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A new genus and two new species of unarmed hymenolepidid cestodes (Cestoda: Hymenolepididae) from geomyid rodents in Mexico and Costa Rica

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Abstract

Two new cestodes of the family Hymenolepididae are described from two species of rodents of the family Geomyidae collected in Mexico and Costa Rica. One new species of *Hymenolepis* is described from *Cratogeomys planiceps* Merriam 1895 from near Toluca, Mexico and another that we allocate to a new genus is described from *Heterogeomys heterodus* (Peters, 1865) from near Irazú Volcano, Costa Rica. *Hymenolepis s. str.* includes those Hymenolepididae with an apical organ, with no hooks on suckers or apical organ, and three testes. *Hobergia irazuensis* **n. gen., n. sp.** includes a hymenolepidid with an apical organ, unarmed scolex, small pockets termed foveolae, in which the suckers completely retract, and extremely bi-lobed ovary. Multivariate morphometric analysis showed good separation of these species from all other hymenolepidids possessing an apical organ and lacking a well developed rostellum and rostellar hooks in the Nearctic and Neotropical regions.

Key words: bilobed ovary, DAMA Protocol, discriminant analysis, *Hobergia* **n. gen.,** *Hobergia irazuensis* **n. gen., n. sp.**, Hymenolepididae, *Hymenolepis cratogeomyos,* new genus, new species, morphology

Introduction

As natural ecological systems on the earth continue to be rapidly obliterated by human activities it is imperative for scientists with knowledge of field biology to report in the scientific literature the results of field-based surveys based on specimens that were collected and deposited in recognized museums, thus establishing a record of the existence of species before they are completely annihilated (Brooks *et al*., 2014; Ceballos *et al*., 2017). Following, we provide descriptions of two new species of cestodes of the family Hymenolepididae recovered from pocket gophers (Rodentia: Geomyidae) collected from relatively high-altitude habitats in both Mexico and Costa Rica of the southern Nearctic and the northern Neotropical regions, respectively. To enable a more complete understanding of the hymenolepidid cestode fauna of pocket gophers, we start this paper by providing a basic introduction to these mammals.

Pocket gophers of the family Geomyidae Bonaparte, 1845 are subterranean rodents that have an extensive geographic and ecological range in the Nearctic and northern Neotropical regions with species representing several genera occupying suitable habitat in mostly the western and far southeastern North America, south through central America into the northern part of South America (Alberico 1990; Hall 1981; Solari 2013).

At the current time, about 40 species of pocket gophers are recognized with these having been allocated to six genera divided among two tribes including: The tribe Geomyini with *Cratogeomys* Merriam 1895, *Geomys* Rafinesque 1817, *Heterogeomys* Merriam 1895, *Pappogeomys* Merriam 1895, and *Zygogeomys* Merriam 1895, and the Tribe Thomomyini, includes only the speciose genus *Thomomys* Wied-Neuwied 1839 (see: Russell 1968; Wilson & Reeder 2005; Spradling *et al*. 2016).

Extant species of *Thomomys* are known only from the western part of the Nearctic but fossils that can be as-

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signed to species included in this genus have been reported from sedimentary deposits as early as Pliocene time on the east coast of North America with records of extinct species of this genus ranging from the states of Maryland to Florida in the USA (Simpson 1928; Kurtén & Anderson 1980; Wilkins 1985).

Published records derived from collections of parasites from Geomyidae in the Nearctic show that cestodes including species of the genus *Hymenolepis* Weinland, 1858 are common parasites of these rodents (Douthitt 1915; English 1932; Rankin 1945; Burnham 1953; Voge 1955; Frandsen & Grundmann 1961; Gardner 1985; Gardner & Schmidt 1988; Gardner *et al*. 2014). A review of this literature shows definitively that the Geomyidae have a specific and diverse helminth fauna especially relative to their hymenolepidid cestodes (Gardner & Schmidt 1988; Makarikov *et al*., 2012; Gardner *et al*. 2014) but understanding the faunal structure and historical ecology of helminth parasitism in the geomyids in the Nearctic is still developing (Douthitt, 1915; English, 1932; Brooks & McLennan, 1993; Bartel & Gardner, 2000) and is still nascent in the northern Neotropical Region.

Up to the present time, investigations of tapeworms of the genus *Hymenolepis* from pocket gophers have mostly focussed on species of these mammals occurring in the western and central Nearctic region (Table 1) (Gardner & Schmidt 1988) and little information is available relative to the helminth fauna of the Geomyidae from south of the United States/Mexico border; in fact, before the current work, no hymenolepidids from geomyid rodents had been reported in the primary literature from Mexico, Central America, or northern South America.

TABLE 1. List of reports of species of the family Hymenolepididae from Geomyidae in the Nearctic and northern Neotropical regions.

Host	Species of Hymenolepis	Geographic locality	References
Thomomys bottae (Eydoux and Gervais)	*H. citelli* (McLeod, 1933)	California	Voge, 1955
	Hymenolepis sp. (Weinland, 1858)	California	Voge, 1955
Thomomys bulbivorus (Richardson)	*H. tualatinensis* Gardner, 1985	Willamette Valley, Oregon	Gardner, 1985
Thomomys talpoides (Richardson)	*H. diminuta* (Rudolphi, 1819)	Eastern Washington State	Rankin, 1945
	H. citelli	Utah	Frandsen and Grundmann, 1961
Thomomys umbrinus (Richardson)	*H. citelli*	Utah	Frandsen and Grundmann, 1961
Geomys bursarius (Shaw)	*H. diminuta*	Oklahoma	Burnham, 1953
	H. weldensis Gardner and Schmidt, 1988	Eastern Colorado	Gardner and Schmidt, 1988
	H. geomydis Gardner and Schmidt, 1988	Eastern Colorado	Gardner and Schmidt, 1988
	H. weldensis	Illinois/Indiana	Haukisalmi *et al*., 2010
	Hymenolepis sp.	Texas	English, 1932
Geomys lutescens Merriam	*H. weldensis*	Nebraska	This study
Geomys spp.	*Hymenolepis* spp.	Midwestern United States	Douthitt, 1915
Cratogeomys planiceps (Merriam)	*H. cratogeomyos* n. sp.	Toluca, Mexico	This study

Species of the family Hymenolepididae Perrier, 1897 have a cosmopolitan distribution, sometimes occurring in high prevalence and relatively great numerical densities in the gastrointestinal tracts of birds and mammals (Gardner *et al*. 2014; Makarikov *et al*. 2015). Spasskii (1954) was the first author to exclude the hymenolepidids with armed scolexes from the rest of the members of the family that have no armed rostellum. However, the complete life-histories of most species in the family are, as yet, unknown, but of those for which we have data, evidence shows that most life-cycles of cestodes in the Hymenolepididae are complex, and depending on the species, include a bird or

mammal as the definitive or final-host, and some species of arthropod as the secondary or intermediate host (Gardner & Schmidt 1988).

This paper reports two new species of cestodes that can be allocated to the family Hymenolepididae. Both were discovered during focussed surveys of pocket gophers in Mexico and Costa Rica. These new species may seem insignificant in the scheme of modern humanity, but the knowledge of their existence in rodents at a specific place and time provides a snapshot view of the ecological complexity that occurred there at that specific moment in time thus providing details about the local environment that would otherwise remain hidden (Manter, 1966; Brooks & McLennan, 1993; Gardner & Campbell, 1992). Subsequent work defining the phylogenetic relationships among these species will be important to enable us to understand the origin of these species relative to their host mammals; this information is essential to both implement and conduct studies based on the DAMA protocol (Brooks *et al*., 2014) which we fully support.

Materials and methods

Specimens used in the following description of a new genus and species of hymenolepidid were collected in 1990 from agricultural fields and pasture-land at the northeastern edge of the village/city of Potrero Cerrado in the province of Cartago in Costa Rica, elevation 2,140 m (Bonino & Hilje, 1992). While pocket gophers identified as *Heterogeomys heterodus* (Peters, 1865) were collected and examined for cestodes, no information is available relative to other parasites that may have occurred in or on these same gophers. All cestodes recovered were preserved and stored in 70% ethanol and sent to SLG by Robert M. Timm, University of Kansas. Specimens of *H. heterodus* collected during the survey were not deposited in a museum in Costa Rica nor anywhere else that we could find (R.M. Timm, pers comm, 1/11/2020).

Material used for the description of the new species of *Hymenolepis* from *Cratogeomys planiceps* (Merriam 1895) was collected in 1998 during field surveys led by Mark S. Hafner, Curator Emeritus, Museum of Natural Sciences, Louisiana State University, Baton Rouge, LA. Individuals of *C. planiceps* were collected from an area consisting of agricultural fields and mixed pine forest near the Parque Nacional Nevado de Toluca, México (Hafner *et al*. 2004). During this work, one individual of *C. planiceps* was fortuitously discovered to harbor several tapeworms. The cestodes were preserved directly in 95% ethanol without pre-processing and sent to SLG. The individual pocket gopher from which the cestodes were recovered was deposited in the mammal collection of the LSU museum of Natural Sciences (LSUMZ36120).

