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The Occurrence of an Abdominal Fauna in an Articulated Tapir (*Tapirus polkensis*)

Recovered from the Miocene Gray Fossil Site, Northeast Tennessee

A thesis

presented to

the faculty of the Department of Biological Sciences

East Tennessee State University

In partial fulfillment

of the requirements for the degree

Master of Science in Biology

by

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May 2010

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Keywords: Abdominal Fauna, *Tapirus polkensis*, Gray Fossil Site, Miocene

ABSTRACT

The Occurrence of an Abdominal Fauna in an Articulated Tapir (*Tapirus polkensis*)

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The analysis of samples recovered from the abdominal area of an articulated tapir from the Late Miocene (4.5-7 million bp) Gray Fossil Site, revealed a rich palyno-fauna comprised of about 94% egg/oocyst – like structures and 6 % pollen and other palynomorphs. In addition, a tight grouping of six hickory nuts (*Carya*) was recovered from the same area suggesting that the samples represent the abdominal contents. The analysis of a sample from immediately outside the tapir produced a sample with 98 % pollen and less than 0.5 % egg – like structures. The size, shape, and general morphology of egg - like structures were analyzed with light and scanning electron microscopy and were compared to a variety of intestinal eggs found in extant ungulates, and in particular the Perissodactyla. We also compared the fossil structures to the numbers and kind of intestinal parasites recovered from fecal samples from the Baird's tapir (*Tapirus bairdii*) in Costa Rica and from samples collected from the Lowland tapir (*T. terrestris*) from Ecuador to assess their similarity to our fossil sample. Based on these data we discuss what role parasites may have played in the biology of *T. polkensis* during the late Miocene – early Pliocene.

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CHAPTER 1

INTRODUCTION

Parasites have evolved in almost every phylum of animals (Roberts and Janvov 2005). Parasitism can be defined as a relationship in which a parasite either harms the host or benefits from the host in some way (Roberts and Janvov 2005). Parasites can be found on (ectoparasite) or within (endoparasite) the host and can have a variety of pathogenic effects on the host including but not limited to: interactions of the host immune/inflammatory responses, trauma (mechanical injury), nutrition robbing, and the production of toxins (Roberts and Janvov 2005). The study of parasitism is also of economic importance because it affects both wild and domestic animals.

Paleoparasitology, the study of fossil parasites, might give clues to the antiquity of a given host-parasite complex and potentially the origin and evolution of certain parasites (Araújo et al. 1998, Araújo and Ferreira 2000, Littlewood and Donovan 2003). In the past, sources for both human and animal parasite remains have come from coprolites, latrines sediments, middens, and mummified tissues (Bouchet 1999, Bouchet et al. 2003a). It is rare to find remains of parasites or their developmental stages (Bouchet et al. 2003b). At one time it was believed that parasites left no fossil remains (Cameron 1952). Evidence of parasites has been found at paleontologic sites from 1.5 million years ago as well as 500,000 years ago, preserved in organic material (Ferreira et al. 1993, Jouy-Avantin et al. 1999). Typically parasites will occupy niches, in or on the host, that are not prone to preservation (fur, feathers, digestive tract, and soft tissue). Unfortunately, parasite remains are rare in the fossil record, and this proves to be a constant problem in determining divergence in parasite phylogenies (Poinar and Poinar

2007). The most abundant evidence of parasites throughout time has come from trace materials like coprolites (Ditmar 2009). Parasitological evidence that is commonly found in trace materials like coprolites is the eggs of endoparasites and occasionally larvae and/or adults (Horne 1985, Reinhard et al. 1988, Aspöck et al. 1999, Bouchet et al. 1999, Bathurst 2005). The study of paleoparasitology may lead to an understanding of host-parasite relationships throughout time and provide information on their origin and evolution (Araújo and Ferreira 2000).

Parasite remains have been discovered in the fossil record, but tracing the lineage of species and their relationship with a given host is complicated. A complete understanding of parasite evolution and host-parasite coevolution is not possible, but the occasional association of parasites with well preserved fossil animals may provide a better understanding of the host - parasite relationships and processes of the past (Poulin 2006). It may not be possible to determine the phylogeny among many parasites because it is impossible to know how many lineages of parasites have become extinct without leaving any evidence (Poulin 2006). Evidence of certain host-parasite relationships have been discovered in the fossil record but do not exist in modern counterparts, which proves that certain lineages of parasites have disappeared over time (Poulin 2006). Parasite evidence has been reported in both human and animal coprolites. Evidence of parasites from the early Cretaceous in dinosaur coprolites has provided examples of protozoan cysts and a variety of helminth eggs (Poinar and Boucot 2006). Evidence of *Toxacara canis* eggs have been reported in carnivore mammals in Brittany, France (300,000 to 500,000 thousand years old) (Bouchet et al. 2003a). Helminth eggs and possible protozoan oocysts have been identified from coprolite remains of the extinct

Shasta ground sloth (10,000 +/- 180 yrs old) (Schmidt et al. 1992). New methods or tools in paleoparasitology and molecular paleoparasitology have helped in advancing the study of host-parasite environment systems (Goncalves et al. 2003).

Tapirs belong to a small order of animals, the Perissodactyla that contains Tapiridae, Rhinocerotidae, and Equidae. The family Tapiridae consists of four species: the Baird's tapir (*Tapirus bairdii*), the Lowland Tapir (*T. terrestris*), the mountain tapir (*T. pinchaque*) all distributed in the new world, and the Malayan tapir (*T. indicus*). Tapirs generally remain inactive in forest and thickets during the day and become active feeders during the night within a home range that may be as large as 2.6 km²; however, this varies depending on carrying capacity of the habitats (Eisenberg 1997, Ayala 2003, Noss et al. 2003, Medici et al. 2007b). This results in a population density of about 1 or fewer tapirs per km⁻². Tapirs generally feed in grassy or scrubland habitats, marshes, lakes and streams, or ephemerally flooded habitats (Padilla and Dowler 1994, Medici et al. 2007a, Medici 2010). Tapirs exploit over 170 species of fruit from 60 different families (Bodmer 1990a, 1990b, Bodmer 1991a, 1991b, Rodriguez et al. 1993, Salas and Fuller 1996, Olmos 1997, Herrera et al. 1999, Fragoso and Huffman 2000, Henry et al. 2000, Galetti et al. 2001, Tofoli 2006, Tobler 2008, Medici 2010). Tapirs, however, are known to eat leaves, twigs, bark, flowers, and aquatic vegetation (Terwilliger 1978, Janzen 1982, Williams 1984, Bodmer 1991a, 1991b, Naranjo 1995, Salas and Fuller 1996, Tobler 2002, Tofoli 2006, Tobler 2008). Tapirs are considered semiaquatic mammals and stay in close proximity to riparian or lacustrine habitats (Barnett and Napier 1953, Gingerich 2003).

In this study sediment associated with the abdominal region of an articulated Miocene – Pliocene *Tapirus polkensis*, recovered from the Gray Fossil Site (GFS), Gray TN was examined for evidence of abdominal fauna. There have been limited studies on the intestinal faunas of extant Tapirs and this will be the first analysis from an extinct Tapir. Parasites from extant Tapirs were evaluated from both literature and from samples collected from wild Tapirs in Central and South America.

CHAPTER 2

MATERIALS AND METHODS

Gray Fossil Site Material

The Gray Fossil Site located in northeast Tennessee is an outlying group of sediments that formed by the collapse of multiple asynchronous sinkholes ultimately forming a depression that formed a late Miocene Lake leaving a series of lacustrine sediments between 4.5 - 7 million years ago (Shunk et al. 2006, Whitelaw et al. 2008). The lacustrine sediments consist of a 40 m layer of dark unlithified silty-clay covered with over 5 m of alluvium and colluvium (Shunk et al. 2006). The sediments have preserved a rich fauna and flora indicative of the latest Miocene – earliest Pliocene.

Sediment samples were collected from the abdominal region of an articulated *T. polkensis* (See Figure 1). Multiple 20 gram samples, some from the abdominal region of the extinct Tapir (*T. polkensis*), and the others (a presumed coprolite containing almost identical palynological assemblage) were processed for palynomorphs using basic palynological methods (Barrs and Williams 1973). A control sample collected from around the same skull of the tapir was processed for comparison.

There are several types of endoparasites including: Trematodes (flukes), Cestodes (tapeworms), Nematodes (roundworms), and Coccidia (enteric protozoa). Tentative identification was performed, looking for distinctive characteristics related to certain species and information from modern parasite databases. In order to make tentative identifications of the egg-like structures in *T. polkensis*, we looked for specific characteristics that would suggest parasitic origin or similarities to modern parasite eggs.

