Dissertations and Theses in Biological Sciences

Biological Sciences, School of

5-2009

Taxonomic Revision of Species of the Genus *Monoecocestus* (Cestoda: Anoplocephalidae)

Terry R. Haverkost
University of Nebraska - Lincoln, haverkost@gmail.com

TAXONOMIC REVISION OF SPECIES OF THE GENUS *MONOECOCESTUS*

(CESTODA: ANOPLOCEPHALIDAE)

By

Terry R. Haverkost

A DISSERTATION

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Doctor of Philosophy

Major: Biological Sciences

Under the Supervision of Professor Scott L. Gardner

Lincoln, Nebraska

May, 2009

TAXONOMIC REVISION OF SPECIES OF THE GENUS *MONOECOCESTUS*

(CESTODA: ANOPLOCEPHALIDAE)

Terry R. Haverkost

University of Nebraska, 2009

Advisor: Scott L. Gardner

My dissertation research is an important contribution to the taxonomy of anoplocephalid cestodes. Almost all research conducted for these chapters was done by staining, mounting, and measuring anoplocephalid cestodes from the Bolivian Biodiversity Survey conducted in Bolivia from 1984-2000. These specimens were collected and processed in the field and deposited in the Harold W. Manter Laboratory of Parasitology. I was particularly interested in species of the genus *Monoecocestus* Beddard, 1914 that parasitize caviid and sigmodontine rodents. In all instances, the material studied has lead to the description of new species or the redescription of existing species of *Monoecocestus*. In one instance, I was able to resurrect the genus *Lentiella* Rego, 1964 based on specimens representing a new species of that genus. In general, the research is indicative of the lack of proper representation of species by quality voucher specimens, i.e. the few specimens available from a geographically small region (Bolivia) in South America has increased the known species in the genus *Monoecocestus* by 40%. The research results presented in these chapters should be convincing evidence that the increased sampling effort for tapeworms and other parasites of caviid and sigmodontine rodents throughout South America would yield a truly massive number of previously

unknown species. Also included in this dissertation are appendices of works that I have completed in my time at the University of Nebraska.

The work herein is not issued for public and permanent scientific record, or for purposes of zoological nomenclature, is not published within the meaning of the International Code of Zoological Nomenclature.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

Taxonomic history of the genus *Monoecocestus* Beddard, 1914

In his description of the genus *Schizotaenia* Janicki, 1904, Janicki (1904)

described a new species, *S. hagmanni* Janicki, 1904 but designated the type of the genus

Schizotaenia decrescens (=*Taenia decrescens* Diesing, 1856). Upon examination of

specimens, Baer (1927) synonymized *S. hagmanni* into *S. decrescens*. Baer (1927)

comments on the poor condition of the specimens collected by Diesing (1856) but was

confident enough in the characters present to consider the two species identical. Baer

(1927) redescribed *S. decrescens* based on specimens obtained from *Hydrochoerus*

Brisson, 1762 (the type host for *S. hagmanni*). Rego (1961) collected numerous

peccaries (*Tayassus (Dicotyles) albirostris*), the type host of *S. decrescens*, found many

cestodes, but no species of *Monoecocestus*. Rego (1961) goes on to speculate that the

specimens collected by Natterer in 1825 and viewed by Diesing in 1856 (and later by

Baer [1927]) were likely mislabeled and that the only likely host for *S. decrescens* is

Hydrochoerus hydrochoeri.

Hughes (1941) discovered that *Taenia decrescens* Diesing, 1856 was actually a

homonym of *Taenia decrescens* Rudolphi (in Creplin, 1849). Hughes supplied a *nomen*

novem, *Schizotaenia diesingi* Hughes, 1941, but, according to Freeman (1949), likely did

so being unaware of the synonymy of *S. hagmanni* by Baer (1927) and the preoccupation

of *Schizotaenia* Cook, 1895 discovered by Fuhrmann (1932). Freeman (1949)

subsequently recombined the new type of the genus as *Monoecocestus hagmanni*

(Janicki, 1904). Spasskii (1951) cites Lühe (1895) to refute Baer's (1927) synonymy of

M. hagmanni into *M. decrescens*, maintaining *M. decrescens* as the type species of the

genus. Spasskii (1951) does recognize the inadequacy of data in the literature when presenting *M. hagmanni* as a separate species in his work. Because of the overwhelming evidence to support their claims, the work herein maintains the opinion of Baer (1927), Freeman (1949), and Rego (1961), placing *M. hagmanni* as the type of *Monoecocestus* and *M. decrescens* as a junior synonym of *M. hagmanni*.

Spasskii (1999) not only disagrees with Baer (1927) that *S. decrescens* and *S. hagmanni* were incorrectly synonymized (see Spasskii, 1951), but separates them even further by partitioning *S. decrescens* and 1 other species (*M. hydrochoeri*) into the new genus *Pecarezia* Spasskii, 1999. This new genus is based on one described character (filamentous vs. capped pyriform apparatus). However, it has recently been shown that the pyriform apparatus filaments are folds of the internal membrane of the egg where they meet the pyriform apparatus (Denegri et al., 2003; Beveridge, 2007; Haverkost and Gardner, 2008). Spasskii (1999) reinstates *Perutaenia* Parra, 1953 and *Lentiella* Rego, 1964 despite Beveridge's (1994) mentioning of insufficient material to properly delineate the taxa into new genera. In the following chapters the work of Spasskii (1999) is disregarded due to the work of (Denegri et al., 2003; Beveridge, 2007; Haverkost and Gardner, 2008) and because there is no mention the paper that Spasskii (1999) viewed new or existing material in his analysis.

Current research

At the beginning of my studies, there were 14 South American species in the genus *Monoecocestus* Beddard, 1914 (see Table I). All but one of these species (*M. mackiewickzi* Schmidt and Martin, 1978) are found in hystricognath rodents. The

chapters within show that there are an additional 6 species of *Monoecocestus*, 3 of those species parasitizing sigmodontine rodents like *M. mackiewiczi*.

In chapter 1, I describe 6 new species of *Monoecocestus* and redescribe *M. mackiewiczi* from the type material. Specimens studied in this chapter are all from the Bolivian Biodiversity Survey and deposited in the H. W. Manter Laboratory of Parasitology. This chapter discusses the uterine development of these new species, as uterine development is an important taxonomic character of the family. The presence of a vaginal dilation in these (and other *Monoecocestus* species) species is discussed, as this character is of potential taxonomic importance. With 3 of these new species found in sigmodontine rodents, this chapter also discusses the potential evolutionary history and biogeography of these parasites.

In chapter 2, I formally redescribe 3 species of *Monoecocestus* from South America. *Monoecocestus minor* Rego, 1960 and *M. macrobursatus* Rego, 1961 were redescribed from the material housed at the helminthological collection of the Instituto do Oswaldo Cruz, Rio de Janeiro, Brazil. *Monoecocestus threlkeldi* (Parra, 1952) is redescribed based on new material collected in Bolivia. These new specimens are undoubtedly *M. threlkeldi*, though they were found in a different genus (*Holochilus* Brandt, 1835) than the type material (found in *Lagidium peruanum* Meyen, 1833). These specimens also lend support to the decision to make *Perutaenia* Parra, 1953 a junior synonym of *Monoecocestus*, as proposed by Beveridge (1994).

In chapter 3, I validate the genus *Lentiella* Rego, 1964, that had been placed in synonomy with *Monoecocestus*. Cestode specimens collected from *Proechimys simonsi* Thomas, 1900 in Bolivia are described as *Lentiella lamothei* n. sp. and can be confidently

placed in the genus *Lentiella* by the presence of a tubular, not reticulate, uterus. This tubular uterus is shown to be distinct from the tubular uterus of the North American anoplocephalid cestode species belonging to the genus *Anoplocephaloides* Baer, 1923.

LITERATURE CITED

Baer, J. G. 1927. Monographie des cestodes de la familie des Anoplocephalidae. Bulletin Biologique de la France et de la Belgique (Supplement). **10**: 1-241.

Beveridge, I. 1994. Family Anoplocephalidae Cholodkovsky, 1902. *in* Keys to the cestode parasites of vertebrates., L. F. Khalil, A. Jones, and R. A. Bray (ed.). CAB International, Cambridge, 315-366 p.

Beveridge, I. 2007. Revision of the *Progamotaenia zschokkei* (Janicki, 1905) complex (Cestoda: Anoplocephalidae), with the description of six new species. Systematic Parasitology. **66**: 159-194.

Creplin, F. C. 1849. Nachträge von Creplin zu Gurlt's verzeichnisse deer Thiere, in welchen endozeen gefunden worden sind. Archiv für Naturgeschichte. **15**: 52-80.

Denegri, G., M. C. Dopchiz, M. C. Elissondo, and I. Beveridge. 2003. *Viscachataenia* n. g., with the redescription of *V. quadrata* (von Linstow, 1904) n. comb. (Cestoda: Anoplocephalidae) in *Lagidium viscacia* (Rodentia: Chinchillidae) from Argentina. Systematic Parasitology. **54**: 81-88.

Diesing, K. M. 1856. Zwanzig Arten von Cephalocotyleen. Denkschriften Akademie Wiss. Wien Math. Naturwiss. Kl. Abt. I. **12**: 23-38.

Freeman, R. S. 1949. Notes on the morphology and life cycle of the genus
Monoecocestus Beddard, 1914 (Cestoda: Anoplocephalidae) from the Porcupine.
Journal of Parasitology. **35**: 603-612.

Fuhrmann, O. 1932. Les Ténias des oiseaux. Mémoires de Universite de Neuchâtel. **8**:
381.

Haverkost, T. R., and S. L. Gardner. 2008. A new species of *Lentiella* (Cestoda:
Anoplocephalidae) from *Proechimys simonsi* (Rodentia: Echimyidae) in Bolivia.
Revista Mexicana de Biodiversidad. **79**: 99S-106S.

Hughes, R. C. 1941. The Taeniae of yesterday. Bulletin of the Oklahoma Agricultural
and Mechanical College. **38**: 1-83.

Janicki, C. 1904. Zur Kenntnis einger Säugetiercestoden. Zoologischer Anzeiger. **27**:
770-782.

Lühe, M. 1895. Mitteilungen über einige wenig becannte bezw. neue südamericanische
Taenien des K.K. naturhistorischen Hof-Museums. Wien. Arch. für Naturgesch,
Berlin. **61**: 199-212.

Rego, A. A. 1961. Revisão do genero *Monoecocestus* Beddard, 1914 (Cestoda,
Anoplocephalidae). Memórias do Instituto Oswaldo Cruz. **59**: 325-354.

Spasskii, A. A. 1951. Essentials of Cestodology, Anoplocephalate tapeworms of
domestic and wild animals, The Academy of Sciences of the USSR, Moscow, 783
p.

Spasskii, A. A. 1999. Taxonomical analysis of the combined genus *Monoecocestus*
(Cestoda, Anoplocephalidae). Vestnik-Zoologii. **33**: 7-12.

Table I. South American species of *Monoecoestus* Beddard, 1914 including type locality (by country), and type host. Entries marked with (*) are described as new species in the following chapters. Entries marked with (†) are redescribed in the following chapters. Hosts marked with (‡) belong to various families in the infraorder Hystricognathi (Rodentia: Hystricomorpha). Hosts marked with (§) belong to the subfamily Sigmodontinae (Myomorpha: Muroidea: Cricetidae).

Name	Type locality	Type Host
Monoecocestus andersoni n. sp.*	Bolivia	*Graomys domorum*§
Monoecocestus diplomys Nobel & Tesh 1974	Panama	*Diplomys darlingi*‡
Monoecocestus eljefe n. sp.*	Bolivia	*Galea musteloides*‡
Monoecocestus gundlachi Vigueras 1943	Cuba	*Capromys pilorides*‡
Monoecocestus hagmanni (Janicki 1904)	Brazil	*Hydrocoerus hydrochaeri*‡
Monoecocestus hydrocoeri (Baylis 1928)	Paraguay	*Hydrocoerus hydrochaeri*‡
Monoecocestus jacobi Sinkoc, Müller & Brum 1998	Brazil	*Hydrocoerus hydrochaeri*‡
Monoecocestus machadoi (Rego 1964) †	Brazil	*Proechimys gayennensis*‡
Monoecocestus mackiewiczi Schmidt & Martin 1978 †	Paraguay	*Graomys sp.* §
Monoecocestus macrobursatus Rego 1961 †	Brazil	*Hydrocoerus hydrochaeri*‡
Monoecocestus microcephalus n. sp.*	Bolivia	*Graomys domorum*§
Monoecocestus minor Rego 1960 †	Brazil	*Cavia aperia*‡
Monoecocestus myopotami Sutton 1973	Argentina	*Myocastor coypus*‡
Monoecocestus parcitesticulatus Rego 1960	Brazil	*Cavia porcellus*‡
Monoecocestus petiso n. sp.*	Bolivia	*Galea musteloides*‡
Monoecocestus poralus n. sp.*	Bolivia	*Phyllotis caprinus*§
Monoecocestus rheiphilus Voge & Read 1953	Peru, Chile	*Pterocnemia pennata*
Monoecocestus sininterus n. sp.*	Bolivia	*Phyllotis wolffsohni*§
Monoecocestus threlkeldi (Parra 1952) †	Peru	*Lagidium peruanum*‡
Monoecocestus torresi Olsen 1976	Chile	*Ctenomys maulinus* ‡

CHAPTER 1

ANOPLOCEPHALIDAE (CESTODA: CYCLOPHYLLIDEA) OF

NEOTROPICAL RODENTS (CAVIIDAE AND SIGMODONTINAE)

Terry R. Haverkost and Scott L. Gardner

Harold W. Manter Laboratory of Parasitology, University of Nebraska State Museum and School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588-0514

ABSTRACT: Anoplocephalid cestodes have a world-wide distribution, but relatively few species are known from South American rodents. By examining the collections of the Harold W. Manter Laboratory of Parasitology and the United States National Parasite Collection, 6 new species of *Monoecocestus* Beddard, 1914 are described, along with a redescription of *Monoecocestus mackiewiczi* Schmidt and Martin, 1978 based on the type specimens. The discussion includes commentary about uterine development, an important taxonomic character of the family, the vaginal dilation in immature proglottids (a character of potential taxonomic importance), and the implication of host usage to the evolutionary history and biogeography of species in this genus.

INTRODUCTION

Anoplocephalid cestodes have been reported from mammals from all major zoogeographic regions but relatively few species have been described from the

Neotropics. Up to the present time, the relative dearth of species of cestodes reported and described from mammals in the Neotropics most likely is due to lack of adequate sampling (see Gardner and Campbell, 1992). Recent studies of the helminth faunas of mammals that have relatively great numerical density in parts of their range have yielded the discovery of several new taxa (Beveridge, 2008; Denegri et al., 2003; Haverkost and Gardner, 2008). At the present time, fewer than 20 species of anoplocephaline cestodes have been described from mammals in the Neotropics, and those that have been reported all occur in hystricognath and sigmodontine rodents (Rego, 1961; Haverkost and Gardner, 2008; Haverkost and Gardner, in press; but see Voge and Read, 1953).

General biological survey work conducted with National Science Foundation support that took place throughout Bolivia from the 1980's through 2000 resulted in the collection and necropsy of approximately 20,000 mammal specimens. The present work is based on material collected during the Bolivian Parasite Biodiversity Survey that is stored in the parasite collections of the Harold W. Manter Laboratory of Parasitology (HWML). For this study, specimens examined also include material from the United States National Parasite Collection (USNPC) in Beltsville, Maryland.

MATERIALS AND METHODS

Mammals collected in the field were immediately killed with chloroform, and quickly examined for both ecto and endo-parasites (Gardner, 1996). Cestodes found were relaxed in distilled or fresh water, killed and preserved in either 10% formalin or 70% ethanol, and transported and stored in the solutions used for fixation. For study in the laboratory, specimens were stained in Semichon's acetic carmine or Erlich's acid

hematoxylin, dehydrated in an alcohol series, cleared in either terpineol or cedarwood oil and xylene, and permanently mounted on slides in Damar Gum (Spectrum, Gardena, CA) (Gardner, 1996; Pritchard and Kruse, 1982) Superficial tissues, including tegument and muscles, were removed from the dorsal or ventral surface of mature proglottids to observe internal organs. Measurements of the strobila were made with an ocular micrometer. Measurements of proglottids were made by drawing the proglottid with the aid of a drawing tube and measuring the subsequently scanned picture with SigmaScan 5.0 (SPSS, Chicago, IL). From each strobila studied, 1-3 proglottids were drawn and measured. Eggs were studied by freeing them from gravid segments, clearing in lactophenol, and mounting temporarily on a microscope slide. Some eggs were released from gravid proglottids just prior to permanent mounting in Damar Gum. Measurements of the eggs were made from digital photographs. Figures were made with the aid of a drawing tube. Some individuals were dehydrated, cleared, embedded in paraffin, and sectioned in the transverse or sagittal plane in 15-30 μm sections.

Scolex length was measured from the anterior extremity to the posterior margin of the suckers. Neck length was measured from the posterior margin of the suckers to the first visible sign of segmentation. Lateral alternation of the genital pores is presented as the number of times the genital pore switched sides per 100 proglottids. Thus, a higher number corresponds to more regular alternation. The widths of dorsal and ventral osmoregulatory canals were recorded at the midpoint of the proglottid on the antiporal side. Distribution of testes in segments was measured as the distance between the two distal extreme testes (Haukisalmi et al., 2004). The index of asymmetry was calculated as the ratio of the distance between the midpoint of the vitelline gland and the poral

extremity/the total width of the proglottid (Sato et al., 1993). Measurements provided include the range, followed by mean, and the number of measurements if different than that given initially. All measurements are provided in micrometers unless otherwise specified.

Principle Components Analysis (PCA) was performed on the standard proglottid measurements of the group of worms including the type specimens of *M. mackiewiczi* Schmidt and Martin, 1978 and the group of unidentified *Monoecocestus* Beddard, 1914 specimens from host species representing the genera *Phyllotis* Waterhouse, 1837 and *Graomys* Thomas, 1916 from Bolivia. PCA is an ordination method that rotates the coordinate axes of the original variables to create completely uncorrelated variables (principal components) (Manly, 1986). We used PCA in an effort to look for the clustering of certain specimens based on orthogonal principle components created from putatively covariant variables. Variables used in the analysis include 20 standard measurements of proglottids: proglottid length and width, length and width of the vitelline gland, ovary, external and internal seminal vesicle, seminal receptacle, cirrus sac, width of the transverse, ventral, and dorsal osmoregulatory canals, testis mean diameter, testis distribution, and the index of asymmetry. Six random specimens (out of 20) potentially representing *M. microcephalus* n. sp. from *G. domorum* (Thomas, 1902) were chosen for the analysis to reduce the weight of these specimens in the analysis. The PCA was repeated using a different subset of these specimens and results were similar regardless of the subset used. Statistical analyses were performed with SAS 6.12 (SAS Institute, Cary, NC) on a UNIX platform. The results are shown in graphical form (Fig. 19).

Rego (1961) made *M. decrescens* (Diesing, 1856) a junior synonym of *M. hagmanni* (Janicki, 1904), since the original name *Taenia decrescens* Diesing, 1856 was a homonym of *Taenia decrescens* Rudolphi, 1849. Both were represented by identical specimens (Baer, 1927) and no representatives of *M. decrescens* have been found in *Tayassu pecari* (Link, 1795) (a likely mislabeled host) since their original collection by Natterer in 1825. It is assumed that *Hydrochoerus hydrochaeris* (Linnaeus, 1766) is the type host for *M. hagmanni*. In the following descriptions, we conduct the differential diagnosis of redescribed and new species against *M. hagmanni* (Janicki, 1904) sensu Rego (1961). Measurements for *M. thelkeldi* (Parra, 1952), *M. minor* Rego, 1960, and *M. macrobursatus* Rego, 1961 are taken from Haverkost and Gardner (in press). Measurements of *M. diplomys* Nobel and Tesh, 1974 are original measurements taken by TRH from the Holotype (USNPC72960). A table of representative measurements is provided in Table (I and II).

Records of hosts are listed by their NK numbers or by Museum of Southwestern Biology (MSB) accession numbers (in Albuquerque, New Mexico) and given symbiotype designation if specimens were given the MSB accession number.

DESCRIPTIONS

Monoecocestus eljefe n. sp.

