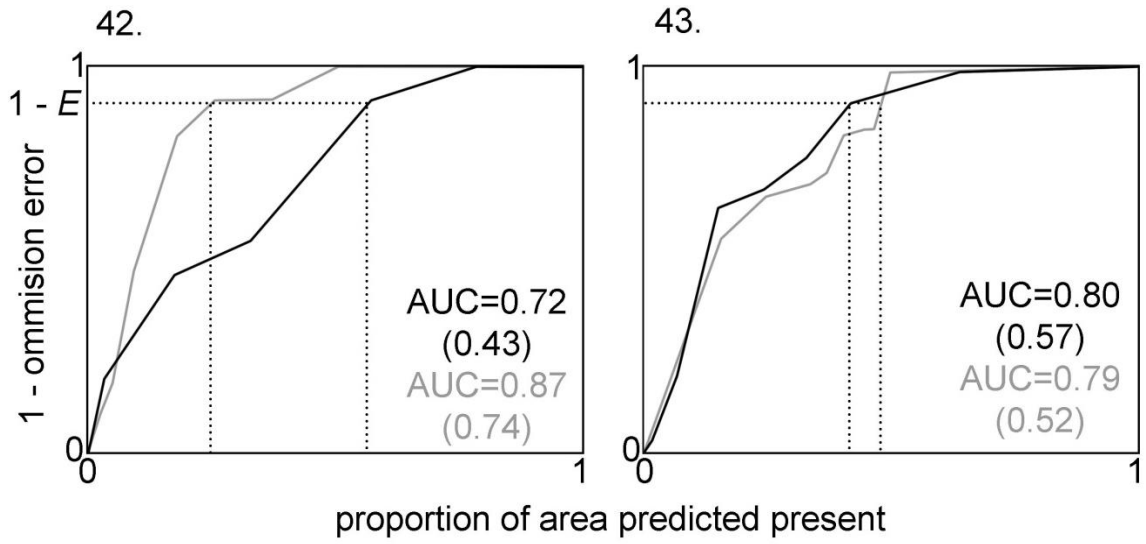


Figure 41: Marginal response curves for the 3 most important variables in Maxent models of *Eimeria* spp. (A,B,C) and *Meriones* spp. (D,E,F) distributions.



Figures 42,43: ROC plots and AUC scores for models of distributions of *Eimeria* spp. (42) and *Meriones* spp. (43). Lines and AUC values are in black for Maxent and grey for GARP. Full AUC values given with partial AUC values with user defined error of $E = 0.1$.

V. DISCUSSION

Taxonomy

Taxonomic revisions

Considering the 10 species this study recommends be considered junior synonyms or *species inquirendae*, the number of species of *Eimeria* infecting gerbils would be reduced by ~20% from 49 to 39, and the number of species of Eimeriidae by ~18% from 56 to 46. The validity these revisions depends heavily on the extent of host specificity in the coccidia of gerbils.

For lack of more knowledge, these revisions were made assuming species of *Eimeria* are usually capable of infecting congeners of their known host. Even though taxonomic ranking above the species level is arbitrary (Brooks and McLennan, 2002), this assumption appears to be valid, more often than not (Levine and Ivens, 1988). However, while the implementation of this assumption works well as a general rule, it is far from universal. For instance, *Eimeria langebarteli* Ivens, Kruidenier, and Levine, 1959 could not be experimentally transmitted from *Peromyscus leucopus* Rafinesque, 1818 to its congener *P. maniculatus* Wagner, 1845 (Hnida and Duszynski, 1999a), while *Eimeria chinchillae* can be transmitted between members of 3 rodent families (De Vos, 1970). If the eimerians infecting gerbils are as host specific as the *E. langebarteli*, then these revisions may have gone too far, wrongfully declaring morphologically indistinguishable species which occur in different species of *Meriones*, such as *E. jersenica* and E. *karschinica*, to be synonymous. However, if eimerians infecting gerbils are more similar to *E. chinichillae* in their host specificity or lack thereof, then the recommendations for

revisions in this study may not be extensive enough, failing to recognize morphologically similar eimerians which occur in different host genera, such as *E. kostencovi* (which occurs in *Meriones meridianus)* and *E. conveni* (which occurs in *Rhombomys opimus*) as synonymous.