These characteristics included: size (length/width), shape, thickness of outer shell, shell



Figure 1 The articulated *Tapirius polkensis* skeleton still in the field jacket showing the pelvic region from which the samples were removed for this study, The arrowheads indicate hickory nuts that were probably present in the stomach or intestinal track at death.

surface, presence/absence of operculum, and polar plugs (See Table 1). Scanning Electron microscopy (SEM) was also performed on samples to examine the surface structure of specific egg-like structures in closer detail.

Table 1 Table shows characteristics used to identify parasite eggs including size, shape, shell thickness, surface structure, and the presence of an operculum and polar plugs.

Type of Parasite	Size	Shape	Outer shell Thickness	Outer Shell Surface	Operculum	Polar Plugs
Trematoda (Flukes)	Large to 500 um	Spherical to oval	Thin shell	Smooth	Present	Absent
Cestoda (Tapeworms)	20-40um	Round Oval Triangular	Usually Thick	Usually Striated	Absent	Absent
Nematoda (Roundworms)	Variable	Round to Oval	Thick or Thin	Rough or Smooth	Absent	Sometimes
Coccidia	10-40um	Round to Oval	Thin	Smooth	Absent	Absent

Modern Material

Samples for modern comparison were collected from Sirena Biological Station in Corcovado National Park, Costa Rica (April 2009). Several samples were collected from various locations (See Figure 2) and brought back to ETSU where traditional flotation methods were applied for parasitic egg analysis. Samples collected in Costa Rica are from the Baird's tapir (*T. bairdii*). Additional samples were collected in Ecuador (July 2009), probably from the Lowland tapir (*T. terrestris*), and processed using traditional flotation methods for analysis. All samples were processed using Sheather's Sucrose Solution (a saturated solution of sucrose w/ specific gravity of 1.275) or a saturated sugar solution. (Dryden et al. 2005). Specimens were examined under light microscopy. They were measured, identified, and compared to eggs derived from known modern stomach and intestinal parasites. Samples from llamas with known *Capillaria* infection were

processed and photographed for comparison to structures from the Gray Fossil Site (GFS).

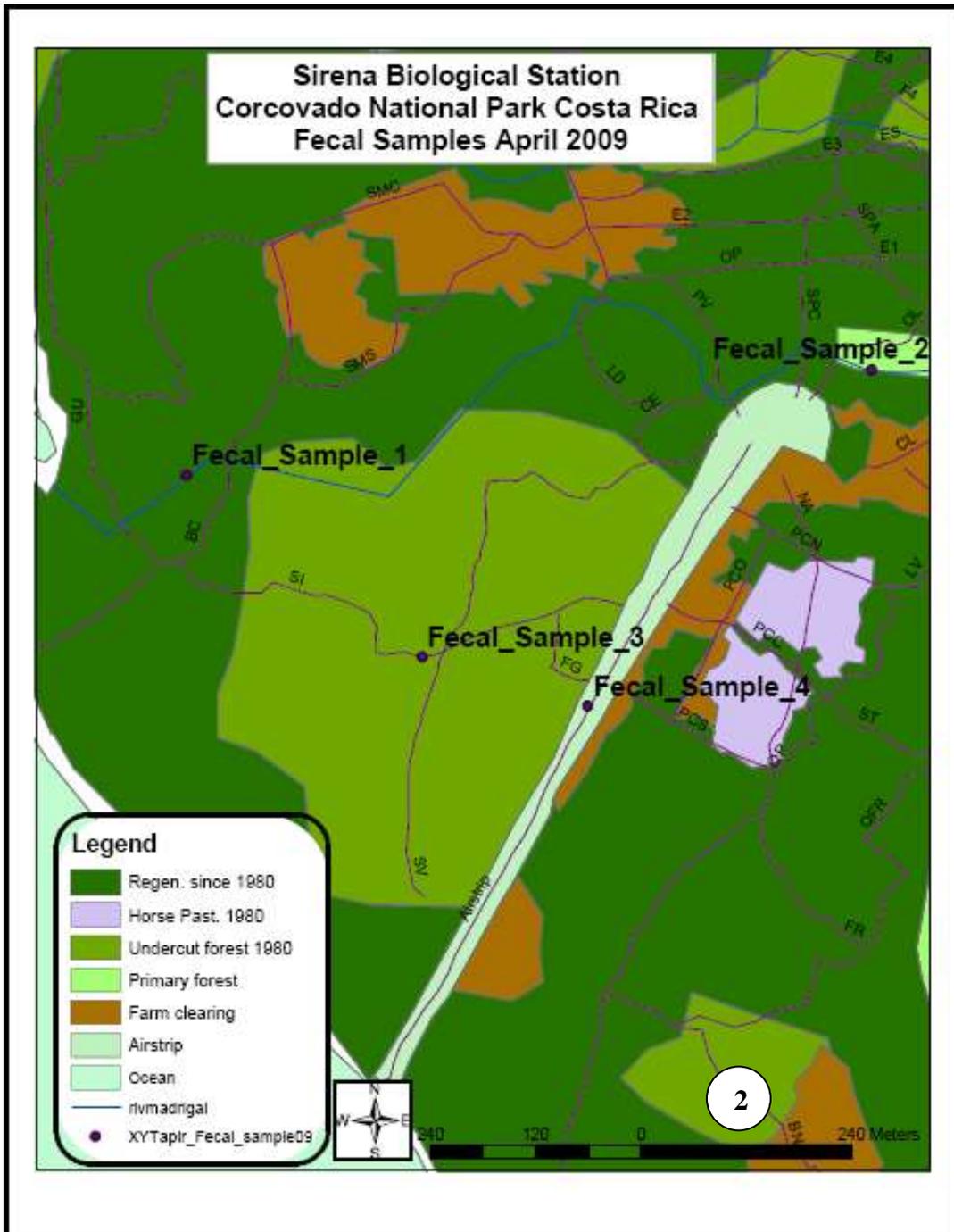


Figure 2 A map showing the locations of fecal samples, collected from the Baird's tapir for analysis of parasite species, at the Sirena Biological Station, Costa Rica (Courtesy of Kendra Abbott from her work with the Baird's tapir Project of Costa Rica).

Measurements were made using a calibrated ocular micrometer and data were collected for statistical analysis (See Appendix). All suspected structures were classified by size and shape. Most noteworthy structures were further analyzed using a Hitachi 640 scanning electron microscope (SEM).

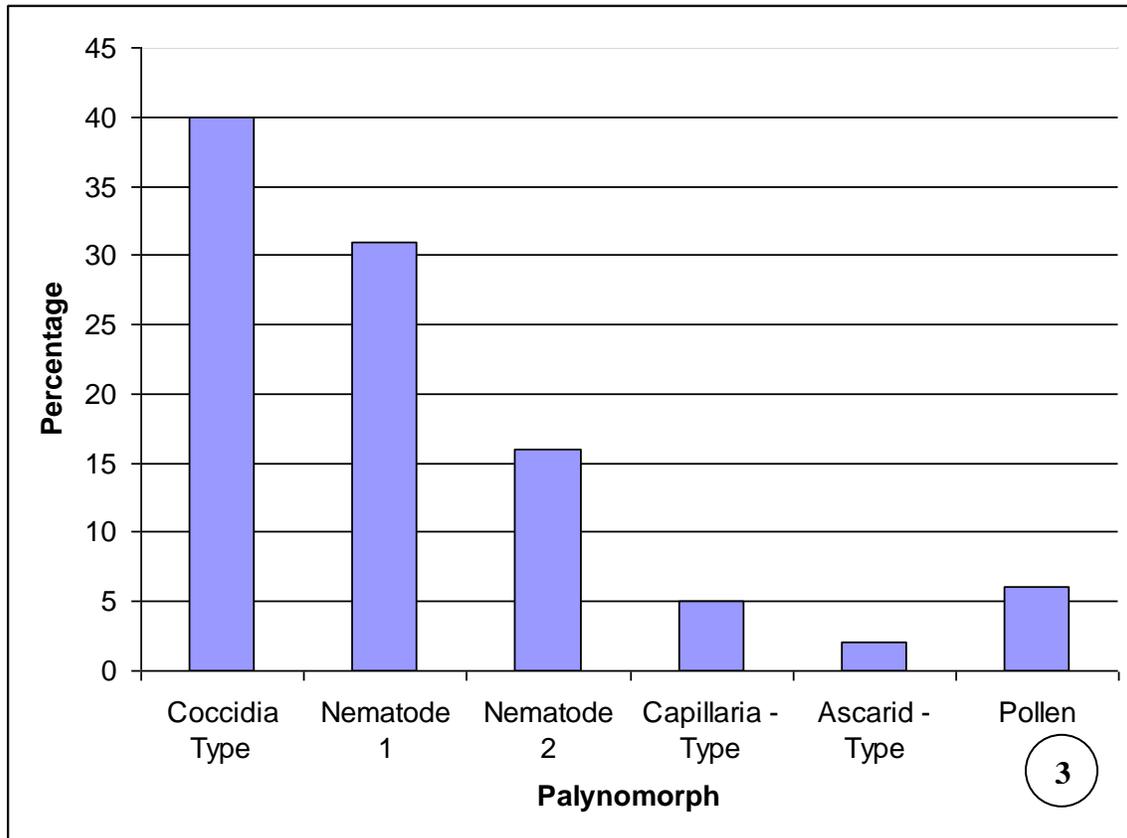


Figure 3 Histogram showing the percent abundance of the various types of egg-like structures from the abdominal sample. Note that these egg - like comprise 94 % of the abdominal palynoflora. A control sample taken outside of the articulated tapir's skull region produced palynoflora 98 % pollen and less than 0.5 % egg - like structures.