(Fig. 1)

Based on 5 complete individuals and 15 proglottid measurements. Strobila total length 96-167 mm (129 mm), maximum width 1373-1934 (1671). Adult cestodes have 178-264 (208) proglottids. Scolex 124-192 (167) long, 288-368 (338) wide. Suckers

directed laterally or anterio-laterally, 116-168 (150, n=20) in diameter. Neck 200-720 (328) long, minimum width 260-348 (302). Proglottids craspedote. Immature proglottids 144-374 (270) long, 768-1123 (939) wide. Length:width ratio of immature proglottids 0.18-0.34 (0.28). Mature proglottids 331-807 (605) long, 1146-1604 (1363) wide. Length:width ratio of mature proglottids 0.23-0.54 (0.42). Gravid proglottids 718-1498 (1148) long, 1467-1872 (1660) wide. Length:width ratio of gravid proglottids 0.38-1.00 (0.72). Genital pores alternate irregularly, switching lateral margins 34-52 (44) times per 100 proglottids. Genital pores alternate approximately every 2 proglottids. Egg diameter 46-60 (50, n=25). Embryophore takes the form of pyriform apparatus, measures 18-27 (22, n=25) long. Pyriform apparatus blunted at terminus, no horns observed. Oncosphere 8-12 (10, n=25) in diameter. Genital ducts pass osmoregulatory canals dorsally. Dorsal canal 14-32 (23) wide, distal to ventral canal. Ventral canal 16-347 (94) wide with one transverse canal per proglottid. Transverse canal 8-240 (81) wide. Cirrus sac measures 105-272 (183) long, 51-100 (80) wide. Cirrus often everted in postmature proglottids. Cirrus sac may cross dorsal and ventral osmoregulatory canals in immature and mature proglottids, but crosses neither in older segments unless swollen ventral canal forces contact. In such a case the cirrus sac is forced to the anterior. Measurements of the internal seminal vesicle are unreliable as it may be oblong when the cirrus is everted or when the cirrus sac is pressured by the ventral osmoregulatory canal. Internal seminal vesicle appears in mature proglottids and remains prominent throughout postmature proglottids. External seminal vesicle absent. Vagina enters genital atrium anterior or anterio-ventral to cirrus. Seminal receptacle ovoid, reaching maximum of 254 long and 97 wide in mature proglottids. Seminal receptacle remains visible into gravid proglottids.

Seminal receptacle dorsal to ovary, ventral to testes. Maximum dimensions for cirrus sac and seminal receptacle reached in postmature proglottids. Vitelline gland globular, measures 91-176 (126) long, 106-195 (138) wide; vitelline gland posterior to ovary. Ovary small, central in segment, 106-295 (207) long, 277-559 (361) wide. Index of asymmetry 0.46-0.50 (0.48). Testes spherical or ovoid, 49-79 (63, n=75) in diameter. If ovoid, testis often elongated laterally. Testes posterior and lateral to vitelline gland, number 38-60 (48) per proglottid. Testes may overlap vitelline gland, seminal receptacle, and posterior margins of ovary, ventral and transverse osmoregulatory canals. Testis distribution 430-616 (482). Uterus first appears as a series of lobes or overlapping tubes radiating from the oocapt. Uterus arises dorsal to ovary, ventral to testes. Developing eggs are seen with the first sign of uterine development. Uterine lobes gradually elongate and become either long and thin, stretching laterally or widen if directed anteriorly or posteriorly. Many tubes radiate from the center, and fenestrations are not seen during development. Fully gravid uterus has few anterior or posterior diverticula; many finger-like projections seen directed laterally across the ventral osmoregulatory canal. Uterine diverticulations cross ventral canal both dorsally and ventrally.

Diagnosis

Monoecocestus eljefe n. sp. can be distinguished from *M. threlkeldi*, *M. minor*, *M. macrobursatus*, and *M. hagmanni* by having a much greater total length, greater number of proglottids, and larger testes. *Monoecocestus eljefe* n. sp. can be distinguished from *M. hydrochoeri* by having a smaller scolex width, narrower vitelline gland width, narrower ovary width, and fewer testes. *Monoecocestus eljefe* n. sp. can be distinguished from *M.*

diplomys by having a smaller total length, greater length:width ratio in mature

proglottids, shorter cirrus sac length, smaller distribution of testes, and a smaller index of

asymmetry. *Monoecocestus eljefe* n. sp. can be distinguished from *M. jacobi* Sinkoc,

Müller, and Brum, 1998 by having a smaller total length, smaller scolex width, sucker

diameter, cirrus sac length, vitelline gland width and ovary width. *Monoecocestus eljefe*

n. sp. can be distinguished from both *M. mackiewiczi* by having a greater length:width

ratio in all proglottids, smaller scolex width, greater neck length, smaller cirrus sac

length, vitelline gland width and ovary width.

Taxonomic summary

Host: Galea musteloides Meyen, 1832 (NK 23329)

Locality: Bolivia, Santa Cruz; 53km E Boyuibe, 18°16' S, 63°11'W, 500 m

elevation, July1991

Prevalence and intensity: 1 of 1 host captured with 6 individual cestodes.

Specimens deposited: Holotype (HWML 61289A) and Paratypes (HWML61289

B-F), deposited in the H.W. Manter Laboratory of Parasitology, Lincoln, Nebraska

Etymology: Monoecocestus eljefe n. sp., "the boss," is named in honor of the late

Dr. Terry Lamon Yates, a leader in mammalogy and the study of infectious disease and

who shared a similar nickname throughout the years of field research in both the

Neotropics and the Nearctic region.

Remarks

Galea musteloides Meyen, 1832 occurs in suitable habitat throughout the central Andean region with a known distribution extending from southern Peru south through Bolivia in the west high altitude, the central high and mid altitude, and lowland chaco into northwestern Argentina and Northern Chile (Wilson and Reeder, 2005; Eisenberg and Redford, 1992; Anderson, 1997).

Monoecocestus petiso **n. sp.**

(Fig. 2)

Based on 5 complete individuals and measurement from 15 separate segments. Stobila length 13.8-18.5 mm (15.5 mm), maximum width 1001-1075 (1045). Adult cestodes have 49-55 (51) proglottids. Scolex 150-196 (173) long, 290-354 (319) wide. Suckers directed laterally or anterio-laterally, 127-173 (159, n=20) in diameter. Neck 155-219 (202) long, minimum width 90-136 (115). Proglottids craspedote. Immature proglottids 103-155 (140) long, 258-368 (333) wide. Length:width ratio of immature proglottids 0.40-0.47 (0.42). Mature proglottids 254-350 (307) long, 680-797 (729) wide. Length:width ratio of mature proglottids 0.33-0.49 (0.42). Gravid proglottids 626-788 (920) long, 810-994 (948) wide. Length:width ratio of gravid proglottids 0.63-1.00 (0.84). Genital pores alternate regularly, switching lateral margins 94-100 (98) times per 100 proglottids. Egg diameter 45-57 (49, n=25). Embryophore takes the form of pyriform apparatus, measures 18-23(21, n=25) long. Pyriform apparatus blunted at terminus, no horns observed. Oncosphere 7-14 (10, n=25) in diameter. Genital ducts pass osmoregulatory canals dorsally. Dorsal canal 2-10 (4) wide, distal to ventral canal.

Ventral canal 18-50 (39) wide with one transverse canal per proglottid. Transverse canal 3-24 (9) wide. Cirrus often everted. Cirrus sac 130-241 (169) long, 73-86 (79) wide. Cirrus sac maximum width 295. Genital atrium reaches ventral osmoregulatory canal most often in mature proglottids. Genital atrium becomes more distal as cirrus everts in post mature proglottids. Proximal end of cirrus sac nearly reaches median line of proglottid in mature and postmature proglottids. Internal seminal vesicle appears in late-mature proglottids and remains prominent in proglottids throughout remaining strobila; internal seminal vesicle 25-53 (37, n=12) long by 41-25 (32, n=12) wide. External seminal vesicle absent. Vagina enters genital atrium anterior to cirrus sac. Vaginal dilation appears in immature proglottids, remains prominent until late-mature proglottids. Vagina remains visible in proglottids throughout strobila. Seminal receptacle ovoid, reaching maximum of 92 long and 68 wide in mature proglottids. Seminal receptacle appears in proglottids as the vaginal dilation disappears. Maximum dimensions for cirrus sac and seminal receptacle (40, n=6) reached in postmature proglottids. Vitelline gland globular, measures 56-81 (72) long, 63-129 (106) wide; posterior to ovary. Vitelline gland is laterally elongated and may form a shallow horseshoe shape. Ovary measures 170-246 (208) long, 262-376 (304) wide. Ovary with very large lobes, almost fills entire proglottid. Index of asymmetry 0.48-0.55 (0.52). Testes spherical or ovoid, 28-45 (36, n=75) in diameter, 15-26 (22) per segment. Testes arranged in a field in the center of the segment, overlapping vitelline gland and ovary posteriorly, rarely overlapping ventral osmoregulatory canal. Testis distribution 234-330 (271). Uterus begins sac-like, develops fringes and lobes. The uterus can be divided by two prominent lobes as uterus forms around vitelline gland.

Diagnosis

Monecocestus petiso n. sp. can be distinguished from *M. mackiewiczi*, *M. eljefe* n. sp., *M. diplomys*, *M. hagmanni*, *M. hydrochoeri*, and *M. jacobi* by having a much smaller total length. *Monecocestus petiso* n. sp. can be distinguished from *M. minor*, *M. threlkeli*, and *M. macrobursatus* by having a greater length:width ratio in all proglottids, smaller scolex width and sucker diameter than *M. macrobursatus*, smaller proglottid width in all proglottids, smaller vitelline gland width and ovary width than *M. macrobursatus* and *M. threlkeldi*.

Taxonomic summary

Host: Galea musteloides Meyen, 1832 (NK30468)

Locality: Bolivia, Cochabamba, 7.5 km SE Rodeo Curubamba, 4000m, 17°40'31"S 65°36'04"W, July 1993

Prevalence and intensity: 1 of 2 hosts infected with 5 worms.

Specimens deposited: HWML62702D (Holotype) HWML62702 A-C, E (Paratypes) deposited in the H.W. Manter Laboratory of Parasitology, Lincoln, Nebraska

Etymology: Monoecocestus petiso n. sp., "the small one," is named because of the small size of the representatives of this species.

Monoecocestus microcephalus n. sp.

(Figures 7, 8, 14, 16)

Description based on 10 specimens and measurements of 30 proglottids. Total length 58-140 mm (85 mm, n=9). Full specimens with 147-227 (183, n=9) craspedote segments per strobila. Maximum width 3900-4850 (4269). Immature proglottids 156-312 (228) long, 1435-2870 (2168) wide. Length:width ratio of immature proglottids 0.08-0.15 (0.11). Mature proglottids 310-610 (402) long, 3055-4479 (3492) wide. Length:width ratio of mature proglottids 0.09-0.14 (0.11). Gravid proglottids 998-1872 (1415) long by 2028-3977 (3107) wide. Length:width ratio of gravid proglottids 0.29-0.69 (0.47). Genital pores alternating irregularly with 54-86 (44) switches per 100 proglottids. Genital pores alternate on average every 1.5 (n=3) proglottids. No more than 6 proglottids in each unilateral set. Scolex 368-488 (433, n=9) wide, 200-248 (222, n=9) long. Suckers not in grooves, directed anteriad, 128-200 (164, n=36) in diameter. Neck 528-712 (632, n=9) wide by 160-280 (223, n=9) long. Eggs 44-64 (55, n=45) in diameter. Oncospheres 8-16 (10, n=45) in diameter, surrounded by a pyriform apparatus 16-25 (20, n=45) long. Pyriform apparatus blunt. Testes numerous, 89-136 (109, n=29) per proglottid, each 30-102 (60, n=150) in diameter; testis distribution 1825-3465 (2314) and continuous through the width of each segment, the testicular field pushing more posteriad near vitelline gland, otherwise distributed evenly through each segment. Testes overlap vitelline gland, ovary, and occasionally ventral osmoregulatory canal. Testes overlap all organs dorsally. Testes not extending beyond ventral canal. Genital ducts crossing osmoregulatory canals dorsally. Vaginal dilation appearing in immature proglottids, disappearing in mature proglottids. Vaginal dilation reaches similar width as seminal receptacle in same

proglottid. Vaginal dilation evident from seminal receptacle through the genital atrium. Vagina visible in proglottids throughout entire strobila. Vagina 657-971 (831) long. Cirrus sac extends proximally beyond dorsal and ventral canals. Dorsal canal distal to ventral canal, 24-68 (45) wide. Ventral canal 46-175 (113) wide with a single transverse canal extending across the posterior of the proglottid at 17-217 (101) wide. Additional anastomoses may project from ventral canal. Cirrus often everted; cirrus sac 337-509 (432) long by 109-117 (145) wide. Internal seminal vesicle present, of variable width and length due to everted cirrus. External seminal vesicle absent. Seminal receptacle ovoid, 271-481 (368) long, 92-226 (170) wide in mature proglottids. Vitelline gland wider than long, 127-277 (183) long by 286-679 (389) wide, often bilobed with thin connection attaching two portions. Ovary 274-514 (345) long by 959-2261 (1242) wide. Ovary and vitelline gland slightly poral. Index of asymmetry 0.34-0.45 (0.41). Uterus begins as a lobed sac, with size and number of lobes filling the proglottid. Uterus shows reticulations. Uterine diverticulations directed in all directions. Gravid uterus crosses osmoregulatory canals dorsally and ventrally.

Diagnosis

Monoecocestus microcephalus n. sp. can be distinguished from almost all other species of *Monoecocestus* by having its scolex inset into its neck and prominently anteriorly-facing suckers, traits only shared by *M. mackiewiczi*. *Monoecocestus microcephalus* n. sp. can be distinguished from *M. mackiewiczi* by having a greater total length, greater mature proglottid width, ovary width, testis distribution and smaller index of asymmetry. *Monoecocestus microcephalus* n. sp. can be distinguished from *M. petiso*

n. sp., *M. macrobursatus*, *M. minor*, and *M. threlkeldi* by having a greater total length and more proglottids. *Monoecocestus microcephalus* n. sp. can be distinguished from *M.eljefe* n. sp. by having a smaller length:width ratio in all proglottids, a greater scolex width, testis distribution, vitelline gland width, ovary width, and a smaller index of asymmetry. *Monoecocestus microcephalus* n. sp. can be distinguished from *M. diplomys* by having a smaller gravid proglottid length:width ratio, a smaller neck length, neck width, cirrus sac width, greater mature proglottid width, vitelline gland width, ovary width, testis distribution, and a smaller index of asymmetry. *Monoecocestus microcephalus* n. sp. has a smaller scolex width, scolex length, sucker diameter, and vitelline width than *M. hagmanni*. *Monoecocestus microcephalus* has a smaller scolex width, scolex length, sucker diameter, cirrus sac length, egg diameter and fewer testes than *M. hydrochoeri* and *M. jacobi*.

Taxonomic summary

Host: Graomys domorum (Thomas, 1902) (NK23821, NK23886, NK23855) (DGR Mamm 30348))

Locality: Bolivia, Tarija, 11.5 km N and 5.5 km E of Padcaya , 21° 47'S, 64° 40'W, 1900m August 1991

Prevalence and intensity: 3 of 36 hosts infected with an average intensity of 4.5 worms per infected host

Specimens studied/deposited: HWML61646B (Holotype) HWML61646 A, C-F (Paratypes) HWML61596, HWML61622

Etymology: *Monoecocestus microcephalus* n. sp. is named for the small scolex.

Remarks

The inclusion of one specimen (HWML61596) in the description of *M. microcephalus* n. sp. greatly skews 2 measurements for this species. HWML 61596 has a much greater length at 250.7 mm and has 319 proglottids. The inclusion of these 2 measurements makes the total length 58.2-250.7 mm (102 mm) and the number of proglottids 147-319 (194). These 2 measurements were not included in the redescription, we think that they represent outlying measurements and do not think that these two measurements indicate that HWML61596 represents a different species as this individual is indistinguishable from the *M. microcephalus* with regards to the other measurements.

Four species of *Graomys* are known with a distribution including Bolivia, Paraguay, and Argentina. In Bolivia, three species occur including *Graomys gresioflavus* (Waterhouse, 1837); *G. pearsoni* Meyers, 1977, and *Graomys domorum*. Of the three species from Bolivia, *G. domorum* has a great altitudinal range occurring in Bolivia from as high as 3700 meters to as low as 600 m. These rodents appear to occur only in the Yungas and mountainous regions of central Bolivia being common in the transitional areas from Yungas to Chaco on the south east part of the Andes of Bolivia (Anderson, 1997, Gardner pers. obs). Species of *Graomys* evidently share many general ecological characteristics with species of rodents in the genus *Phyllotis*, which are omnivorous, consuming seeds, arthropods, lichens, and forbs (Eisenberg and Redford, 1992). Species of both *Phyllotis* and *Graomys* likely share their general ecological characteristics because of their phylogenetic history, both belonging to the tribe Phyllotini with a

presumed common ancestor with shared genetic and ecological history (D'Elía, 2003,

Steppan, 2007).

Monoecocestus andersoni n. sp.

(Figures 3, 4, 11)

Description based on the 2 specimens and 6 proglottids. Cestodes measure 99-112

mm (106 mm) in total length. Full specimens have 165-205 (185) proglottids per strobila.

Maximum width 5044-5141 (5092). Proglottids craspedote. Immature proglottids 250-

312 (281) long, 1778-2309 (2043) wide. Length:width ratio of immature proglottids 0.14.

Mature proglottids 400-536 (445) long, 3482-3882 (3698) wide. Length:width ratio of

mature proglottids 0.10-0.15 (0.12). Gravid proglottids 1030-1746 (1388) long by 5044-

5117 (5080) wide. Length:width ratio of gravid proglottids 0.29-0.69 (0.47). Genital

pores alternate irregularly with 68-84 switches per 100 proglottids. Genital pores

alternate, on average, every 1.3 proglottids; no more than 5 proglottids in each unilateral

set. Scolex 420-436 (428) wide, 180-188 (184) long. Suckers directed laterally or anterio-

laterally, 138-150 (145, n=8) in diameter. Neck long, not as wide as scolex, minimum

width 388-408 (398). Neck 320-620 (470) long. Eggs 55-70 (62, n=10) in diameter.

Oncospheres 8-13 (9, n=10) in diameter, surrounded by a pyriform apparatus 15-20 (18,

n=10) long. Pyriform apparatus blunted. Testes number 58-109 (80) in each proglottid,

each 66-118 (94, n=30) in diameter. Testis distribution 2492-2886 (2672). Testes present

throughout proglottid, may occasionally intersect ventral and transverse osmoregulatory

canal. Genital ducts cross osmoregulatory canals dorsally. Vagina enters genital atrium

anterior to cirrus sac. Vaginal dilation appears in immature proglottids, disappears in

mature proglottids. Vagina visible in proglottids throughout entire strobila. Vagina 626-1090 (785) long. Cirrus sac extends proximally beyond dorsal and ventral canals. Dorsal canal distal to ventral canal, 3-37 (24) wide. Ventral canal 38-122 (71) wide with a single transverse canal extending across the posterior of the proglottid at 4-32 (17) wide. Additional anastomoses may project from ventral canal. Cirrus often everted, cirrus sac 433-480 (451) long by 165-194 (179) in diameter. Internal seminal vesicle appears in postmature proglottids, often oddly shaped from everted cirrus. External seminal vesicle absent. Seminal receptacle ovoid, 373-469 (436) long, 139-218 (179) wide in mature proglottids. Vitelline gland wider than long, 208-249 (226) long by 352-382 (370) wide; vitelline gland often bilobed with thin connection attaching two portions. Ovary 390-428 (405) long by 1384-1615 (1439) wide. Ovary and vitelline gland slightly poral. Index of asymmetry 0.38-0.41 (0.40). Uterine diverticulations directed in all directions. Gravid uterus crosses osmoregulatory canals dorsally and ventrally. Uterus appears reticulate early in development, turning into sac with many lateral branches.

