J. Parasitol., 96(3), 2010, pp. 580–595

NEW SPECIES IN THE GENUS *MONOECOCESTUS* (CESTODA: ANOPLOCEPHALIDAE) FROM 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, Nebraska 68588-0514. *e-mail: slg@unl.edu*

ABSTRACT: Anoplocephalid cestodes have a worldwide 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 segments (a character of potential taxonomic importance), and the implication of host usage to the evolutionary history and biogeography of species in this genus.

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 South America has probably been due to lack of adequate sampling (see Gardner and Campbell, 1992). Recent studies of the helminth fauna of mammals that have relatively great numerical density in parts of their range have yielded descriptions and redescriptions of several taxa (Denegri et al., 2003; Beveridge, 2008; Haverkost and Gardner, 2008). At the present time, fewer than 30 species of anoplocephaline cestodes (mostly *Monoecocestus* spp.) have been described from mammals in the Neotropics, and those that have been reported all occur in hystricognath and sigmodontine rodents (see Table I) (Voge and Read, 1953: Rego, 1961; Haverkost and Gardner, 2008, 2009).

MATERIALS AND METHODS

General biological survey work conducted with National Science Foundation support that took place throughout Bolivia from the 1980s 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, which is stored in the parasite collections of the Harold W. Manter Laboratory of Parasitology (HWML). For the present study, specimens examined also include material from the United States National Parasite Collection (USNPC) in Beltsville, Maryland.

Mammals collected in the field were immediately killed with chloroform and quickly examined for both ecto- and endoparasites (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. Some specimens were preserved in 95% ETOH and in liquid nitrogen for future molecular studies. 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, transferred subsequently to xylene, and permanently mounted on slides in Damar Gum. Superficial tissues, including tegument and muscles, were removed from the dorsal or ventral surface of mature segments to observe internal organs. Measurements of the strobila were made with an ocular micrometer. Measurements of segments were made by drawing the segment with the aid of a drawing tube and measuring the subsequently scanned picture with SigmaScan 5.0 (SPSS, Chicago, Illinois). From each strobila studied, 1–3 segments 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 segments 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.

Scolex length was measured from the anterior extremity of the scolex 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 segments. Thus, a higher number corresponds to more regular alternation. The widths of dorsal and ventral osmoregulatory canals were recorded at the midpoint of the segment on the antiporal side. Distribution of testes in segments 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 vitelline gland and the poral extremity/the total width of the segment (Sato et al., 1993). Measurements provided include the range, followed by mean, and the number of measurements if different than that given initially. When possible, 5 testes were measured per segment, and 5 eggs were measured per specimen. All measurements are provided in micrometers unless otherwise specified.

Records of host mammals are listed by their NK, DRG, or MSB catalog numbers (all housed in the Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico) and given symbiotype designation if specimens were given an MSB number. The host of *Monoecocestus mackiewiczi* had been deposited (after being collected in Paraguay) and was recently found at the University of Connecticut Museum in Storrs, Connecticut, and is listed by its UCM number.

DESCRIPTIONS

Monoecocestus andersoni n. sp.
(Fig. 1)

Diagnosis (based on 2 specimens and 6 segments): Cestode total length 99–112 mm (106 mm). Maximal width 5,044–5,141 (5,092). Scolex 180–188 (184) long, 420–436 (428) wide. Suckers directed laterad or anterio-laterad, 138–150 (145, n = 8) in diameter. Neck 320–620 (470) long, minimal width 388–408 (398). Adult cestodes with 165–205 (185) segments per strobila. Segments craspedote. Immature segments 250–312 (281) long, 1,778–2,309 (2,043) wide. Length:width ratio of immature segments 0.14. Mature segments 400–536 (445) long, 3,482–3,882 (3,698) wide. Length:width ratio of mature segments 0.10–0.15 (0.12). Gravid segments 1,030–1,746 (1,388) long by 5,044–5,117 (5,080) wide. Length:width ratio of gravid segments 0.29–0.69 (0.47). Dorsal osmoregulatory canal distal to ventral canal, 3–37 (24) wide. Ventral osmoregulatory canal 38–122 (71) wide; 1 transverse canal extending across the posterior of the segment at 4–32 (17) wide. Additional anastomoses may project from ventral and transverse canal. Testes number 58–109 (80) in each segment, each 66–118 (94, n = 30) in diameter. Testes posterior in segment, may occasionally intersect ventral and transverse osmoregulatory canal. Testicular distribution 2,492–2,886 (2,672). External seminal vesicle absent. Internal seminal vesicle present in postmature segments, of variable width and length due to variation in everted cirrus. Cirrus spined, often everted; cirrus sac 433–480 (451) long by 165–194 (179) in diameter. Cirrus sac extends beyond dorsal and ventral canals. Genital pores alternate irregularly, 68–84 switches per 100 segments. Genital pores alternate, on average, every 1.3 segments; no more than 5 segments in each unilateral set. Genital ducts cross osmoregulatory canals dorsally. Ovary 390–428

Received 5 March 2009; revised 21 July 2009; accepted 12 January 2010.
* To whom correspondence should be addressed.
DOI: 10.1645/GE-2089.1

TABLE I. South American species of *Monoecoestus* Beddard, 1914, including type locality (by country) and type host. Hosts marked with (‡) belong to various families in the infraorder Hystricognathi (Rodentia: Hystricomorpha). Hosts marked with (§) belong to the subfamily Sigmodontinae (Myomorpha: Muroidea: Cricetidae).

Scientific 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 hydrochoeri (Baylis 1928)	Paraguay	*H. hydrochaeri*‡
Monoecocestus jacobi Sinkoc, Müller & Brum 1998	Brazil	*H. hydrochaeri*‡
Monoecocestus mackiewiczi Schmidt & Martin 1978	Paraguay	*Graomys griseoflavus*§
Monoecocestus macrobursatus Rego 1961	Brazil	*H. hydrochaeri*‡
Monoecocestus microcephalus n. sp.	Bolivia	*G. 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	*G. musteloides*‡
Monoecocestus poralus n. sp.	Bolivia	*Phyllotis caprinus*§
Monoecocestus rheiphilus Voge & Read 1953	Peru	*Pterocnemia pennata*
Monoecocestus sininterus n. sp.	Bolivia	*Phyllotis wolffsohni*§
Monoecocestus threlkeldi (Parra 1952)	Peru	*Lagidium peruanum*‡
Monoecocestus torresi Olsen 1976	Chile	*Ctenomys maulinus* ‡

(405) long, 1,384–1,615 (1,439) wide. Ovary and vitelline gland slightly poral. Vitelline gland wider than long, 208–249 (226) long by 352–382 (370) wide; vitelline gland often bilobed with thin connection attaching 2 portions. Index of asymmetry 0.38–0.41 (0.40). Seminal receptacle ovoid, 373–469 (436) long, 139–218 (179) wide in mature segments. Vagina enters genital atrium anterior to cirrus sac. Vagina visible in segments throughout entire strobila. Vagina 626–1,090 (785) long. Vaginal dilation appears in immature segments and disappears in mature segments. Uterine diverticula 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. Eggs 55–70 (62, n = 10) in diameter. Embryophore in the form of pyriform apparatus 15–20 (18, n = 10) long. Oncospheres 8–13 (9, n = 10) in diameter.

Taxonomic summary

Host: Graomys domorum (Thomas, 1902) (Myomorpha: Cricetidae).

Locality: Bolivia, Cochabamba, 1.3 km W of Jamachuma, 2,800 m, 17°31′32″S, 66°07′29″W, July 1993.

Symbiotype designation: G. domorum (MSB70543).

Prevalence and intensity: One of 2 individuals infected with 2 worms.

Specimens deposited: HWML62672A (Holotype), HWML62672B (Paratype).

Etymology: The new species is named in honor of Dr. Sydney Anderson, Curator Emeritus at the American Museum of Natural History, New York, a fellow field biologist, leader in the field of Bolivian mammalogy, and good friend and mentor.

Remarks

Monoecocestus andersoni n. sp. can be distinguished from *Monoecocestus diplomys* by having a lesser total length, fewer proglottids, a greater maximal width, greater scolex width, smaller suckers, larger eggs, larger testes, a wider vitelline gland and ovary, more extensive distribution of testes, and genitalia oriented more porally. The new species can be distinguished from *Monoecocestus gundlachi* Vigueras, 1943, by having a lesser total length, smaller scolex, smaller pyriform apparatus, larger testes, lesser cirrus sac length, and greater vitelline gland and ovary width. *Monoecocestus andersoni* n. sp. can be distinguished from *Monoecocestus hagmanni* (Janicki, 1904) Rego, 1961, *Monoecocestus hydrochoeri* (Baylis, 1928) Spasskii, 1951, and *Monoecocestus jacobi* Sinkoc, Müller, and Brum, 1998, by having the following characters: lesser total length, scolex width, sucker diameter, cirrus sac length, vitelline gland width, and ovary width. The new species can be distinguished from *M. mackiewiczi* by having a greater total length, greater maximum width, greater scolex width and length, longer neck, greater vitelline gland and ovary width, and genitalia oriented more porad. *Monoecocestus andersoni* is different from *Monoecocestus minor* Rego, 1960, and *Monoecocestus threlkeldi* (Parra, 1952) by being larger in almost every measurement and having more poral genitalia, and from *Monoecocestus macrobursatus* Rego, 1961, by being longer and wider and having more proglottids, more numerous and larger testes, longer cirrus sac, wider vitelline gland, and greater width of ovary. The new species also has a smaller scolex in both length and width, smaller suckers, and a smaller pyriform apparatus than *M. macrobursatus*; it can be distinguished from *Monoecocestus myopotami* Sutton, 1973, by having a shorter strobila, more narrow scolex, and fewer but larger testes, and from *Monoecocestus rheiphilus* Voge and Read, 1953, by having a shorter strobila, lesser width of segments, narrower scolex and smaller sucker diameter, smaller eggs, and smaller diameter of pyriform apparatus. *Monoecocestus andersoni* is different from *Monoecocestus parcitesticulatus* Rego, 1960, and *Monoecocestus torresi* Olsen, 1976, by having a greater total length, greater scolex width, greater testes diameter, greater cirrus sac length, and a greater vitelline gland and ovary width.