CHAPTER 3

RESULTS

Gray Fossil Site Material

A low percentage of palynomorphs was observed in the sample, including bisaccate, stephanoporate, periporate, triporate, and tricolpate pollen (Figures 4G-4O). Other unidentifiable structures were recovered from the GFS sample. Among the palynomorphs recovered from the GFS samples were pollen, fungal spores, cuticle, tentatively identified egg – like structures, and a variety of unidentified structures. The most abundant egg – like structure is a small, round structure most closely resembling a coccidia – oocyst like structure (Coccidia - Type) (See Figure 3, Table 2, Figures 5A-5H). They usually appear to have a smooth surface structure (See Figures 5B-5F), although some atypical specimens appear to be spinate (See Figures 5A, 5G-5H) or even operculate (See Figure 5E). These structures resemble a coccidia-type oocyst.

The second most abundant egg-like structure is tentatively considered a Nematode egg (Nematode –Type 1) (See Figure 3, Table 2, Figures 6A-6F). The third most abundant egg-like structure is also tentatively identified as a Nematode (Nematode – Type 2) and is characterized by a smooth outer shell ranging from oval to long and thin (See Figure 3, Table 2, Figures 7A-7J). Frequently the shells are longitudinally split (See Figure 3, Table 2, Figures 7A-7J).

The fourth most abundant type (See Figure 3, Table 2) is tentatively identified as a *Capillaria sp.* egg (Capillaria Type). Specimens resembling *Capillaria sp.* eggs demonstrated similar surface structures as modern *Capillaria sp.*, having similar shapes

and sizes. They were consistently oval or barrel-shaped with surface characteristics similar to the modern eggs, textured with striations/reticulations or wrinkles and pits (See Figures 8B-8G). This type shares many features with modern *Capillaria* except for the distinctive polar plugs (See Figures 8B-8G compare to modern egg in Figures 8A). The fifth most abundant type (See Figure 3, Table 2) and most distinctive is the Ascarid – Type that are round and exhibit a regulated outer shell (See Figures 9B-9G compare to modern egg in Figure 9A). This type shares the most characteristics with its presumed modern counterpart.

Table 2 Table summarizing the distinctive characteristics of all the egg – like structures recovered from the abdominal sample in *Tapirus polkensis*. These distinctive characteristics were used as evidence to support identification. Polar plugs are absent in all structures and operculum may be present in the Coccidia Type oocysts.

Egg Type	Size (Avg. LxW)	Shape	Outer Shell Thickness	Outer Shell Surface
Coccidia Type	15 um (dia.)	Round	Thin	Smooth and Spinate
Nematode Type 1	55x43 um	Round	Thin	Smooth
Nematode Type 2	54x32 um	Oval	Thin	Smooth
Ascarid Type	48x42 um	Oval	Thick	Rough
Capillaria Type	54x30 um	Oval	Thin	Rough
Tapeworm Egg (Modern)	30x27 um	Round	Thick	Smooth with distinct hooks.
Ascarid Egg (Modern)	60x50 um	Oval	Thick	Rough

Modern Material

Modern fecal samples collected from Costa Rica and Ecuador were analyzed and produced possible evidence of parasitism in 2 species of tapirs (*T. bairdii* and *T. terrestris*). The samples collected from Costa Rica also provided possible evidence of parasites, but one sample in particular (sample 3) showed several specimens of a species of tapeworm (See Figure 4F). Most samples also contained evidence of mites that were ingested. There was very little evidence of pollen and spores, while plant debris such as cuticle was plentiful. Monolete and trilete spores were observed in samples (See Figures 4A-4D) along with angiosperm pollen (See Figure 4E). Parasite eggs were identified as tapeworm from the family Anoplocephalidae. These parasite eggs have distinct hooklets dispersed in a fan-like array (See Figure 4F).

Fecal samples collected from Ecuador provided more evidence of pollen and spores than parasite remains. There were a few artifacts that did resemble parasite eggs, specifically the tapeworm (See Figure 4E) and ascarid (See Figure 9A) eggs. Structures consistent with tapeworm eggs were identified and appeared to have distinct hooklets that distinguish these eggs from others. The possible ascarid egg is of comparable size to known *Ascaris sp.* and has a comparable surface structure to a fertilized egg, appearing rugulate. A variety of pollen and spores was recovered from fecal samples collected in Ecuador which included: bisaccate pollen (*Pinus sp.*), monolete, scabrate spores (probably Polypodiaceae), trilete spores, and a periporate, spinate pollen resembling Asteraceae.

Samples were collected from horses in Jonesborough, TN for analysis of common parasites in a related, extant species. Fecal samples from llama with known *Capillaria* infection were processed and images taken for comparison to suspected *Capillaria sp.* in *T. polkensis*. Both *Capillaria sp.* and *Trichurus sp.* were identified from these samples. *Trichurus* have very distinct polar plugs and *Capillaria* is distinctly barrel-shaped with polar caps or plugs. Table 3 contains a list of all known parasites in extant and fossil tapirs.

Table 3 Table showing known parasites found in different species of extant tapirs and the tentatively identified taxa found in the extinct species, *Tapirus polkensis*.

Tapir	Reference	Parasites
<i>T. bairdii</i> (Baird's tapir)	Cruz et al. 2006(1) Ramsay and Zainuddin, 1993(3) This Study (5)	<u>Nematodes</u> : <i>Agristoma sp.</i> , <i>Lacandoria sp.</i> , <i>Neomushidia sp.</i> , <i>Trichostrongylus sp.</i> , <i>Strongylus sp.</i> , <i>Brachylumus sp.</i> (1) Tapeworm (Anoplocephalidae) (5) <u>Protozoan's</u> : <i>Eimeria sp.</i> , <i>Balantidium coli</i> (1) Ciliophora, mastigophora, Balantidium and Giardia sp. (3)
<i>T. terrestris</i> (Lowland tapir)	Durett-Desset et al. 1997(2) This Study (5)	<u>Nematodes</u> : <i>Tapironema coranatum</i> (2) Tapeworm (Anoplocephalidae) (5) Ascarid (5) <u>Protozoan's</u> : Ciliophora, mastigophora, Balantidium and Giardia sp. (3)
<i>T. pinchaque</i> (Mountain tapir)	Ramsay and Zainuddin, 1993(3) Gale and Sedgwick, 1968(4)	<u>Nematodes</u> : Ascarid ova, <i>Strongylus</i> and <i>Strongyloides</i> (4) <u>Protozoan's</u> : giardia (3 and 4) Ciliophora, mastigophora, Balantidium (3)
<i>T. indicus</i> (Malayan tapir)	Ramsay and Zainuddin, 1993(3)	<u>Protozoan's</u> : Ciliophora, mastigophora, Balantidium (3)
<i>T. polkensis</i>	This Study (5)	Coccidia Type Nematode Type 1 and 2 Ascarid Type Capillaria Type