Species descriptions

The species descriptions in this study represent an important milestone in the taxonomy of gerbil coccidia. Other than two species from *Gerbilliscus guineae* Thomas, 1910 (Modrý et al., 2008), these are the first species descriptions of gerbil coccidia since 1983 (Ismailov and Gaibova). Discounting *Eimeria akeriana* as an invalid species (see 'Taxanomic revisions' in chapter IV), this study contains the first *valid* species descriptions of gerbil coccidia since 1975 (Mirza and Al-Rawas, cited from Duszynski et al., 2000). Furthermore, this study is only the second in which coccidian species from *M. unguiculatus* have been described, the first being by (Machul'skii) in 1949.

This study also represents the first descriptions of gerbil coccidia to utilize photosyntypes (Bandoni and Duszynski, 1988) as type material. In fact, to the best of the author's knowledge, this is the first study which presents any photographs of sporulated oocysts of gerbil coccidia. Also to the best of the author's knowledge, this study contains the first descriptions of gerbil coccidia which contain data on the presence or absence of the substieda and parastieda body and which present mean, range, and standard deviation for measurement data.

Although their accuracy has been called into question (Bebber et al., 2007), species discover curves have been widely used to estimate numbers of undiscovered species since

the middle of the twentieth century. Essentially, as sample size increases in regard to the localities, individuals or length of time sampled, the number of species discovered at first increases proportionally. However, as the sample size continues to increase, the rate at which new species are discovered decreases until, theoretically, all species have been discovered (Steyskal, 1965). When one considers that of the seven species of *Eimeria* found in this study, only two had been previously described, and only two were found in more than one individual host, it is clear that the number of eimerian species from gerbils in Mongolia discovered is far less than the number that must exist. Therefore, it seems likely that the number of eimerian species discovered would continue to increase with the number of Mongolian gerbils examined.

Statistical analyses

The variable with which the correlation with infection by species of *Eimeria* was most significant was host species, with a p-value of .07 ($X^2 = 3.20$). While the correlation between infection by species of *Isospora* and the year the host was collected was the next most significant (p=.14) (Table 6), the results of the Chi-squared test are somewhat misleading, as 6 of the 8 individual hosts infected with isosporans were from the same locality and were collected on the same day. The rest of these relationships lacked significance, with the next most significant correlation being that between host sex and infection by eimerians (p = .27).

In light of the ability of *M. unguiculatus* to serve as a host for a wide variety of experimental infections, it is not surprising that infections would be especially prevalent in this species. However, a search of a commonly used peer reviewed literature database

with "*Meriones meridianus"* and "experimental infection" as keywords returned only a single result, while a search for "*Meriones unguiculatus*" and "experimental infection" in the same database produced 43 results. Though it is needless to state that more literature concerning experimental infections using *M. unguiculatus* and *M. meridianus* as hosts must exist, this discrepancy likely reflects an actual scarcity of experimental infections using *M. meridianus* as a host, whether the infections were successful or not. In other words, the susceptibility of *M. meridianus* to a variety of pathogens is understudied, especially compared to that of *M. unguiculatus*. Therefore, it is not possible to attribute the higher prevalence of eimerian infection in *M. unguiculatus* relative to *M. meridianus* to greater susceptibility to other pathogenic organisms until more experimental infections have been attempted with *M. meridianus*.