***Monoecocestus eljefe* n. sp.**

(Figs. 2, 8)

Diagnosis (based on measurements of 5 specimens and 15 segments): Cestode total length 96–167 mm (129 mm), maximal width 1,373–1,934 (1,671). Scolex 124–192 (167) long, 288–368 (338) wide. Suckers directed laterad or anterio-laterad, 116–168 (150, n = 20) in diameter. Neck 200–720 (328) long, minimal width 260–348 (302). Adult cestodes with 178–264 (208) segments. Segments craspedote. Immature segments 144–374 (270) long, 768–1,123 (939) wide. Length:width ratio of immature segments 0.18–0.34 (0.28). Mature segments 331–807 (605) long, 1,146–1,604 (1,363) wide. Length:width ratio of mature segments 0.23–0.54 (0.42). Gravid segments 718–1,498 (1,148) long, 1,467–1,872 (1,660) wide. Length:width ratio of gravid segments 0.38–1.00 (0.72). Dorsal osmoregulatory canal 14–32 (23) wide, distal to ventral canal. Ventral osmoregulatory canal 16–347 (94) wide with 1 transverse canal per segment. Transverse osmoregulatory canal 8–240 (81) wide. Testes spherical or ovoid, 49–79 (63, n = 75) in diameter. Testes posterior and lateral to the vitelline gland, number 38–60 (48) per segment. Testicular distribution 430–616 (482). Testes may overlap vitelline gland, seminal receptacle, and posterior margins of ovary, ventral, and transverse osmoregulatory canals. External seminal vesicle long, sinuous. Internal seminal vesicle present. Measurements of the internal seminal vesicle are unreliable because it may be oblong when the cirrus is everted or when the cirrus sac is pressured by the ventral osmoregulatory canal.

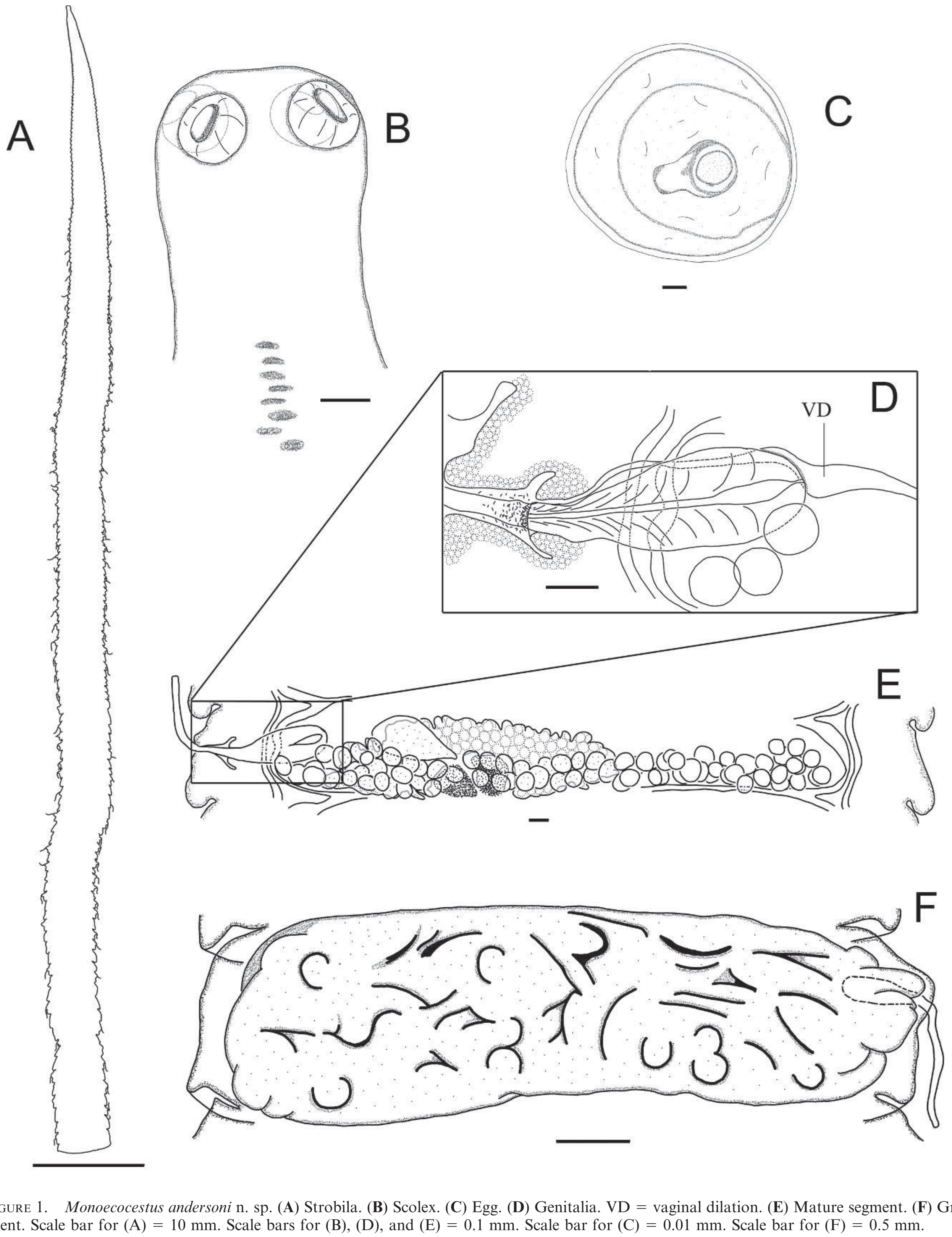

FIGURE 1. *Monoecocestus andersoni* n. sp. (**A**) Strobila. (**B**) Scolex. (**C**) Egg. (**D**) Genitalia. VD = vaginal dilation. (**E**) Mature segment. (**F**) Gravid segment. Scale bar for (A) = 10 mm. Scale bars for (B), (D), and (E) = 0.1 mm. Scale bar for (C) = 0.01 mm. Scale bar for (F) = 0.5 mm.

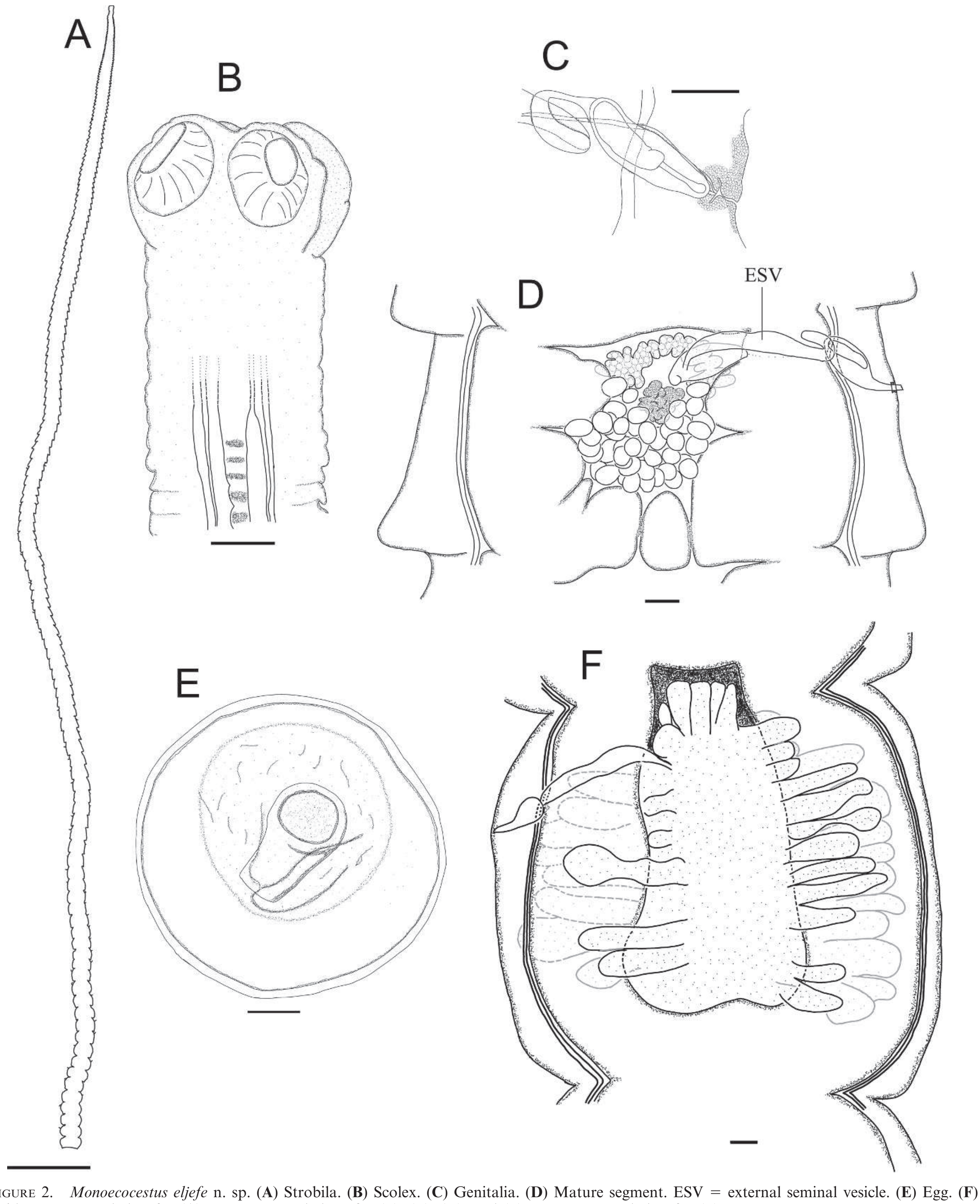

FIGURE 2. *Monoecocestus eljefe* n. sp. (**A**) Strobila. (**B**) Scolex. (**C**) Genitalia. (**D**) Mature segment. ESV = external seminal vesicle. (**E**) Egg. (**F**) Gravid segment. Scale bar for (A) = 10 mm. Scale bars for (B), (C), (D), and (F) = 0.1 mm. Scale bar for (E) = 0.01 mm.