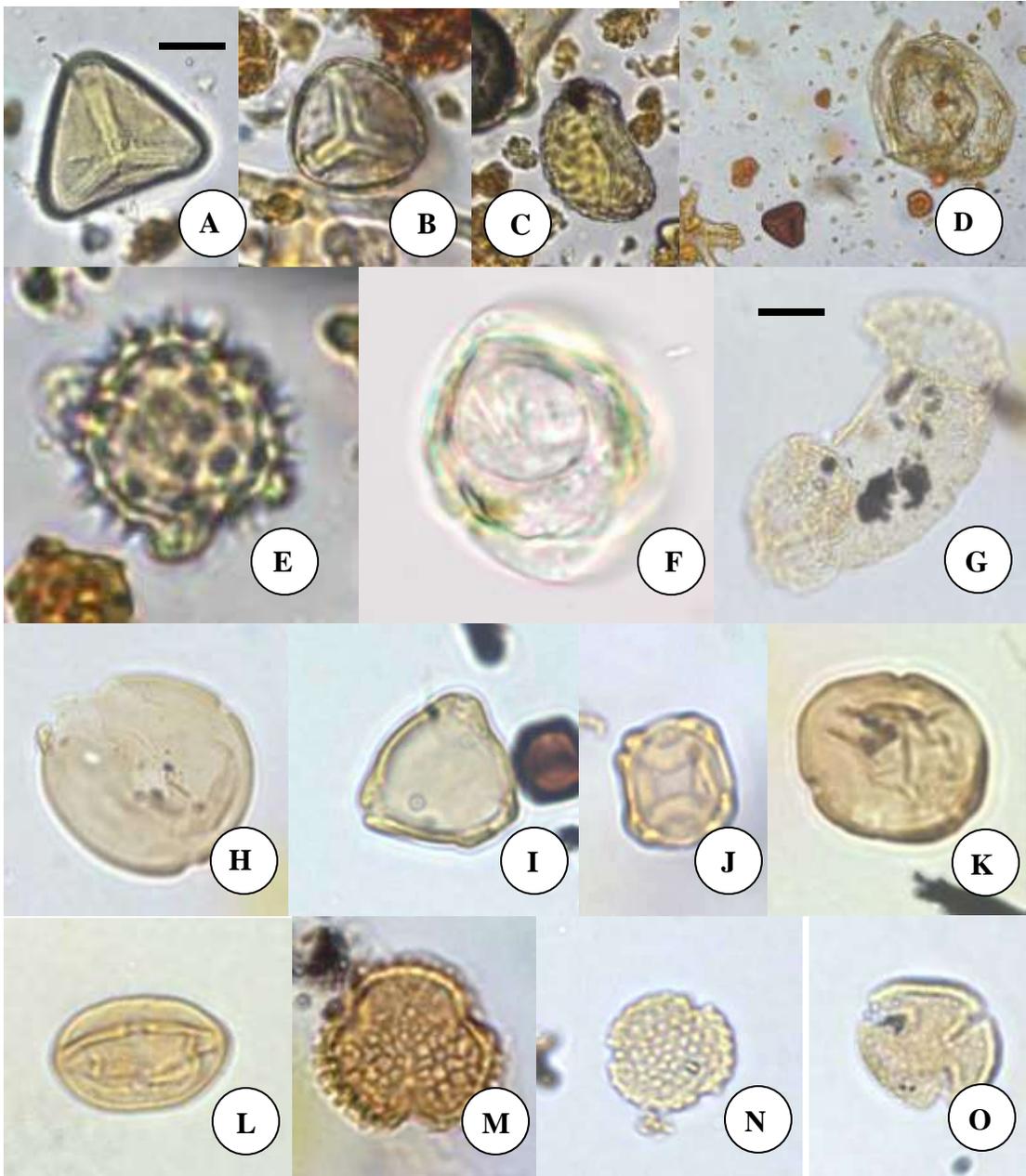


Figure 4 Pollen recovered from the fecal samples of extant tapirs. Scale Bar = 10 um, applies to Figures 4A-4E. Figure 4A Trilete fern spore. Figure 4B Trilete fern spore. Figure 4C Monolete fern spore. Figure 4D. Large oval wrinkled structure recovered from fecal samples of an extant tapir similar to Nematode Type 1 found in *T. polkensis*. Compare with Figures 6A-6F. Picture 4E Pollen grain of the Asteraceae (High Spine). Figure 4F Tapeworm egg recovered from extant fecal sample. Figures 4G-4O Pollen recovered from the abdominal sample of *Tapirus polkensis*. Scale Bar = 10 um applies to Figures 4G-4O. Figures 4G Bisaccate gymnosperm pollen showing some corrosion due to intestinal acids. Figures 4H Pollen grain of Hickory also exhibiting some breakage and corrosion. Figures 4I -4J showing the triporate and tetraporate pollen of *Alnus*. Figures 4K Degraded pollen, probably of Hickory. Figures 4L Pollen that cf. with *Quercus*. Figure 4M. Unidentified tricolporate type. Figures 4N Pollen grain of the Asteraceae (Low Spine). Figure O Pollen that cf. with *Quercus*.

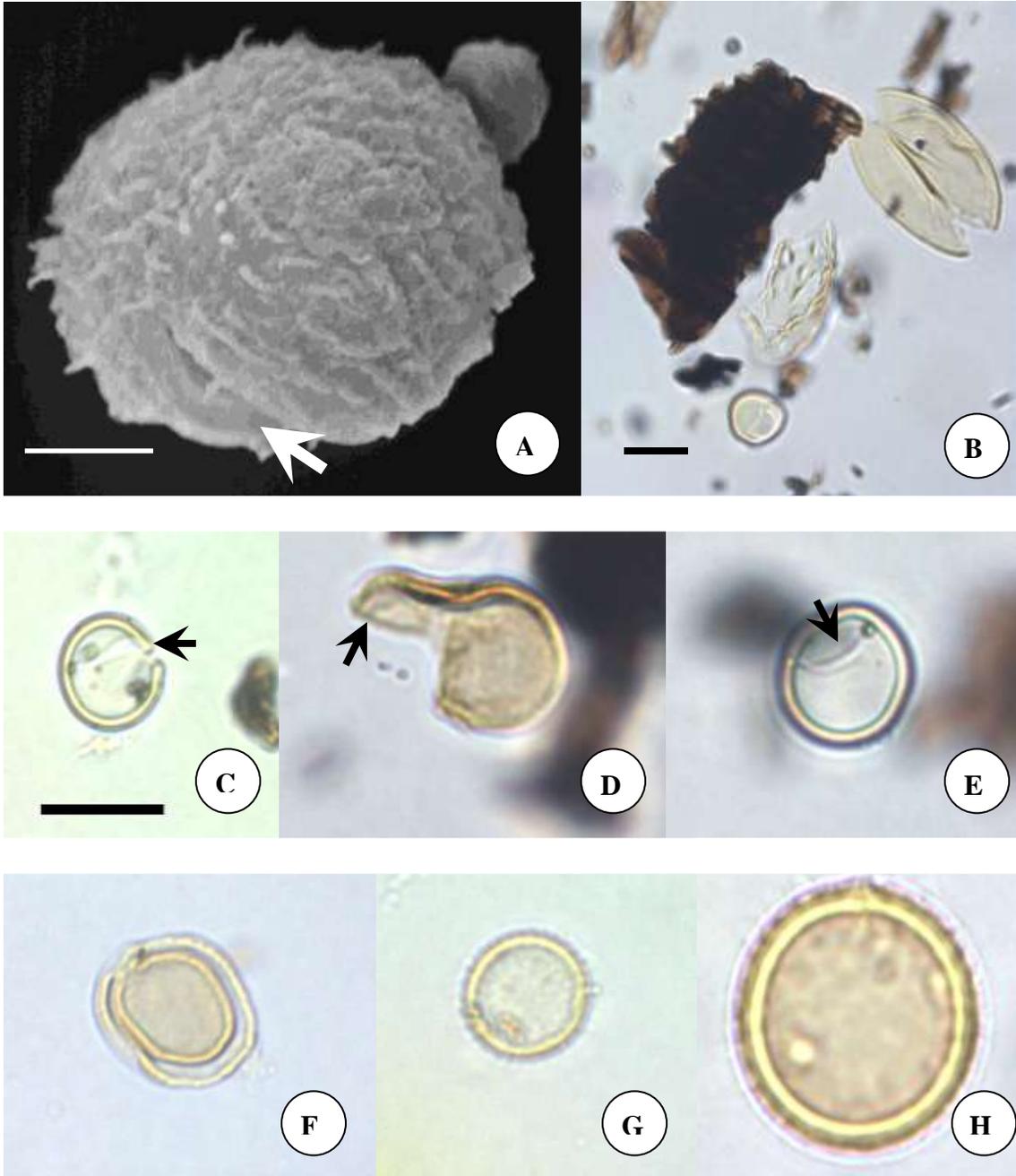


Figure 5 Coccidia type oocyst. Figure 5A SEM showing an ornamented form of the coccidian type; note the split that may be the operculum like structure (arrow). Scale bar = 5 μ m. Figure 5B Low magnification of the coccidia type note its small size in comparison to the other 2 parasite like eggs. Scale bar = 20 μ m. Figures 5C-5E Coccidia type showing the common presentation of a cap (operculum, arrows) like structure. Figures 5F An unidentified palynomorph similar to the coccidian oocyst. Figure 5G Coccidia type oocyst that appears ornamented (see Figure 5A), showing no evidence of an operculum. Figure 5H A large unidentified structure similar to the coccidian type. Scale bar in Figure 5C = 20 μ m (applies to Figures 5C-5H).