Diagnosis

Monoecocestus andersoni n. sp. can be distinguished from *M. mackiewiczi* by having a greater total length, scolex width, neck width, vitelline gland width and ovary width. *Monoecocestus andersoni* n. sp. can be distinguished from *M. microcephalus* n. sp. by having a greater gravid proglottid width, neck length, smaller scolex length and neck width. *Monoecocestus andersoni* n. sp. can be distinguished from *M. petiso* n. sp., *M. macrobursatus*, *M. minor*, and *M. threlkeldi* by having a greater total length and more proglottids. *M. andersoni* n. sp. can be distinguished from *M. eljefe* n. sp. by having a

greater proglottid width but smaller length:width ratio in all proglottids, greater scolex width, neck width, vitelline gland width, ovary width, testis distribution and a smaller index of asymmetry. *Monoecocestus andersoni* n. sp. can be distinguished from *M. diplomys* by having a smaller total length, fewer proglottids, greater scolex width, mature proglottid width, vitelline gland width, ovary width, testis distribution, and a smaller index of asymmetry. *Monoecocestus andersoni* n. sp. can be distinguished from *M. hagmanni*, *M. hydrochoeri*, and *M. jacobi* by having a smaller total length, scolex width, sucker diameter, cirrus sac length, vitelline gland width, and ovary width.

Taxonomic summary

Host: Graomys domorum (Thomas, 1902)

Locality: Bolivia, Cochabamba, 1.3 km W of Jama Chuma, 2800m, 17°31'32"S 66°07'29"W, July 1993

Symbiotype designation: Graomys domorum (MSB Mamm 70543))

Prevalence and intensity: 1 of 2 hosts infected with 2 worms.

Specimens studied/deposited: HWML62672A (Holotype), HWML62672B (Paratype)

Etymology: Monoecocestus andersoni n. sp. is named in honor of Dr. Sydney Anderson, a fellow field biologist and good friend and mentor.

Monoecocestus sininterus n. sp.

(Figures 5, 6, 12)

Description based on 1 specimen and 3 proglottids. Cestode measures 115 mm in total length. Full specimen has 211 proglottids per strobila. Maximum width 4850. Proglottids craspedote. Immature proglottids 156 long, 1685 wide. Length:width ratio of immature proglottids 0.09. Mature proglottids 261-321 (291) long, 2925-3544 (3182) wide. Length:width ratio of mature proglottids 0.08-0.10 (0.09). Gravid proglottids 1746 long by 3783 wide. Length:width ratio of gravid proglottids 0.46. Genital pores alternate irregularly with 82 switches per 100 proglottids. Genital pores form unilateral pairs, on average, every 4 proglottids. Scolex 620 wide, 320 long. Scolex small, flush with neck; suckers anteriorly directed, 218-232 (224, n=4) in diameter. Neck slightly wider than scolex, minimum width 704. Neck 400 long. Eggs 55-63 (60, n=5) in diameter. Oncospheres 10-13 (11, n=5) in diameter, surrounded by a pyriform apparatus 18-23 (20, n=5) long. Pyriform apparatus blunted. Testes number 49-69 (61) in each proglottid, each 36-84 (54, n=15) in diameter. Testis distribution 1623-2280 (1894). Testes present throughout proglottid. Testes may intersect, but do not wholly overlap ventral osmoregulatory canal. Genital ducts cross osmoregulatory canals dorsally. Genital atrium reaches dorsal osmoregulatory canal in immature and mature proglottids, becomes more shallow as cirrus everts in postmature proglottids. Vagina enters genital atrium anterior to cirrus sac. Vaginal dilation appears in immature proglottids, disappears in late mature proglottids. Vaginal dilation has greater width than seminal receptacle in the same proglottid. Vaginal dilation distended from seminal receptacle through the genital atrium. Seminal receptacle appears in the same proglottids as the vaginal dilation. Peduncle

often forms around cirrus sac in postmature proglottids. Cirrus sac overlaps or reaches

proximally beyond ventral osmoregulatory canal. Dorsal canal distal to ventral canal, 47-

56 (53) wide. Ventral canal 70-116 (95) wide with a single transverse canal extending

across the posterior of the proglottid at 2-49 (24) wide. Additional anastomoses may

project from ventral canal. Cirrus often everted; cirrus sac 312-445 (357) long by 126-

195 (151) wide. Internal seminal vesicle small, does not appear until postmature

proglottids. External seminal vesicle absent. Seminal receptacle ovoid, 0-283 (186) long,

0-117 (77) wide in mature proglottids. Vitelline gland wider than long, 149-176 (161)

long by 241-352 (296) wide, often bilobed with thin connection attaching two portions.

Ovary 231-325 (269) long by 1137-1469 (1269) wide. Ovary and vitelline gland slightly

poral. Index of asymmetry 0.45-0.48 (0.47). Uterine diverticulations directed in all

directions. Gravid uterus crosses osmoregulatory canals dorsally and ventrally.

Diagnosis

Monoecocestus sininterus n. sp. can be distinguished from M. mackiewiczi by

having a greater total length, more proglottids, greater scolex width, neck width, sucker

diameter, and ovary width. Monoecocestus sininterus n. sp. can be distinguished from M.

andersoni n. sp. by having a greater total length, more proglottids, smaller width in all

proglottids, greater scolex width, neck width, sucker diameter, smaller vitelline gland

width, testis distribution, and a greater index of asymmetry. Monoecocestus sininterus n.

sp. can be distinguished from M. petiso n. sp., M. minor, M. macrobursatus, and M.

threlkeldi by having a greater total length and more proglottids. Monoecocestus sininterus

n. sp. can be distinguished from M. microcephalus n. sp. by having a greater scolex

width, sucker diameter, smaller testes and a greater index of asymmetry. *Monoecocestus sininterus* n. sp. can be distinguished from *M. eljefe* n. sp. by having greater width in all proglottids but a smaller length:width ratio in all proglottids, a greater scolex width, neck width, sucker diameter, cirrus sac length, ovary width, and testis distribution. *Monoecocestus sininterus* n. sp. can be distinguished from *M. diplomys* by having a smaller total length, fewer proglottids, greater scolex width, neck width, mature proglottid width, cirrus sac length, vitelline gland width and ovary width. *Monoecocestus sininterus* n. sp. can be distinguished from *M. hagmanni*, *M. jacobi*, and *M. hydrochoeri* by having a smaller total length, scolex width, sucker diameter, vitelline gland width, and ovary width.

Taxonomic summary

Host: Phyllotis wolffsohni Thomas, 1902 (NK 30396)

Locality: Bolivia, Cochabamba, 1.3 km W of Jama Chuma, 2800m, 17°31'32"S 66°07'29"W, July 1993

Prevalence and intensity: 1 of 19 hosts infected with 1 worm.

Specimens studied/deposited: HWML62667 (Holotype)

Etymology: Monoecocestus sininterus n. sp., "uninteresting," is given this name as this specimen lacks any distinctive qualitative characters and recognizing this species as separate from other *Monoecocestus* species requires numerous quantitative measurements.

Monoecocestus poralus n. sp.

(Figures 9, 10, 13, 15)

Based on 1 complete individual and 3 proglottids. Stobila total length 116 mm, maximum width 5529. Adult cestode has 230 proglottids. Scolex 190 long, 372 wide. Suckers directed laterally or anterio-laterally, 138-140 (139, n=4) in diameter. Neck 520 long, minimum width 408. Proglottids craspedote. Immature proglottids 250 long, 1966 wide. Length:width ratio of immature proglottids 0.13. Mature proglottids 460-475 (468) long, 3076-3151 (3106) wide. Length:width ratio of mature proglottids 0.15. Gravid proglottids 874 long, 4056 wide. Length:width ratio of gravid proglottids 0.22. Genital pores alternate regularly, switching lateral margins 92 times per 100 proglottids. Genital atrium deep in immature proglottids, peduncles common in mature and postmature proglottids. Egg diameter 58-70 (63, n=10). Embryophore takes the form of pyriform apparatus, measures 18-23 (21, n=10) long. Pyriform apparatus blunted at terminus, no horns observed. Oncosphere 13-15 (13, n=10) in diameter. Genital ducts pass osmoregulatory canals dorsally. Dorsal canal 37-45 (42) wide, distal to ventral canal. Ventral canal 37-65 (55) wide with one transverse canal per proglottid. Transverse canal 19-31 (23) wide. Many anastomoses connecting ventral and transverse osmoregulatory canals. Cirrus sac extends proximally from ventral osmoregulatory canal if cirrus not extended in peduncle, measures 343-486 (436) long, 179-197 (186) wide. Internal seminal vesicle appears in mature proglottids. Internal seminal vesicle large and remains visible throughout remaining stages of development. Internal seminal vesicle 60-120 (90) long by 66-90 (78) wide. External seminal vesicle absent. Vaginal dilation appears in immature proglottids and disappears in mature proglottid. Vagina enters genital atrium

anterior or anterio-ventral to cirrus sac. Seminal receptacle ovoid, reaching maximum of 154-170 (161) long and 101-117 (109) wide in mature proglottids. Maximum dimensions for cirrus sac and seminal receptacle reached in postmature proglottids. Vitelline gland resembles horseshoe, measures 124-173 (151) long, 320-350 (347) wide; posterior to ovary. Ovary does not reach midline of proglottid.; measures 345-350 (347) long, 584-631 (615) wide. Index of asymmetry 0.34-0.35 (0.34). Testes spherical or ovoid, 55-69 (64, n=5) in diameter. Testes number 51-71 (62) per proglottid. Testes extend far enough proximally to reach ovary of subsequent proglottid. Testis distribution 1170-1279 (1210). Testes may overlap ventral and transverse osmoregulatory canals. Uterus reticulate with no prominent lobes or branches. Uterus doesn't extend far distally beyond ventral osmoregulatory canal, but does overlaps both dorsally and ventrally.

Diagnosis

Monoecocestus poralus n. sp. can be distinguished from *M. petiso* n. sp., *M. macrobursatus*, *M. threlkeldi*, and *M. hagmanni* by having greater total length and more proglottids. *Monoecocestus poralus* n. sp. can be distinguished from *M. mackiewiczi* by having smaller scolex width, ovary width, and index of asymmetry. *Monoecocestus poralus* n. sp. can be distinguished from *M. eljefe* n. sp. by having greater width in all proglottids but a smaller length:width ratio in all proglottids, greater scolex width, egg diameter, cirrus sac length, vitelline gland width and ovary width. *Monoecocestus poralus* n. sp. can be distinguished from *M. diplomys* by having a smaller sucker diameter, greater egg diameter, mature proglottid width, vitelline gland width, and ovary width. *Monoecocestus poralus* n. sp. has a smaller ovary width and testis distribution than

M. microcephalus n. sp., *M. andersoni* n. sp., and *M. sininterus* n. sp. *M. poralus* n. sp. can further be distinguished from both *M. microcephalus* n. sp. and *M. andersoni* n. sp. by having a smaller scolex length and width, neck length, and seminal receptacle length.

Taxonomic summary

Host: Phyllotis caprinus Pearson, 1958 (NK23566)

Locality: Bolivia; Tarija: Serrania Sama; 3200m; 21°21'S, 64°52'W. July 1991

Prevalence and intensity: 1 of 19 hosts infected with 1 worm per host.

Specimens deposited: HWML 61440 (Holotype)

Etymology: M. poralus n. sp. is named for the poral nature of the genitalia.

REDESCRIPTION

Monoecocestus mackiewiczi Schmidt and Martin, 1978

Observations based on 2 type specimens, 6 proglottids. Total length 46-75 mm (60.5 mm). Full specimens with 120-176 (148) proglottids per strobila. Maximum width 3340-3686 (3513). Proglottids craspedote. Immature proglottids 300-312 (306) long, 2440-2746 (2593) wide. Length:width ratio of immature proglottids 0.11-0.12 (0.12). Mature proglottids 280-370 (326) long, 2400-3180 (2821) wide. Length:width ratio of mature proglottids 0.09-0.15 (0.11). Gravid proglottids 1000-1248 (1124) long by 1940-3557 (2749) wide. Length:width ratio of gravid proglottids 0.35-0.52 (0.43). Genital pores alternate irregularly, switching lateral margins 64 times per 100 proglottids. Scolex 360-400 (380) wide, 188-240 (214) long. Suckers not in grooves, directed anteriorly, 125-160 (144, n=8) in diameter. Neck wider than scolex, 272-420 (346) wide. Neck

short, 188-230 (209) long. Eggs 52-58 (58, n=5) in diameter. Oncospheres 7-13 (11, n=5) in diameter, surrounded by a pyriform apparatus 16-23 (20, n=5) long. Pyriform apparatus blunted. Testes number 52-96 (66) in each proglottid, each 35-70 (50, n=30) in diameter. Testis distribution 1050-1810 (1552). Testes scattered throughout proglottid, overlapping vitelline gland, ovary, transverse osmoregulatory canal, poral and antiporal ventral osmoregulatory canals often. Testes overlap all organs dorsally. Testes to do not extend beyond ventral canal. Genital ducts cross osmoregulatory canals dorsally. Genital atrium reaches dorsal osmoregulatory canal in immature and mature proglottids. Vagina enters genital atrium anterior to cirrus sac. Vaginal dilation appears in immature proglottids, disappears in mature proglottids. Vaginal dilation distends from seminal receptacle to genital atrium. Vaginal dilation similar width as seminal receptacle in same proglottid. Cirrus everted in late mature proglottids throughout rest of strobila, may form a peduncle. Dorsal canal distal to ventral canal, 15-34 (28) wide. Ventral canal 50-135 (95) wide with single transverse canal extending across the posterior of the proglottid at 5-50 (16) in diameter. Additional anastomoses may project from ventral canal. Cirrus sac 350-411 (381) long by 135-175 (155) wide. Internal seminal vesicle appears in late mature proglottids. External seminal vesicle absent. Seminal receptacle ovoid, 150-306 (227) long, 65-150 (114) wide in mature proglottids. Seminal receptacle forms early, enlarges before vaginal dilation appears. Vitelline gland wider than long, 115-176 (148) long by 230-310 (267) wide, often bilobed with thin connection attaching two portions. Ovary 100-268 (190) long by 320-930 (736) wide. Ovary and vitelline gland slightly poral. Index of asymmetry 0.43-0.48 (0.45). Uterus begins as a lobed sac, with size and number of lobes filling the proglottid. Reticulations present in developing uterus. Uterine

diverticulations directed in all directions. Uterus crosses osmoregulatory canals dorsally and ventrally.

Diagnosis

Monoecocestus mackiewiczi can be distinguished from *M. petiso* n. sp., *M. macrobursatus*, *M. minor*, and *M. threlkeldi* by having a much greater total length, more proglottids, greater cirrus sac length and greater proglottid width in all (immature, mature, gravid) proglottids. *Monoecocestus mackiewiczi* has a greater scolex width than *M. petiso* n. sp. and *M. minor*, smaller suckers than *M. macrobursatus* and *M. minor*. *M. maciewiczi* can be distinguished from *M. eljefe* n. sp. by having a smaller length:width ratio in all proglottids, a greater scolex width, vitelline gland width, and ovary width. *M. mackiewiczi* can be distinguished from *M. poralus* n. sp. by having a greater ovary width, scolex width, and index of asymmetry than *M. poralus* n. sp.

Taxonomic summary

Host: Graomys sp.

Locality: Juan de Zalazar, Boqueron, Paraguay

Specimens studied/deposited: USNPC73083 (Holotype), USNPC73084 (Paratype)

DISCUSSION

Ordination by PCA separated the four species (*M. mackiewiczi*, *M. sininterus* n. sp., *M. andersoni* n. sp., and *M. microcephalus* n. sp.) into 2 groups, one group including

M. mackiewiczi and *M. sininterus* n. sp. and one including *M. microcephalus* n. sp. and *M. andersoni* n. sp. The purpose of the PCA was to see if there was support for the separation of the two opposite pairs: *M. andersoni* n. sp. vs. *M. sininterus* n. sp. and *M. mackiewiczi* vs. *M. microcephalus* n. sp. *Monoecocestus mackiewiczi* and *M. microcephalus* n. sp. are similar in that they both have small scoleces that are more narrow than the neck. *Monoecocestus andersoni* n. sp. and *M. sininterus* n. sp. are similar in that they both lack any striking morphologically distinctive features. The PCA showed good separation of the pairs in question, and the separation of these pairs can be supported by numerous quantitative measurements of the strobila and/or mature proglottid.

The ontological/morphological development of the uterus in species of the Anoplocephalinae is one of the most important taxonomic characters to assign species to various genera (Rausch, 1976; Tenora et al., 1986; Wickstrom et al., 2005). It has recently been noted (Haverkost and Gardner, in press) that species can be assigned to the genus *Monoecocestus* by virtue of the uterus crossing the osmoregulatory canals both dorsally and ventrally. The uterine development of the South American species of *Monoecocestus* differs slightly than that of their North American counterparts. The early uterus of the South American species can be described as the development of a lobed sac, with subsequent lobes overlapping the previous distally. Reticulations may be present as a thickened uterine wall, but rarely as fenestrations (windows). This pattern was observed in the species described and observed in this work and alluded to by many other researchers (Vigueras, 1943; Rego, 1960; Rego, 1961; Noble and Tesh, 1974; Olsen, 1976; Schmidt and Martin, 1978). Figures 17 and 18 show this development of the uterus

in *M. eljefe* n. sp. and *M. microcephalus* n. sp., respectively. Few anterior and posterior

diverticulations similar to species of *Anoplocephaloides* and *Paranoplocephala* are seen.

The uterus eventually fills the proglottid and becomes a simple sac full of eggs.

In species of *Monoecocestus*, the vagina develops in a way not seen in other

species of anoplocephalines. This unique development is noted by many authors in many

species (Douthitt, 1915; Chandler and Suttles, 1922; Spasskii, 1951; Noble and Tesh,

1974; Rausch and Maser, 1977; Schmidt and Martin, 1978) and discussed in detail by

Freeman (1949). In most species of *Monoecocestus*, the vagina develops in immature

proglottids and the medial section of the vagina can dilate to 3-4 times the width of either

end. Often this dilation abates as the seminal receptacle begins to form. The vagina often

disintegrates and is not visible in mature and post-mature proglottids. The presence of the

vaginal dilation and the pattern of its development does seem to vary slightly among

species. We chose to include the information in our descriptions, as this character may be

of taxonomic importance. Additional specimens would be necessary to confirm if this

feature is taxonomically informative. Figure 5 and 9 show the vaginal dilation in *M.*

sininterus n. sp. and *M. poralus* n. sp, respectively.

The sampling effort attained by the Bolivian Biodiversity Survey in its

expeditionary phase was generally meant to target as many mammals as possible and was

not focused on a single group. Targeted and focused sampling of hystricognath and

sigmodontine rodents throughout the Neotropical Region is likely to yield many more

new taxa of anoplocephaline cestodes and other parasites. The material available from the

Bolivian Biodiversity Survey that is stored in the HWML is immense, and similar efforts

of focused research on different host/parasite groups at the HWML will yield similar

results of several new species. For example see: Gardner et al., 1988; Campbell and

Gardner, 1992; Campbell and Gardner, 1992a; Brant and Gardner, 1997; Gardner and

Hugot, 1997; Hecksher et al., 1999; Hugot and Gardner, 2000; Gardner and Pérez-Ponce

de León, 2002; Jiménez-Ruiz and Gardner, 2003; Jiménez-Ruiz and Gardner, 2003a;

Jiménez-Ruiz et al., 2008; Haverkost and Gardner, 2008; Haverkost and Gardner 2008a.

Hystricognath rodents are the dominant host for species of *Monoecocestus*, but

this study indicates that the sigmodontine rodents (Myomorpha: Cricetidae:

Sigmodontinae) are suitable hosts for these helminths, as 4 species of *Monoecocestus*

described herein are found thus far only in sigmodontines. It is assumed that species of

Monoecocestus originated in South America from an unknown ancestor since 20 of the

27 species of *Monoecocestus* are found in South America and it is more parsimonious to

assume this diversification happened with their hosts before the great biotic interchange.

However, unless we do a phylogenetic analysis, we will not know the true nature of this

diversification since common does not equal primitive (this is being done now).   At any

rate, in this scenario the parasites could have infected new hosts in North America as the

ancestral erethizontid mammal migrated north as early as 2.6 million years ago during the

great biotic interchange across the Panamanian land bridge (Marshall, 1985). Since

sigmodontine rodents are found in South America prior to the final development of the

Panamanian land bridge, it is assumed that these hosts were infected after their arrival to

South America. Such hypotheses have yet to be tested and would require the acquisition

of more specimens suitable for molecular phylogenetic analysis.