In the laboratory, specimens were stained with Semichon's acetic carmine, dehydrated in ethanol, cleared in terpineol and xylene, and mounted permanently on slides in Canada balsam. Specimens were studied using a Zeiss Axiophot™ microscope using both bright-field and Normarsky illumination. Images were prepared using software from Zeiss [AxioVision™ (V4.6.3.0)] and Photoshop CS5™. Line drawings were prepared directly from images using "layers" in Adobe Photoshop and a Wacom-Intuos™ tablet and stylus.

Terminology for morphological characters of adults and larval cestodes (eggs) follows Chervy (2009), Maggenti (2005), and Gardner & Schmidt (1988). All specimens of cestodes were deposited as voucher and type specimens in the H.W. Manter Laboratory of Parasitology Parasite Collections (HWML).

Multivariate canonical discriminant (CANDISC), stepwise discriminant (STEP), and principal component analyses (PCA) were conducted with SAS ® software, version 9.4 using 17 quantitative characters taken from six different species of *Hymenolepis* spp. and *Hobergia irazuensis* **n. gen., n. sp.** (Tables 1 & 2). Measurement data from original archival computer files maintained by the Manter Laboratory, for the species *H. diminuta* (Rudolphi, 1819), *H. geomydis* Gardner & Schmidt, 1988, *H. weldensis* Gardner & Schmidt, 1988, *H. tualatinensis* Gardner, 1985, *H. weldensis* Gardner & Schmidt, 1988, and *H. robertrauschi* Gardner *et al*., 2014 were taken from data originally archived in the HWML from the combined data set of Gardner at al. (2014). All measurements of cestodes collected from the pocket gophers *C. planiceps* and *H. heterodus* were taken from individual specimens deposited in the Manter Laboratory (HWML No. 139035-139054). An *a-priori* level of significance of $p < 0.05$ was set for all statistical analyses. Any deviations from normality in the mensural data were estimated via calculations of skewness and kurtosis using SAS and Microsoft Excel™. Variables with distributions not conforming to statistical

TABLE 2. Quantitative and qualitative characters of *Hymenolepis* and *Hobergia* n. gen., n. sp. of the Nearctic and Northern Neotropical Region (all units in micrometers unless otherwise indicated).

Characters	***H. citelli*** [1];*	***H. diminuta*** [2];[4];[8];*	***H. folkertsi*** [3];*	***H. geomydis*** [4];*	***H. pitymi*** [5];*	***H. robertrauschi*** [6];*
Strobila length	23–29 mm	128–329 mm	99–116 mm	72–168 mm	23–24 mm	42–83 mm
Strobila width	0.70–0.73 mm	1.44–2.94 mm	1.71–1.85 mm	1.98–3.30 mm	0.75–0.76 mm	1.18–2.54 mm
No. of proglottids	424–754	1025–1188	790–850	456–697	481	284–454
Scolex width	184–197	188–244	168–175	194–245	159	199–257
Sucker size	87–96 x 114–133	176–235 x 188–244	70–86 x 93–102	65–94 x 92–124	45–55 x 63–76	82–95 x 119–164
Apical organ sac length	125–140	82–93	67–73	68–74	49–73	86–92
Testes size	185–232 x 84–107	94–223 x 89–202	75–112 x 44–62	55–180 x 81–180	37–47 x 30–36	99–165 x 73–128
External seminal vesicle	59–67 x 31–39	141–247 x 38–73	65–98 x 31–49	45–202 x 27–130	103–115 x 24–26	119–160 x 36–75
Internal seminal vesicle	122–137 x 35–45	202–388 x 31–49	78–110 x 26–33	40–177 x 32–70	52–56 x 20–23	84–157 x 26–53
Cirrus–sac size	173–188 x 43–54	202–388 x 31–49	138–154 x 30–39	83–160 x 36–67	71–87 x 29–35	147–232 x 33–61
Cirrus armature	Armed	Armed	Armed	Armed	Armed	Armed
Ventral canals width	26–34	16–17	25–52	23–90	10–11	21–38
Ovary width	253–266	108–329	147–217	180–484	42–50	130–297
Vitelline Gland width	70–87 x 123–146	47–103 x 176–235	30–57 x 55–98	61–137 x 101–209	15–16 x 18–23	45–102 x 46–118
Seminal receptacle size	220–229 x 37–46	71–540 x 28–200	275–365 x 37–62	99–369 x 55–89	183–210 x 42–51	190–246 x 45–102
Egg size	74–90 x 54–69	67–83 x 61–77	54–75 x 40–53	76–85 x 72–83	42–61 x 28–42	57–76 x 44–58
Embryo hooks **						
Large	17–20 x 3–5	16–18 x 3.7–5	15–18 x 3–4.3	18–20 x 3.5–5	14–18 x 3–4.8	16–18 x 3.5–4.4
Small	17–20 x 2.2–3.2	15–17 x 2.1–3	15–17.8 x 2–2.8	19–21 x 2.7–3	13–17 x 2–3	15.5–19 x 2–2.5
Middle	16–19 x 1.7–2.2	16–18 x 2.5–2.9	15–20 x 2–2.7	17–21 x 2.3–3	12–15 x 1.62–1.95	16–18 x 1.7–2.2

....*Continued next page*

TABLE 2, (Continued)

Characters	*H. scalopi*[7];*	*H. tualatinensis*[8];*	*H. weldensis*[4];*	*H. cratogeomyos* n. sp.*	*H. irazuensis n. gen.*, n. sp.*
Strobila length	100–200 mm	24–210 mm	112–165 mm	88–129 mm	53–65 mm
Strobila width	2.57 mm	0.39–1.58 mm	1.87–2.29 mm	2.72–3.41 mm	1.69–2.18 mm
No. of proglottids	999–1070	274–602	821–943	1257–1266	531–640
Scolex width	170–232	150–272	126–288	209–227	334–426
Sucker size	55–62 x 86–92	70–122 x 113–120	85–106 x 109–126	84–89 x 109–117	110–161 x 102–146
Apical organ sac length	121	51–75	77–88	55–59	96–128
Testes size	101–123 x 87–113	58–141 x 54–141	94–127 x 92–166	141–190 x 95–121	132–179 x 78–107
External seminal vesicle	136–175 x 52–65	28–134 x 11–49	63–183 x 20–78	181–197 x 92–97	219–289 x 70–90
Internal seminal vesicle	72–84 x 42–49	41–80 x 14–40	87–159 x 20–48	80–93 x 31–41	85–112 x 34–44
Cirrus–sac size	125–159 x 45–53	56–153 x 26–49	149–194 x 34–51	121–145 x 45–57	145–197 x 41–56
Cirrus armature	Armed	Armed	Armed	Armed	Armed
Ventral canals width	74–84	14–38	43–137	87–95	42–57
Ovary width	192–220	82–216	90–293	168–203	125–166
Vitelline Gland width	68–83 x 78–92	34–109 x 37–132	50–112 x 54–106	45–53 x 62–80	57–79 x 132–199
Seminal receptacle size	533–597 x 60–68	48–169 x 23–73	175–552 x 43–148	746–919 x 75–93	369–483 x 55–74
Egg size	65–80 x 49–62	57–89 x 42–68	70–81 x 67–77	62–94 x 40–63	34–45 x 25–42
Embryo hooks **					
Large	16–19.5 x 3.6–4.3	16–19.7 x 3–4.3	16–19.2 x 3.2–4.7	16–20 x 3.4–4.8	9–12 x 2–2.8
Small	16–21 x 2.1–2.8	17.6–21 x 2.–2.5	16–18.7 x 2.3–3	14–20 x 2.3–3.3	9–12.6 x 1.5–2
Middle	16–21 x 1.8–2.4	16–19 x 2–2.4	17–19 x 2–2.6	15–19 x 1.6–2.3	11–14 x 1.4–2

[1]Measurements from McLeod (1933); [2] Genov (1984); [3]Makarikov *et al.* (2015); [4]Gardner & Schmidt (1988); [5]Yarinsky (1952); [6]Gardner *et al.* 2014; [7]Schultz (1939); [8]Gardner (1985); * measurements were taken in present study. **(Total hook length x guard width).

normality were log transformed (log_{10}) and reassessed for normality; any characters that deviated from normality after transformation were not used in the analyses. Log-transformed data were used for all subsequent analyses.