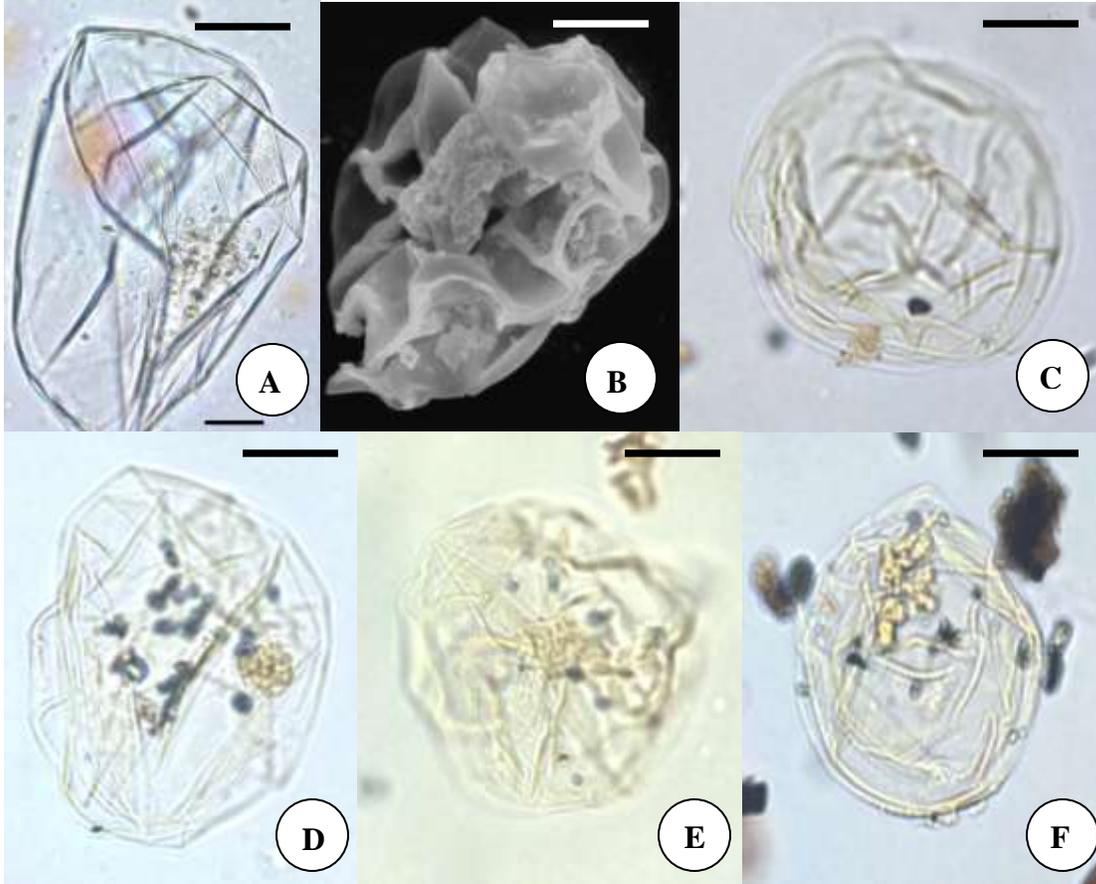


Figure 6 Nematode Type 1 parasitic eggs. Scale Bar = 20 μm . Figures 6A, 6C-6F Light micrographs showing the typical oval shape, thin wall and invariable folded wall. Figure 6B SEM showing a similar form to those in Figures 6A, 6C-6F.

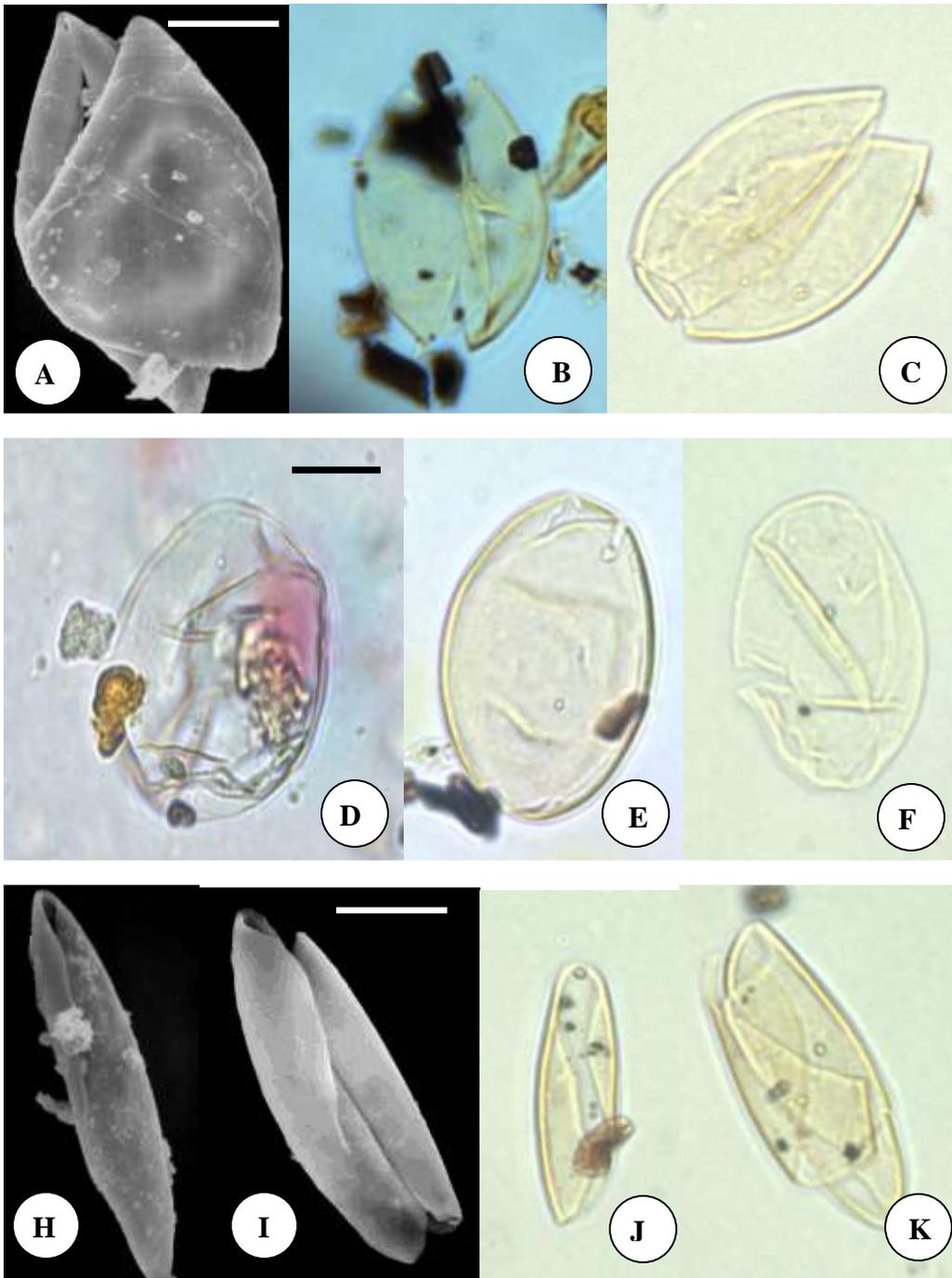


Figure 7 Light and Scanning Electron photographs of Nematode Type II parasitic eggs. Figure 7A SEM of Nematode Type II showing smooth outer shell and oval to round shape. Note that the shell is longitudinally split a common occurrence in this type. Figures 7B-7C Light micrograph of Nematode Type II showing the same characteristics as in Figure 7A. Figure 7D Light micrograph of Nematode Type II intact. Figures 7E-7F Nematode Type II showing an apical and lateral split. Figures 7G-7H SEM of a form similar to Nematode Type II but appearing more fusiform, they have smooth walls, longitudinal split. Figures 7I-7J Light micrograph of Nematode Type II in Figure 7G-7H. Note in all cases this Nematode lacks the prominent wrinkling observed in Nematode Type I. Scale Bars in Figure 7D = 20 μ m (applies to Figures 7B-7F, 7I-7J). Scale Bars in Figures 7A and 7H = 20 μ m (applies to Figures 7A, 7G-7H).