ACKNOWLEDGEMENTS

LITERATURE CITED

Anderson, S. 1997. Mammals of Bolivia, taxonomy and distribution. Bulletin of the American Museum of Natural History. **231**: 1-652.

Baer, J. G. 1927. Monographie des cestodes de la familie des Anoplocephalidae. Bulletin Biologique de la France et de la Belgique (Supplement). **10**: 1-241.

Beveridge, I. 2008. *Mathevotaenia niuguiniensis* n. sp. (Cestoda: Anoplocephalidae: Linstowiinae) from the water-rat *Parahydromys asper* (Thomas) in Papua New

Guinea, with a list of species of *Mathevotaenia* Akumyan, 1946. Systematic Parasitology. **71**: 189-198.

Brant, S. V., Gardner, S. L. 1997. Two new species of *Litomosoides* (Nemata: Onchocercidae) from *Ctenomys opimus* (Rodentia: Ctenomyidae) from the Altiplano of Bolivia. Journal of Parasitology. **83**: 700-705.

Chandler, A. C., and C. L. Suttles. 1922. A new rat tapeworm, *Schizotaenia sigmodontis*, from North America. Journal of Parasitology. **8**: 123-128.

D'Elía, G. 2003. Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics. **19**: 307-323.

Denegri, G., M. C. Dopchiz, M. C. Elissondo, and I. Beveridge. 2003. *Viscachataenia* n. g., with the redescription of *V. quadrata* (von Linstow, 1904) n. comb. (Cestoda: Anoplocephalidae) in *Lagidium viscacia* (Rodentia: Chinchillidae) from Argentina. Systematic Parasitology. **54**: 81-88.

Douthitt, H. 1915. Studies on the cestode family Anoplocephalidae. Illinois Biological Monographs. **1**: 1-97.

Eisenberg, J. F., and K. H. Redford. 1992. Mammals of the Neotropics: the central Neotropics, University of Chicago, Chicago, Illinois, 609 p.

Freeman, R. S. 1949. Notes on the morphology and life cycle of the genus *Monoecocestus* Beddard, 1914 (Cestoda: Anoplocephalidae) from the Porcupine. Journal of Parasitology. **35**: 603-612.

Gardner, S. L., Rausch, R. L., Camacho, O. C. J. 1988. *Echinococcus vogeli* Rausch and Bernstein, 1972 from the paca, *Cuniculus paca* L. (Rodentia: Dasyproctidae) in the Departamento de Santa Cruz, Bolivia. Journal of Parasitology. **74**: 399-402.

Gardner, S. L., Campbell, M. L. 1992. Parasites as probes for biodiversity. Journal of Parasitology. **78**: 596-600.

Gardner, S. L., Campbell, M. L. 1992a. A new species of *Linstowia* Zschokke, 1899 (Cestoda: Anoplocephalidae) from marsupials in Bolivia with comments on the biogeography of cestodes of the genus *Linstowia*. Journal of Parasitology. **78**: 795-799

Gardner, S. L. 1996. Field Parasitology Techniques for Use with Mammals. *in* Measuring and Monitoring Biological Diversity: Standard Methods for Mammals, D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster (ed.). Smithsonian Institution Press, Washington, 291-298 p.

Gardner, S. L., Hugot, J.-P. 1997. A new pinworm, *Didelphoxyuris thylamisis*, n gen., n. sp. (Nemata: Oxyurida) from *Thylamys elegans* (Waterhouse, 1839) (Marsupialia: Didelphidae) in Bolivia. Research and Reviews in Parasitology. **55**: 139-147.

Gardner, S. L., Pérez-Ponce de León, G. 2002. *Yungasicola travassosi* gen. n., sp. n. (Digenea: Dicrocoeliidae: Eurytrematinae) from two species of grass mice *Akodon* Meyen (Rodentia: Muridae) from the Yungas of Bolivia. Comparative Parasitology. **69**: 51-57.

Haukisalmi, V., L. M. Wickström, H. Henttonen, J. Hantula, and A. Gubányi. 2004. Molecular and morphological evidence for multiple species within

Paranoplocephala omphalodes (Cestoda, Anoplocephalidae) in *Microtus* voles (Arvicolinae). Zoologica Scripta. **33**: 277-290.

Haverkost, T. R., and S. L. Gardner. 2008. A new species of *Lentiella* (Cestoda: Anoplocephalidae) from *Proechimys simonsi* (Rodentia: Echimyidae) in Bolivia. Revista Mexicana de Biodiversidad. **79**: 99S-106S.rausch 1976

Haverkost, T. R., Gardner, S. L. 2008a. A review of species in the genus *Rhopalias* (Rudolphi, 1819). Journal of Parasitology. **94**: 296-298.

Haverkost, T. R., and S. L. Gardner. 2009. A redescription of three species of *Monoecocestus* (Cestoda: Anoplocephalidae) including *Monoecocestus threlkeldi* based on new material. Journal of Parasitology. accepted. in press

Hecksher, S. K., Wickesberg, B. A., Duszynski, D. W., Gardner, S. L. 1999. Three new species of *Eimeria* (Apicomplexa: Eimeriidae) from Bolivian marsupials (Didelphiomorphia: Didelphidae). International Journal for Parasitology. **29**: 275-284.

Hugot, J.-P., Gardner, S. L. 2000. *Helminthoxys abrocomae* n. sp. (Nematoda: Oxyurida) from *Abrocoma cinerea* in Bolivia. Systematic Parasitology. **47**: 223-230.

Jiménez-Ruiz, A., Gardner, S. L. 2003. Aspidoderid nematodes from Bolivian armadillos, with the description of a new species of *Lauroia* (Heterakoidea: Aspidoderidae). Journal of Parasitology. **89**: 978-983.

Jiménez-Ruiz, A., Gardner, S. L. 2003a. The nematode fauna of long-nosed mice *Oxymycterus* spp. from the Bolivian Yungas. Journal of Parasitology. **89**: 299-308.

Jiménez-Ruiz, A., Braun, J. K., Campbell, M. L., Gardner, S. L. 2008. Endoparasites of Fat-tailed Mouse Opossums (*Thylamys*: Didelphidae) from northwestern Argentina and southern Bolivia, with the description of a new species of tapeworm. Journal of Parasitology. **94**: 1098-1102.

Manly, B. F. J. 1986. Multivariate statistical methods: A primer. Chapman and Hall: New York. 159 p.

Marshall, L. G. 1985. Geochronology and Land-Mammal Biochronology of the Transamerican Faunal Interchange. *in* The Great American Biotic Interchange, F. G. Stehli and S. D. Webb (ed.). Plenum Press, New York, 49-85 p.

Noble, G. A., and R. B. Tesh. 1974. *Monoecocestus diplomys* sp.n. (Cestoda:Anoplocephalidae) from the rat, *Diplomys darlingi*. Journal of Parasitology. **60**: 605-607.

Olsen, O. W. 1976. *Monoecocestus torresi* n.sp. (Cestoda: Cyclophyllidea: Anoplocephalidae) from tuco-tuco *Ctenomys maulinus brunneus* Osgood, 1943 (Hystrichomorpha: Rodentia). Revista Ibérica de Parasitología. **36**: 209-217.

Prichard, M. H., and G. O. W. Kruse. 1982. The collection and preservation of animal parasites, University of Nebraska Press, Lincoln, 141 p.

Rausch, R. L. 1976. The genera *Paranoplocephala* Lühe, 1910 and *Anoplocephaloides* Baer, 1923 (Cestoda: Anoplocephalidae) with particular reference to species in rodents. Ann. Parasitol. Human Comp. **51**: 513-562.

Rausch, R. L., and C. Maser. 1977. *Monoecocestus thomasi* sp.n. (Cestoda: Anoplocephalidae) from the northern flying squirrel, *Glaucomys sabrinus* (Shaw), in Oregon. Journal of Parasitology. **63**: 793-799.

Rego, A. A. 1960. Nota prévia sóbre um novo Monoecocestus parasito de preá (Cestoda: Cyclophyllidea). Atas da Sodedade de Biología do Rio de Janeiro. **4**: 73.

Rego, A. A. 1961. Revisão do genero *Monoecocestus* Beddard, 1914 (Cestoda, Anoplocephalidae). Memórias do Instituto Oswaldo Cruz. **59**: 325-354.

Schmidt, G. D., and R. L. Martin. 1978. Tapeworms of the Chaco Boreal, Paraguay, with two new species. Journal of Helminthology. **52**: 205-209.

Spasskii, A. A. 1951. Anoplocephalate tapeworms of domestic and wild animals, The Academy of Sciences of the USSR, Moscow, 783 p.

Steppan, S. J., O. Ramirez, J. Banbury, D. Huchon, V. Pacheco, L. I. Walker, and A. E. Spotorno. 2007. A molecular reappraisal of the systematics of the leaf-eared mice *Phyllotis* and their relatives. *in* The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson., D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (ed.). University of California Publications in Zoology, 799-826 p.

Sato, H., H. Kamiya, F. e. Tenora, and M. Kamiya. 1993. *Anoplocephaloides dentatoides* sp. n. from the gray-backed vole, *Clethrionomys rufocanus bedfordiae*, in Hokkaido, Japan. Journal of the Helminthological Society of Washington. **60**: 105-110.

Tenora, F. e., É. Murai, and C. Vaucher. 1986. On *Andrya* Railliet, 1893 and *Paranoplocephala* Lühe, 1910 (Cestoda, Monieziinae). Parasitologica Hungarica. **19**: 43-75.

Vigueras, I. P. 1943. Un genero y cinco especies nuevas de helmintos Cubanos. Rev. Univ. Habana. **48**: 315-356.

Voge, M., and C. P. Read. 1953. *Diplophallus andinus* n.sp. and *Monoecocestus rheiphilus* n.sp., avian cestodes from the high Andes. Journal of Parasitology. **39**: 558-567.

Wickström, L. M., V. Haukisalmi, S. Varis, J. Hantula, and H. Henttonen. 2005. Molecular phylogeny and systematics of anoplocephaline cestodes in rodents and lagomorphs. Systematic Parasitology. **62**: 83-99.

Wilson, D. E., and D. M. Reeder. 2005. Mammal Species of the World, Johns Hopkins University Press, Baltimore, 2,142 p.

Table I. Selected measurements of *Monoecocestus* species. All measurements in micrometers unless otherwise stated.

Species	*M. mackiewiczi*		*M. mackiewiczi*		*M. microcephalus* n. sp.		*M. andersoni* n. sp.		*M. sininterus* n. sp.
Host	*Phyllotis* sp.		*Phyllotis* sp.		*Graomys domorum*		*Graomys domorum*		*Phyllotis wolffsohni*
Source	Schmidt and Martin, 1978		Type material, this study		this study		this study		this study
		n		n		n		n	n
No. of proglottids	200		120-176 (148)	2	147-319 (196)	10	165-205 (185)	2	211	1
Total length (mm)	70-115		46-75 (60)	2	58-250 (101)	10	99-112 (106)	2	115	1
Max. width (mm)	3.5-4.5		3.3-3.6 (3.5)	2	3.90-4.85 (4.27)	10	5.04-5.14 (5.09)	2	4.85	1
Genital alternation	--		--		54-86 (44)	10	68-84	2	82	1
Scolex width	360-415		360-400 (380)	2	368-488 (433)	9	420-436 (428)	2	620	1
Sucker diameter	120-160		125-160 (144)	8	128-200 (164)	36	138-150 (145)	8	218-232 (224)	4
Egg width	58-60		52-58 (58)	5	44-64 (55)	45	55-70 (62)	10	55-63 (60)	5
No. of testes	--		52-96 (66)	6	89-136 (109)	29	58-109 (80)	6	49-69 (61)	3
Testis width	30-48		35-70 (50)	30	30-102 (60)	150	66-118 (451)	30	36-84 (54)	15
Cirrus sac length	360-440		350-411 (381)	6	337-509 (432)	30	433-480 (451)	6	312-445 (357)	3
Ovary Width	240-320		320-930 (736)	6	959-2261 (1242)	30	1384-1615 (1439)	6	1137-1469 (1269)	3
Vitelline gland width	--		230-310 (267)	6	286-679 (389)	30	352-382 (370)	6	241-352 (296)	3
Index of asymmetry	--		0.43-0.48 (0.45)	6	0.34-0.45 (0.41)	30	0.38-0.41 (0.40)	6	0.45-0.48 (0.47)	3

Table II. Selected measurements of additional *Monoecocestus* species. All measurements in micrometers unless otherwise stated.

| Species | M. poralus n. sp. | | M. petiso n. sp. | | M. eljefe n. sp. | |
| Host | Phyllotis caprinus | | Galea musteloides | | Galea musteloides | |
Source	this study	n	this study	n	this study	n
No. of proglottids	230	1	49-55 (51)	5	178-264 (208)	5
Total length (mm)	116	1	13.8-18.5 (15.5)	5	96-167 (129)	5
Max. width (mm)	5.53	1	1.00-1.07 (1.04)	5	1.37-1.93 (1.67)	5
Genital alternation	92	1	94-100 (98)	5	34-52 (44)	5
Scolex width	372	1	290-354 (319)	5	288-368 (338)	5
Sucker diameter	138-140 (139)	4	127-173 (159)	20	108-168 (149)	20
Egg width	58-70 (63)	10	45-57 (49)	25	40-60 (50)	25
No. of testes	51-71 (62)	3	15-26 (22)	15	38-60 (48)	15
Testis width	55-69 (64)	5	28-45 (36)	75	49-79 (63)	75
Cirrus sac length	343-486 (436)	3	130-241 (167)	15	105-272 (183)	15
Ovary Width	584-631 (615)	3	262-376 (303)	15	277-559 (361)	15
Vitelline gland width	320-350 (347)	3	63-129 (106)	15	106-195 (138)	15
Index of asymmetry	0.34-0.35 (0.34)	3	0.51-0.52 (0.51)	2	0.46-0.50 (0.48)	15

Figure 1. *Monoecocestus eljefe* n. sp., (A) Scolex (B) Mature proglottid, (C) Egg, (D) Gravid Proglottid. Scale bars = 0.1 mm for (A), (B), and (D). Scale bar for (C) = 0.01 mm.
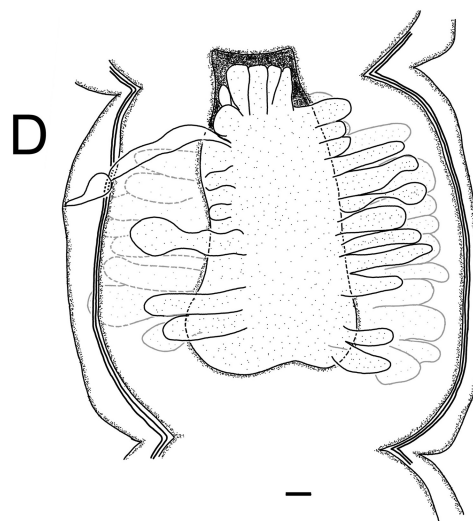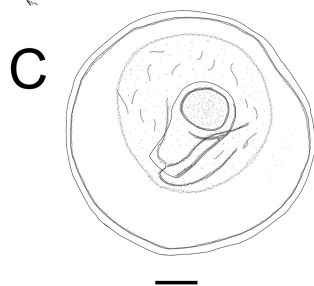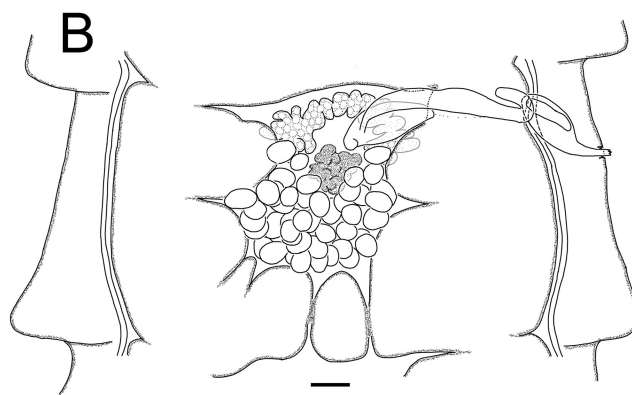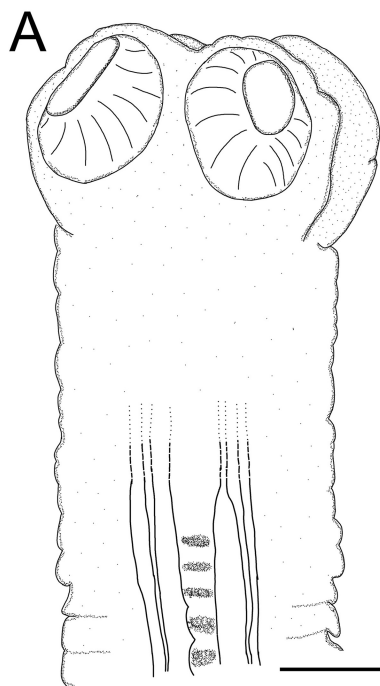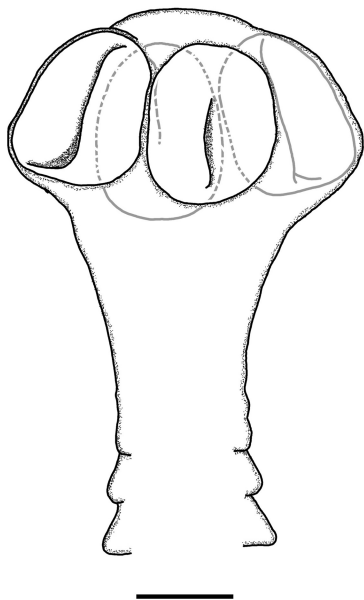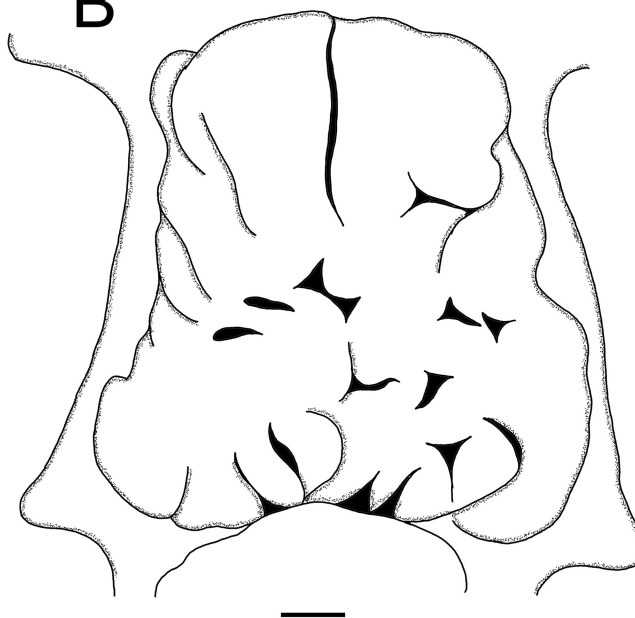
Figure 2. *Monoecocestus petiso* n. sp., (A) Scolex, (B) Gravid Proglottid, (C) Mature Proglottid. All scale bars = 0.1 mm.