Internal seminal vesicle appears in mature segments and remains prominent throughout postmature segments. Cirrus sac 105–272 (183) long, 51–100 (80) wide. Cirrus spined, often everted in postmature segments. Cirrus sac may cross dorsal and ventral osmoregulatory canals in immature and mature segments. Genital pores alternate irregularly, 34–52 (44) switches per 100 segments. Genital pores alternate approximately every 2 segments. Genital ducts pass osmoregulatory canals dorsally. Ovary 106–295 (207) long, 277–559 (361) wide. Vitelline gland globular, 91–176 (126) long, 106–195 (138) wide; vitelline gland posterior to ovary. Index of asymmetry 0.46–0.50 (0.48). Seminal receptacle ovoid, maximally 254 long, 97 wide in mature segments. Vagina enters genital atrium anterior or anterio-ventral to cirrus sac. 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 observed with the first sign of uterine development. During uterine development, uterine lobes gradually elongate and become either long and thin, stretching laterad or widen if directed anteriorly or posteriorly. Many tubes radiate from center and fenestrations not seen during development. Fully gravid uterus with few anterior or posterior diverticula; many finger-like projections directed laterad across ventral osmoregulatory canal. Uterine diverticula cross ventral canal both dorsally and ventrally. Egg 46–60 (50, n = 25) in diameter. Embryophore in form of pyriform apparatus, measures 18–27 (22, n = 25) long. Oncosphere 8–12 (10, n = 25) in diameter.

Taxonomic summary

Host: Galea musteloides Meyen, 1832 (Hystricomorpha: Caviidae) (NK23329).

Locality: Bolivia, Santa Cruz; 53 km E Boyuibe, 18°16′S, 63°11′W, 500 m elevation, July 1991.

Prevalence and intensity: One host examined, harboring 6 individual cestodes.

Specimens deposited: Holotype (HWML61289A) and paratypes (HWML61289 B–F).

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 diseases, who shared a similar nickname throughout the year of field research in both the Neotropic and the Nearctic Regions. We treat the epithet *eljefe* as a random combination of letters (International Code of Zoological Nomenclature, 1999, Article 11.3) in the masculine gender because it is appropriate, compact, euphonious, and memorable (International Code of Zoological Nomenclature, 1999, Rec. 25C).

Remarks

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 segments, and larger testes, and from *M. hydrochoeri* by having lesser width of the scolex, narrower vitelline gland width, narrower ovary width, and fewer testes. The new species can be distinguished from *M. diplomys* by having a lesser total length, greater length:width ratio in mature segments, shorter cirrus sac length, lesser testicular distribution, and a smaller index of asymmetry. *Monoecocestus eljefe* is distinguished from *M. jacobi* by having a lesser total length, lesser scolex width, sucker diameter, cirrus sac length, vitelline gland width, and ovary width, and from *M. mackiewiczi* by having a greater length:width ratio in all segments, lesser scolex width, greater neck length, lesser cirrus sac length, vitelline gland width, and ovary width. The new species is different from *M. andersoni*, *M. myopotami*, and *M. gundlachi* by having a lesser scolex width, fewer testes, lesser cirrus sac length, and lesser vitelline gland and ovary width, and a lesser total length than *M. myopotami*. The new species is different from *M. rheiphilus* by having a lesser total length, maximal width, egg diameter, and cirrus sac length, and from *M. parcitesticulatus* by having a lesser maximal width, scolex width, cirrus sac length, vitelline gland and ovary width, pyriform apparatus length, and a greater total length. *Monoecocestus eljefe* can be distinguished from *M. torresi* by having a greater total length, number of proglottids, number of testes, and a lesser maximal width, scolex width, and cirrus sac length.

***Monoecocestus microcephalus* n. sp.**

(Figs. 3, 9)

Diagnosis (based on 10 specimens and 30 segments): Cestode total length 58.2–250.7 mm (102 mm). Maximal width 3,900–4,850 (4,269). Scolex 368–488 (433, n = 9) wide, 200–248 (222, n = 9) long. Suckers directed anteriad, 128–200 (164, n = 36) in diameter. Neck 160–280 (223, n = 9) long, minimal width 528–712 (632, n = 9). Neck wider than scolex. Adult cestodes have 147–319 (194) segments per strobila. Segments craspedote. Immature segments 156–312 (228) long, 1,435–2,870 (2,168) wide. Length:width ratio of immature segments 0.08–0.15 (0.11). Mature segments 310–610 (402) long, 3,055–4,479 (3,492) wide. Length:width ratio of mature segments 0.09–0.14 (0.11). Gravid segments 998–1,872 (1,415) long by 2,028–3,977 (3,107) wide. Length:width ratio of gravid segments 0.29–0.69 (0.47). Dorsal osmoregulatory canal distal to ventral canal, 24–68 (45) wide. Ventral osmoregulatory canal 46–175 (113) wide with 1 transverse canal extending across posterior of segment at 17–217 (101) wide. Additional anastomoses may project from ventral and transverse osmoregulatory canal. Testes number 89–136 (109, n = 29) per segment, each 30–102 (60, n = 150) in diameter. Testicular distribution 1,825–3,465 (2,314). Testes posterior, in continuous field across each segment. Testes dorsally overlap vitelline gland, ovary, and occasionally ventral osmoregulatory canal. Testes not extending beyond ventral canal. External seminal vesicle absent. Internal seminal vesicle present, of variable width and length due to everted cirrus. Cirrus spined, often everted; cirrus sac 337–509 (432) long by 109–117 (145) wide. Cirrus sac extends proximad beyond dorsal and ventral canals. Genital pores alternating irregularly with 54–86 (44) switches per 100 segments. Genital pores alternate on average every 1.5 (n = 3) segments. No more than 6 segments in each unilateral set. Genital ducts crossing osmoregulatory canals dorsally. Ovary 274–514 (345) long, 959–2,261 (1,242) wide. Ovary and vitelline gland slightly poral. Vitelline gland wider than long, 127–277 (183) long by 286–679 (389) wide, often bilobed with thin connection attaching 2 portions. Index of asymmetry 0.34–0.45 (0.41). Seminal receptacle ovoid, 271–481 (368) long, 92–226 (170) wide in mature segments. Vagina visible in segments throughout entire strobila. Vagina 657–971 (831) long. Vaginal dilation appearing in immature segments, disappearing in mature segments. Uterus begins as a lobed sac, with size and number of lobes filling the segment. Uterus becoming reticulate. Uterine diverticula directed in all directions. Gravid uterus crosses osmoregulatory canals dorsally and ventrally. 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.

Taxonomic summary

Host: Graomys domorum (Thomas, 1902) (Myomorpha: Cricetidae) (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, 1,900 m, August 1991.

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

Specimens deposited: HWML61646B (holotype) HWML61646 A, C–F (paratypes) HWML61596 (voucher), HWML61622 (voucher).

Etymology: The new species is named for the small scolex.

Remarks

Monoecocestus microcephalus n. sp. can be distinguished from almost all other species of *Monoecocestus* since the neck of *M. microcephalus* is wider than its scolex and has its scolex inset into its neck with prominently anteriorly-facing suckers, traits shared only by *M. mackiewiczi*. The new species can also be distinguished from *M. mackiewiczi* by having a greater total length, greater mature segment width, ovary width, testicular distribution, and smaller index of asymmetry. *Monoecocestus microcephalus* can be separated from *M. macrobursatus*, *M. minor*, and *M. threlkeldi* by having a greater total length and more segments, and from *M. eljefe* by having a smaller length:width ratio in all segments, a greater scolex width, testicular distribution, vitelline gland width, ovary width, and a smaller index of asymmetry. *Monoecocestus microcephalus* is distinguished from *M. diplomys* by having a lesser gravid segment length:width ratio, a lesser neck length, neck width, cirrus sac width, greater mature segment width, vitelline gland width, ovary width, testicular distribution, and a smaller index of asymmetry, and from *M. hagmani*, which has a lesser scolex width, scolex length, sucker diameter, and vitelline width. The new species has a lesser scolex width, scolex length, sucker diameter, cirrus sac length, egg diameter, and fewer testes than *M. hydrochoeri* and *M. jacobi*. *Monoecocestus microcephalus* n. sp. can be distinguished from *M.*