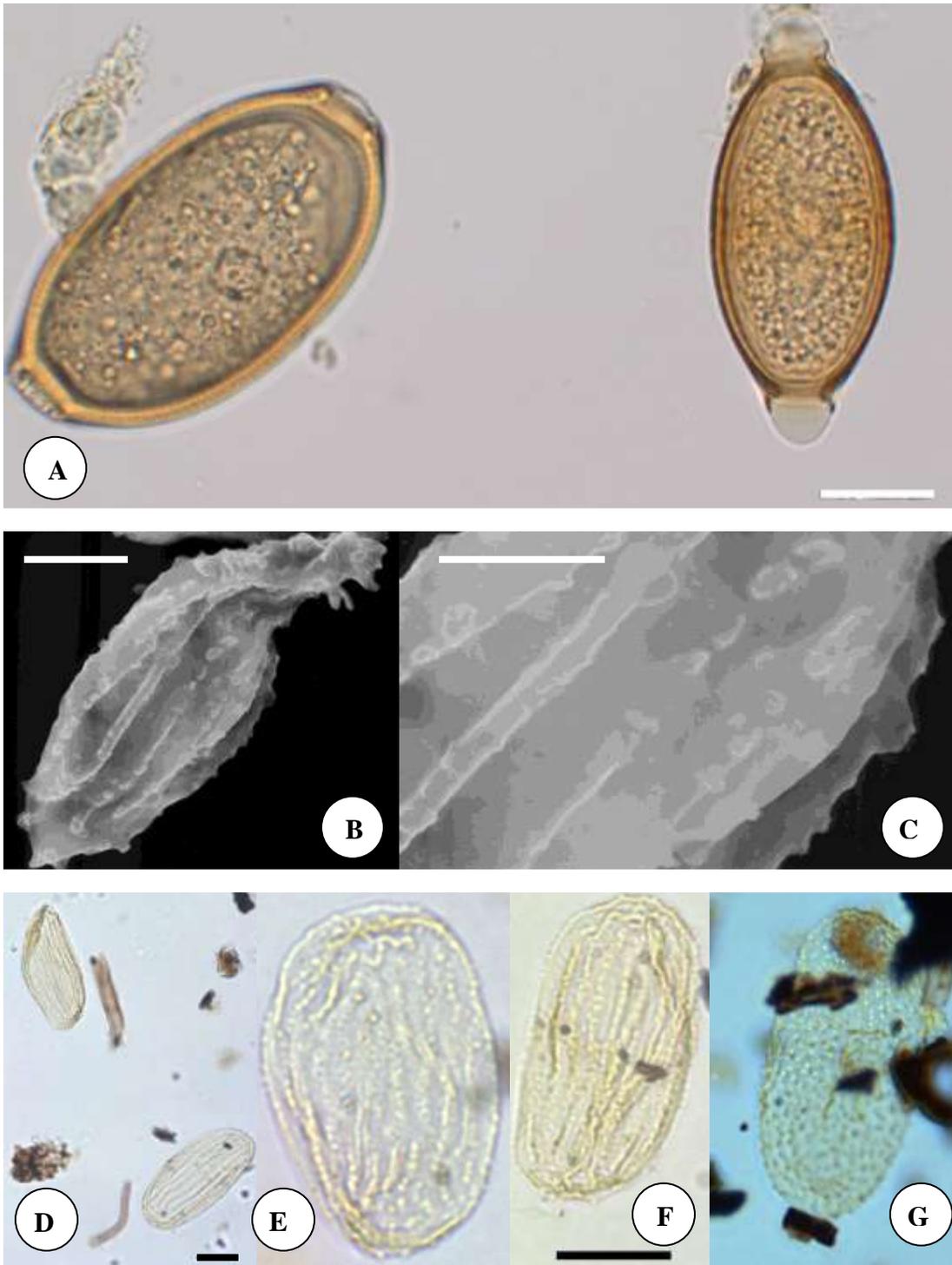


Figure 8 *Capillaria* Type parasitic eggs. Figure A Modern *Capillaria* sp. showing the polar bodies that are indicative of many modern taxa. Scale Bar = 20 μ m. Figures 8B-8C SEM of the *Capillaria* Type showing the shape, size and ornamentation comparable to modern taxa, however, polar bodies appear to be lacking. Note that two types of ornamentation can occur on the same individual. Scale Bar in Figure 8B = 20 μ m, Scale Bar in Figure 8C = 10 μ m. Figures 8D-8G Showing variation in ornamentation, i.e., longitudinal striae, granules, and specimens with both (also see Figures 8B-8C). Scale Bar in Figure 8D = 20 μ m. Scale Bar in Figure 8F = 20 μ m (applies to Figures 8E-8G).

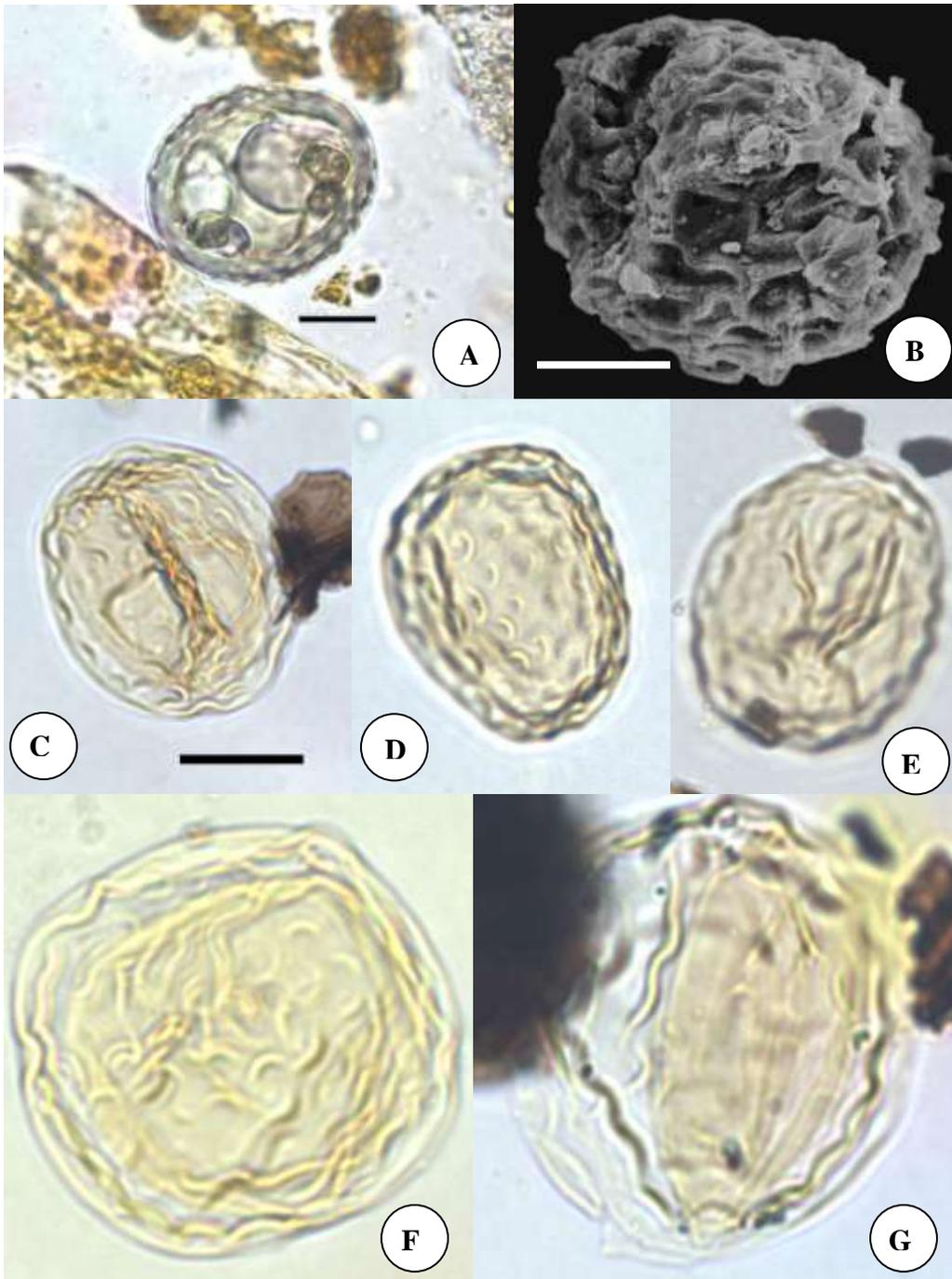


Figure 9 SEM and Light micrographs of the Ascarid Type parasitic egg. Figure 9A A modern Ascarid egg recovered from a tapir fecal sample in Costa Rica. Scale Bar = 20 um. Figure 9B SEM of a fossil Ascarid type egg showing the highly regulated outer wall. Scale Bar = 20 um. Figure 9C-9G Light micrographs showing the variation in the rugulations from different specimens recovered from the abdominal region of *Tapirus polkensis*. Scale Bar in Figure 9C = 20 um (applies to Figures 9C-9G).