In the following, six species of both *Hymenolepis* and *Hobergia* **n. gen.** from Rodentia were included in a canonical variates analysis using 17 quantitative-mensural characters from 41 individual cestodes (see: Table 3 and Figs. 10 & 11). To examine the data-set for well-defined groups the data were first analyzed with a PCA and subsequently analyzed using CANDISC. Five of the six *Hymenolepis* species analyzed are found exclusively in the Americas; however, *H. diminuta* as it is currently understood as a species, is cosmopolitan with a global distribution, probably made so via synanthropic hosts which are usually species of the genus *Rattus* Fischer 1803, but many other species of mammals have been reported as definitive or final hosts for this tapeworm (Burt, 1980). A phylogenetic analysis was conducted using a complex suite of morphological characters, the results of which are being published elsewhere (Gardner & Racz, in review).

TABLE 3. List of characters with loadings on canonical axes and variation in canonical structure. CAN I, with more than 50% of the variation shown in the analysis is influenced most by the seminal receptacle length and external seminal vesicle length and width; CAN II which contributes about 25% to the total variation in the analysis shows number of proglottids and length of strobila to be most important in separating species.

Variable	CAN I	CAN II	CAN III	CAN IV
Maximum strobila length	-0.15	-0.56	-0.26	0.60
Maximum strobila width	0.33	-0.01	0.06	0.70
Number of proglottids	0.42	-0.68	-0.24	0.50
Cirrus sac length	0.39	0.38	-0.61	0.41
Cirrus sac width	0.44	0.12	0.45	0.15
Internal seminal vesicle length	0.39	0.27	-0.66	0.38
Internal seminal vesicle width	0.12	0.32	0.32	0.30
External seminal vesicle length	0.68	0.39	-0.07	0.33
External seminal vesicle width	0.69	0.23	-0.02	0.39
Testes length	0.51	0.10	-0.13	0.33
Testes width	0.07	-0.13	-0.14	0.65
Seminal receptacle length	0.82	-0.04	-0.09	0.21
Seminal receptacle width	0.25	0.02	-0.25	0.49
Ovary length	0.35	-0.40	0.25	0.00
Ovary width	0.36	0.31	0.33	0.70
Vitelline gland width	0.33	0.20	0.60	0.36
Vitelline gland length	0.02	0.08	0.09	0.66
Percentage of variation of each canonical axis (CI)	51.04%	25.10%	12.66%	7.59%
Summed variation accounted for by each CI	51.04%	76.15%	88.81%	96.40%

Results

For the following descriptions, all measurements are given in micrometers unless otherwise specified. Character number 3 refers to number of proglottids. Number of individuals examined is indicated by (N) and numbers in parentheses are mean ± standard deviation (Tables 1 & 2). From complete strobilae, measurements of organs from mature regions were taken from each of the 5 proglottids immediately anterior to those proglottids in which eggs begin to appear in the uterus.

Class Cestoda van Beneden, 1849

Order Cyclophyllidea van Beneden, 1850

Family Hymenolepididae Perrier, 1897

Subfamily Hymenolepidinae Perrier, 1896

***Hobergia* n. gen.**
(Figs. 1–6)
LSIDurn:lsid:zoobank.org:act:439BC5C8-B0AE-4108-94ED-044B34E1DB9D

Type and only species: *Hobergia irazuensis* **n. gen., n. sp.**

Diagnosis: Hymenolepididae, Hymenolepidinae. Strobila elongate, widest at level just anterior to terminal gravid proglottids. Strobila attenuated and narrowest in neck region, posteriad to scolex. Scolex with four fully developed and separate suckers (Fig. 1). Each sucker with foveola and associated structures. Foveolae completely contain suckers when suckers are retracted (Fig. 2). Apical organ, piriform (Fig. 1). Anterior most part of osmoregulatory canals not penetrating apical organ sac. Transverse tubes connect ventral osmoregulatory canals. Genital ducts pass dorsal to osmoregulatory canals. Genital pores dextral, marginal, and unilateral. Cirrus sac, internal seminal vesicle, and external seminal vesicle dorsal to seminal receptacle, ovary, vitelline gland, and Mehlis' gland. Vitelline and Mehlis' glands posterior and slightly ventral to divided ovary. Two laterally extended lobes of ovary, connected by narrow isthmus, clearly lie on each side of vitelline gland. Gravid proglottids with transverse saccular uterus. Terminology of egg morphology follows Ubelaker (1980). Eggs (Fig. 6) subspherical, embryophore larvae with three pairs of hooks, including: 1st pair dimorphic consisting of 1 small and 1 large hook, 2nd (middle pair) monomorphic delicate, 3rd pair dimorphic consisting of 1 small and 1 large hook. Large embryo hooks have a wide and thick guard compared to the small embryo hooks of both the middle pair and the paired small-hooks of 1st and 3rd pairs. Middle pair of embryo hooks identical, with falcate blade having shallow curve and with most delicate and narrow guard of all three embryo hook types (Fig. 6).

Etymology: The new genus is named in honor of Dr. Eric P. Hoberg who was the last curator of the United States National Parasite Collection. We honor Eric's life-long dedication and acknowledge his tireless studies of the taxonomy, systematics, phylogenetics, historical ecology, and biodiversity of parasites of planet earth.

Remarks: Definition of a new structure in the Cestoda. Scolex with pockets or depressions = foveolae (see definition in Maggenti *et al*., 2009) into which suckers can be retracted. This structure has also been observed in tapeworms of the genus *Linstowia* Zschokke, 1899 (Cestoda: Anoplocephalidae) from marsupials and monotremes (Gardner & Campbell, 1992a, b).

***Hobergia irazuensis* n. gen., n. sp.**
(Figures 1–6)
LSIDurn:lsid:zoobank.org:act:84C2C2D1-5ACC-4177-9EC4-BE630DC7FB8

Type Host: *Heterogeomys heterodus* (Peters, 1865).

Type locality: Agricultural field, approximately 12 km from Irazú volcano, on the northeastern edge of Potrero Cerrado, Cartago, Costa Rica, altitude 2,140 m; lat. 9°55´18" N, long. 83°52´41" W.

Symbiotype host: (See Frey *et al*., 1992) Variable pocket gopher, *Heterogeomys heterodus* (Peters 1865) (Rodentia: Geomyidae).

Symbiotype catalog number: Not available.

Type locality/collection date: Potrero Cerrado, Cartago, Costa Rica, Elevation: 2,140 m; lat. 9°55´18" N, long. 83°52´41" W; 28 March 1990.

Collector: Dr. Never Bonino and students.

Site of infection: Small intestine.

Prevalence: (5.3%) 2 of 38 specimens of *Heterogeomys heterodus* infected, one male and one female.

Specimens deposited: Holotype, HWML139040

Specimens examined: Paratypes: HWML39041, HWML139042, HWML139043, HWML139044, HWML139045, HWML13946, HWML13947, HWML13948, HWML13949, HWML13950, HWML13951, HWML13952, HWML13953, HWML139054.