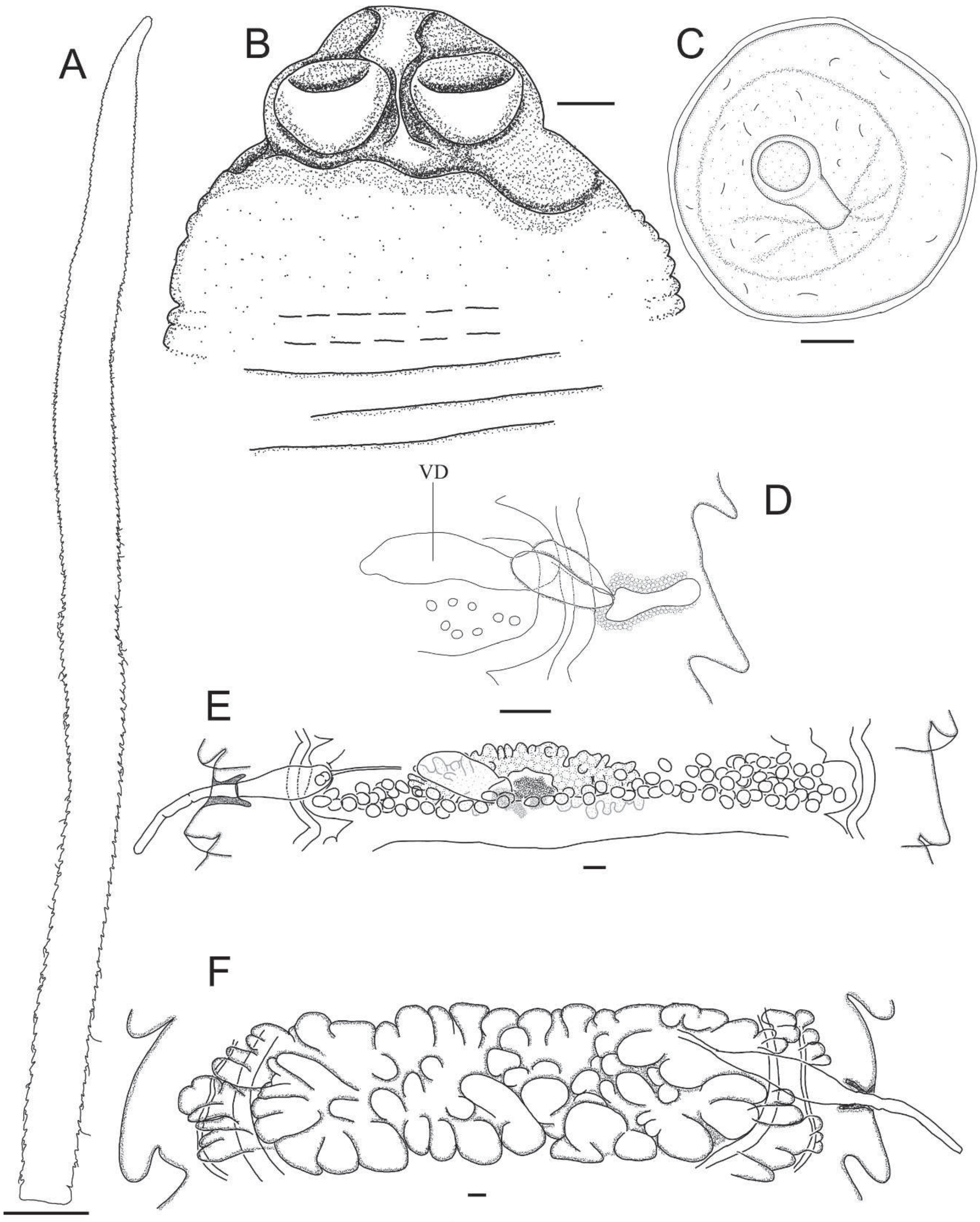

FIGURE 3. *Monoecocestus microcephalus* n. sp. (**A**) Strobila. (**B**) Scolex. (**C**) Egg. (**D**) Genitalia. VD = vaginal dilation. (**E**) Mature segment. (**F**) Gravid segment. Scale bar for (A) = 5 mm. Scale bars for (B), (D), (E), and (F) = 0.1 mm. Scale bar for (C) = 0.01 mm.

gundlachi by having a lesser maximal width, lesser scolex width, lesser cirrus sac length, but a greater number of testes, and from *M. myopotami* by having a lesser total length, scolex width, sucker diameter, number of testes, and ovary width. The new species is different from *M. parcitesticulatus* by having a lesser scolex width, but greater number and width of testes, greater vitelline gland, and ovary width, but a lesser pyriform apparatus length, and from *M. rheiphilus* by having a lesser maximal width, scolex width, sucker diameter, and egg diameter, but a greater number of testes. *Monoecocestus microcephalus* n. sp. is different from *M. torresi* in having a greater number of proglottids, greater total length, maximal width, number of testes, and ovary width. It is very similar to *M. andersoni*, but can be distinguished by having a lesser maximal length, lesser pyriform apparatus length, but a greater scolex length and neck length.

Monoecocestus petiso n. sp.
(Fig. 4)

Diagnosis (based on 5 specimens and 15 segments): Cestode total length 13.8–18.5 mm (15.5 mm). Maximal width 1,001–1,075 (1,045). Scolex 290–354 (319) wide, 150–196 (173) long. Suckers directed laterad or anterio-laterad, 127–173 (159, n = 20) in diameter. Neck 155–219 (202) long, minimal width 90–136 (115). Adult cestodes with 49–55 (51) segments per strobila. Segments craspedote. Immature segments 103–155 (140) long, 258–368 (333) wide. Length:width ratio of immature segments 0.40–0.47 (0.42). Mature segments 254–350 (307) long, 680–797 (729) wide. Length:width ratio of mature segments 0.33–0.49 (0.42). Gravid segments 626–788 (920) long, 810–994 (948) wide. Length:width ratio of gravid segments 0.63–1.00 (0.84). Dorsal osmoregulatory canal 2–10 (4) wide, distal to ventral canal. Ventral osmoregulatory canal 18–50 (39) wide with 1 transverse canal per segment. Transverse osmoregulatory canal 3–24 (9) wide. Testes spherical or ovoid, 28–45 (36, n = 75) in diameter, 15–26 (22) per segment. Testes posterior, overlapping vitelline gland and ovary, rarely overlapping ventral osmoregulatory canal. Testicular distribution 234–330 (271). Internal and external seminal vesicles appears in late-mature segments and remains prominent in segments throughout remaining strobila; internal seminal vesicle 25–53 (37, n = 12) long, 41–25 (32, n = 12) wide. External seminal vesicle surrounded by thick cellular coating. Cirrus sac 130–241 (169) long, 73–86 (79) wide. Cirrus spined. Genital pores alternate regularly, switching lateral margins 94–100 (98) times per 100 segments. Genital ducts pass osmoregulatory canals dorsally. Ovary measures 170–246 (208) long, 262–376 (304) wide. Ovary with very large lobes, almost fills entire segment. Vitelline gland globular, measures 56–81 (72) long, 63–129 (106) wide; posterior to ovary. Vitelline gland laterally elongated, may form shallow horseshoe shape. Index of asymmetry 0.48–0.55 (0.52). Vagina enters genital atrium anterior to cirrus sac. Vaginal dilation appears in immature segments, remains prominent until late-mature segments. Vagina visible throughout strobila. Seminal receptacle ovoid, reaching maximum of 92 long and 68 wide in mature segments. Seminal receptacle appears in segments as vaginal dilation disappears. Maximum dimensions for seminal receptacle 40 (n = 6), reached in postmature segments. Uterus begins sac-like, develops fringes and lobes. The uterus divided by 2 prominent lobes as uterus forms around vitelline gland. Egg diameter 45–57 (49, n = 25). Oncosphere 7–14 (10, n = 25) in diameter surrounded by pyriform apparatus 18–23(21, n = 25) long.

Taxonomic summary

Host: Galea musteloides Meyen, 1832 (Hystricomorpha: Caviidae) (NK30468).

Locality: Bolivia, Cochabamba, 7.5 km SE Rodeo Curubamba, 4,000 m, 17°40′31″S, 65°36′04″W, July 1993.

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

Specimens deposited: HWML62702D (holotype) HWML62702 A–C, E (paratypes).

Etymology: The new species, "the small one," is named because of the small size of the representatives of this species.

Remarks

Monecocestus petiso n. sp. differs from *M. andersoni*, *M. eljefe*, *M. diplomys*, *M. gundlachi*, *M. mackiewiczi*, *M. hagmanni*, *M. hydrochoeri*, *M. jacobi*, *M. microcephalus*, *M. myopotami*, *M. parcitesticulatus*, and *M. rheiphilus* by having a much lesser total length. The new species can be distinguished from *M. macrobursatus* by having a greater length:width ratio in all segments, lesser scolex width and sucker diameter than *M. macrobursatus*, a lesser segment width in all segments, lesser vitelline gland width and ovary width than *M. macrobursatus* and *M. threlkeldi*, and from *M. torresi* by having a lesser maximal width, scolex width, cirrus sac length, and number and width of testes.

Monoecocestus poralus n. sp.
(Fig. 5)

Diagnosis (based on 1 specimen and 3 segments): Cestode total length 116 mm, maximal width 5,529. Scolex 190 long, 372 wide. Suckers directed laterad or anterio-laterad, 138–140 (139, n = 4) in diameter. Neck 520 long, minimal width 408. Adult cestode has 230 segments. Segments craspedote. Immature segments 250 long, 1966 wide. Length:width ratio of immature segments 0.13. Mature segments 460–475 (468) long, 3,076–3,151 (3,106) wide. Length:width ratio of mature segments 0.15. Gravid segments 874 long, 4,056 wide. Length:width ratio of gravid segments 0.22. Dorsal osmoregulatory canal 37–45 (42) wide, distal to ventral canal. Ventral osmoregulatory canal 37–65 (55) wide with 1 transverse canal per segment. Transverse osmoregulatory canal 19–31 (23) wide. Many anastomoses connecting ventral and transverse osmoregulatory canals. Testes spherical or ovoid, 55–69 (64, n = 5) in diameter. Testes number 51–71 (62) per segment. Testicular distribution 1,170–1,279 (1,210). Testes may overlap ventral and transverse osmoregulatory canals. External seminal vesicle absent. Internal seminal vesicle 60–120 (90) long by 66–90 (78) wide. Cirrus sac extends proximad from ventral osmoregulatory canal unless cirrus extended in peduncle. Cirrus sac 343–486 (436) long, 179–197 (186) wide. Cirrus spined. Genital pores alternate regularly, switching lateral margins 92 times per 100 segments. Genital atrium deep in immature segments, peduncles common in mature and postmature segments. Genital ducts pass osmoregulatory canals dorsally. Ovary does not reach midline; 345–350 (347) long, 584–631 (615) wide. Vitelline gland resembles horseshoe, 124–173 (151) long, 320–350 (347) wide; posterior to ovary. Index of asymmetry 0.34–0.35 (0.34). Seminal receptacle ovoid, 154–170 (161) long, 101–117 (109) wide in mature segments. Vagina enters genital atrium anterior or anterio-ventral to cirrus sac. Vaginal dilation appears in immature segments, disappears in mature segment. Uterus reticulate, with no prominent lobes or branches. Uterus does not extend far distally beyond ventral osmoregualtory canal, overlaps ventral canal both dorsally and ventrally. Egg diameter 58–70 (63, n = 10). Oncosphere 13–15 (13, n = 10) in diameter surrounded by pyriform apparatus 18–23 (21, n = 10) long.

Taxonomic summary

Host: Phyllotis caprinus Pearson, 1958 (Myomorpha: Cricetidae) (NK23566).

Locality: Bolivia; Tarija: Serrania Sama; 3,200 m; 21°21′S, 64°52′W, July 1991.

Prevalence and intensity: One of 19 hosts infected with a single worm.

Specimens deposited: HWML 61440 (holotype).

Etymology: The new species is named for the poral nature of the genitalia.