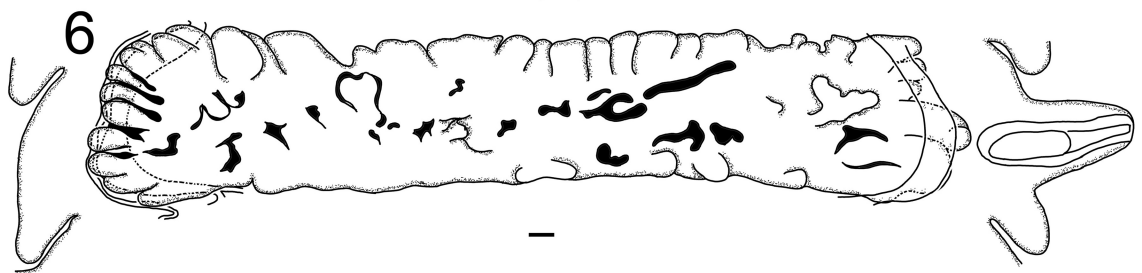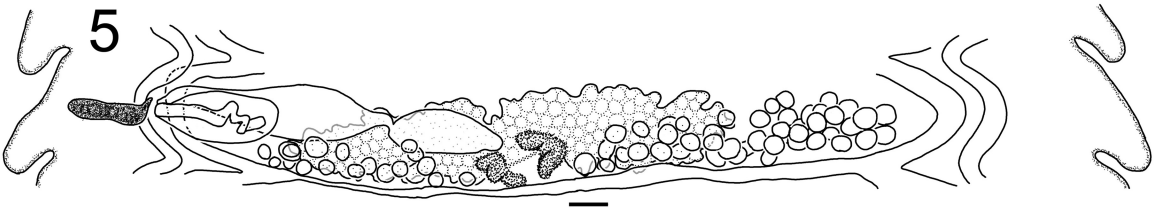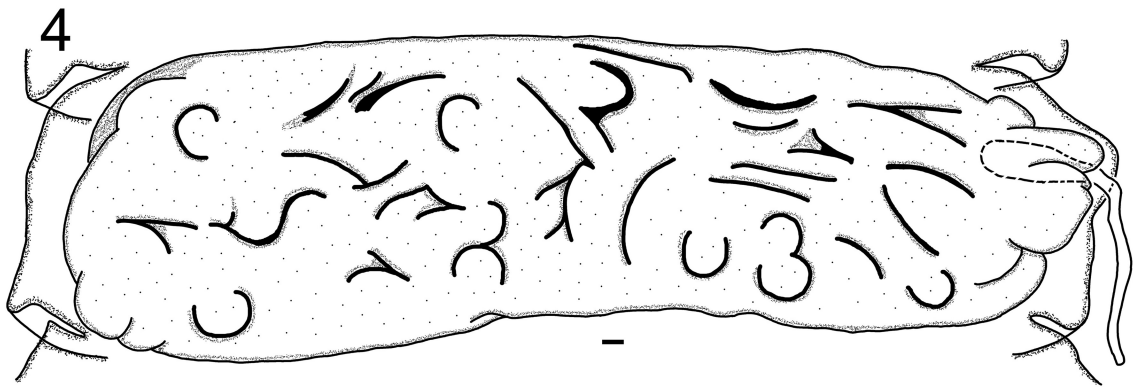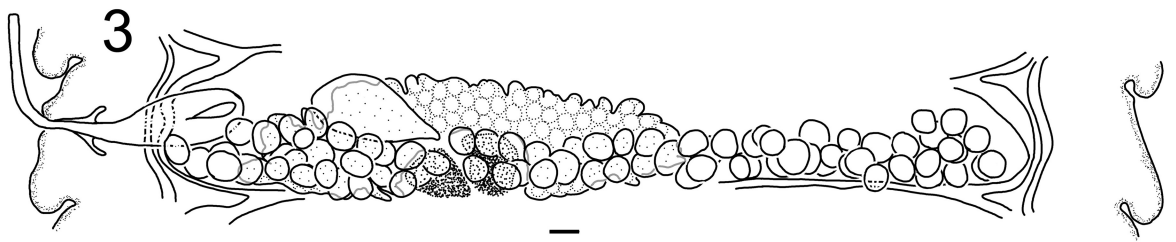Figures 3-6. Mature and gravid proglottids of *Monoecocestus andersoni* n. sp. and *Monoecocestus sininterus* n. sp. (3) *Monoecocestus andersoni* n. sp. mature proglottid. (4) *M. andersoni* n. sp. gravid proglottid. (5) *Monoecocestus sininterus* n. sp. mature proglottid. (6) *M. sininterus* n. sp. gravid proglottid. All scale bars = 0.1 mm.

Figures 7-10. Mature and gravid proglottids of *Monoecocestus microcephalus* n. sp. and *Monoecocestus poralus* n. sp. (7) *Monoecocestus microcephalus* n. sp. mature proglottid. (8) *M. microcephalus* n. sp. gravid proglottid. (9) *Monoecocestus poralus* n. sp. mature proglottid. (10) *M. poralus* n. sp. gravid proglottid. All scale bars = 0.1 mm.

7

8

9

10
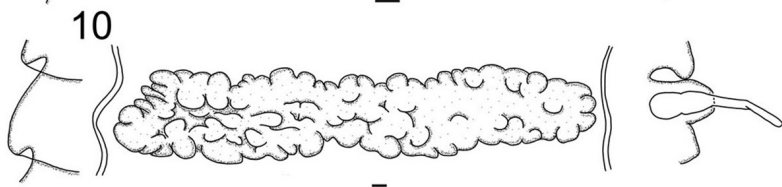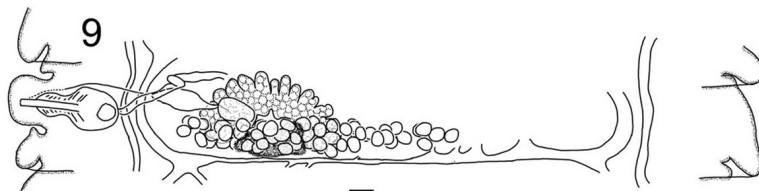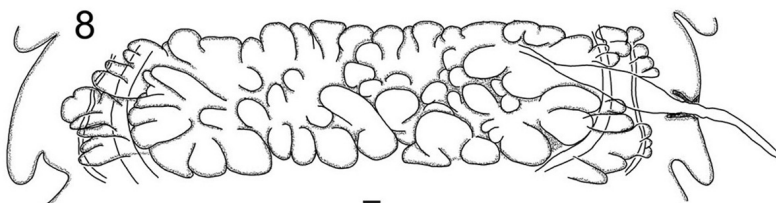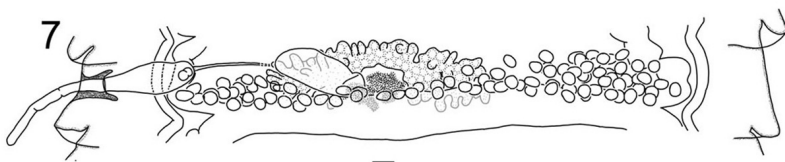
Figures 11-16. Scoleces and eggs of 4 new species of *Monoecocestus*. (11) *M. andersoni* n. sp. scolex. (12) *M. sininterus* n. sp. scolex. (13) *M. poralus* n. sp. scolex. (14) *M. microcephalus* n. sp. scolex. (15) *M. poralus* n. sp. egg. (16) *M. microcephalus* n. sp. egg. Scale bars for Fig. 11-14 = 0.1 mm. Scale bars for Fig. 15-16 = 0.01 mm.
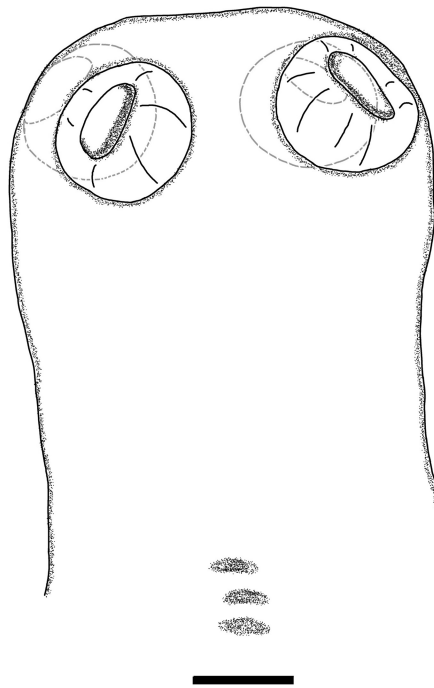
11

12
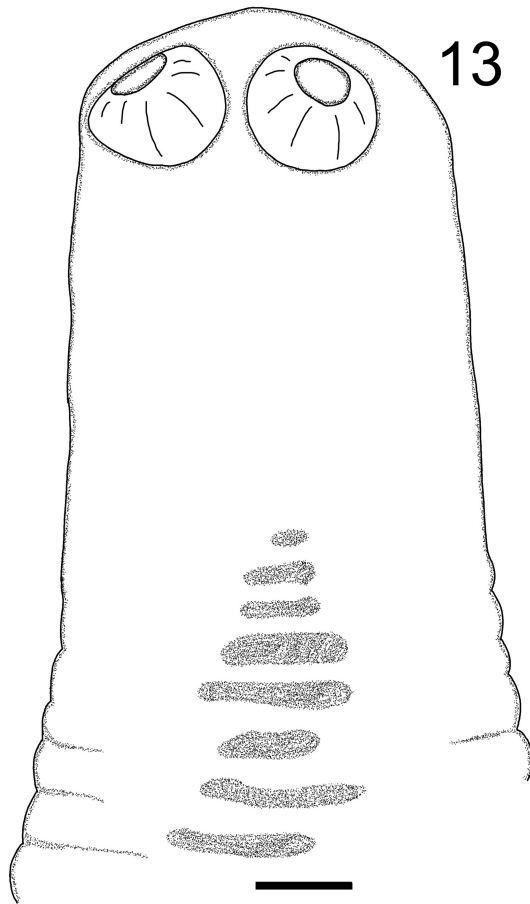
13
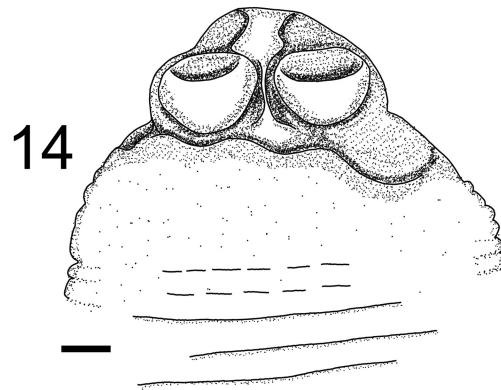
14
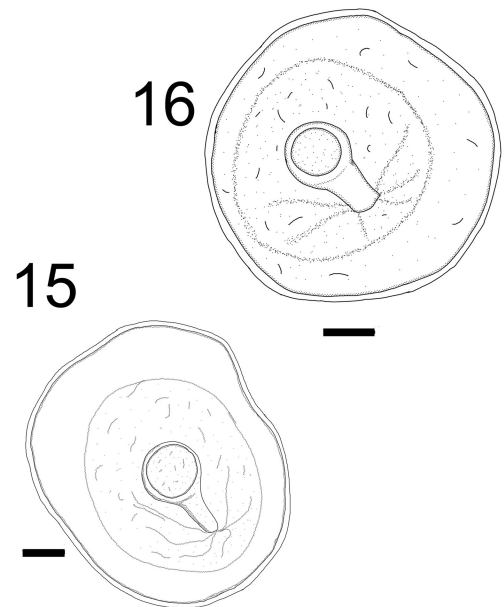
15
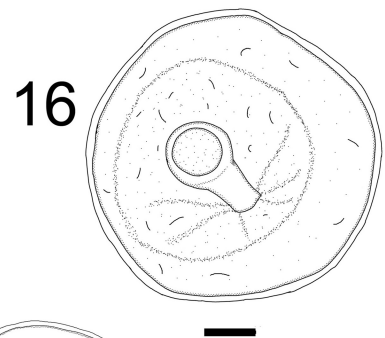
16

Figure 17. Uterine development in a series of proglottids from *M. eljefe* n. sp.

Figure 18. Uterine development in a series of proglottids from *M. microcephalus* n. sp.
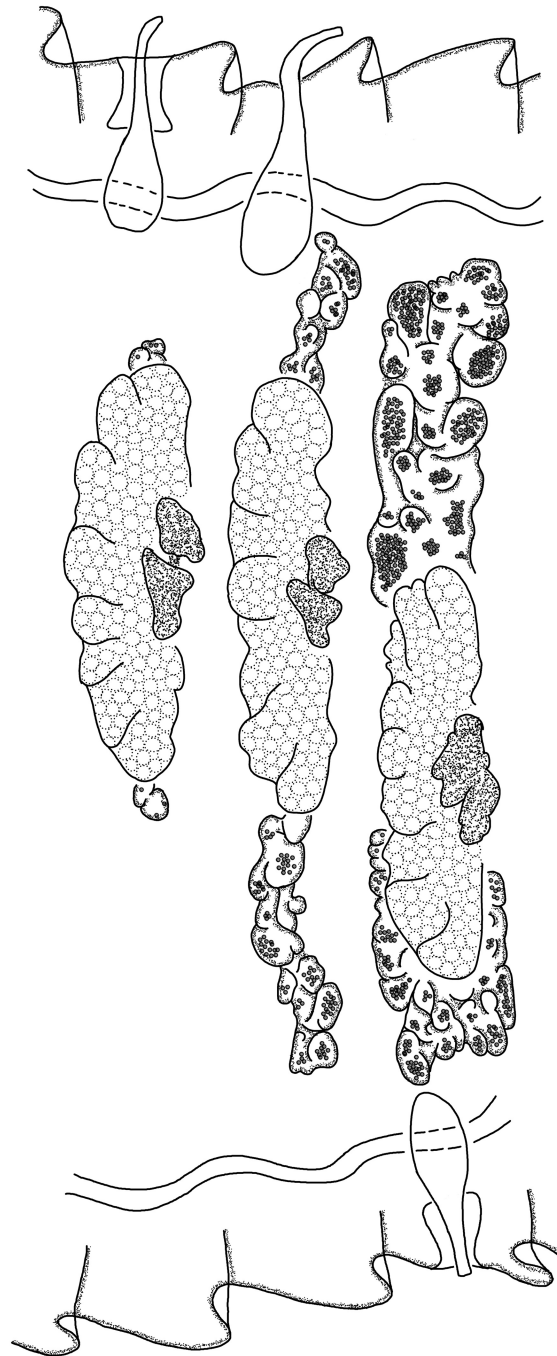
Figure 19. PCA separating four species of *Monoecocestus* based on measurements of the proglottids. *Monoecocestus mackewickzi* = Δ; *M. microcephalus* n. sp. = O; *M. sininterus* n. sp. = +; *M. andersoni* n. sp. = X. Scale for the two axes are expressed in prinicple component scores.
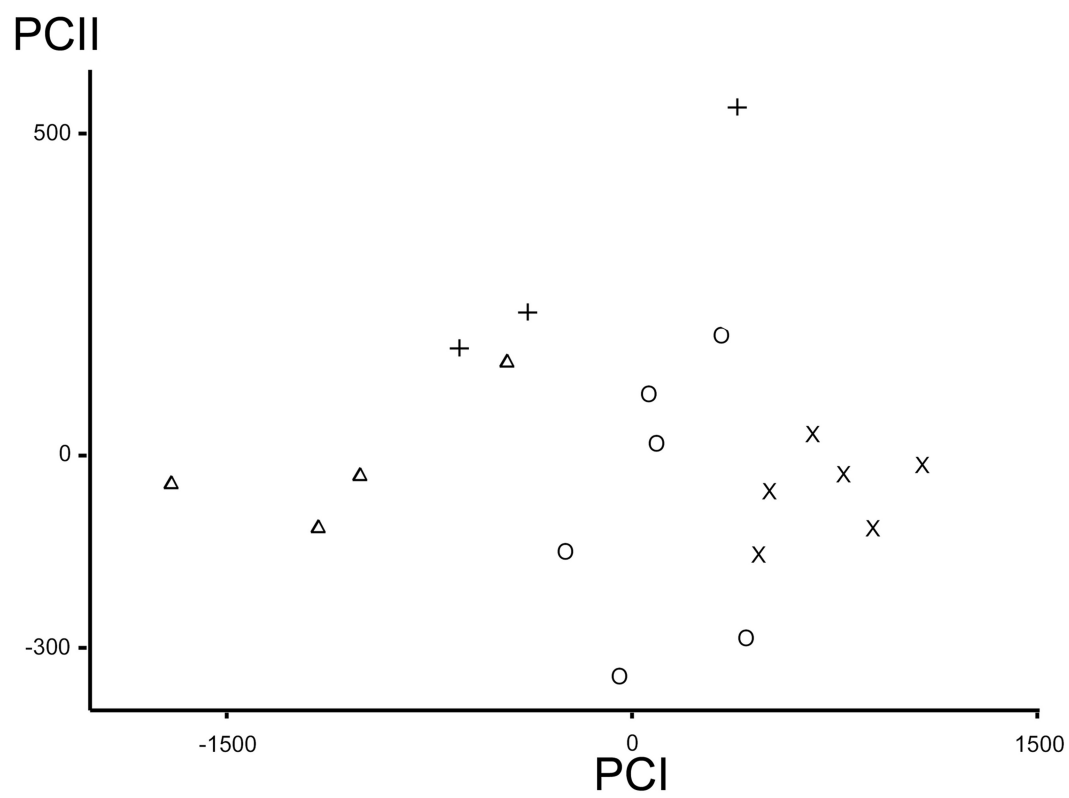
CHAPTER 2

Citation: Haverkost, Terry R. and Scott L. Gardner. A redescription of

three species of *Monoecocestus* (Cestoda: Anoplocephalidae) including

***Monoecocestus threlkeldi* based on new material. Journal of**

Parasitology (In Press)

A REDESCRIPTION OF THREE SPECIES OF *MONOECOCESTUS* (CESTODA: ANOPLOCEPHALIDAE) INCLUDING *MONOECOCESTUS THRELKELDI* BASED ON NEW MATERIAL

Terry R. Haverkost and Scott L. Gardner

The Harold W. Manter Laboratory of Parasitology, University of Nebraska State

Museum, Lincoln, Nebraska 68588-0514. *e-mail: slg@unl.edu*

ABSTRACT: Because we have new and detailed data on species in the genus, herein we redescribe both *M. macrobursatus* and *M. minor* based on existing museum specimens. We also redescribe *M. threlkeldi* (Parra, 1952) using material collected in Bolivia. Based on the specimens representing *M. thelkeldi*, we affirm that *Perutaenia* Parra, 1953 should remain a junior synonym of *Monoecocestus*.

INTRODUCTION

After an examination of the type material, Beveridge (1994) considered *Perutaenia* a junior synonym of *Monoecocestus* Beddard, 1914. The type material of *M. threlkeldi*, the type species of *Perutaenia*, was admittedly of marginal quality, but the key character in his decision (vagina entering genital atrium anterior to cirrus sac) was seen clearly in mature proglottids. The type specimens of *M. thelkeldi* do not have gravid segments and it is likely that measurements based on these specimens do not reflect those seen in fully gravid specimens. For a more solid taxonomic determination to be made, additional gravid specimens representing this species are necessary.

In 1985, research teams from the Museum of Southwestern Biology and the American Museum of Natural History were surveying mammals and their parasites throughout lowland Bolivia. During this study, 1 specimen of *Holochilus brasiliensis* (Desmarest, 1819) was collected by SLG and found to host over 50 anoplocephalid cestodes throughout its small intestine.

This paper redescribes *M. thelkeldi* based on specimens obtained from *H. brasilensis*. In addition, we provide new measurements and redescriptions from museum specimens of *M. macrobursatus* Rego, 1961 and *M. minor* Rego, 1960, 2 species closely resembling *M. thelkeldi*.

MATERIALS AND METHODS

All specimens of mammals that were collected were processed using standard methods (Gardner, 1996). Voucher specimens of the hosts are housed at the American Museum of Natural History (AMNH) in New York City, New York, or at the Museum of

Southwest Biology (NK) at the University of New Mexico in Albuquerque, New Mexico. Rodents were collected in the field and necropsy was performed immediately after death. The intestinal tract was opened via transverse cut with blunt nosed scissors in saline solution, cestodes recovered were immediately relaxed and in fresh river water, and immediately killed and fixed in either 10% formalin solution (v/v) or 70% ethanol. Specimens were preserved, transported, and stored in the same solution as was used for fixation. Specimens were stained in Semichon's acetic carmine, dehydrated in an ethanol series, cleared in cedarwood oil and xylene, and mounted on slides in Damar Gum. After staining, the tegument and ventral or dorsal longitudinal muscles were removed to allow for a better view of the internal organs. Voucher specimens examined representing *M. minor* and *M. macrobursatus* were loaned from the Coleção Helmintologica do Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Brazil.

All measurements of individual proglottids were taken by first drawing the proglottid with the aid of a drawing tube, digitizing the drawing, and measuring the digitized image using SigmaScan Pro 5.0 (SPSS, Chicago, Illinois). Measurements of the strobila were made with an ocular micrometer on a Jenaval compound microscope. Measurements of eggs were made with the compound microscope using SigmaScan Pro 5.0 from digital images. Measurements were taken from 1-2 proglottids per specimen. Scolex length was measured from the anterior of the scolex to the posterior margin of the suckers. Neck length was measured from posterior margin of the suckers to the beginning of visible segmentation. Sinistral/dextral alternation of the genital atrium among segments was recorded or standardized as the number of changes per 100 proglottids. The index of asymmetry was calculated from the ratio of the distance between the midpoint of

the vitelline gland and the poral extreme/the total width of the proglottid (Sato et al., 1993). Testis distribution is measured as the transverse distance between the two most distal testes in the proglottid (Haukisalmi and Henttonen, 2003). Maximum cirrus sac measurements were not recorded because the cirrus is usually everted, likely skewing these measurements. All measurements are provided in micrometers unless otherwise specified and include the range followed by the mean in parentheses, and the number of measurements if different than that given initially. Selected measurements are shown in Table I.