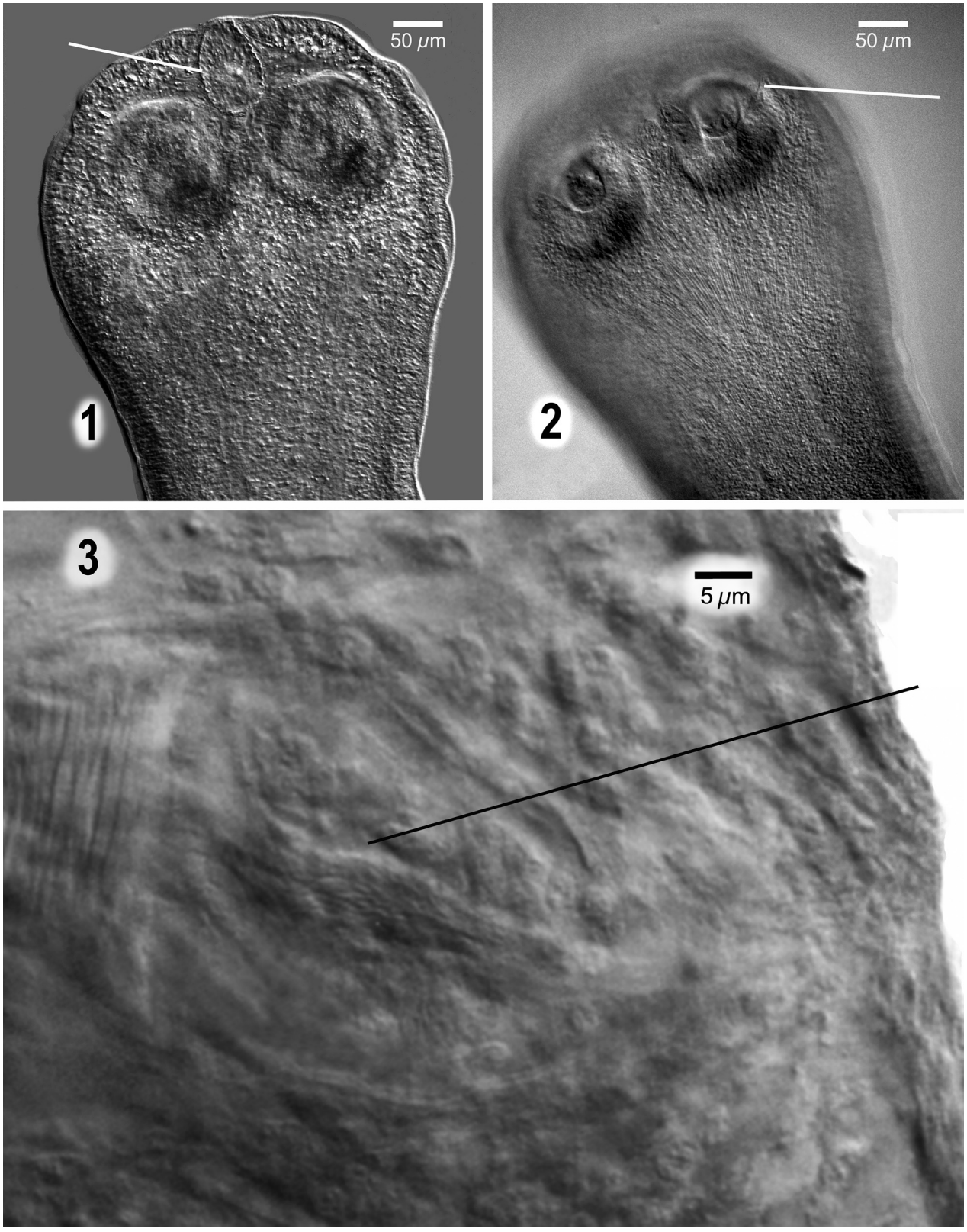
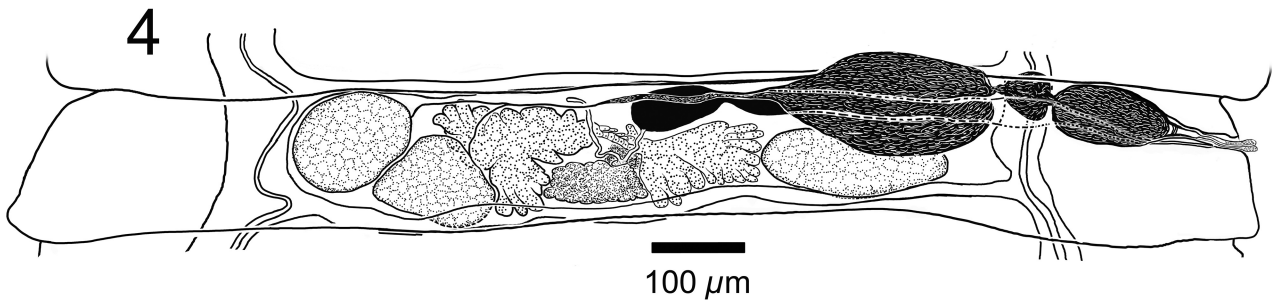


FIGURE 1. Scolex of *Hobergia irazuensis* **n. gen., n. sp.** showing details of apical organ and apical organ sac. Line indicates apical organ sac.

FIGURE 2. Scolex of *Hobergia irazuensis* **n. gen., n. sp.** showing detail of membranes on the scolex that cover the suckers creating a foveola or pocket into which each sucker can be retracted. Line indicates pocket opening.

FIGURE 3. Image of distal end of cirrus sac of *Hobergia irazuensis* **n. gen., n. sp.** showing the spinose nature of the cirrus (line).



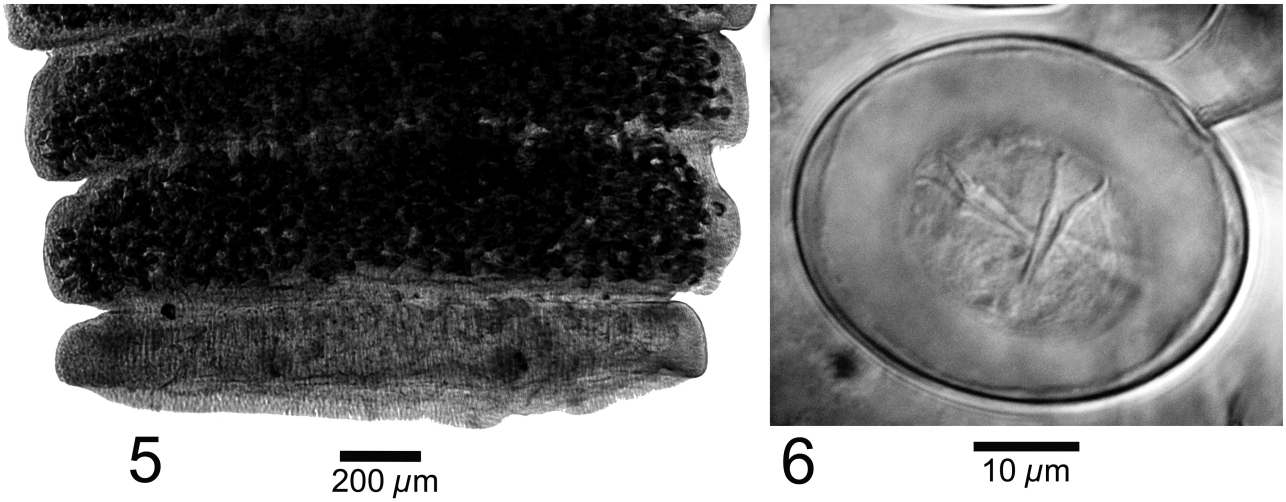


FIGURE 4. Line drawing of last mature proglottid of *Hobergia irazuensis* **n. gen., n. sp.**

FIGURE 5. Image of terminal gravid proglottids of *Hobergia irazuensis* **n. gen., n. sp.** showing the uterus filled completely with eggs in the subterminal proglottid and the terminal segment with no eggs evident (anapolytic).

FIGURE 6. Egg of *H. irazuensis* **n. gen., n. sp.** showing extent of development of embryo hooks with usual dimorphic hooks of the lateral pairs and the monomorphic hooks of the central pair in the embryophore larva.

Description: Fourteen specimens were studied for the following description, not all specimens had all characters visible. Scolex unarmed (Fig. 1), N = 5, 334–426 (393 ± 30) in maximum width. Apical organ (AO) present, N = 13, 20–32 (24 ± 3) in length. Each osmoregulatory duct terminates in the scolex near posterior end of AO but none penetrate the AO sac (posterior part of the AO) [Figure 1]. Apical organ sac, N = 12, 96–128 (114 ± 9) long by N= 9, 61–75 (68 ± 5) wide. Apical organ sac not reaching beyond the posterior margins of suckers. Suckers, N = 48, 102–146 (128 ± 11) long by N = 53, 110-161 (134 ± 11) wide. Well-defined foveolae present (Figure 2). Neck, N = 8, 708–899 (801 ± 66) long by N= 12, 261-307 (284 ± 17) in maximum width. Strobila, N = 4, 52.85 mm–64.64 mm (60.00 ± 5.13 mm) long, with N = 8, 531–640 (587 ± 34) proglottids; maximum width N = 7, 1.69–2.18 mm (1.91 ± 0.19 mm) occurs in gravid proglottids immediately anterior to terminal proglottids. Strobilar margins craspedote with intersegmental divisions clearly evident in mature and gravid proglottids; length-width ratio of mature and gravid proglottids 0.09–0.12 (N = 17) and 0.15–0.19 (N = 13). Proglottids wider than long. Genital pores unilateral, dextral, non-alternating. Genital atrium depth, N = 7, 14–18 (16 ± 2). Vaginal opening posterior and slightly ventral to cirrus opening. Genital ducts pass dorsally to longitudinal excretory canals. Dorsal canals, N = 15, 5–7 (6 ± 1) wide. Ventral canals, N = 20, 42–57 (51 ± 5) wide. Anlagen of genitalia first appearing N = 2,828–852 (840 ± 17) from anterior end. Cirrus sac piriform, N = 22, 145–197 (165 ± 16) in maximum length by N = 21, 41–56 (47 ± 5) in maximum width, antiporal end not overlapping excretory canals. Cirrus claviform, armed with minute spines, N = 11, 1.1-1.5 (1.2 ± 0.1) in length. Cirrus armature patterned in well-defined gridded rows (Fig. 3). Internal seminal vesicle piriform, N = 12, 85–111 (98 ± 9) long by N = 14, 34–44 (38 ± 4) wide. External seminal vesicle (ESV), N =24, 220–289 (251 ± 23) long by N = 15, 70–90 (80 ± 5) in maximum width. ESV, elongate, fusiform, situated anterior to poral testis. Testes N = 58, 132–179 (155 ± 15) long by N = 36, 78–107 (91 ± 9) wide, one poral and two antiporal. Testes arrangement usually triangular, sometimes more linear, arrangement depends on level of contrac-