Remarks

Monoecocestus poralus n. sp. can be distinguished from *M. hagmanni*, *M. macrobursatus*, *M. minor*, *M. parcitesticulatus*, *M. petiso*, *M. threlkeldi*, and *M. torresi* by having greater total length and more segments, and from *M. mackiewiczi* by having lesser scolex width, ovary width, and index of asymmetry. The new species differs from *M. eljefe* by having greater width in all segments, but a smaller length:width ratio in all segments, and a greater scolex width, egg diameter, cirrus sac length, vitelline gland width, and ovary width. It is different from *M. diplomys* in having a smaller sucker diameter, and a greater egg diameter, mature segment width, vitelline gland width, and ovary width. *Monoecocestus poralus* has a lesser ovary width and testicular distribution than *M. microcephalus* and *M. andersoni*, and can further be distinguished from both *M. microcephalus* and *M. andersoni* by having a lesser scolex length and width, neck length, and seminal receptacle length. The new species can be separated from *M. gundlachi*, *M. hydrochoeri*, and *M. myopotami* by having a greater total length, scolex width, sucker diameter, and ovary width, and from *M. hydrochoeri* having larger but fewer testes, lesser cirrus sac length, vitelline

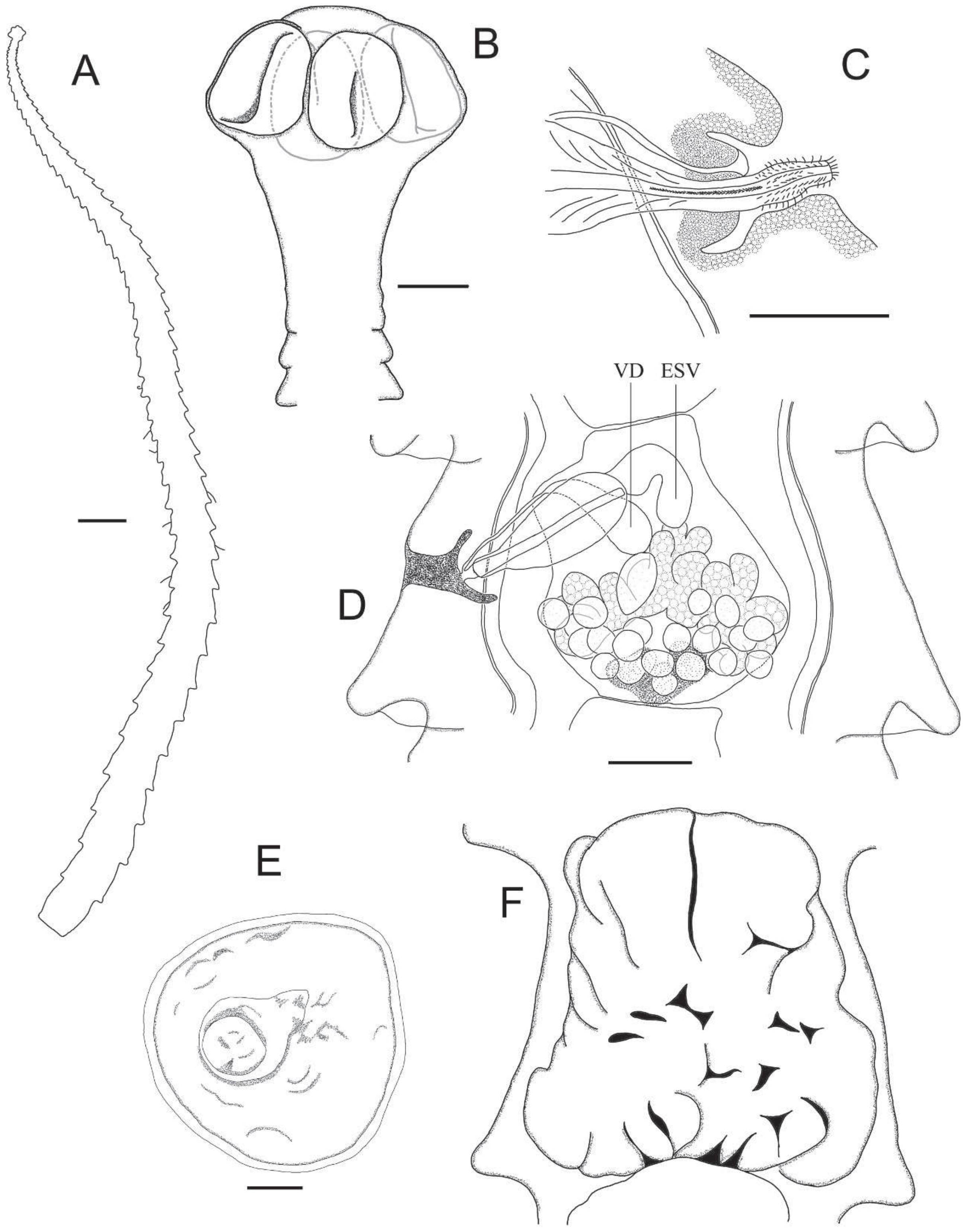

FIGURE 4. *Monoecocestus petiso* n. sp. (**A**) Strobila. (**B**) Scolex. (**C**) Genitalia. (**D**) Mature segment. VD = vaginal dilation, ESV = external seminal vesicle. (**E**) Egg. (**F**) Gravid segment. Scale bar for (A) = 1 mm. Scale bars for (B), (C), (D), and (F) = 0.1 mm. Scale bar for (E) = 0.01 mm.

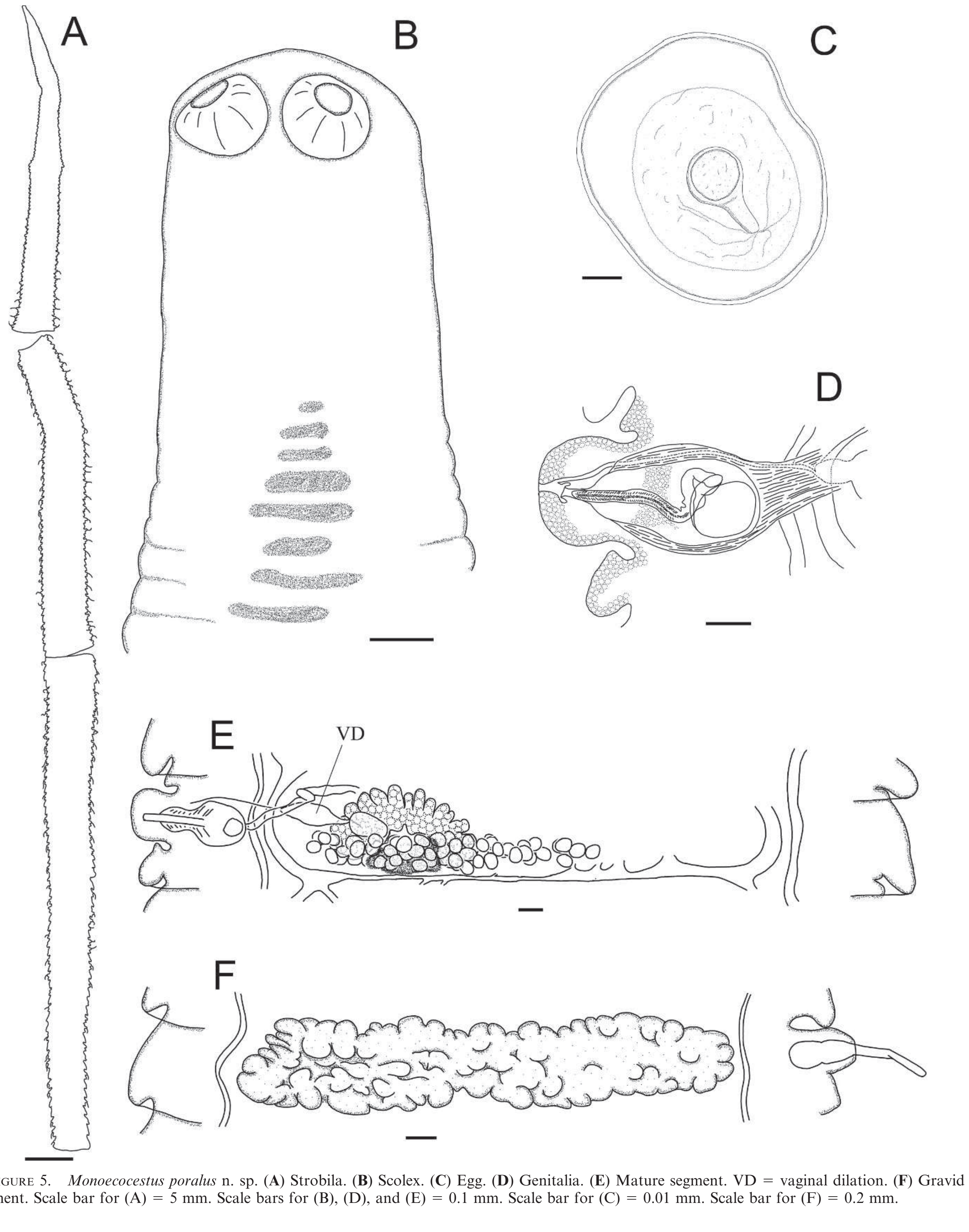

FIGURE 5. *Monoecocestus poralus* n. sp. (**A**) Strobila. (**B**) Scolex. (**C**) Egg. (**D**) Genitalia. (**E**) Mature segment. VD = vaginal dilation. (**F**) Gravid segment. Scale bar for (A) = 5 mm. Scale bars for (B), (D), and (E) = 0.1 mm. Scale bar for (C) = 0.01 mm. Scale bar for (F) = 0.2 mm.