REDESCRIPTIONS

Monoecocestus macrobursatus **Rego, 1961**

(Fig. 2, 3, 7)

Diagnosis (measurements based on voucher specimens, 8 individuals and 10 mature proglottids): Scolex 280-600 (413, n=7) long, 544-840 (701, n=7) wide. Suckers face laterally or antero-laterally. Suckers 232-468 (323, n=27) in diameter. Neck 0-240 (151) long, 372-720 (555) wide. Specimens with 62-91 (78, n=7) proglottids. Strobila total length 9.4-19.6 mm (15.0 mm, n=7). Strobila maximum width 1.4-2.6 mm (2.2 mm, n=7). Immature proglottids 48-176 (96, n=7) long, 840-2040 (1205, n=7) wide. Length/width ratio of immature proglottids 0.04-0.17 (0.09, n=7). Mature proglottids 156-291 (213) long, 1384-2243 (2130) wide. Length/width ratio of mature proglottids 0.08-0.18 (0.13). Gravid proglottids 312-811 (629) long, 1104-2309 (1745) wide. Length/width ratio of gravid proglottids 0.15-0.65 (0.39). Genital pores alternate regularly, 98-100 (100, n=7) switches per 100 proglottids. Genital peduncle forms as

cirrus everts in post-mature proglottids. Testes number 51-53 (52, n=2), 22-38 (29, n=25) in diameter. Testis distribution 479-508 (494, n=2), do not overlap osmoregulatory canals. Testes overlap cirrus sac, ovary, seminal receptacle, and vitelline gland dorsally. Cirrus with spines. Cirrus sac 191-388 (273) long, 95-213 (151) wide. Genital atrium deep, often extending to osmoregulatory canals. Cirrus sac extends mediad beyond canals. Internal seminal vesicle present. Vas deferens a dilated tube surrounded by dark staining cellular coating. Seminal receptacle 86-108 (95, n=4) long, 74-99 (90, n=4) wide. Vitelline gland 69-136 (110) long, 177-313 (232) wide. Index of asymmetry 0.44-0.54 (0.48). Ovary 117-237 (182) long, 446-833 (589) wide. Vagina indistinct in mature proglottids. Vagina enters genital atrium anterior to cirrus sac. Uterus ventral to seminal receptacle and testes, dorsal to ovary. Uterus crosses ventral excretory canals ventrally and dorsally. Gravid uterus reticulate, prominently with anterior and posterior diverticula, becoming sac-like later in development. Eggs 45-70 (57, n=27) in diameter. Embryophore in form of pyriform apparatus, often blunt or with short horns. Genital organs crossing excretory canals dorsally. Dorsal and ventral osmoregulatory canal present with single transverse canal. Ventral canals 20-66 (45) wide, dorsal canals 6-20 (13) wide, transverse canals 16-23 (20, n=2) wide.

Taxonomic summary

Host: Hydrochoerus hydrochaeris (Linnaeus, 1766).

Locality: Angra dos Reis, State of Rio de Janeiro; Salobra and S. João (type locality), State of Mato Grosso, Brazil. *Specimens studied*: From the CHIOC (all vouchers): 27.733 b-d,f-g; 27.734 a,c; 27.735

Remarks

Because the species-group name does not match the gender of the generic name,
we formally change *Monoecocestus macrobursatum* to *Monoecocestus macrobursatus* in
accordance with Article 34.2 of the International Code of Zoological Nomenclature
(ICZN, 1999). *Monoecocestus macrobursatus, M. threlkeldi,* and *M. minor* are the 3
currently described species of *Monoecocestus* that have a total length less than 100 mm.
All other species of *Monoecocestus* have a total length greater than 150 mm. Hence, the
diagnoses to follow only compare the 3 species mentioned above. *Monoecocestus
macrobursatus* can be distinguished from *M. minor* and *M. threlkeldi* by having a larger
scolex, larger diameter of the suckers, and a larger minimum neck width. *Monoecocestus
macrobursatus* has more numerous and smaller testes than *M. threlkeldi*, and has more
proglottids in fully gravid specimens; *M. macrobursatus* has a larger cirrus sac than *M.
minor* and a larger cirrus sac / proglottid width ratio.

Monoecocestus threlkeldi **(Parra, 1952) Beveridge, 1994**

syn. *Paranoplocephala threlkeldi* Parra, 1952

Perutaenia threlkeldi Parra, 1953

(Fig. 5)

*Diagnosis (measurements based on voucher specimens, 5 fully gravid individual
and 10 mature proglottids):* Scolex 180-228 (205) long, 288-480 (411) wide. Suckers
face laterally or antero-laterally. Suckers 138-192 (176, n=20) in diameter. Neck 180-240
(214) long, minimum width 260-356 (324). Fully gravid specimens with 34-49 (40)

proglottids. Strobila total length 9.5-20.0 mm (14.4 mm). Strobila maximum width 1.4-1.9 mm (1.8 mm). Immature proglottids 120-200 (154) long, 656-880 (765) wide. Length/width ratio of immature proglottids 0.16-0.24 (0.20). Mature proglottids 123-248 (200) long, 941-1301 (1120) wide. Length/width ratio of mature proglottids 0.12-0.22 (0.18). Gravid proglottids 640-1248 (902) long, 1,392-1,872 (1,726) wide. Length/width ratio of gravid proglottids 0.44-0.73 (0.52). Genital pores alternate regularly with 98-100 (100) changes per 100 proglottids. Genital peduncle forms as cirrus everts in post-mature proglottids. Testes number 17-30 (24) per proglottid, each testis 42-60 (49, n=50) in diameter. Testis distribution 353-570 (489). Testes may overlap ventral and transverse osmoregulatory canal, always crossing canal dorsally. Testes overlap ovary, seminal receptacle, and vitelline gland dorsally. Cirrus sac 205-284 (234) long, 92-124 (112) wide. Cirrus usually everted. Cirrus with spines. Genital atrium deep, often reaching osmoregulatory canals. Cirrus sac crosses canals, often extending further mediad, terminating near midline of proglottid. Internal seminal vesicle present. Vas deferens a dilated tube surrounded by dark-staining cellular coating. Seminal receptacle ovoid to spherical, 73-129 (112) long, 63-98 (81) wide. Vitelline gland 67-111 (86) long, 135-167 (150) wide. Index of asymmetry 0.46-0.51 (0.49). Ovary 138-211 (182) long, 386-560 (471) wide. Vagina dilated in immature proglottids. Vagina indistinct in mature proglottids. Vaginal dilation dissipates as seminal receptacle forms. Vaginal dilation overlaps cirrus sac, reaches to developing seminal receptacle, does not reach distally past cirrus sac. Vagina enters genital atrium anterior to cirrus sac. Uterus dorsal to ovary, ventral to seminal receptacle and testes. Uterus crosses ventral excretory canals ventrally and dorsally. Gravid uterus reticulate with anterior, posterior, and lateral diverticula.

Eggs 44-56 (49, n=25) in diameter. Embryophore in form of a pyriform apparatus, 14-21 (18, n=25) long. Pyriform apparatus blunt or with very short horns. Oncosphere 8-10 (10, n=25) in diameter. Genital organs crossing osmoregulatory canals dorsally. Dorsal and ventral excretory canals present with one transverse anastomosis. Ventral canals 14-87 (48) wide, dorsal canals 5-13 (9) wide, transverse canals 7-46 (29) wide.

Taxonomic summary

Host: Holochilus brasiliensis (Desmarest, 1819) NK 13169, AMNH 261985

Locality: Rio Tijamuchi, Beni, Bolivia, 1985. 14.56°S, 65.9°W, 240 meters elevation

Specimens deposited: (5 specimens): HWML 60426 d-e, g-h, k deposited in the Harold W. Manter Laboratory of Parasitology Parasite Collection.

Prevalence and intensity: One individual rodent with > 50 worms.

Remarks

Monoecocestus threlkeldi can be distinguished from *M. minor* and *M. macrobursatus* by having fewer testes that are twice the size; *M. threlkeldi* has fewer total proglottids in fully gravid specimens than both *M. minor* and *M. macrobursatus*. *Monoecocestus thelkeldi* has a larger scolex diameter, sucker diameter, and cirrus sac length than *M. minor*. Additional comparisons to *M. macrobursatus* show that *M. thelkeldi* has smaller scolex diameter, sucker diameter, and a smaller vitellarium width.

The early uterus and its subsequent development in *M. threlkeldi* matches the descriptions of uterine structure and development in other *Monoecocestus* species. The

uterus is first seen as a transverse tube, quickly developing lobes in all directions. This development is shown in Figure 8.

Monoecocestus minor Rego, 1960

(Fig. 1, 4, 6)

Diagnosis (measurements based on paratype and voucher specimens, 4 individuals and 8 mature proglottids): Scolex 125-173 (143) long, 250-325 (291) wide. Suckers face laterally or antero-laterally. Suckers 45-125 (89, n=16) in diameter. Neck 0-88 (52) long, 288 (n=1) wide. Specimens with 51-82 (67) proglottids. Strobila total length 6.1-15.7 mm (10.9 mm). Strobila maximum width 1.2-1.6 mm (1.4 mm). Immature proglottids 60-112 (87) long, 540-1,400 (1,037) wide. Length/width ratio of immature proglottids 0.07-0.11 (0.09). Mature proglottids 121-207 (169) long, 1,194-1583 (1,394) wide. Length/width ratio of mature proglottids 0.08-0.17 (0.12). Gravid proglottids 240-655 (454) long, 920-1,560 (1231) wide. Length/width ratio of gravid proglottids 0.26-0.45 (0.35). Genital pores alternate regularly, 88-94 (90) switches per 100 proglottids. Genital peduncle not visible in post-mature proglottids. Testes 15-42 (28, n=38) in diameter. Testes overlap ovary and vitelline gland dorsally. Cirrus with spines. Cirrus sac 87-186 (135) long, 41-90 (64) wide. Genital atrium deep, cirrus sac overlaps the osmoregulatory canals, does not extend far mediad beyond canals. Internal and external seminal vesicle present. Seminal receptacle 177 (n=1) long, 49 (n=1) wide. Vitelline gland 45-100 (64) long, 83-187 (137) wide. Index of asymmetry 0.45-0.52 (0.47). Ovary 69-160 (106) long, 235-546 (385) wide. Vagina indistinct in mature proglottids. Vagina enters genital atrium anterior to cirrus. Uterus ventral to seminal

receptacle and testes, dorsal to ovary. Uterus crosses ventral excretory canals ventrally

and dorsally. Gravid uterus reticulate with predominately anterior and posterior

diverticulae, eventually becoming sac-like. Eggs 45-53 (49, n=10) in diameter.

Embryophore in form of pyriform apparatus. Pyriform apparatus blunted or with short

horns. Genital organs crossing osmoregulatory canals dorsally. Dorsal and ventral

osmoregulatory canals present with single transverse anastomosis. Ventral canals 29-41

(35, n=2) wide, dorsal canals 6-8 (7, n=2) wide, transverse canals 16 (n=1) wide.

Taxonomic summary

Host: Cavia aperea Erxleben, 1777.

Locality: Rio de Janeiro, State of Guanabara, Brazil.

Specimens studied: From the CHIOC : 27.719 b-c (vouchers); 27.720 a-b

(paratypes).

Remarks

Monoecocestus minor is the smallest of the 3 species discussed here. Compared to

M. threlkeldi and *M. macrobursatus*, *M. minor* has a smaller scolex diameter, smaller

sucker diameter, and a smaller cirrus sac length with a smaller cirrus sac/proglottid width

ratio. Alternation of the genital atrium is slightly more irregular than *M. thelkeldi* and *M.*

macrobursatus. Testes were very difficult to distinguish in the specimens available for

our study and were not counted. Rego (1960) states that *M. minor* has 50-80 testes, but

cites their diameter (46 μm) as larger than that of our study (15-42 [28]). In this case, we

trust our own measurement for testis diameter and Rego's (1960) measurement of testes

number to be greater than 50. This would give *M. minor* roughly double the number of testes relative to *M. threlkeldi*.

DISCUSSION

We agree with Beveridge (1994), who considered *Perutaenia* to be a junior synonym of *Monoecocestus* based on the entrance of the vagina being anterior to the cirrus sac at the genital atrium. We are also in agreement with Beveridge (1994) that the type specimens of *M. thelkeldi* (USNPC 37380) are not of high enough quality to make solid taxonomic decisions, but it is clear that the worms we collected from *Holochilus brasiliensis* are *M. threlkeldi*. Differences between the published description (Parra, 1953) of *M. threlkedi* and the specimens we examined from Bolivia include the size and position of the testes relative to the female genital organs. Based on Parra's (1953) description and her Figure 3, it appears that the position and size of the testes were based on the measurements made from immature proglottids. In specimens representing various species of *Monoecocestus*, it is common to see the testes migrate posteriad throughout the segment during development, with the testes starting off anterior to the ovary in immature proglottids and becoming mediad, and eventually posterior to the ovary in mature segments. Testis size also increases in more mature proglottids of anoplocephalid cestodes. Our measurements also show *M. threlkeldi* to have a greater total length than reported by Parra (1953). We believe this discrepancy is caused by our measurements being based on gravid specimens and the type specimens of *M. threlkeldi* being immature, having not yet reached their maximum total length.

Prior to this study, species of *Monoecocestus* from South America were found almost exclusively in hystricognath rodents, with the exception of *M. rheiphilus* Voge and Reed, 1953 from Darwin's rhea (*Pterocnemia pennata*) in Peru and *M. mackiewiczi* Schmidt and Martin, 1978 from *Phyllotis* sp. (Myomorpha: Sigmodontinae) in Paraguay. *Holochilus brasiliensis*, also a sigmodontine rodent, is the third host species of *Monoecocestus* found outside of the Hystricomorpha.

It is possible that the specimens from *H. brasiliensis* represent a cryptic species. However, the measurements of the specimens from *H. brasiliensis* were very similar to the description of *M. thelkeldi*, and we feel that occurrence of a parasite in a specific species or group of species of hosts per se is not sufficient to differentiate a species and is not a valid character in a species diagnosis of a parasite. The knowledge of the taxonomic relationships of anoplocephaline cestodes historically has been limited by the lack of useful taxonomic characters and recent work in the area has relied more heavily on data from DNA sequencing to provide additional characters. Based purely on morphological evidence, it is clear that our specimens from *H. brasiliensis* represent *M. thelkeldi.* This hypothesis remains to be tested with molecular characters.

Haukisalmi and Wickström (2005) showed that generic level classification can be achieved with certain anoplocephalines by noting where the gravid uterus crosses the osmoregulatory canals. The work herein, and additional observations of numerous other specimens, shows that in all species assigned to *Monoecocestus*, the gravid uterus crosses the osmoregulatory canals both dorsally and ventrally. This pattern should be observed across multiple proglottids, as in a single proglottid, the uterus may overlap the osmoregulatory canals ventrally, dorsally, or both. When the uterus overlaps these canals

both dorsally and ventrally in the same proglottid, it may overlap the dextral canals dorsally and the sinistral canals ventrally or it may overlap one side both dorsally and ventrally. Our observations indicate that this character is stable and observable in well prepared specimens and can be given taxonomic weight on the generic level for *Monoecocestus*.

ACKNOWLEDGMENTS

LITERATURE CITED

Beveridge, I. 1994. Family Anoplocephalidae Cholodkovsky, 1902. *In* Keys to the
cestode parasites of vertebrates, L. F. Khalil, A. Jones, and R. A. Bray (eds.).
CAB International, Cambridge, U.K., p. 315-366.

Gardner, S. L. 1996. Field parasitology techniques for use with mammals. *In* Measuring and monitoring biological diversity: Standard methods for mammals, D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C., p. 291-298.

Haukisalmi, V., and H. Henttonen. 2003. What is *Paranoplocephala macrocephala* (Douthitt, 1915) (Cestoda: Anoplocephalidae)? Systematic Parasitology **54:** 53-69.

Haukisalmi, V., AND L. M. WICKSTRÖM. 2005. Morphological characterization of *Andrya* Railliet, 1893, *Neandrya* n.g. and *Paranoplocephala* Lühe, 1910 (Cestoda: Anoplocephalidae) in rodents and lagomorphs. Systematic Parasitology **62:** 209-219.

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, 4th. The International Trust for Zoological Nomenclature, 306 p.

Parra, O. B. 1953. *Perutaenia threlkeldi* n.g., n.sp. (Cestoda: Anoplocephalidae) from *Lagidium peruanum*. Journal of Parasitology **39:** 252-255.

Rego, A. A. 1960. Nota prévia sóbre um novo *Monoecocestus* parasito de preá (Cestoda: Cyclophyllidea). Atas da Sodedade de Biología do Rio de Janeiro.**4:** 73.

Sato, H., H. Kamiya, F. E. Tenora, and M. Kamiya. 1993. *Anoplocephaloides dentatoides* sp. n. from the gray-backed vole, *Clethrionomys rufocanus* bedfordiae, in Hokkaido, Japan. Journal of the Helminthological Society of Washington **60:** 105-110.

Table I. Selected measurements from specimens representing three species of *Monoecocestus*. All measurements in micrometers unless otherwise stated.