tion (or relaxation) of strobila (relaxed strobila always with testes arranged in triangular pattern (Fig. 4). Seminal receptacle, N = 12, 369–482 (419 ± 41) long by N = 18, 55–74 (64 ± 6) in maximum width, extending anterior to ovary. Ovary N = 19, 125–166 (148 ± 15) in maximum length by N = 45, 288–405 (341 ± 32) in maximum width. Ovary markedly bilobed, each lobe subdivided into globular fan-shaped lobules extending laterad. Lateral lobes connected centrally in segment via thin isthmus (Fig. 4). Vitelline gland, N = 42, 132–199 (172 ± 17) wide by N = 31, 57–79 (67 ± 6) in maximum length, margins with small lobules, situated medially and posterior to ovary and anterior to transverse ducts of ventral osmoregulatory canals. Uterus first appearing as undefined tube extending bilaterad from area of oötype, appearing quickly in developing mature proglottids with uterus extending transversely through segment before eggs are evident within. Gravid proglottids filled entirely by saccular uterus. Internal organs, displaced by gravid uterus, persist in gravid proglottids (Fig. 5). Strobila with anapolytic proglottids. Eggs N = 51, 34–45 (39 ± 3) long by N = 51, 25–42 (34 ± 3) wide, sub-spherical. Embryo, N = 51, 20–28 (24 ± 2) long by N = 51, 18–27 (21 ±2) wide (Fig. 6), with sub-spherical shape. Embryo hooks as follows: larger hooks of first and third pairs, total length, N = 51, 9–12 (11 ± 1) long by N = 51, 2–3 (2 ± 0.2) wide at guard. Handle, N = 51, 4–7 (6 ± 1) long, blade, N = 51, 3–5 (4 ± 0.3) long. Larger hooks of first and third pairs have robust, wide guards. Smaller hooks of first and third pairs, total length, N = 45, 9–13 (11 ± 1) long by N = 46, 1–2 (1.8 ± 0.2) wide at guard. Handle, N = 46, 4–7 (6 ± 1) long, blade, N = 46, 3–5 (4 ± 0.4) long. Smaller hooks of first and third pairs have narrow, more delicate guards. Middle pair of hooks, total length, N = 24, 11–14 (12 ± 1) long by N = 24, 1–2 (1.7 ± 0.2) wide at guard, handle, N = 24, 6–8 (7 ± 1) long, blade, N = 24, 4–6 (5 ± 1) long. Middle pair of hooks usually longer than hooks of 1st and 3rd pairs with a less tapered guard and deeply rounded blade.

Etymology: *Hobergia irazuensis* **n. sp.** was named for the Volcán Irazú near the type locality, Costa Rica, northern Neotropical region.

Remarks: *Hobergia irazuensis* **n. gen., n. sp.** exhibits the characteristics of *Hymenolepis* as defined by Schmidt (1986) but refined and complemented by Makarikov & Tkach (2013). The following comparisons are restricted to members of the genus *Hymenolepis* known to occur in mammals of the Nearctic region, see Gardner (1985) and Gardner & Schmidt (1988).

Comparison of *H. irazuensis* n. gen., n. sp. with other hymenolepidids found in the Nearctic

Hobergia irazuensis **n. gen.**, **n. sp.** is readily distinguishable from all other known species of Hymenolepididae in the Nearctic by the presence of sucker foveolae on the scolex. Each of the four suckers on the scolex has a pocket-like foveola in which the sucker can retract. The tissue of the foveola covers each sucker with a thin membrane (Fig. 2) which appears striated and likely involved in foveola structure or function in retraction of the suckers into the foveolae. Additionally, *H. irazuensis* can be differentiated from species of *Hymenolepis s. str.* in the Nearctic by the following characters: Ovary extremely bilobed with a central thin isthmus only a few cells in diameter; no other described species of *Hymenolepis s. str.* has this structure. In addition, the new species has a much longer and wider scolex and wider neck relative to all described species.

Hymenolepis cratogeomyos n. sp.

(Figs. 7–9)

LSIDurn:lsid:zoobank.org:act:BB0861E9-71F4-4618-92BB-601F156C12F0

Symbiotype host: (see Frey *et al*., 1992). Volcán De Toluca Pocket Gopher, *Cratogeomys planiceps* Merriam 1895 (Rodentia: Geomyidae).

Symbiotype catalog number: LSUMZ 36120.

Type locality/collection date. Mexico, 10 km S, 16 km W Toluca, 3,000 m; lat. 19° 11’ 52.8”N, long. 99° 48’ 36”W; 17 February 1998.

Collector: Mark S. Hafner.

Site of infection: Small intestine.

Prevalence: 100% of those examined; one infected of one specimen examined.

Specimens deposited: Holotype, HWML139035.

Specimens examined: Paratypes: HWML139036, HWML139037, HWML139038, HWML139039.

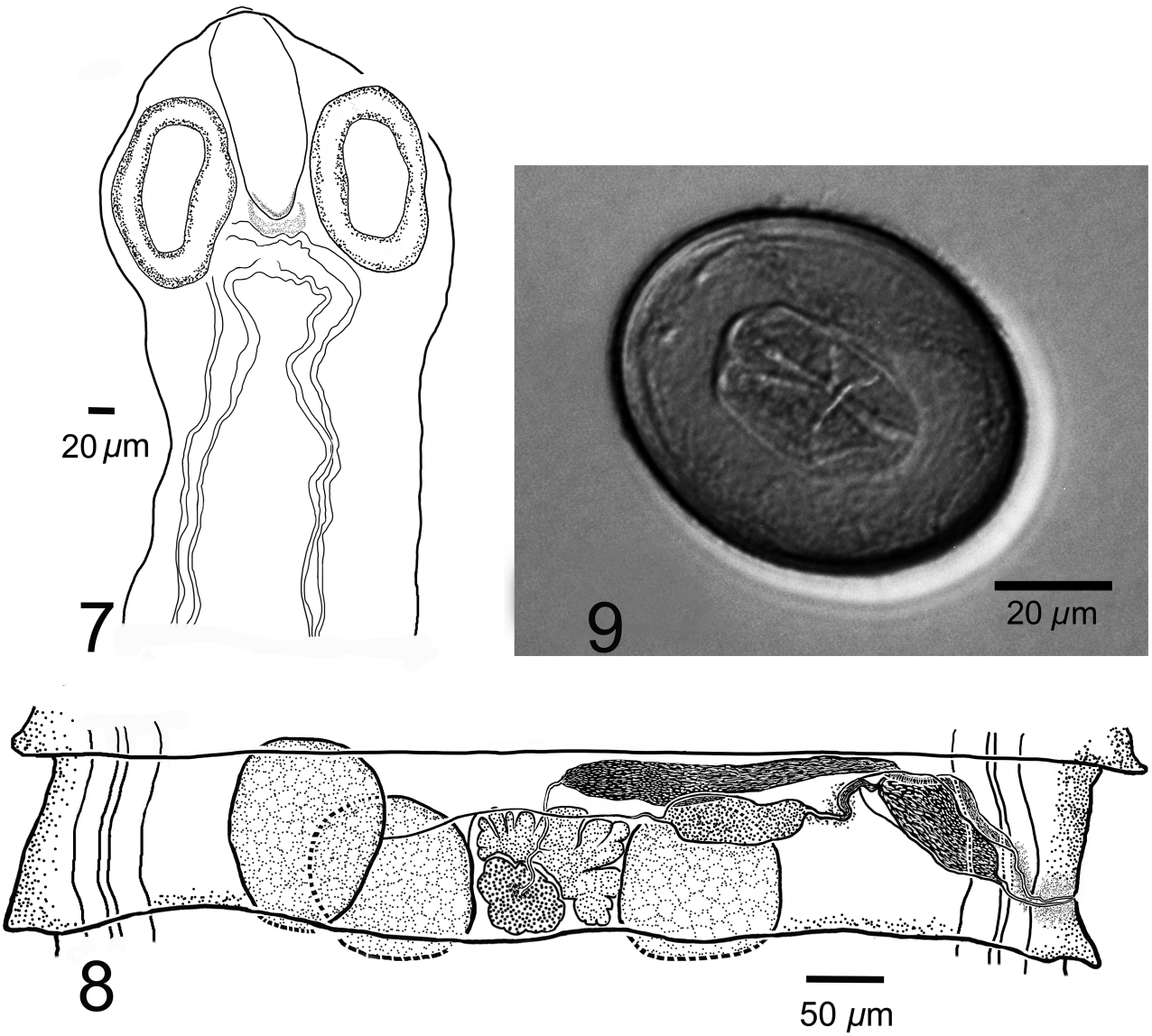


FIGURE 7. Scolex of *Hymenolepis cratogeomyos* **n. sp.** showing relatively large apical organ sac.
FIGURE 8. Line drawing of one of the last mature proglottids (see text for definition) of *Hymenolepis cratogeomyos* **n. sp.**
FIGURE 9. Egg of *Hymenolepis cratogeomyos* **n. sp**. showing relatively delicate of development of embryo hooks with usual dimorphic hooks of the lateral pairs and the monomorphic hooks of the central pair in the embryophore larva.