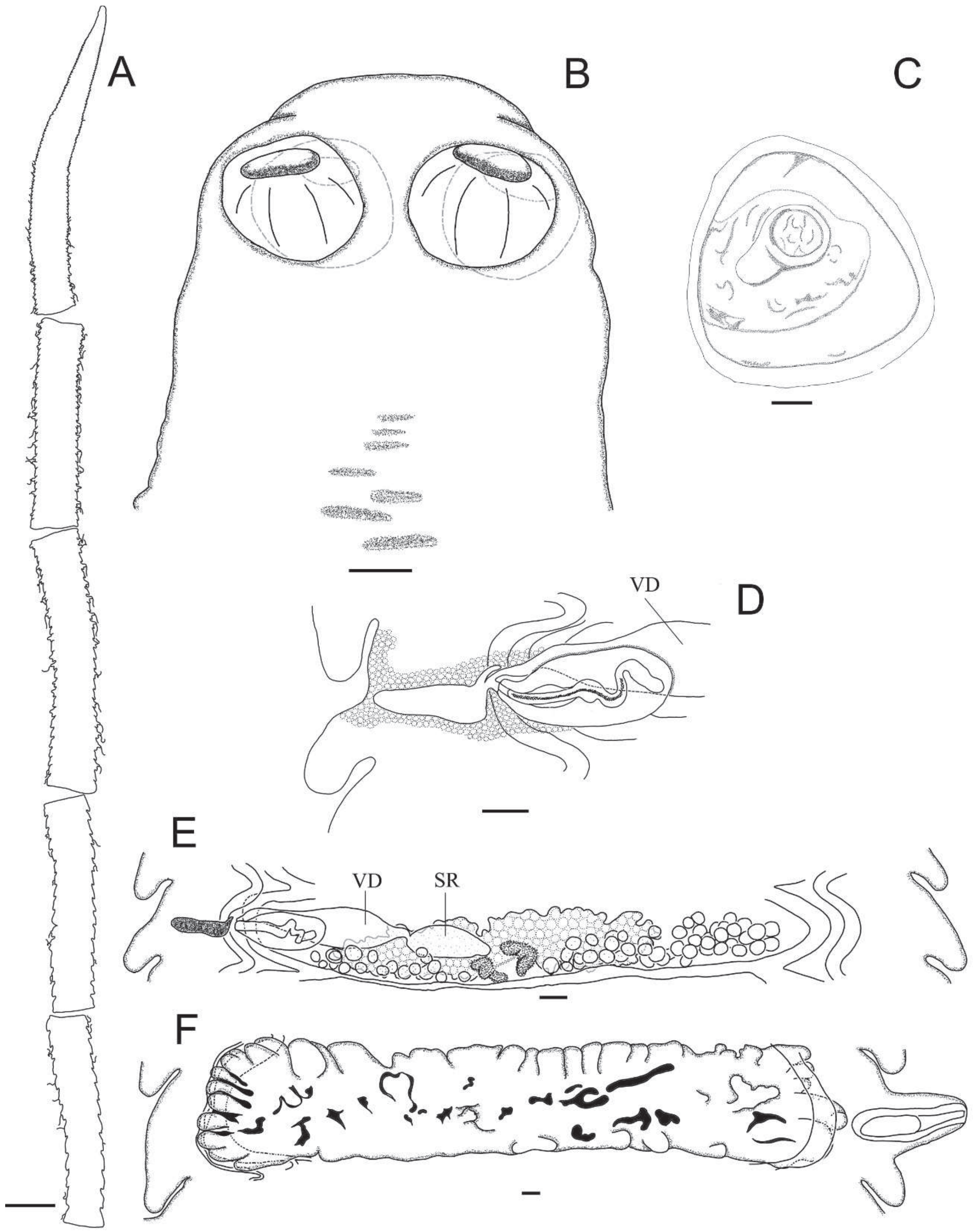

FIGURE 6. *Monoecocestus sininterus* n. sp. (**A**) Strobila. (**B**) Scolex. (**C**) Egg. (**D**) Genitalia. VD = vaginal dilation. (**E**) Mature segment. SR = seminal receptacle. (**F**) Gravid segment. Scale bar for (A) = 5 mm. Scale bars for (B), (D), (E), and (F) = 0.1 mm. Scale bar for (C) = 0.01 mm.

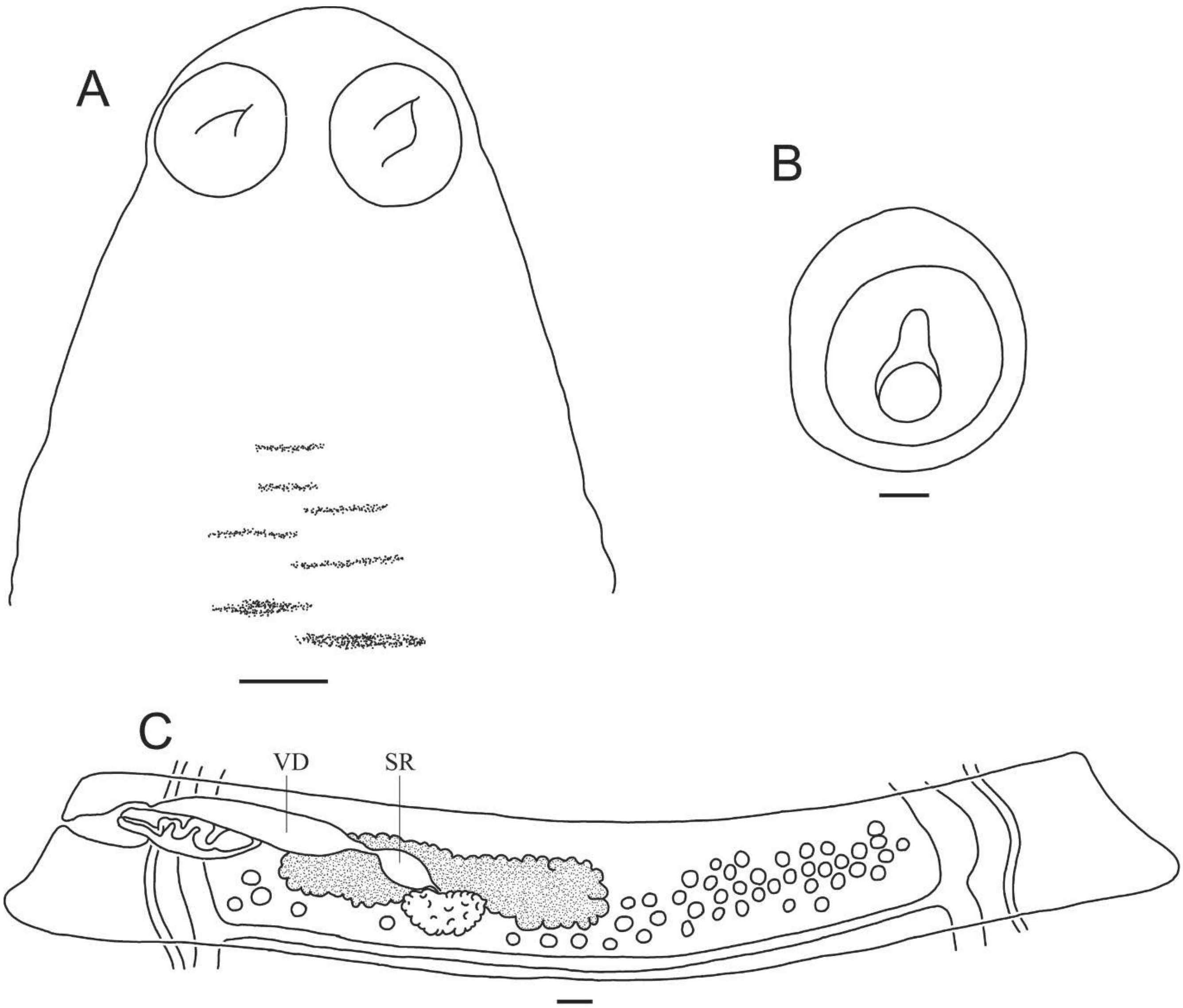

FIGURE 7. *Monoecocestus mackiewiczi*. Redrawn from Schmidt and Martin, 1978. (**A**) Scolex. (**B**) Egg. (**C**) Mature segment. VD = vaginal dilation, SR = seminal receptacle. Scale bars for (A) and (C) = 0.1 mm. Scale bar for (B) = 0.01 mm.

gland width, and a lesser pyriform apparatus length. *Monoecocestus poralus* is distinguished from *M. jacobi* by having fewer proglottids, a lesser total length, maximal width, scolex width, sucker diameter, cirrus sac length, and ovary and vitelline gland width, and from *M. rheiphilus* by having more poral genitalia, a greater total length, pyriform apparatus length, and testes diameter, but a lesser scolex width.

Monoecocestus sininterus n. sp.

(Fig. 6)

Diagnosis (based on 1 specimen and 3 segments): Cestode total length 115 mm. Maximal width 4,850. Scolex 620 wide, 320 long. Scolex small, flush with neck; suckers directed anteriad, 218–232 (224, n = 4) in diameter. Neck slightly wider than scolex, minimal width 704. Neck 400 long. Full specimen has 211 segments per strobila. Segments craspedote. Immature segments 156 long, 1,685 wide. Length:width ratio of immature segments 0.09. Mature segments 261–321 (291) long, 2,925–3,544 (3,182) wide. Length:width ratio of mature segments 0.08–0.10 (0.09). Gravid segments 1,746 long by 3,783 wide. Length:width ratio of gravid segments 0.46. Dorsal osmoregulatory canal distal to ventral canal, 47–56 (53) wide. Ventral osmoregulatory canal 70–116 (95) wide with single transverse canal extending across posterior of segment at 2–49 (24) wide. Additional anastomoses may project from ventral canal. Testes number 49–69 (61) in each segment, each 36–84 (54, n = 15) in diameter. Testicular distribution 1,623–2,280 (1,894). Testes extend length of segment in posterior field. Testes may intersect but do not wholly overlap ventral osmoregulatory canal. Internal seminal vesicle small, does not appear until postmature segments. External seminal vesicle absent. Peduncle often forms around cirrus sac in postmature segments. Cirrus sac overlaps or reaches proximad beyond ventral osmoregulatory canal. Cirrus spined, often everted; cirrus sac 312–445 (357) long by 126–195 (151) wide. Genital pores alternate irregularly with 82 switches per 100 segments. Genital pores form unilateral pairs, on average, every 4 segments. Genital ducts cross osmoregulatory canals dorsally. Genital atrium reaches dorsal osmoregulatory canal in immature and mature segments, becomes more shallow as cirrus everts in postmature segments. Ovary 231–325 (269) long by 1,137–1,469 (1,269) wide. Ovary and vitelline gland slightly poral. Index of asymmetry 0.45–0.48 (0.47). Seminal receptacle ovoid, 0–283 (186) long, 0–117 (77) wide in mature segments. Vagina enters genital atrium anterior to cirrus sac. Vaginal dilation appears in immature segments, disappears in late mature

TABLE II. Selected measurements of *Monoecocestus* species.