Cladistic analysis

Across all analyses, the placement of *E. arizonensis*, a parasite of New World cricetid rodents, makes the eimerians occurring in Mongolian gerbils (Old World murid rodents) a paraphyletic group. The presence or absence of an oocyst residuum is not an indicator of two distinct monophyletic clades of *Eimeria* of rodents, according to these analyses (Figs. 36, 37). Whether the species was recovered from *M. meridianus* or *M. unguiculatus* does not seem to be phylogenetically informative, either. However, considering only 5 of the seven species of *Eimeria* in this study were found in only a single host individual, this observation merits little to no credence. Furthermore, as none of these analyses produced a tree score distribution with a g1 value of a magnitude greater than -0.5, all results of these analyses should be regarded as preliminary, at best.

The failure of morphological data to produce phylogenetic information in this study indicated by the weakness of the skew of tree scores is indicative of the problems with making phylogenetic inferences based on morphological features of the oocyst observable through light microscopy. The existence of oocyst polymorphism within a species (eg. Parker and Duszynski, 1986) and oocyst monomorphism between species (eg. Duszynski et al., 1992; Upton et al., 1992; Hnida and Duszynski, 1999a) demonstrate the complex relationship between coccidian species and the morphology of their oocysts. Such uncertainty regarding the interpretation of oocyst morphology at the species level does not bode well for the use of oocyst morphology in systematics above the species level.

However, this is not to say that no features of the oocyst are phylogenetically informative. While the findings of Morrison et al. (2004) were not in agreement with those of Zhao and Duszynski (2001) regarding the oocyst residuum in the *Eimeria* of rodents, they were in agreement with the finding of Carreno and Barta (1999) that the presence or absence of the Stieda body in *Isospora* spp. is phylogenetically informative. This suggests that while oocyst morphology in general may or may not be phylogenetically informative, certain individual characters are. However, until further research reveals in detail the specific relationships between morphological characters and at what scale, if any, they are phylogenetically informative, phylogenetic analyses based on oocyst morphology alone are unlikely to be of much use.

Ecological Niche Modeling

Estimates for the total proportion of area for which *Eimeria* spp. of gerbils are present predicted using Maxent (28.70%) (Fig. 4) and GARP (28.63%) (Fig. 5) are similar. However, the fact that only about half the presence area predicted by each method coincides with that predicted by the other indicates a lack of predictive power by one or both of the methods. There are a number of possible explanations for such an outcome. Both methods may be returning underestimates of the true range of eimerians infecting gerbils, such that the union of the distributions made using both methods is most accurate. Alternatively, one model could be substantially more accurate than the other, such that the presence area predicted by the superior model is mostly reflective of the true distribution, while the presence area predicted only by the inferior model is mostly commission error. Finally, it is possible that the distributions predicted by both models are highly inaccurate, and that coincidence between the predictions made with both methods is mostly due to random chance. Of course, the three aforementioned circumstances are the extreme cases, and the truth is likely a combination of all three.

Which model is more appropriate for this study? For both full and partial AUC, GARP produced higher values for models of the distribution of *Eimeria* spp., while Maxent produced higher values for models of the distribution of *Meriones*. The difference in AUC scores was greater for models of eimerian distribution (0.15 full AUC, 0.31 partial AUC) than for models of the distribution of species of *Meriones* (0.01 full and 0.05 partial AUC). Also, while only 7.88% of the presence area of *Eimeria* spp. predicted by GARP did not coincide with that of *Meriones* spp., the majority (79.12%) of presence area of *Eimeria* spp. predicted by Maxent did not coincide with that of species of

Meriones. By these metrics, it would appear that GARP provided the superior prediction of distribution in this study.

However, one aspect in which GARP has been declared inferior to Maxent by some is the interpretability of the results. Stockman et al. (2006) criticized GARP for being "a 'black box' technique", among other things. Though the study was based on flawed methodology (McNyset and Blackburn, 2006), this particular criticism is not unfounded. In the case of this study, regardless of which predictions were more accurate, the output of the Maxent software was much more useful than that of DesktopGARP for inferring relationships between distributions and ecological variables. While DesktopGARP provided data on which layers were used in which models, all 11 layers were used in all 10 of the best subset models, so it was not possible to infer any relationships without using other methods. Maxent, however, returned a variety of outputs, such as analyses of variable contributions (Table 10), marginal response curves (Fig. 41), and jackknife analyses (not shown in this study).