Description: All specimens available were studied, including one full and 2 partial). At time of collection, specimens were placed directly into 95% ethanol, and so are extremely contracted, with only a few mature proglottids non-contracted and available to examine. Scolex (Fig. 7) unarmed, length N = 2, 198–203 (200 ± 2.6), maximum width N = 2, 209–227 (218 ± 12.6). Apical organ (AO), N = 1, 21.8–21.8 (21.8 ± 0) long. Osmoregulatory ducts terminate at base of AO, but do not appear to penetrate AO (Fig. 7). Apical organ sac, N = 3, 55–59 (57 ± 2) long by, N = 2, 33–37 (34.8 ± 2.9) wide. Apical organ sac not extending farther than posterior margins of suckers. Suckers, N = 6, 109–117 (112 ± 3) long by, N = 4, 84–89 (87 ± 2) wide. Neck, N = 1, 375–375 (375 ± 0) long by N = 2, 169–172 (170 ± 2.3) in maximum width. Strobila, N = 2, 88.28–128.58 mm (108.42 ± 28.49 mm) long, with 1,257–1,266 (1,262 ± 6) proglottids; maximum width 2.72–3.41 mm (3.06 ± 0.49 mm) attained in gravid proglottids. Strobila anapolytic. Strobilar margins craspedote with intersegmental divisions plainly visible in mature and gravid proglottids; length: width ratio of mature and gravid proglottids 0.09–0.178 (N = 4) and 0.11–0.177 (N =4), respectively. Genital pores marginal, dextral, and non-alternating crossing osmoregulatory canals dorsally. Opening of genital pore ringed with deeply staining, densely packed cells. Genital atrium depth, N = 12, 20–25 (22 ± 2). Vaginal opening is anterior to cirrus opening in genital atrium. Dorsal osmoregulatory canals, N = 9, 19–24 (22 ±

2) wide. Ventral osmoregulatory canals, N = 9, 87–95 (92 ± 3) wide. Anlagen of genitalia N =1, 119–119 (119 ± 0) long. Cirrus sac piriform, N = 5, 121–145 (138 ± 10) in maximum length by, N = 5, 45–57 (52 ± 4) in maximum width, the antiporal end of cirrus usually overlapping excretory canal. Cirrus clavate, armed with minute spines. Cirrus armature arranged in welldefined rows. Internal seminal vesicle piriform in shape, N = 7, 80–93 (85 ± 4) long by, N = 8, 31–40 (34 ± 3) wide. External seminal vesicle, elongate fusiform, N = 3, 181–197 (191 ± 9) long by, N = 4, 92–97 (95 ± 2) wide. Testes ovoid, N = 15, 141–190 (167 ± 16) long by, N = 19, 95–121 (106 ± 8) wide, with one poral and two antiporal. Seminal receptacle, N = 4, 745–919 (841 ± 72) long by, N = 8, 75–93 (83 ± 7) wide, positioned anterior and dorsal to ovary and ventral to cirrus sac. Ovary, N = 8, 84–93 (90 ± 3) long by, N = 12, 168–203 (183 ± 12) wide. Ovary deeply lobed, fan shaped and compacted between testes. Vitelline gland, N = 8, 62–80 (72 ± 6) wide by, N = 7, 45–53 (50 ± 3) in maximum long, margins smooth. Vitelline gland near midline, anterior to intersegmental boundaries. Uterus developing laterally from origin in center of proglottid (Fig. 8). Gravid uterus saccular, overlapping osmoregulatory canals and completely filling segment and displacing all internal gonadal tissues. Eggs, N = 52, 62–94 (74 ± 6) long by, N = 52, 40–63 (52 ± 4) wide, sub-spherical. Embryophore (Fig. 9), N = 49, 31–46 (37 ± 3) long by, N = 49, 20–30 (26 ± 3) wide, sub-spherical. Embryo hooks as follows: Description of larger hooks of first and third pairs, hook length, N = 60, 16.0–19.9 (18.0 ± 1.0) by, N = 60, 3.4–4.8 (4.1 ± 0.4) wide at guard. Handle, N = 60, 6.8–11.0 (9.3 ± 0.9) long, blade, N = 60, 5.3–8.6 (7.1 ± 0.6) long. Larger hooks of first and third pairs with robust guard, thick handle, and a broad shallowly-curved, falcate, blade. Smaller hooks of first and third pairs, length, N = 41, 14.2–20.0 (17.5 ± 1.2) long b, N = 41, 2.3–3.3 (2.8 ± 0.2) wide at guard; handle, N = 41, 6.9–10.9 (9.1± 0.9) long, blade, N = 41, 5.4–8.6 (7.0 ± 0.7) long. Smaller hooks of first and third pairs narrow with thin guard and sub-falcate blade. Length of middle hooks, N = 21, 15.4–18.9 (17.1± 1.0) by, N = 21 1.6–2.3 (1.9 ± 0.2) wide at guard; handle, N = 21, 7.5–10.0 (9.0 ± 0.77) long; blade, N = 21, 5.6–8.2 (7.1 ± 0.6) long. Guard of middle pairs of hooks reduced relative to large outer hooks, blade deeply curved and falcate (Fig. 9).

Etymology: This tapeworm species was named after the generic name of its type host "*cratogeomyos*" meaning "of *Cratogeomys*."

Differential Diagnosis: *Hymenolepis cratogeomyos* **n. sp.** exhibits characteristics of *Hymenolepis* as defined by Yamaguti (1959) and Schmidt (1986) but later refined by Makarikov & Tkach (2013). There is no evidence that geomyid rodents have ever occurred in the Palearctic region (Kurtén & Anderson, 1980) therefore we restrict comparison of this species with those of the genus *Hymenolepis* known to occur in mammals from the Nearctic and Neotropical regions, see Gardner (1985) and Gardner & Schmidt (1988). *Hymenolepis cratogeomyos* **n. sp.** can be recognized as distinct from all known species of *Hymenolepis* from the Nearctic region by possessing a greater width of dorsal osmoregulatory canal, longer seminal receptacle, and an apical organ sac with lightly crenulated margins.

Comparisons of *H. cratogeomyos* with other hymenolepidids from geomyid rodents

Hymenolepis cratogeomyos differs from *H. geomydis* in having a greater number of proglottids, longer apical organ, shorter and narrower apical organ sac, shorter neck, smaller vitelline gland, wider ventral osmoregulatory canals, longer and wider external seminal vesicle, smaller width of egg and embryo, anlagen of genitalia appearing earlier, wider guard of first and third pairs of large hooks, more compact ovary, and smooth vitelline gland margins.

Hymenolepis cratogeomyos **n. sp.** can be separated from *H. weldensis* by the following characters: wider strobila, a greater number of proglottids, longer apical organ, shorter and narrower apical organ sac, shorter neck, shorter cirrus sac, longer testes, longer and wider external seminal vesicle, expanded ovary, deeper genital atrium, narrower embryo, and earlier anlagen of genitalia. *Hymenolepis cratogeomyos* also differs from *H. weldensis* in the shape and armature pattern of the cirrus, the cirrus of *H. cratogeomyos* is partially clavate with well-defined gridded rows of minute hooks. *Hymenolepis cratogeomyos* differs from *H. tualatinensis* in being larger in all respects except that *H. cratogeomyos* has eggs possessing embryophores that are smaller and the anlagen appears earlier in the strobila. In addition, *H. cratogeomyos* differs from *H. tualatinensis* in having an ovary that is compact, fan-shaped, and with multiple lobes, genital pores, a cirrus that is clavate and with a different pattern of spines, and eggs with hooks that are much more robust than those in *H. tualatinensis*.

Hymenolepis cratogeomyos can be readily distinguished from *H. irazuensis* by the more compact ovary (not extremely bilobed as in *H. cratogeomyos*) and the fact that the scolex has no sucker pockets. *Hymenolepis cratogeo-*

myos can be readily distinguished from *H. irazuensis* in having a longer and wider strobila, greater number of proglottids, shorter and narrower apical organ sac, narrower neck, wider seminal receptacle, shorter and wider ovary, smaller vitelline gland, shorter and wider external seminal vesicle, deeper genital atrium, wider ventral excretory canal, and longer and wider eggs and embryo. The embryo hooks of *H. cratogeomyos* differ from the hooks of *H. irazuensis* by the following characters: a longer handle, blade, and total length and a narrower guard of the big and small hooks of the first and third pairs, and greater total length of the middle embryo hooks. Additionally, *H. cratogeomyos* has an ovary that is multilobed with deep small lobes and not extremely bilobed, cirrus sac that partially overlaps the ventral excretory canal, and a smooth-edged vitelline gland.

Comparisons of *H. cratogeomyos* with *Hymenolepis* species from Sciurid, Cricetid, and Murid Rodents in the Nearctic.