CHAPTER 4

DISCUSSION

This is the first effort to identify evidence of parasitic infection in an extinct tapir (*T. polkensis*). The contrast between the palynomorphs recovered from the abdominal region and the exterior of the articulated skeletal material and its association with a cluster of hickory nuts suggest that the former is in fact an intestinal fauna (See Figure 3). Tentative identifications of the intestinal fauna were made based on size, shape, and ornamentation (See Tables 1 and 2). Specimens exhibit a number of features suggestive of a variety of groups of abdominal parasites.

There are few studies of parasites in extant tapirs and limited data on all members of Perrisodactyla excluding horses. A specific Trichostrongylid nematode has been identified in the lowland tapir, *Tapironema coronatum* (Durette-Desset et al. 1997). Other species have been listed but they all provide inadequate descriptions of morphology and measurements. Tapirs can be infected by a variety of parasites including tapeworms, *Strongyloides* sp., strongylids, Ascarid, *Capillaria* (See Table 3) (Ramsey and Zainuddin 1993). Protozoans including *Balantidium* sp. and *Girardia* sp. have also been identified in the tapir (Ramsey and Zainuddin 1993). In the La Sepultura Biosphere Reserve, Chiapas Mexico, 19 fecal samples (Baird's tapir) were analyzed as well as samples from a single male tapir from the Montes Azules Biosphere Reserve (Chiapas, Mexico). Nematodes and protozoans were found in fecal samples from the Baird's tapir. Among these nematodes and protozoans were: *Agriostomum* sp., *Lacandoria* sp., *Neomurshidia* sp., *Trichostrongylus* sp., *Strongylus* sp., *Brachylumus* sp., an unidentified species of ancylostomidae, *Eimeria* sp., and *Balantidium coli* (Cruz et al. 2006). There is

evidence of *Giardia* (protozoan) and nematodes, *Strongylus*, *Strongyloides*, ascarids, and the tapeworm *Flabellioskrjabinia* in the mountain tapir (Gale and Sedgewick 1968).

As a result of limited studies of parasitic infection in tapirs, an investigation into the parasitic infections of related species of the order Perissodactyla was conducted. Common internal parasites of Equidae, the horses, include: *Strongylus vulgaris*, small strongyles or cyathostomes, *Oxyuris equi*, *Gastrophilus* spp., *Parascaris equorum*, *Habronema* spp., *Strongyloides westeri*, *Anoplocephala* spp., and *Babesia* spp. (Foreyt 2001). *Capillaria hepatica* may also infect horses (Jones et al. 1997).

Rhinocerotidae, the rhinoceroses, can be infected by a variety of endoparasites including numerous members of phylum Platyhelminthes (flatworms and tapeworms), Nematodes, and Protozoans. The trematode *Brumptia bicanda* inhabits the intestine of both the black and white rhinoceros. Tapeworms have been identified in the rhinoceros including *Anoplocephala* that has been reported in both captive and wild rhinoceroses. The tapeworms *A. diminuta* and *A. gigantean* have been reported in the Javan rhinoceros. The tapeworm, *A. vulgaris* has been identified in captive one-horned rhinoceros and in wild black rhinoceros (Ramsey and Zainuddin 1993). Nematodes have also been identified in rhinoceroses including, the ascarid, *Probastamayria vivipara* (found in captive one-horned rhinoceros), Strongylids, *Strongyloides*, and *Crossocephalus* sp. (found in the Sumatran rhinoceros). The black rhinoceros has demonstrated evidence of *Parquilonia brumpti* and *Murshidia*, *Buisoon*, and *Khalilia* sp. in the small intestine. Extreme intestinal infestations by *Strongylus tremletti* has been found in the black rhinoceros. Evidence of *Memphisia*, *Henryella*, *Kiluluma*, and *Quilonia* sp., and *Oxyuris*

karamoja, *Parabronema rhinocerotis*, and *Pteridopharynx omoensis* have been identified from the large bowel and cecum of the black rhinoceros (Ramsey and Zainuddin 1993).

Hookworms have been identified in rhinoceroses. *Grammocephalus clathrotus* has been identified in the bile duct of both African rhinoceroses, and *G. intermedius* was identified in the large bowel of the black rhinoceros. *Capillaria* have been identified in the white rhinoceros. Spirurid worms (an order of nematodes) *Drascheia megastoma* and *Habronima khalili* have been seen in the intestines of black rhinoceroses (Ramsey and Zainuddin 1993). Protozoans identified in the white rhinoceros include *Balantidium* sp. and trophozoites of *Entamoeba* sp. that may be pathogenic. Both black and white rhinoceroses have been observed as hosts to ciliated protozoa and *Phalodinium*, *Arachnodinium*, *Monoposthium*, and *Rhinozeta* sp. (Ramsey and Zainuddin 1993).

Another study on the black and white rhinoceroses of Southern Africa identified several helminth species including: *Probstmayria vivipara* (the most abundant parasite in each rhinoceros), *Draschia megastoma*, *Parabronema roundi*, *Kiluluma* sp., *Kiluluma goodeyi*, *Kiluluma magna*, *Khalilia rhinocerotis*, *Oxyuris karamoja*, and *Anoplocephala gigantea* (Knapp et al. 1997).

The fecal specimens examined in this study of tapirs from Central and South America contained a variety of plant artifacts and very little pollen and spores but did provide definitive evidence for the identification of parasites eggs. A sample from Sirena Biological Station tested positive for a tapeworm species (See Figure 4F). Although we did not find the Trichostrongylid nematode species, endemic to tapirs, we did find a tapeworm in the family Anoplocephalidae that may not have been previously described in tapirs (See Figure 4F). The tapeworm recovered from a tapir in Costa Rica is comparable

to known tapeworm eggs based on size, shape, and morphology. These eggs have the distinct hook/hooklets that are indicative of tapeworm eggs. These tapeworm eggs were not plentiful and did not suggest an infestation. All other samples collected from various locations throughout Sirena Biological Station showed no definitive evidence of parasites. Samples from Ecuador contained a variety of plant artifacts, pollen, and spores. They also contained possible tapeworm and ascarid eggs. The tapeworm eggs appear to have hooklets, a characteristic of the tapeworm egg and the potential ascarid egg conforms to the shape and characteristics of eggs from species of ascarids.

In the fossil tapir *T. polkensis* there are a number of different morphological types that are suggestive of parasitic groups, but their suite of characteristics are common to a number of parasitic groups. One palynomorph resembles an ascarid - type egg especially based on studies with the SEM; however, this egg-type does appear to have similar surface structures observed in modern ascarid eggs with ridges and grooves (Figures 9B-9G). Another palynomorph was found that has characteristics of *Capillaria sp.* Based on measurements and distinct morphological features these palynomorphs resemble modern *Capillaria sp.* With an average length of 54 μm and average width of 30 μm these structures have similar measurements of modern specimens. *Capillaria* have a distinct surface structure that is either granular in appearance or striated. The suspected structures from *T. polkensis* also exhibit these surface structures that suggest affinity with the capillarids; however, a distinct difference is the lack of polar plugs in the fossil, a feature that is highly conserved in modern *Capillaria sp.* (See Figures 8A-8G). Statistical analysis was performed for all egg-like structures and is summarized in the Appendix.

Numerous structures have been recovered from the abdominal sample in *T. polkensis*, some sharing characteristics in modern parasite eggs. A variety of nematodes and protozoans have been identified in extant wild tapirs including ascarid species, but *Capillaria* species are not generally found in populations today. This poses the question why capillarids might have been present in extinct tapirs and not extant ones?