Direct exposure to UV radiation quickly kills oocysts (Duszynski et al., 2000). In light of this knowledge, the ranking of NDVI and aspect as the first and third most important variables in determining the presence or absence of *Eimeria* spp. (Table 10) stands to reason. The shape of the response curve of the log contribution to raw output of NDVI is reasonable, as well (Fig. 41). Because higher NDVI values are indicative of greater vegetative cover, it is reasonable to conclude that the greater the NDVI, the greater the cover, and the less the risk of oocysts being killed by UV radiation. The shape of the response curve of log contribution to raw output of aspect is less reasonable. As the study area is in the Northern hemisphere and UV radiation kills eimerian oocysts, the behavior

of the curve between values of 0 and 180 makes sense; oocysts on the northern face of a slope would be less exposed to UV radiation than oocysts on the southern face. However, the monotonicity of the curve is concerning. For example, such monotonicity implies that oocysts on a slope facing 359.9° are less likely to survive than those on a slope facing 0.1°.

Examining the shape of the response curves of the log contribution to raw prediction to NDVI for both *Meriones* spp. and *Eimeria* spp. (Figs. 41) reveals an interesting relationship. Specifically, while the response to NDVI for *Eimeria* spp. is monotonically increasing, the response to NDVI for *Meriones* spp. is generally decreasing, though not monotonically. As gerbils are highly adapted to desert environments, it is understandable that they would be less likely to occur in densely vegetated habitats, whether this is a function of their fundamental or realized niche. This highlights a potential trade-off in the distribution of the *Eimeria* spp. of gerbils: habitats with less vegetative cover are more likely to harbor their hosts but are also less conducive to the survival of oocysts. Conversely, habitats with greater vegetative cover are less likely to harbor their hosts, but are more conducive to the survival of oocysts.

When trade-offs such as this are viewed in light of the mechanisms of Maxent, the methodology of this study is called into question. Specifically, is it valid to assume distributions inferred from occurrence data of a parasite group occurring in species of a host group represent the *only* the distribution of species occurring in that particular host group, rather than all species of the parasite group? Because the presence of a suitable host is a prerequisite to the presence of a parasite, the distribution of the parasites specific to any host group should be subject to the all the constraints of the distribution of the host

group, plus additional constraints which affect the parasite more than the host. I therefore assumed that a model of a parasite's distribution which predicts parasites occurring outside the range of their hosts predicted with the same methods and environmental data was indicative of a model with low predictive power. However, because Maxent works by fitting distributions across ecological space to occurrence data, if the distribution of the subset of hosts which are infected with the parasite is atypical of the distribution of all potential hosts, then the data used to infer the parasite distribution will lack important information regarding the host distribution, and the predicted distribution of the parasite may not be constrained to that of the host. In the case of this study, this means that the distribution of *Eimeria* spp. predicted with Maxent may be more representative of the distribution of all *Eimeria* spp. in general than of the distribution of only the species of *Eimeria* infecting hosts of the genus *Meriones*.

Conclusions

The main objectives of this study were to discover what species of coccidia occur in gerbils of Mongolia, contribute to and revise eimeriid taxonomy by describing new species and recommending taxonomic revisions concerning previously described species. In identifying 7 species of *Eimeria* and 1 species of *Isospora,* describing the new species *E. tsogoi*, *E. sarae*, *E. ivgeeltensis* and *E. briansmithi*, and recommending 10 species be considered junior synonyms or *species inquirendae*, these objective have been accomplished. The lesser objectives of this study were to predict the spatial distribution of eimeriid parasites occurring in gerbils in Mongolia and identify any apparent ecological trends, and to investigate the phylogenetic relationships among the eimeriids which were found in this survey. Though the predicted distributions made through

developing ENM's and the phylogenies produced from morphological data are very tentative, they may serve as a starting point for future investigators.

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