	Monoecocestus andersoni n. sp.		*Monoecocestus eljefe* n. sp.		*Monoecocestus microcephalus* n. sp.		*Monoecocestus mackiewiczi*	*M. mackiewiczi*	
Host	*Graomys domorum*		*Galea musteloides*		*G. domorum*		*Graomys griseoflavus*	*G. griseoflavus*	
Source	This study	n	This study	n	This study	n	Schmidt and Martin, 1978	Type material, this study	n
No. of segments	165–205 (185)	2	178–264 (208)	5	147–319 (196)	10	200	120–176 (148)	2
Total length (mm)	99–112 (106)	2	96–167 (129)	5	58–250 (102)	10	70–115	46–75 (60)	2
Max. width (mm)	5.04–5.14 (5.09)	2	1.37–1.93 (1.67)	5	3.90–4.85 (4.27)	10	3.5–4.5	3.3–3.6 (3.5)	2
Scolex width	420–436 (428)	2	288–368 (338)	5	368–488 (433)	9	360–415	360–400 (380)	2
Scolex length	180–188 (184)	2	124–192 (167)	5	200–248 (222)	9	175–225	188–240 (214)	2
Sucker diameter	138–150 (145)	8	108–168 (149)	20	128–200 (164)	36	120–160	125–160 (144)	8
Neck width (min)	388–408 (398)	2	260–348 (302)	5	528–712 (632)	9	—	188–230 (209)	2
No. of testes	58–109 (80)	6	38–60 (48)	15	89–136 (109)	29	—	52–96 (66)	6
Testis width	66–118 (451)	30	49–79 (63)	75	30–102 (60)	150	30–48	35–70 (50)	30
Cirrus sac length	433–480 (451)	6	105–272 (183)	15	337–509 (432)	30	360–440	350–411 (381)	6
Ovary width	1,384–1,615 (1,439)	6	277–559 (361)	15	959–2,261 (1,242)	30	240–320	320–930 (736)	6
Vitelline gland width	352–382 (370)	6	106–195 (138)	15	286–679 (389)	30	—	230–310 (267)	6
Genital alternation	68–84	2	34–52 (44)	5	54–86 (44)	10	—	—	—
Egg width	55–70 (62)	10	40–60 (50)	25	44–64 (55)	45	58–60	52–58 (58)	5
Index of asymmetry	0.38–0.41 (0.40)	6	0.46–0.50 (0.48)	15	0.34–0.45 (0.41)	30	—	0.43–0.48 (0.45)	6

segments. Vaginal dilation has greater width than seminal receptacle in the same segment. Vitelline gland wider than long, 149–176 (161) long by 241–352 (296) wide, often bilobed with thin connection attaching 2 portions. Uterine diverticula directed in all directions. Gravid uterus crosses osmoregulatory canals dorsally and ventrally. 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.

Taxonomic summary

Host: *Phyllotis wolffsohni* Thomas, 1902 (Myomorpha: Cricetidae) (NK30396).

Locality: Bolivia, Cochabamba, 1.3 km W of Jama Chuma, 2,800 m, 17°31′32″S, 66°07′29″W, July 1993.

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

Specimens deposited: HWML62667 (holotype).

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

Remarks

Monoecocestus sininterus n. sp. can be distinguished from *M. mackiewiczi* by having a greater total length, more segments, greater scolex width, neck width, sucker diameter, and ovary width, and from *M. andersoni* by having a greater total length, more segments, smaller width in all segments, greater scolex width, neck width, sucker diameter, smaller vitelline gland width, testes distribution, and a greater index of asymmetry. The new species differs from *M. minor*, *M. macrobursatus*, *M. parcitesticulatus*, *M. petiso*, *M. threlkeldi*, and *M. torresi* by having a greater total length and more segments, and from *M. microcephalus* by having a greater scolex width, sucker diameter, smaller testes, and more central genitalia. *Monoecocestus sininterus* is separated from *M. eljefe* by having greater width in all segments, but a smaller length:width ratio in all segments, a greater scolex width, neck width, sucker diameter, cirrus sac length, ovary width, and testes distribution. The new species is different from *M. diplomys* by having a lesser total length, fewer segments, greater scolex width, neck width, mature segment width, cirrus sac length, vitelline gland width, and ovary width, and from *M. hagmanni*, *M. jacobi*, and *M. hydrochoeri* by having a lesser total length, scolex width, sucker diameter, vitelline gland width, and ovary width. The new species can be distinguished from *M. gundlachi* by having a lesser total length, pyriform apparatus length, cirrus sac length, but greater maximal width, sucker diameter, and vitelline gland width, and from *M. myopotami* by having a lesser total length, maximal width, scolex width, sucker diameter, pyriform apparatus length, and ovary width. *Monoecocestus sininterus* differs from *M. poralus* by having a greater scolex width, sucker diameter, and distribution of testes, but a lesser maximal width and number of proglottids. The new species is distinguished from *M. rheiphilus* by having a lesser maximal width, scolex width, sucker diameter, egg diameter, and pyriform apparatus length.

REDESCRIPTION

Monoecocestus mackiewiczi Schmidt and Martin, 1978

(Fig. 7)

Observations (based on 2 type specimens, 6 segment measurements): Total length 46–75 mm (60.5 mm). Maximal width 3,340–3,686 (3,513). Scolex 360–400 (380) wide, 188–240 (214) long. Suckers not in grooves, directed anteriad, 125–160 (144, n = 8) in diameter. Neck wider than scolex, 272–420 (346) wide. Neck short, 188–230 (209) long. Strobila with 120–176 (148) segments. Segments craspedote. 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 segment at 5–50 (16) in diameter. Additional anastomoses may project from ventral canal. Immature segments 300–312 (306) long, 2,440–2,746 (2,593) wide. Length:width ratio of immature segments 0.11–0.12 (0.12). Mature segments 280–370 (326) long, 2,400–3,180 (2,821) wide. Length:width ratio of mature segments 0.09–0.15 (0.11). Gravid segments 1,000–1,248 (1,124) long by 1,940–3,557 (2,749) wide. Length:width ratio of gravid segments 0.35–0.52 (0.43). Testes number 52–96 (66) in each segment, each 35–70 (50, n = 30) in diameter. Testicular distribution 1,050–1,810 (1,552).

TABLE III. Selected measurements of additional *Monoecocestus* species.

	Monoecocestus petiso n. sp.		*Monoecocestus poralus* n. sp.		*Monoecocestus sininterus* n. sp.	
Host	*Galea musteloides*		*Phyllotis caprinus*		*Phyllotis wolffsohni*	
Source	This study	n	This study	n	This study	n
No. of segments	49–55 (51)	5	230	1	211	1
Total length (mm)	13.8–18.5 (15.5)	5	116	1	115	1
Max. width (mm)	1.00–1.07 (1.04)	5	5.53	1	4.85	1
Scolex width	290–354 (319)	5	372	1	620	1
Scolex length	150–196 (173)	5	190	1	320	1
Sucker diameter	127–173 (159)	20	138–140 (139)	4	218–232 (224)	4
Neck width (min)	90–136 (115)	5	408	1	704	1
No. of testes	15–26 (22)	15	51–71 (62)	3	49–69 (61)	3
Testis width	28–45 (36)	75	55–69 (64)	5	36–84 (54)	15
Cirrus sac length	130–241 (167)	15	343–486 (436)	3	312–445 (357)	3
Ovary width	262–376 (303)	15	584–631 (615)	3	1,137–1,469 (1,269)	3
Vitelline gland width	63–129 (106)	15	320–350 (347)	3	241–352 (296)	3
Genital alternation	94–100 (98)	5	92	1	82	1
Egg width	45–57 (49)	25	58–70 (63)	10	55–63 (60)	5
Index of asymmetry	0.51–0.52 (0.51)	2	0.34–0.35 (0.34)	3		

Testes scattered throughout segment in posterior field, 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. Internal seminal vesicle appears in late mature segments. External seminal vesicle absent. Cirrus everted in late mature segments throughout rest of strobila, may form a peduncle. Cirrus sac 350–411 (381) long by 135–175 (155) wide. Cirrus spined. Genital pores alternate irregularly, switching lateral margins 64 times per 100 segments. Genital ducts cross osmoregulatory canals dorsally. Genital atrium reaches dorsal osmoregulatory canal in immature and mature segments. Ovary 100–268 (190) long by 320–930 (736) wide. Index of asymmetry 0.43–0.48 (0.45). Seminal receptacle ovoid, 150–306 (227) long, 65–150 (114) wide in mature segments. Seminal receptacle forms early, enlarges before vaginal dilation appears. Vagina enters genital atrium anterior to cirrus sac. Vaginal dilation appears in immature segments, disappears in mature segments. Vitelline gland wider than long, 115–176 (148) long by 230–310 (267) wide, often bilobed with thin connection attaching 2 portions. Uterus begins as lobed sac, with size and number of lobes filling segment. Reticulations present in developing uterus. Uterine diverticula directed in all directions. Uterus crosses osmoregulatory canals dorsally and ventrally. 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.

Taxonomic summary

Type host: Graomys griseoflavus (Myomorpha: Cricetidae) (UCM16499).

Locality: Juan de Zalazar, Boqueron, Paraguay.

Specimens studied: USNPC No. 73083 (holotype), USNPC No. 73084 (paratype).

Remarks

In the original paper (Schmidt and Martin, 1978) the type host of *M. mackiewiczi* was listed as a potential new species of *Phyllotis*. The vertebrate collections manager from the University of Connecticut found the host specimens in the collections and informed us that the host was later identified as *Graomys griseoflavus* (S. Hochgraf, pers. comm.). Because it is impossible to trace which host in the series of *G. griseoflavus* was the host, we give the symbiotype designation to UCM16499.