	M. minor		*M. minor* (N=4)	*M. macrobursatum*		*M. macrobursatum* (N=8)		*M. threlkeldi* (N=5)	*M. threlkeldi*
Country	Brazil		Brazil	Brazil		Brazil		Bolivia	Peru
Host	*Cavia aperea*		*Cavia aperea*	*Hydrochoerus hydrochaeris*		*Hydrochoerus hydrochaeris*		*Holochilus brasiliensis*	*Lagidium peruanum*
Source	Rego, 1960	n	Present study	Rego, 1961	n	Present study	n	Present study	Parra, 1953
Total length (mm)	8.4-15.4	4	6.1-15.7 (10.9)	12.1-22.4	7	9.4-19.6 (15.0)	5	9.5-20.0 (14.4)	6-14
Max. Width (mm)	1.8	4	1.2-1.6 (1.4)	3.28	7	1.4-2.6 (2.2)	5	1.4-1.9 (1.8)	0.4-2
No. of proglottids	55-80	4	51-82 (67)	85-100	7	62-91 (78)	5	34-49 (40)	--
Immature prog. L/W	--	4	0.07-0.11 (0.09)	--	7	0.04-0.17 (0.09)	5	0.16-0.24 (0.20)	--
Gravid prog. L/W	--	4	0.26-0.45 (0.35)	--	8	0.15-0.65 (0.39)	5	0.44-0.73 (0.52)	--
Scolex diameter	392	4	250-325 (291)	920	7	544-840 (701)	5	288-480 (411)	440-530
Sucker diameter	122	16	45-125 (89)	398	27	232-468 (323)	20	138-192 (176)	160-190
Neck length	--	4	0-88 (52)	--	8	0-240 (151)	5	180-240 (214)	--
Neck min. width	--	1	288	--	8	372-720 (555)	5	260-356 (324)	--
Gen. alternation	--	4	88-94 (90)	--	7	98-100 (100)	5	98-100 (100)	--
Testes number	50-80		--	--	2	51-53 (52)	5	17-30 (24)	15-20
Testis width	46	38	15-42 (28)	46	25	22-38 (29)	50	42-60 (49)	30
Cirrus sac length	435	8	87-186 (135)	996	10	191-388 (273)	10	205-284 (234)	360-440
Vitellarium width	261	8	83-187 (137)	365	10	177-313 (232)	10	135-167 (150)	--
Ovary width	609	8	235-546 (385)	1029	10	446-833 (589)	10	386-560 (471)	--
Index of asymmetry	--	8	0.45-0.52 (0.47)	--	10	0.44-0.54 (0.48)	10	0.46-0.51 (0.49)	--
Testes distribution	--		--	--	2	479-508 (494)	10	353-570 (489)	--
Ventral canal width	--	2	29-41 (35)	--	10	20-66 (45)	10	14-87 (48)	--
Egg diameter	50	10	45-53 (49)	58	27	45-70 (57)	25	44-56 (49)	60-66
Pyriform length	25		--	29		--	25	14-21 (18)	--

Figures 1-4. (**1**) *Monoecocestus minor*. Scolex. CHIOC 27.719B. (**2**) *Monoecocestus macrobursatus*. Scolex. CHIOC 27.734A. (**3**) *Monoecocestus macrobursatus*. Mature proglottid. CHIOC 27.734A. (**4**) *Monoecocestus minor*. Mature proglottid. CHIOC 27.720A. All scale bars = 0.1 mm
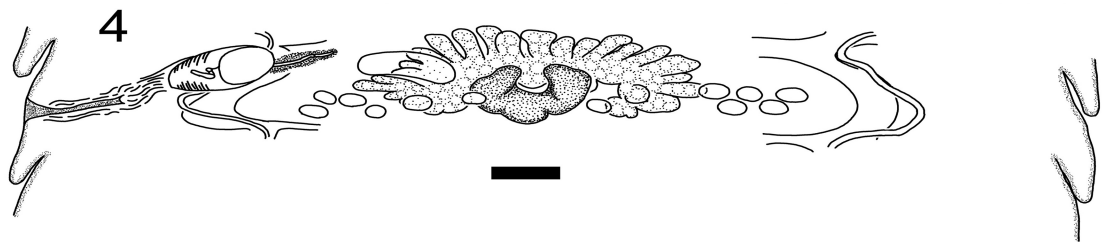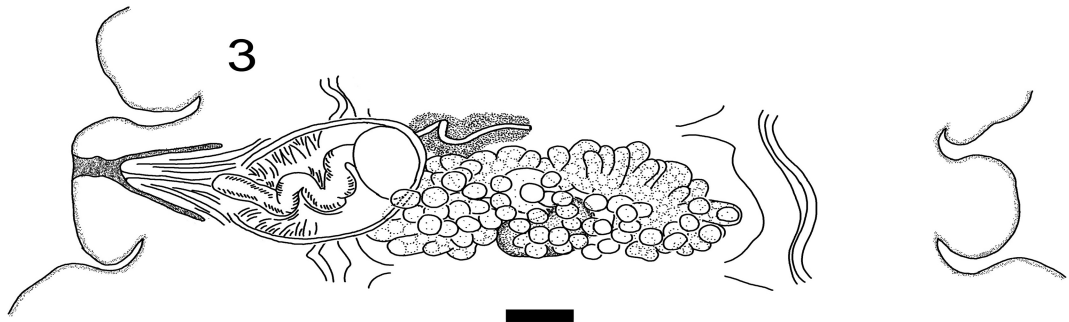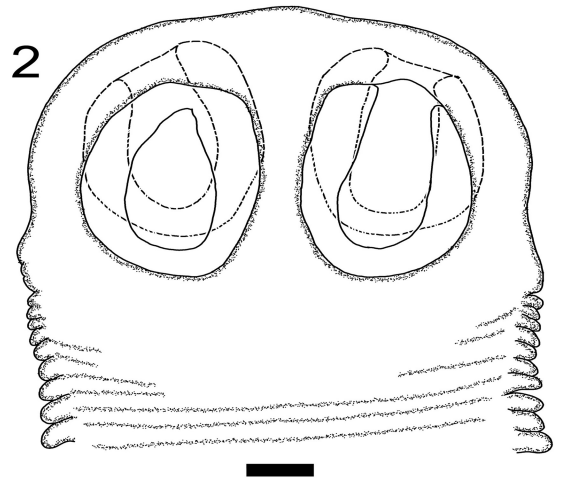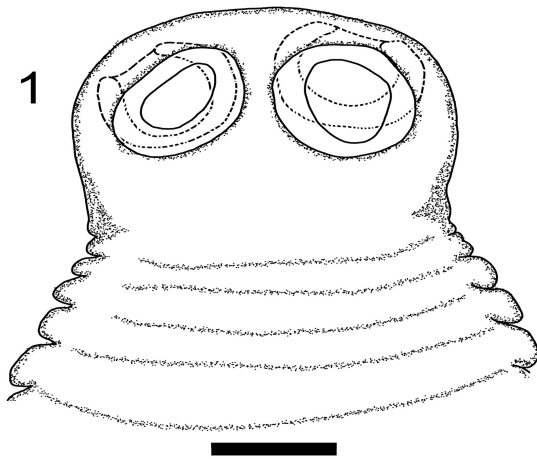
1

2

3

4

Figure 5. *Monoecocestus threlkeldi.* (**a**) Full strobila HWML 60426E. Scale bar = 0.5 mm. (**b**) Scolex. HWML 60426I. Scale bar = 0.1 mm. (**c**) Egg. Scale bar = 0.01 mm. (**d**) Mature proglottid. HWML 60426H. Scale bar = 0.1 mm.
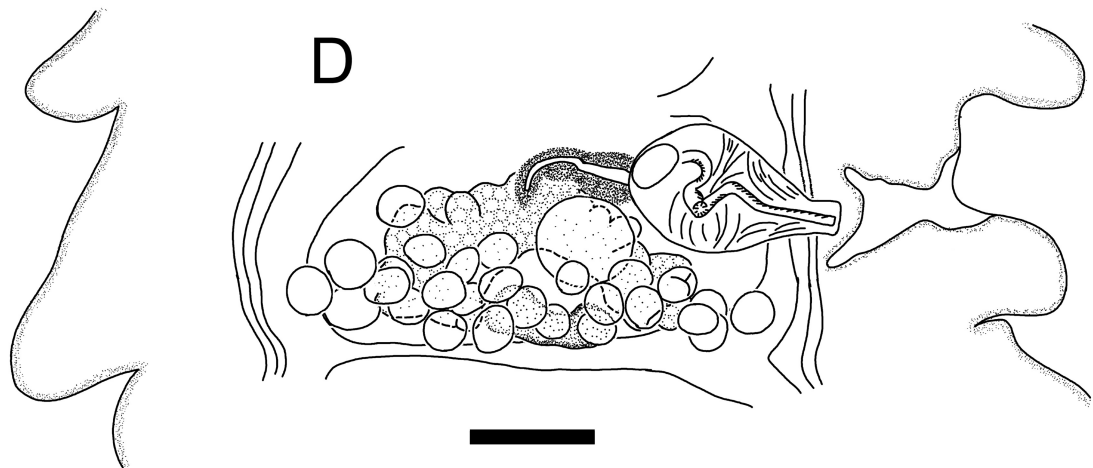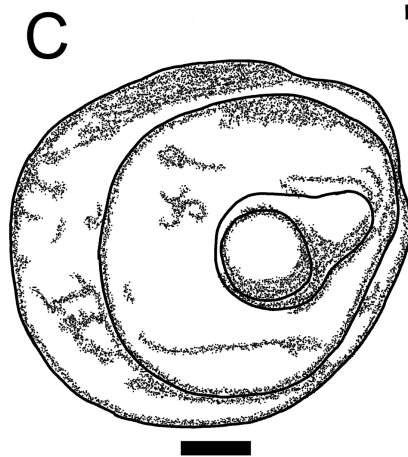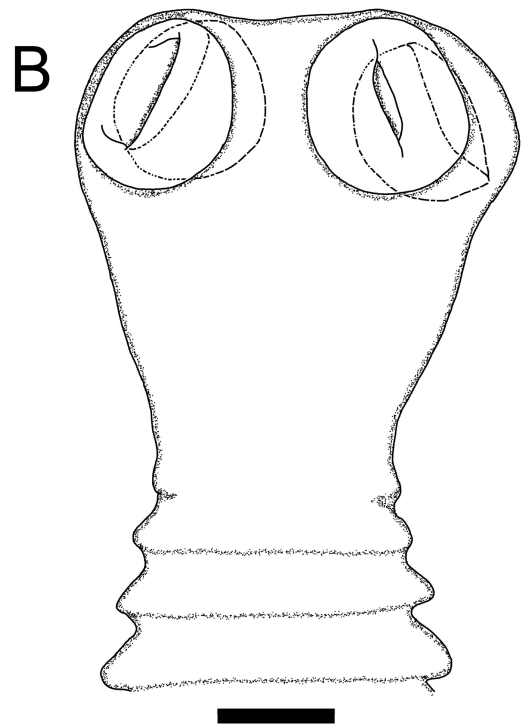
Figure 6-7. (**6**) *Monoecocestus minor*. Full strobila. CHIOC 27.719B. (**7**) *Monoecocestus macrobursatus*. Full strobila. CHIOC 27.733C. Both scale bars = 0.5 mm.

6 7

Figure 8. The developing uterus of *Monoecocestus threlkeldi*. Other organs and structures not shown for clarity. HWML 60426K. All scale bars = 0.1 mm.

CHAPTER 3

Citation: Haverkost, Terry R. and Scott L. Gardner. 2008. A new species of

   Lentiella **(Cestoda: Anoplocephalidae) from *Proechimys simonsi***

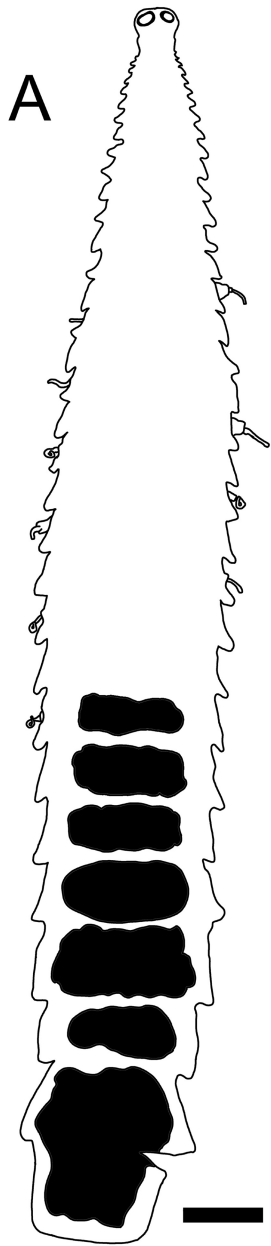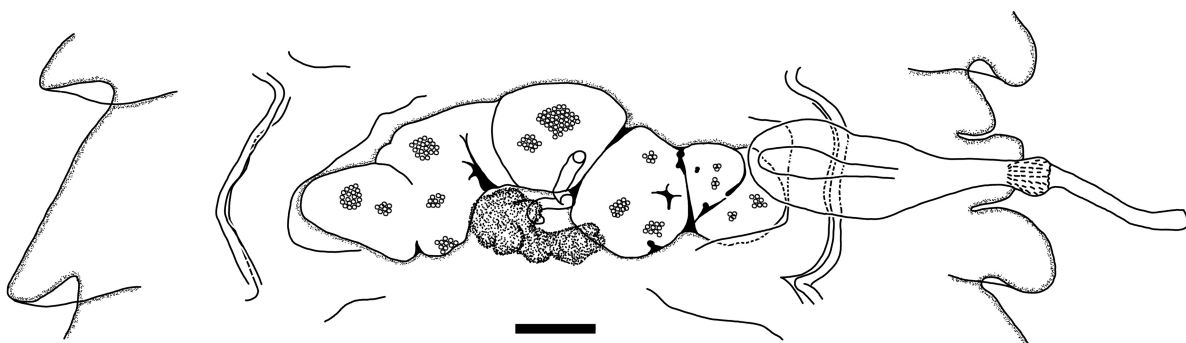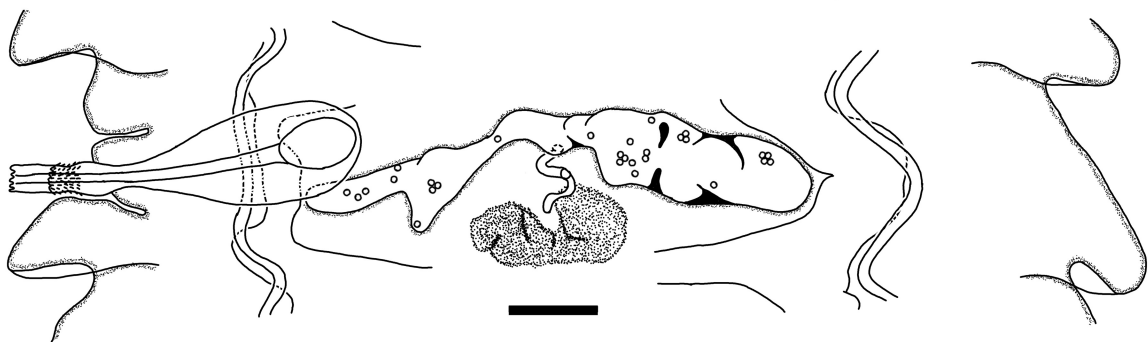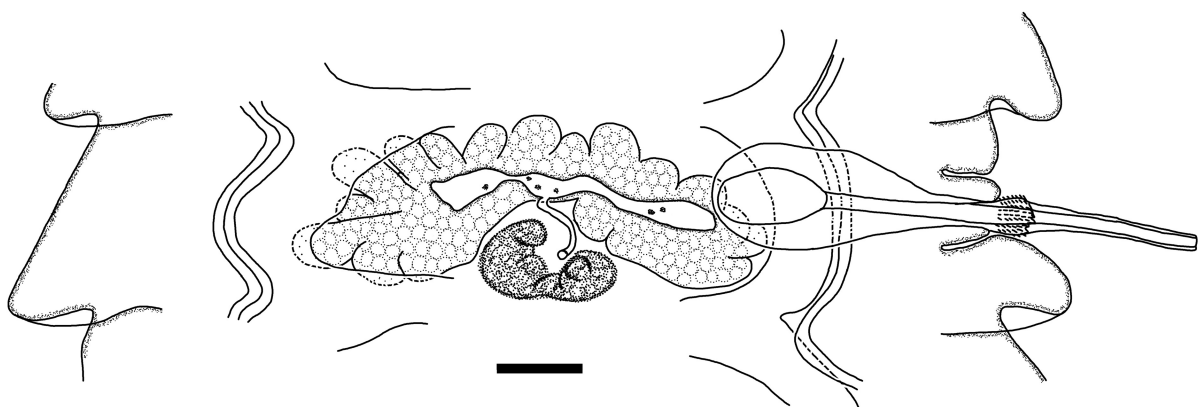   **(Rodentia: Echimyidae) in Bolivia. Revista Mexicana de**

   Biodiversidad 79**: 99S- 106S**

A NEW SPECIES OF *LENTIELLA* (CESTODA: ANOPLOCEPHALIDAE) FROM

  PROECHIMYS SIMONSI **(RODENTIA: ECHIMYIDAE) IN BOLIVIA**

Terry R. Haverkost and Scott Lyell Gardner

Harold W. Manter Laboratory of Parasitology W-529 Nebraska Hall, The University of

Nebraska State Museum, University of Nebraska, Lincoln,

Nebraska 68588-0514, USA.

  ABSTRACT: During a biodiversity survey of mammals and their parasites in the Beni, Bolivia in the summer of 2000, several spiny rats, *Proechimys simonsi* Thomas, 1900, were collected and examined for parasites. Herein we describe *Lentiella lamothei* n. sp. from one of these hosts. This species is can be distinguished from *L. machadoi* Rego, 1964 by having a greater total length but smaller maximum width, a greater number of segments, a smaller cirrus sac, a smaller scolex diameter, and in the eggs, a larger pyriform apparatus. In addition, we formally validate the genus *Lentiella* Rego, 1964, that had been placed in synonymy with *Monoecocestus* Beddard, 1914.

INTRODUCTION

This contribution is one of the many publications that have resulted from data collected as a result of our collaborative, long-term expeditionary research on the biodiversity of mammals and their parasites from the Republic of Bolivia (Gardner and Campbell, 1992; Anderson, 1997; Dick et al., 2007; Notarincola et al., 2007). In the year 2000, research teams from the Museum of Southwestern Biology and the Harold W. Manter Laboratory of Parasitology traveled through east-central lowland Bolivia and collected small and medium-sized mammals and their parasites from the departments of Beni and Santa Cruz. The work was primarily focused on a survey of potential hosts for Machupo virus, the causative agent of Bolivian hemorrhagic fever. During this survey, many species of mammals were obtained, examined, and deposited in museums. From our work, several specimens of spiny rats (*Proechimys simonsi* Thomas, 1900) were collected and examined for parasites and 2 individuals were found to be infected with an undescribed species of anoplocephalid cestode.

Species of the genus *Proechimys* Allen, 1899 occur throughout lowland tropical evergreen forests of South America from east-central Honduras (*P. semispinosus* (Tomes, 1860)) south through northern Paraguay (*P. longicaudatus* (Rengger, 1830)). *Proechimys simonsi* is known to occur in suitable habitats in Ecuador, Peru, Bolivia, and western Brazil (Eisenberg and Redford, 1992; Wilson and Reeder, 2005). During work carried out in the north eastern part of South America, the anoplocephalid cestode, *Lentiella machadoi* Rego ,1964 was described from 8 whole specimens taken from the small intestine of an individual of *Proechimys guyannensis* (Geoffroy, 1803) collected in

Abaeté, Estado do Pará, Brazil (Rego, 1964). In this paper Rego (1964) established the genus *Lentiella* based on morphological characters of the species *L. machadoi*. For clarity we reproduce the original diagnosis of the genus here:

Lentiella Rego (1964)

Diagnose – Anoplocefalídeos de reduzidas dimensões e siples genitália. Escolex e ventosas grandes. Pescoço inexistente ou reduzido. Proglotes mais largos que longos, com segmentação linear. Póros genitais regular ou irregularmente alternos. Testículos pouco numerosos, dispostos nap arte posterior do segmento, em fi la contínua, posteriormente ao ovário e vitelino. Bôlsa do cirro, grande, provida de cirro espinoso. Vagina ventral á bôlsa do cirro. Ovário bastante lobado, ligeiramente anti-poral, Vitelino compacto, de posição mediana nos segmentos, mas poral em relação ao ovário. Receptáculo seminal pequeno. Útero tubular, que se ramitica, mas não ocupa a parte posterior dos segmentos. Ovos con aparéelo piriforme pouco desenvolvido. Sistema excretor? Adultos em roedores.

As noted above, the details of the excretory system were not recorded; however, the general characteristics of the type species appear to be well enough defined that Rego (1964) was able to describe the species in a new genus (*Lentiella* n. gen.).

Beveridge (1994) examined the type specimens in the Helminthological Collection of the Instituto do Oswaldo Cruz (IOC 29.770a) and stated:

The testes lie in the posterior part of the medulla and the vagina, which is only clearly visible in 2 proglottids, opens to the genital atrium anterior to the cirrus-sac, in contradistinction to Rego's (1964) description. The uterus is prominently lobed and appears to be slightly reticulated; however, in the only specimen available, from the collection… …(IOC 29.779)[sic], the proglottids in which the critical stages of uterine development occur are damaged. More material is required for a detailed study of uterine development, and pending this, the genus is made a synonym of Monoecocestus.

We note here that in his description, Rego (1964) did not mention where the vagina enters the genital atrium; however, mediad from the genital atrium, the vagina passes ventrally to the cirrus sac. Therefore, based on our observations of both the description by Rego and of specimens that we collected in Bolivia, we verify that the genus *Lentiella* is valid and herein we describe a new species of anoplocephalid cestode collected from *P. simonsi* in the Beni Dept., Bolivia. The description is based on 5 fully developed specimens with gravid segments and sections of additional specimens.

MATERIALS AND METHODS

Captured mammals were processed immediately following standard protocols (Gardner, 1996). The complete gastrointestinal tract, liver, lungs, pleural, and peritoneal cavities were examined separately for helminths using a dissecting microscope. Cestodes found were placed immediately in a large volume of distilled water to relax the strobila for later morphological examination. Specimens were killed and preserved in either 10% formalin or 70% ETOH and were transported in the same solution to the laboratory for

staining and subsequent study by light microscopy. Specimens used in the present study were stained in Semichon's acetic carmine or Erlich's acid hematoxylin, dehydrated in an alcohol series, cleared in terpineol and xylene, and mounted in Dammar gum. After staining, superficial tegument and tissues, including either dorsal or ventral longitudinal and transverse muscles, were removed from some specimens to allow observation of internal organs. Eggs were viewed by clearing a gravid proglottid with lactophenol and viewing free eggs with the aid of a microscope. Serial cross sections were prepared from one specimen to allow observation of the relative placement of organs.