Nematodes in the family Capillariidae parasitize a diverse array of host species in all vertebrate groups. There are at least 300 species described from fish, reptiles, amphibians, birds, and mammals. The life cycle biology of this group is quite variable. The systematic classification for this important group of parasites is poorly understood. Traditionally, the group has been treated as a single genus w/ many subgenera and species following the discussion and rationale of Baylis (1931, 1937). Moravec et al. (1987) reviewed the biology of the Capillariidae and provided a convincing rationale for treatment of this nematode group as a family with 22 genera, albeit some of which are monotypic composed of only a single species. Justification for this classification scheme is based on the observed heterogeneity in the range of host-parasite associations, the systems/anatomical sites they parasitize, and the respective life cycle biology's within the group. Still it is worth noting that although over 300 capillarids are known to science, less than 20% of these have been extensively investigated. The adult parasites are very small and difficult to detect. Professor Moravec feels that even though there are no known capillarid species from modern Perissodactylid hosts, this is not unequivocal evidence of their absence in the host group (F. Moravec - personal communication). Indeed, the paucity of parasite studies in modern tapir populations bears witness to the fact there is still much to learn before the present can properly inform the past.

Understanding the evolutionary relationships among the members of the Capillariidae and their host associations is precluded by the near absence of molecular studies of their genetic variation. Thus, it is impossible to ascertain when particular genera diverged from larger ancestral groups and colonized their characteristic host species. Zarlenga et al. (2006) study of genetic variation in the distantly related Trichinellidae posit a divergence from its sister taxa Trichuridae (composed of Capillariinae, Trichuinae, and Trichosomoidinae) approximately 275 mya. They suggest that the present distribution of *Trichinella* species in their vertebrate hosts is the result of post-Miocene expansion, colonization, and multiple occurrences of host switching. It is likely that the extensive biogeographic and host distribution of the capillarids is the result of the same processes, but without the molecular framework the spatial and temporal scales cannot be deduced.

Geophagy, consumption of soil, clay, dirt, termite mound earth, or ground-up rock, is common among a variety of animals including mammals, reptiles, birds, and invertebrates (Wynn and Fougere 2007). An interesting feature of the modern tapirs studied and *T. polkensis* is the preponderance of low levels of infestation. Tapirs are surprisingly parasite free. This is interesting in light of the preliminary geochemical data that suggests the Gray Fossil Site may be an ancient lick. Lowland tapirs have been observed visiting natural clay licks in the Northeastern Brazilian where they consume soil and drink the water (Montenegro 1998, 2004). One theory is that tapirs may frequent natural clay licks in search of mineral supplementation and to detoxify plant secondary compounds it consumed to control parasite infestation (pharmacophagy) (Montenegro 1998, Tobler 2008). Tapirs have been observed eating bark that may contain plant

secondary metabolites (PSM) (Medici 2010). A tapir (*Tapirus veroensis*) was discovered at a late Pleistocene site at Sassafras Cave in the Oklahoma Ozark Highlands. It is predicted that tapirs may have visited caves to find clays to detoxify these consumed plant secondary compounds (Czaplewski et al. 2002). This particular tapir may have been seeking out the clay mineral, Kaolinite, which is believed to be responsible for absorbing a variety of plant biochemical toxins that are consumed by herbivores (Czaplewski et al. 2002). Kaolinite is considered a pure pharmaceutical and animals may actually choose soil types with the properties to bind and deactivate plant toxins (Jain et al. 2008).

The movements and spatial distributions of herbivores may correspond to availability of mineral licks (Montenegro 1998, Adcock 2001, Tobler 2008). Fruits, young leaves, and a variety of other plant parts may contain toxic, teratogenic, or carcinogenic plant secondary compounds (PSM). For example *Vernonia amygdalina* (also see e.g. *Symphonia globulifera*, Ngouela et al. 2006, Lenta et al. 2007a, 2007b) contains 7 steroid glucosides along with 4 sesquiterpene lactones that are efficient in killing parasites that cause serious parasitic diseases including schistosomiasis, malaria, and leishmaniasis (Wynn and Fougere 2007). Chimpanzees and other mammals appear to self-medicate (pharmacophagy) by ingestion of plant allelochemicals with the intent of treating gastrointestinal parasites (Johns and Duquette 1991). Studies in primates supports that regular dirt consumption yields lower parasite loads (Krishnamani 2002). Animals may consume clay or clay enriched water to buffer the effects of PSM (Voigt et al. 2008).

It has also been suggested that geophagy may aid in parasite and disease control, cytoprotection, prevent indigestion, nitrification, or detoxification, and as a mechanical digestion aid (Voigt et al. 2008). Geophagy may encourage a favorable balance between nutrients and toxins but one of its functions might be to counter dietary toxins and may also counter the effects of gastrointestinal parasites (Johns and Duquette 1991). There is evidence of all members of order Perissodactyla frequenting natural clay and mineral licks. Wild ungulates commonly eat soil and visit clay licks (Penzhorn 1982). In the Equids, for example, the mountain zebra has been shown to eat soil and visit mineral licks in the Mountain Zebra National Park in South Africa. As to the exact reason for the zebra to visit these mineral licks it is one theory that they require calcium that is abundant at the locations (Penzhorn 1982). It was also observed that zebras will eat termite mounds made of soil, suggesting that these animals are perhaps eating soil or clay for other reasons other than the chemical constituents (Penzhorn 1982). Free-ranging elephants and rhinoceroses use mineral licks, captive rhinos that are not provided with mineral licks have low circulating Na as compared to free-ranging animals; this may suggest that mineral licks may be used by rhinoceroses to supplement a deficiency of minerals that may be lacking in their diet (Clauss et al. 2007). Rhinoceroses may also visit mineral licks to acquire other supplementation including magnesium, potassium, and calcium (Mukinya 1976). Soil type seems to play an important role in the carrying capacity of the black rhinoceros in that it provides limiting mineral nutrients made available through browsing and soil licks (Adcock 2001). More recent studies do suggest that perhaps the clay is actually the primary component when selecting soil to ingest. Many animals including cattle, giraffes, elephants, rhinoceroses, chimpanzees, gorillas,

and a variety of rain forest birds regularly consume clay-rich termite mound soil (Jain et al. 2008). Clay is the primary ingredient of kaolin, which is found in many over-the-counter treatments for gastrointestinal ailments in humans. Animals may choose clay minerals over plants as a defense against pathogens to avoid the side effects of PSM that are toxic to the pathogen and host (Jain et al. 2008). Although tapirs are known to practice geophagy low parasite loads in tapirs may primarily be due to low population density and the fact that tapirs are primarily solitary, thus reducing the opportunity to be infected by conspecifics (Altizer et al. 2003).

This investigation presents evidence of intestinal parasites in the extinct *T. polkensis*. Tentative identification of parasites based on morphological characteristics of egg-like structures also indicate that the fossil tapir *T. polkensis* like the extant species of tapirs have low levels of infestation. Tapirs may have a long practice of geophagy, and or pharmacophagy. This also suggests that parasite loads in the modern and fossil taxa do not play a major role in lowering the fitness of tapirs, and the extirpation of tapirs in east-central North America is probably more affected by other factors.

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APPENDIX

Statistics of Egg-Like Structures

Descriptive Statistics							
	N	Minimum	Maximum	Mean		Std.	
	Statistic	Statistic	Statistic	Statistic	Error	Deviation	Variance
						Statistic	Statistic
Coccidia Type	169	11	20	14.86	.115	1.492	2.225
Nematode1aLength	53	27	48	38.19	.661	4.812	23.156
Nematode1aWidth	53	18	43	32.36	.837	6.096	37.157
Nematode1bLength	33	50	83	62.36	1.573	9.037	81.676
Nematode1bWidth	33	28	50	41.82	1.011	5.807	33.716
CapillariaLength	170	41	77	53.65	.476	6.206	38.512
CapillariaWidth	170	19	47	29.81	.317	4.134	17.089
Nematode2Length	139	39	88	53.80	.631	7.434	55.263
Nematode2Width	139	22	52	32.01	.385	4.544	20.652
Nematode1cLength	100	54	78	65.13	.615	6.154	37.872
Nematode1cWidth	100	45	72	56.05	.523	5.231	27.361
OvalPitLength	7	46	56	52.14	1.565	4.140	17.143
OvalPitWidth	7	27	48	35.86	3.542	9.371	87.810
NwOvalLength	27	46	75	55.37	1.372	7.131	50.858
NwOvalWidth	27	13	25	18.48	.598	3.105	9.644
AscardLength	14	41	59	48.07	1.344	5.030	25.302
AscardWidth	14	37	45	42.00	.734	2.746	7.538
Valid N (listwise)	7						

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