From this study, we find that the measurements of *M. mackiewiczi* differ from the original in that the specimen has a shorter total length, fewer segments, a lesser maximal width, a smaller egg diameter, and a much wider ovary width. It is unclear why most of these measurements are larger than in the original description. One explanation is that our specimens were based on the measurement of mature segments; it is unclear from the original description which segments were measured (immature, mature, gravid), and what was used to measure them. This redescription is also based on the 2 type specimens available at the USNPC. The 2 voucher specimens deposited by Schmidt and Martin (1978) were examined but not used in this analysis because of their poor quality. Redescriptions based on only 2 of the 4 specimens available could change the measurement ranges for many of the characters used. However, because the ranges of measurements are based on the only 2 quality specimens, we are confident that our measurements more accurately represent *M. mackiewiczi*.

DISCUSSION

There is uncertainty surrounding the name of the type species of this genus, *Monoecocestus decrescens* (Diesing, 1856) Fuhrmann, 1932, or *M. hagmanni* (Janicki, 1904) Freeman, 1949, and the specimens surrounding the confusion. To alleviate future confusion regarding the taxonomy of this species, we include a short synopsis of the renaming of this species and the taxonomy used in the present work.

Rego (1961) considered *M. decrescens* a junior synonym of *M. hagmanni*. Both were represented by specimens with identical measurements (Baer, 1927), and no representatives of *M. decrescens* have been found in its "claimed" host, *Tayassu pecari* (Link, 1795), since the original collection by Natterer in 1825 (see Rego, 1961). Because of these 2 facts, it is assumed by Rego (1961) and us that *Hydrochoerus hydrochaeris* (Linnaeus, 1766) is the type host for the type species of the genus, *M. hagmanni*. In the following descriptions, we compare the redescribed and new species with *M. hagmanni* (Janicki, 1904) sensu Rego (1961), although Spasskii (1999) considers *M. decrescens* the type species for the genus. Measurements for *M. thelkeldi* (Parra, 1952), *M. minor* Rego, 1960, and *M. macrobursatus* Rego, 1961, are taken from Haverkost and Gardner (2009). Measurements of *M. diplomys* Nobel and Tesh, 1974, are original measurements taken by 1 of us (T.R.H.) from the holotype (USNPC72960). A table of representative measurements is provided in Tables II and III.

The ontological/morphological development of the uterus in species of the cestodes of the Anoplocephalinae is one of the most important taxonomic characters that taxonomists use to assign species to various genera (Rausch, 1976; Tenora et al., 1986;

Wickström et al., 2005). It has recently been noted (Haverkost and Gardner, 2009) that species can be assigned to *Monoecocestus* by virtue of the uterus crossing the osmoregulatory canals both dorsally and ventrally. Also, the ontological development of the uterus of species of *Monoecocestus* from South America differs slightly from that of their counterparts from North America. Few anterior and poseterior diverticula similar to species of *Anoplocephaloides* and *Paranoplocephala* are seen. The early uterus of the South American species can be described as the development of a lobed sac, with subsequent lobes overlapping the former distally. Reticulations may be present as the uterine wall thickens, but fenestrations (windows) are rarely seen. This pattern was observed in the species described and observed in this work and alluded to by many other researchers (Vigueras, 1943; Rego, 1960, 1961; Noble and Tesh, 1974; Olsen, 1976; Schmidt and Martin, 1978). Figures 8 and 9 show this development of the uterus in *M. eljefe* and *M. microcephalus*, respectively. In all species the uterus eventually fills the segment 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 segments, 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 segments. The presence of the vaginal dilation and the pattern of its development do seem to vary slightly among species. No specimens studied with this dilation showed the constrictions of an external seminal vesicle (Tinnin et al., 2008). The study of additional specimens is necessary to confirm if this feature is taxonomically informative. Figures 4–7 show the vaginal dilation in *M. petiso*, *M. poralus*, *M. sininterus*, and *M. mackiewiczi*.

It is evident that the best results for studying the eggs of anoplocephalid cestodes are achieved if the eggs are removed from a segment, cleared in lactophenol, and mounted on a slide under a coverslip in lactophenol or other clearing reagent (see Denegri et al., 2003; Beveridge, 2007). By studying the eggs with a compound microscope using the above method, it is clear that the "filaments" of the pyriform apparatus (once thought to be valid and important taxonomic characters for the genus; Spasskii, 1999) are actually folds of the internal membrane of the egg where it meets the pyriform apparatus, as shown by Denegri et al. (2003).

The sampling effort attained by the Bolivian Biodiversity Survey in its expeditionary phase was generally meant to target as many mammals from as many habitats 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 stored there will yield similar results of several new species (for example, see Hugot and Gardner, 2000; Gardner and Pérez-Ponce de León, 2002; Jiménez-Ruiz and Gardner, 2003; Jiménez-Ruiz et al., 2008).

FIGURE 8. Uterine development in a series of segments from *Monoecocestus eljefe* n. sp.

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 well. From our cursory work, a total of 4 species of *Monoecocestus* described herein are found thus far only in sigmodontines. It is assumed that species of *Monoeces-*

FIGURE 9. Uterine development in a series of segments from *Monoecocestus microcephalus* n. sp.

tus originated in South America from an unknown ancestor because 20 of the 27 species of *Monoecocestus* are found in South America, and it is more parsimonious to assume this diversification happened within their hosts before the Great American Interchange (GAM; cf. Marshall, 1985). However, until we perform a phylogenetic analysis, we will not know the true nature of this diversification because characters that are widespread are not necessarily plesiomorphic, or "common does not equal primitive." At any rate, in this scenario, the parasites could have infected new hosts in North America as the ancestral erethizontid migrated north as early as 2.6 million yr ago during the GAM across the Panamanian land bridge. Because sigmodontine rodents are found in South America prior to the final development of the Panamanian land bridge (Smith and Patton, 1999), 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.

The descriptions of *M. poralus* and *M. sininterus* are both based on 1 specimen collected respectively in 1991 and 1993. We recognize that describing new species based on a single specimen is somewhat controversial. Although we are confident that these 2 specimens represent 2 valid new species, the validity of these (and all) species should be tested with new field collections and laboratory research. Because no species of *Monoecocestus* has been described in the past 11 yr, we feel it is more important to describe *M. poralus* and *M. sininterus* as new in the hopes that the current work will stimulate new investigations of Neotropical cestodes.

ACKNOWLEDGMENTS

We would like to thank Eric Hoberg and Pat Pilitt at the USNPC for their hospitality during a visit by T.R.H. to the national museum. The field expeditionary work in Bolivia was funded by the National Science Foundation Survey and Inventory Program (BSR-8612329 to S. L. Gardner, D. W. Duszynski, and T. L. Yates; BSR-9024816 and DEB-9496263 to S. L. Gardner; BSR-8408923 to T. L. Yates; BSR-8316740 to S. A. Anderson). Additional support was provided directly by the American Museum of Natural History, the Museum of Southwestern Biology, and the Tinker Foundation. The following organizations provided either specimens or logistic support in the field: El Museo National de Historia Natural, La Paz, Bolivia; the Museum of Southwestern Biology, the University of New Mexico; and El Instituto Boliviano de Biologia de la Altura, La Paz, Bolivia, and the Harold W. Manter Laboratory of Parasitology Development and Endowment Funds. Special thanks to Joseph A. Cook, Jorge Salazar-Bravo, and Jackie Miralles for all the hard work and camaraderie in the field in Bolivia from 1984 to 2000.

LITERATURE CITED

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

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.

———. 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.

CHANDLER, A. C., AND C. L. SUTTLES. 1922. A new rat tapeworm, *Schizotaenia sigmodontis*, from North America. Journal of Parasitology **8:** 123–128.

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.

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. 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.

———, AND M. L. CAMPBELL. 1992. Parasites as probes for biodiversity. Journal of Parasitology **78:** 596–600.

———, AND G. PÉREZ-PONCE DE LEÓN. 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.

———, AND ———. 2009. A redescription of three species of *Monoecocestus* (Cestoda: Anoplocephalidae) including *Monoecocestus threlkeldi* based on new material. Journal of Parasitology **93:** 695–701.

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

INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE. 1999. International Commission on Zoological Nomenclature, 4th ed. International Trust for Zoological Nomenclature, London, U.K., 306 p.

JIMÉNEZ-RUIZ, A., J. K. BRAUN, M. L. CAMPBELL, AND S. L. GARDNER. 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.

———, AND S. L. GARDNER. 2003. Aspidoderid nematodes from Bolivian armadillos, with the description of a new species of *Lauroia* (Heterakoidea: Aspidoderidae). Journal of Parasitology **89:** 978–983.

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 (eds.). Plenum Press, New York, New York, p. 49–85.

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.

RAUSCH, R. L. 1976. The genera *Paranophlocephala* Luhe, 1910 and *Anoplocephaloides* Baer, 1923 (Cestoda: Anoplocephalidae) with particular reference to species in rodents. Annales de Parasitologie Humaine et Comparee **51:** 513–562.

———, 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: Cyclophilldea). Atas da Sodedade de Biología do Rio de Janeiro **4:** 73.

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

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.

SCHMIDT, G. D., AND R. L. MARTIN. 1978. Tapeworms of the Chaco Boreal, Paraguay, with two new species. Journal of Helminthology **52:** 205–209.

SMITH, M. F., AND J. L. PATTON. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: Evidence from cytochrome b. Journal of Mammalian Evolution **6:** 89–128

SPASSKII, A. A. 1951. Anoplocephalate tapeworms of domestic and wild animals. Academy of Sciences of the USSR, Moscow (English translation, Israel Program for Scientific Translations, Jerusalem, Israel, 1961), 783 p.

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

TENORA, F., É. MURAI, AND C. VAUCHER. 1986. On *Andrya* Railliet, 1893 and *Paranoplocephala* Luhe, 1910 (Cestoda, Monieziinae). Parasitologica Hungarica **19:** 43–75.

TINNIN, D. S., S. L. GARDNER, AND S. GANZORIG. 2008. Helminths of small mammals (Chiroptera, Insectivora, Lagomorpha) from Mongolia with a description of a new species of *Schizorchis* (Cestoda: Anoplocephalidae). Comparative Parasitology **75:** 107–114.

VIGUERAS, I. P. 1943. Un genero y cinco especies nuevas de helmintos Cubanos. Revista Universidad de la 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.