All measurements were taken with the aid of an ocular micrometer. Figures were made with the aid of a drawing tube. Scolex length was measured from the anterior extremity to the posterior margin of the suckers. Neck length was measured from the posterior margin of the suckers to the first visible sign of segmentation. Genital pore alternation is presented as the number of times the genital pore switched sides per 100 proglottids. Thus, a higher number corresponds to more regular alternation. The widths of dorsal and ventral osmoregulatory canals were recorded at the midpoint of the proglottid on the antiporal side. Measurements of the cirrus sac were not taken if the cirrus was everted. Dimensions of the pyriform apparatus were measured from digital photographs. Testis distribution was measured as the distance between the 2 distal extreme testes (Haukisalmi et al., 2004). The index of asymmetry was calculated as the ratio of the distance between the midpoint of the vitellarium and the poral extremity/the total width of the proglottid (Sato et al., 1993). All measurements are provided in micrometers unless otherwise specified. Measurements provided include the mean measurement, followed by

the range in parentheses, and the number of measurements if different than that given
initially.

DESCRIPTION

Lentiella lamothei n. sp.

(Figs. 1-7)

Measurements based on 5 whole gravid individuals from a single host.
Measurements are summarized in Table I. Scolex 752 (673-840) wide, 368 (341-395)
long. Suckers face laterally or antero-laterally. Width of suckers 293 (248-348 n=20),
sucker aperture 179 (132-232 n=20). Neck 615 (360-735) long, 502 (480-540) wide at
narrowest point. Specimens have 41 (37-43) proglottids per gravid strobila. Strobila 19.4
(16.1-21.6) mm in total length. Width at widest point 1.37 (0.78-1.62) mm in mature
proglottids. Immature proglottids 150 (120-180) long, 894 (780-1110) wide. Mature
proglottids 449 (330-660) long, 1323 (1110- 1590) wide. Gravid proglottids 876 (780-
960) long, 1308 (1200-1500) wide. Genital pores alternate regularly, with an average of
90 (82-96) switches per 100 proglottids. The following measurements are based on 15
mature proglottids with 3 proglottids measured per strobila. Testes ovoid, 27 (18-37) per
proglottid, 47 (32-66 n=75) in diameter. Testis distribution 522 (410-650). Testes dorsal
and ventral to transverse excretory canal. Cirrus sac 210 (123-310) long, 120 (76-158)
wide. Internal and external seminal vesicle absent. Seminal receptacle 116 (73-163) long,
69 (41-107) wide. Vitelline gland 95 (70-111) long, 96 (70-114) wide. Index of
asymmetry 0.61 (0.56-0.65). Ovary 224 (180-284) long, 277 (234-332) wide. Midline of
ovary 801 (658-983) from poral extremity, midline of vitelline gland 694 (573-867) from

poral extremity. Vagina dilated distally, when dilated, usually overlapping cirrus sac. Vaginal dilation reaching maximum length of 237 long and 114 wide, appearing in immature segments, not seen or absent in mature proglottids. Vagina 422 (316-664) long, entering genital atrium anterior to cirrus sac. Uterus dorsal to seminal receptacle and ovary, ventral to testes, if contacted. Uterus crosses ventral excretory canals rarely, in gravid segments only. Uterus may cross osmoregulatory canals ventrally or dorsally. Gravid uterus with anterior, posterior, and lateral diverticula. Genital organs crossing excretory canals dorsally. Dorsal and ventral excretory canals present. Ventral canals 25 (16-39) in width, dorsal canals 13 (4-21) wide, transverse canals 18 (8-43) wide. Eggs round, 46 (43-51 n=25) in diameter containing an oncosphere 12 (10-14 n=25) wide surrounded by pearshaped pyriform apparatus. Pyriform apparatus simple, with 2 short horns and no filaments, 31 (25-34 n=12) along its axis.

Taxonomic summary

Type-host: *Proechimys simonsi* Thomas 1900, Symbiotype (see Frey, et al., 1992) deposited in the University of New Mexico, Museum of Southwestern Biology Mammal Division (MSB), MSB98787.

Site of infection: small intestine.

Type-locality: Puesto Militar Casarabe, Dept. Beni, Bolivia, 5.5 km South of Casarabe by road, 14o 53' 44" S 64o 25' 59" W, 188 m elevation.

Type-specimen: holotype, mounted on a microscope slide, collected 26 May, 2000, HWML70023, 9 paratypes from same host symbiotype, mounted on slides, HWML70024, preserved in formalin, HWML63382. All specimens deposited in the

Harold W. Manter Laboratory of Parasitology, Division of Parasitology, The University of Nebraska State Museum, University of Nebraska, Lincoln, Nebraska.

Prevalence and intensity: 2/6 (33%), average 40 specimens from duodenum.

Etymology: this species is named after Dr. Rafael Lamothe-Argumedo, teacher, taxonomist, and one of the leaders in helminthology at UNAM in Mexico.

Lentiella Rego, 1964, emended.

Diagnosis - Anoplocephalids of small size. Scolex and suckers large. Proglottids wider than long in immature, mature, and gravid segments, posterior penultimate and ultimate segments devoid of eggs, always longer than wide. Genital pores regularly alternating. Small but numerous testes, located in posterior part of segment, in continuous line, posterior to ovary and vitelline gland. Testes overlap transverse, but not ventral or dorsal osmoregulatory canals. Cirrus sac large, cirrus spined. Vagina enters genital atrium anterior to cirrus sac. Lateral genital ducts (vagina and cirrus sac) cross osmoregulatory canals dorsally. Ovary lobed, slightly anti-poral. Vitelline gland compact, posterior and poral to the ovary. Small seminal receptacle present. Vaginal dilation present in immature segments. Internal and external seminal vesicles absent. Tubular uterus arching anteriorly from center, not occupying posterior part of the segments. Uterine development abrupt, filling with eggs before uterine wall fully developed. Uterus crosses ventral excretory canals rarely, in gravid segments only. Uterus may cross osmoregulatory canals ventrally or dorsally. Gravid uterus with anterior, posterior, and lateral diverticula. Anapolytic with eggs generally absent from terminal senescent segments. Eggs with simple pyriform apparatus. Adults in rodents, South America.

Remarks

Compared to the only other species in the genus, *L. lamothei* n. sp. differs from *L. machadoi* by having a greater total length but smaller maximum width, a greater number of segments, a smaller cirrus sac, a smaller scolex diameter, and in the eggs, a larger pyriform apparatus. Other measurements may prove useful in distinguishing the 2 taxa. However, due to the condition of the material from Rego (1964), we recommend that new material be collected and measured so a comparison can be made with properly relaxed specimens of *L. machadoi*. Currently, including this report, species of *Lentiella* are known only from hystricognath rodents of the genus *Proechimys* in the Neotropics (Brazil and Bolivia).

Species assigned to the genus *Lentiella* appear superficially similar to species of *Monoecocestus* in that the vagina enters the genital atrium anterior to the cirrus sac. However, *Lentiella* has a tubular uterus while the developing uterus of all known species of *Monoecocestus* is reticular in nature. In addition, the vitelline gland in *Lentiella* is posterior to the ovary and on the poral side compared with the vitelline gland in known species of *Monoecocestus* which are central and posterior to the ovary.

The 2 species of *Lentiella* can be readily distinguished from species of *Viscachataenia* Denegri et al., 2003 with the former having only a single set of genital organs per segment and a tubular uterus.

Comparing *L. lamothei* to known forms of the Anoplocephalidae that also have a uterus that is tubular in nature, it is evident that only species of Nearctic *Anoplocephaloides* have this type of uterine development and structure. However, *L.*

lamothei can be recognized as distinct from species of *Anoplocephaloides* in having a uterus that remains diffuse until the uterine wall becomes immediately recognizable and the uterus is full of eggs. In species of *Anoplocephaloides*, the tubular uterus develops more slowly, forming a definitive uterine wall and lumen before becoming gravid. Finally, the testes of *Lentiella* are always posterior to the ovary and vitelline gland compared to species of *Anoplocephaloides* that have testes that are largely antiporal.

DISCUSSION

Species of *Proechimys* are known to eat seeds, fruits, and fungi (Eisenberg and Redford, 1992), and with the discovery of this cestode, it is clear that they also eat some kind of arthropod. Assuming the close relationship of *Lentiella* spp. to *Monoecocestus* spp., this arthropod is likely an Oribatid mite, since the life cycle of at least one species of *Monoecocestus* has been experimentally verified (Freeman, 1952). We assume the close relationship of *Lentiella* and *Monoecocestus* from the relative position of the vagina to the cirrus sac at the genital atrium, and the posterior position of the testes in the proglottids.

Development of the uterus has been one of the most important taxonomic characters of species included in this family of cestodes, especially in the Anoplocephalinae, where the uterus does not degenerate in gravid proglottids (Rausch, 1976; Spasskii, 1951). It has been established that the development of the early uterus (e.g. reticulate, tubular) is homoplastic (Wickström et al., 2005), but general structure and development of the uterus is still used to discriminate between and among species within a genus. The development of the uterus in *L. lamothei* n. sp. appears to be most similar to

Anoplocephaloides in that it is not reticulate early in development, but differs from *Anoplocephaloides* species in the nature of the development. The uterus in *L. lamothei* n. sp. appears in the segment less than 5 proglottids before it becomes prominent in the strobila; appearing as an aggregation of cells that spans the proglottid, not unlike most other anoplocephalids. However, in *Anoplocephaloides* the uterus develops a recognizable uterine wall and lumen prior to becoming full of developing eggs (Fig. 8). In *L. lamothei* n. sp., development from a simple aggregation of cells to fully gravid uterus takes place in the span of one proglottid, and in the newly formed uterus undeveloped eggs occupy a majority of the uterine area (Fig. 9). The uterine wall in this fully gravid proglottid is has not completely developed, and still looks like an aggregation of densely packed cells. In the following proglottids the uterus grows rapidly, but the number of eggs does not follow its fast development, leaving the uterus partially filled in subsequent proglottids. Soon the uterus develops the anterior and posterior diverticula common in *Monoecocestus* and other anoplocephalid species until it becomes sac-like, filling with eggs. Many specimens examined followed developmental pathways noted by Rego (1964) in that the eggs would sometimes be completely expelled from the last 2 or 3 proglottids. Those senescent segments appear in sharp contrast to those proglottids before them, as they became 2 to 3 times longer than wide.

LITERATURE CITED

Anderson, S. 1997. Mammals of Bolivia, taxonomy and distribution. Bulletin of the American Museum of Natural History 231:1-652.

Beveridge, I. 1994. Family Anoplocephalidae Cholodkovsky, 1902. *In* Keys to the cestode parasites of vertebrates, L. F. Khalil, A. Jones and R. A. Bray (eds.). CAB International, Cambridge. p. 315-366.

Denegri, G., M. C. Dopchiz, M. C. Elissondo and I. Beveridge. 2003. *Viscachataenia* n. g., with the redescription of *V. quadrata* (von Linstow, 1904) n. comb. (Cestoda: Anoplocephalidae) in *Lagidium viscacia* (Rodentia: Chinchillidae) from Argentina. Systematic Parasitology 54:81-88.

Dick, C. W., D. Gettinger and S. L. Gardner. 2007. Bolivian ectoparasites: a survey of bats (Mammalia: Chiroptera). Comparative Parasitology 74:372-377.

Eisenberg, J. F. and K. H. Redford. 1992. Mammals of the Neotropics: the central Neotropics, volume 3. University of Chicago, Illinois. 609 p.

Freeman, R. S. 1952. The biology and life history of *Monoecocestus* Beddard, 1914 (Cestoda: Anoplocephalidae) from the porcupine. Journal of Parasitology 38:111-129.

Frey, J. K., T. L. Yates, D. W. Duszynski, W. L. Gannon and S. L. Gardner. 1992. Designation and curatorial management of type host specimens (symbiotypes) for new parasite species. Journal of Parasitology 78:930-932.

Gardner, S. L. 1996. Field parasitology techniques for use with mammals. *In* Measuring and monitoring biological diversity: standard methods for mammals, D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran and M. S. Foster (eds.). Smithsonian Institution, Washington, D.C. p. 291-298.

Gardner, S. L. and M. L. Campbell. 1992. Parasites as probes for biodiversity. The Journal of Parasitology 78:596-600.

Haukisalmi, V., L. M. Wickström, H. Henttonen, J. Hantula and A. Gubányi. 2004. Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Cestoda, Anoplocephalidae) in *Microtus* voles (Arvicolinae). Zoologica Scripta 33:277-290.

Notarnicola, J., F. A. Jiménez-Ruiz and S. L. Gardner. 2007. A new species of *Dipetalonema* (Filarioidea: Onchocercidae) from *Ateles chamek* from the Beni of Bolivia. Journal of Parasitology 93:661-667.

Rausch, R. L. 1976. The genera *Paranoplocephala* Lühe, 1910 and *Anoplocephaloides* Baer, 1923 (Cestoda: Anoplocephalidae) with particular reference to species in rodents. Annales de Parasitologie Humaine et Comparée 51:513-562.

Rego, A. A. 1964. *Lentiella machadoi* g. n., sp. n. e *Raillietina* (R.) *trinitatae* (Cameron and Reesal, 1951), parasitos de roedor (Cestoda, Cyclophyllidea). Revista Brasileira de Biologia 24:211-220.

Sato, H., H. Kamiya, F. Tenora and M. Kamiya. 1993. *Anoplocephaloides dentatoides* sp. n. from the gray-backed vole, *Clethrionomys rufocanus bedfordiae*, in Hokkaido, Japan. Journal of the Helminthological Society of Washington 60:105-110.

Spasskii, A. A. 1951. Essentials of cestodology, anoplocephalate tapeworms of domestic and wild animals. Academy of Sciences of the USSR, Moscow. 783 p.

Wickström, L. M., V. Haukisalmi, S. Varis, J. Hantula and H. Henttonen. 2005. Molecular phylogeny and systematics of anoplocephaline cestodes in rodents and lagomorphs. Systematic Parasitology 62:83-99.

Wilson, D. E. and D. M. Reeder. 2005. Mammal Species of the World. Johns Hopkins University, Baltimore. 2142 p.

Table 1. Measurements comparing *L. lamothei* n. sp. and *L. machadoi*. All

measurements in micrometers unless otherwise stated.

Measurement	*L. machadoi* Rego, 1964	*L. lamothei* n. sp. Range (mean)
Proglottids, number	24-28	37-43(41)
Total length (mm)	5.4-10.5	16.1-21.6 (19.3)
Strobila width, max	2100	780-1620 (1374)
Mature proglottid	--	
Length	202	330-660 (490)
Width	1830	1140-1620 (1374)
Gravid proglottid	--	
Length	562	780-960 (876)
Width	1420	1200-1500 (1308)
Scolex diameter	1050	673-840 (752)
Scolex length	1120	341-395 (369)
Sucker diameter	300-330	248-348 (293)
Egg, diameter	45	43-51 (46)
Oncosphere, diameter	23	25-34 (31)
Pyriform apparatus, length	--	25-34 (31)
Testes number	20	18-37 (26)
Testes diameter	45	32-66 (47)
Cirrus length	300	123-310 (209)
Cirrus width	112	76-158 (120)
Seminal receptacle	--	
Length	150	73-163 (116)
Width	60	41-107 (69)
Ovary	--	
Length	--	180-284 (224)
Width	--	234-332 (277)
Vitelline Gland	--	
Length	--	70-111 (95)
Width	--	70-114 (96)
Vagina, Length	--	316-664 (422)
Vaginal swelling, max	--	114
Index of asymmetry	--	0.56-0.65 (0.61)

Figures 1-6. *Lentiella lamothei* n. sp. (1) genital atrium of immature proglottid showing vaginal dilation. (2) Scolex (3) Gravid uterus. (4) Egg showing pyriform apparatus and oncosphere. Scale bar = 0.01 mm (5) First postmature proglottid. (6) Mature proglottid. Scale bars = 0.1 mm for Fig. 1-3, 5-6.
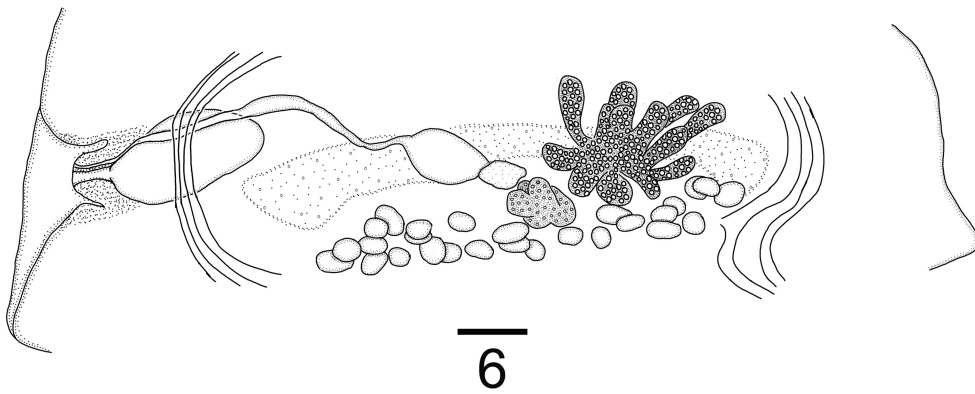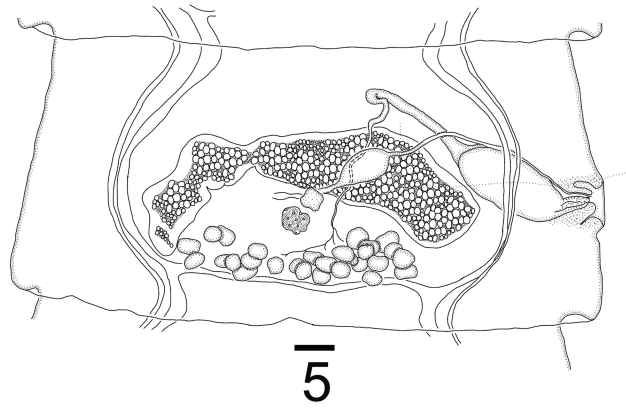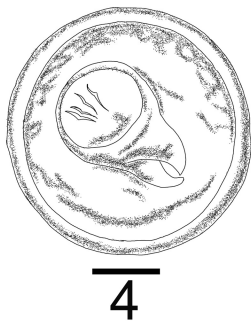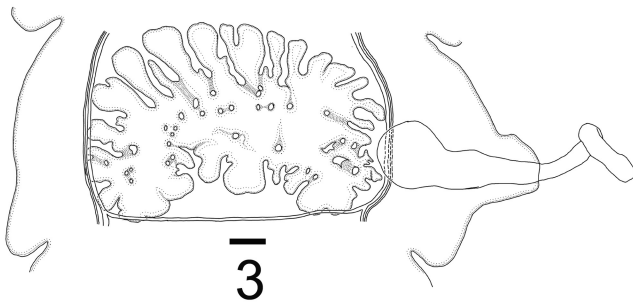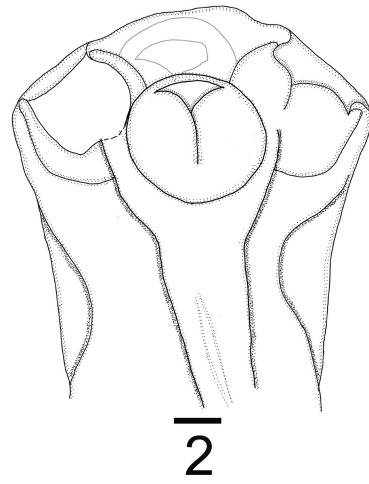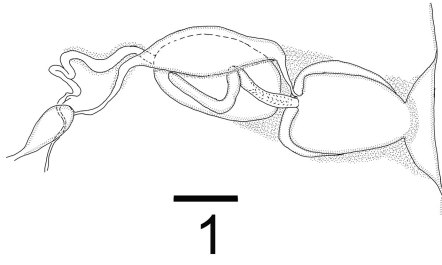
1

2

3

4

5

6

Figure 7-9. (7) *Lentiella lamothei* n. sp. paratype, full strobila. Scale bar=1mm (8)

Detailed view of the uterine development of *Anoplocephaloides* spp. Scale bar=0.1 mm

Specimen the collection of the author (TRH). (9) Detailed view of the uterine

development of *Lentiella lamothei* n. sp. holotype. Scale bar=0.1 mm

7

8

9