Hymenolepis cratogeomyos can be separated from *H. robertrauschi* in having a longer and wider strobila, greater number of proglottids, longer apical organ, shorter cirrus sac, longer and wider external seminal vesicle, wider ventral canals, narrower internal seminal vesicle, narrower embryo, and the anlagen of the genitalia appears earlier in the strobila. In addition, *H. cratogeomyos* differs from *H. robertrauschi* by the following characters: a piriform cirrus sac, cirrus armature arrangement of well-defined rows, and cirrus sac that crosses osmoregulatory canals to the mid line of the ventral canal, this in contrast to the cirrus sac of *H. robertrauschi* that does not touch or cross the osmoregulatory canals.

Hymenolepis cratogeomyos differs from *H. pitymi* by the following characters: longer and wider strobila, greater number of proglottids, shorter apical organ, wider apical organ sac, longer and wider neck, longer and wider cirrus sac, longer and wider external seminal vesicle, longer and wider internal seminal vesicle, wider seminal receptacle, longer and wider ovary, longer vitelline gland, deeper genital atrium, wider ventral excretory canals, longer and wider eggs, wider embryos, and greater total length of middle embryo hooks and a cirrus armature arrangement of well-defined gridded rows.

Hymenolepis cratogeomyos can be recognized as distinct from *H. folkertsi* in having a wider strobila, greater number of proglottids, shorter apical organ, shorter and narrower apical organ sac, deeper genital atrium, wider seminal receptacle, longer and wider external seminal vesicle, longer and wider testes, and wider ventral canals. *Hymenolepis cratogeomyos* can be distinguished from *H. folkertsi* in having the following characters: piriform cirrus sac that usually overlaps the ventral excretory canal, clavate cirrus, and a much more reduced AO relative to that of *H. folkertsi*.

Hymenolepis cratogeomyos is readily distinguishable from *H. diminuta* by the following characters: wider strobila, more great number of proglottids, longer apical organ, shorter and narrower apical organ sac, longer neck, shorter cirrus sac, wider external seminal vesicle, shorter internal seminal vesicle, deeper genital atrium, wider ventral excretory canals, narrower embryo, narrower guard of middle embryo hooks, and earlier anlagen of genitalia. *Hymenolepis cratogeomyos* can be recognized as distinct from *H. diminuta* by the following characters: non-alternating genital pores, a cirrus sac that usually overlaps the ventral excretory canal, and cirrus spines formed in evenly spaced rows and columns.

Generally, the characters that serve to distinguish *H. diminuta* from other species also suffice to distinguish *H. citelli* from other species as the adult characters of *H. diminuta* and *H. citelli* appear indistinguishable (Gardner & Schmidt 1988). *Hymenolepis cratogeomyos* can be recognized as distinct from *H. citelli* by the following characters: wider strobila, shorter apical organ, shorter and narrower apical organ sac, longer and wider neck, longer and wider internal seminal vesicle, longer external seminal vesicle, longer testes, wider seminal receptacle, wider ventral excretory canal, wider cirrus sac, piriform cirrus sac, and a genital pore that is non-alternating. Note: It is the opinion of the authors that new specimens from the type locality of *H. citelli* should be collected to confirm its validity.

Hymenolepis cratogeomyos can be recognized as distinct from *H. scalopi* Schultz, 1939 described from *Scalopus aquaticus* Linnaeus, 1758 collected from the vicinity of Stillwater, Oklahoma by the following characters (see Table 2): wider strobila, greater number of proglottids, longer apical organ, shorter and narrower apical organ sac, earlier anlagen of genitalia, longer and wider external seminal vesicle, longer testes, wider seminal receptacle, shorter ovary, shorter vitelline gland, wider and shorter neck, deeper genital atrium, and a larger ventral excretory canal. In addition, *H. cratogeomyos* can be separated from *H. scalopi* in having a piriform cirrus sac that extends

further than the ventral excretory canal, and a larger ovary that is expanded laterally. Note: It is interesting that this species has never been reported after its initial description. At this time we have been unable to locate the voucher specimens of the type host *H. scalopi* so it remains an enigma as to whether this cestode was actually recovered from a mole collected from near Stillwater, OK.

Prevalence of hymenolepidids in Geomyidae of Costa Rica and México

During the field work by Bonino in Costa Rica (1989–1990), 127 individuals of *H. heterodus,* were collected and examined for helminths. *Hobergia irazuensis* **n. gen., n. sp.** was found in 1.6% of all specimens examined; all infected individual pocket gophers were found at a single collection locality, occurring in 5.3% of those individuals of *H. heterodus* examined at the locality Potrero Cerrado.

Relative to *Hymenolepis cratogeomyos* **n. sp.**, one individual of *C. planiceps* was incidentally found infected with cestodes (Hafner *et al*. 2004).

Statistical Analyses

To examine the extent of morphological divergence among all species of *Hymenolepis* s. str. in the Nearctic and Northern Neotropical regions a PCA and CANDISC were performed. The PCA ordination (Fig. 10) shows relatively good separation of species using the first two components. The CANDISC ordination (discriminant analysis works on previously defined groups and maximizes the differences among the groups) shows distinct separation among all species included in this analysis (Fig. 11). The CANDISC analysis shows that all multivariate means or centroids are significantly different from each of the seven species of hymenolepidids evaluated ($F= 11.34$, $df =102,109.62$, $p < 0.0001$). Characters most important for discriminating among species in this study were determined by stepwise discriminant analysis and include: number of proglottids, cirrus sac length, maximum strobila length, ovary width, seminal receptacle length, vitelline gland width, cirrus sac width, and maximum strobila width. Measurements of scolexes, eggs, and embryophores were not included in the multivariate analysis due to the low number of these characters available for comparative species.

Discussion

The discovery of these two new species of cestodes adds critical new information to our knowledge of the known species of rodent-specific Hymenolepididae in both the Mesa Central of Mexico and the volcanic region of Costa Rica. The record of *Hobergia irazuensis* from *H. heterodus* in the highlands of Costa Rica is the first report of a hymenolepidid from geomyid rodents in the northern neotropics; however, we expect that additional sampling of geomyids throughout their ranges will reveal hidden parasite diversity that has been previously ignored by biodiversitists.

Across the Nearctic and northern Neotropical regions, six species of the genus *Hymenolepis* are now known to occur in species from three of the six genera of Geomyidae. *Hymenolepis citelli* and *H. weldensis* have been reported from more than one species of geomyid rodent (Gardner & Schmidt 1988) and both *H. diminuta* (Table 1) and *H. weldensis* have been transferred experimentally to, and appear to thrive in, experimentally infected species of *Geomys*, *Thomomys*, and *Cratogeomys* (see Gardner & Schmidt 1988). The fact that *Hymenolepis weldensis* and *H. diminuta* were transferred experimentally from geomyids to beetles of the family Tenebrioniidae (*Tenebrio molitor* L.) and then to gophers, indicates that any host specificity of these species of tapeworms to geomyids does not manifest or show physiological or phylogenetic host specificity, but instead is most likely a result of ecological host specificity (separation of host and parasite based on ecology or geographic distances). Based on the potential for ecological fitting (see reviews in Brooks *et al*., 2014 and Weaver *et al*., 2016) of *Hymenolepis* spp. among the diverse and widely distributed species of Geomyidae and the requirements of the complex life cycles of these cestodes combined with the broad geographic distribution of the geomyids, it is clear that additional biodiversity surveys throughout the Nearctic and Neotropical regions are required to understand the dynamic evolutionary and ecological history of the species of Hymenolepididae in geomyid rodents.

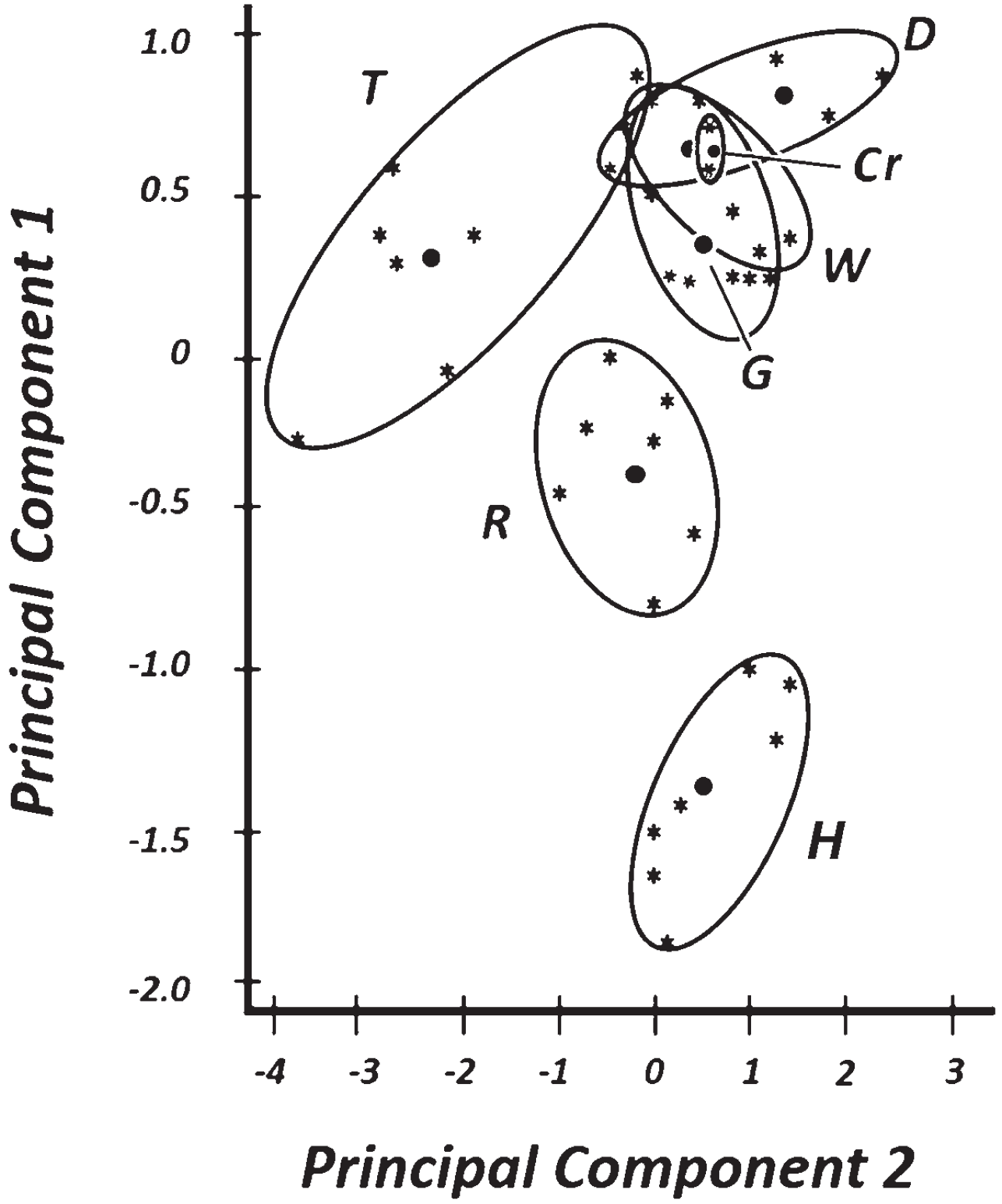


FIGURE 10. Ordination of first two principal components derived from a PCA of morphometric characters of seven species of Hymenolepididae, ellipse labels as follows: H = *Hobergia irazuensis* **n. gen., n. sp.**; Cr = *H. cratogeomyos* n. sp.; D = *H. diminuta*; G = *H. geomydis*; R = *H. robertrauschi*; T = *H. tualatinensis;* W = *H. weldensis.*

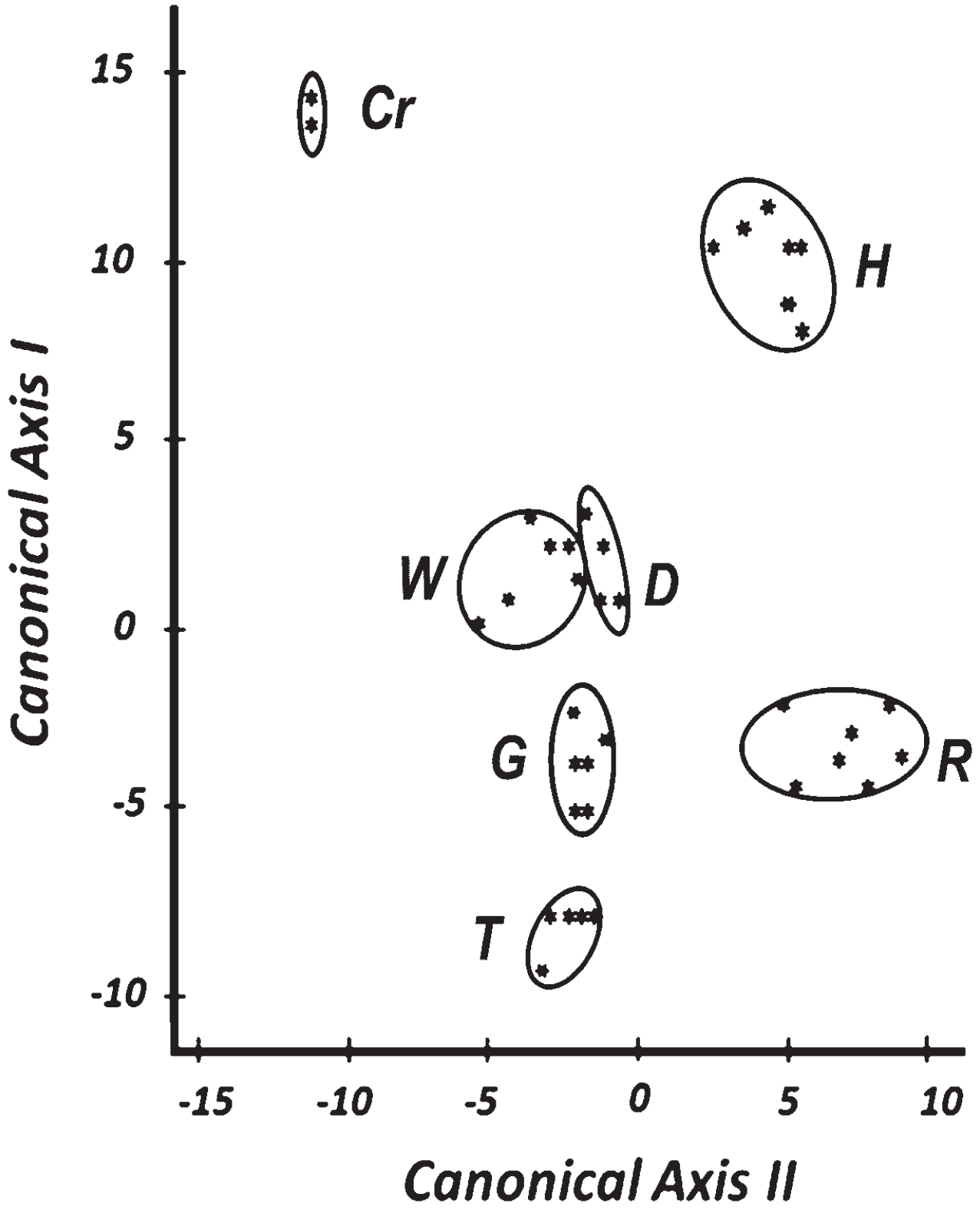


FIGURE 11. Ordination plot of the first two axes derived from a canonical discriminant morphometric analysis (CANDISC) of six species of *Hymenolepis* and *Hobergia irazuensis n.* gen. n. sp. Ellipse labels as follows: H = *H. irazuensis* n. sp.; Cr. = *H. cratogeomyos* n. sp.; D = *H. diminuta*; G = *H. geomydis*; R = *H. robertrauschi*; T = *H. tualatinensis*; W = *H. weldensis*. Asterisks represent the scatter of individuals in discriminant space.

Parasites with complex life-cycles, such as cestodes that occur in species of Geomyidae, are important indicators of biodiversity that is many times hidden with only parts of the fauna of a region or locality functioning in host-

parasite systems (Manter 1966; Brooks & McLennan 1993). If a parasite with a complex life-cycle is shown to be present in one or several host species in an area, it is immediately clear that all essential ecological requirements for both definitive and intermediate hosts are also present in the ecosystem (Gardner & Campbell 1992; Hoberg 1997). Thus, discovery of parasites with complex life-cycles in this case, mammals, but in fact any other vertebrates in any geographic locality serves to immediately expose to examination previously hidden and perhaps unknown and undiscovered biodiversity. Finally, putting the species associated with these discoveries into a phylogenetic context adds historical depth to the discovery of species (Gardner & Campbell 1992; Brooks *et al*. 2014; Racz & Gardner submitted).

With the inclusion of the two new hymenolepidids described herein, we consider the genus *Hymenolepis* to contain 20 species with one new species allocated to a new genus, defined above.

Acknowledgments

We thank the students who worked so hard to collect pocket gophers in both Costa Rica and in Mexico all those years ago. Thanks to Mark S. Hafner, Robert M. Timm, and Never Bonino for sending the specimens of cestodes to SLG and then waiting all this time to see the results. This paper is dedicated to the memory of Dr. Robert L. Rausch, for without his encouragement and guidance, SLG would never have met Eric P. Hoberg. Part of this work was funded by NSF grants to SLG including (DEB-9621395, DEB-0097019, DBI-1458139, and DBI-1756397).

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