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Cestodes of the Genus *Hymenolepis* Weinland, 1858 *Sensu Stricto* from Pocket Gophers *Geomys* and *Thomomys* spp. (Rodentia: Geomyidae) in Colorado and Oregon, with a Discriminant Analysis of Four Species of *Hymenolepis*

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Cestodes found to represent previously undescribed members of the genus *Hymenolepis* s.str. (Yamaguti 1959) were recovered from pocket gophers, *Geomys bursarius* (Shaw), in northeastern Colorado. ***Hymenolepis weldensis*** n.sp. and ***Hymenolepis geomydis*** n.sp., not occurring together in any individual host, were found in 3 and 8%, respectively, of pocket gophers examined for helminths. The life cycle of *H. weldensis* was completed in the laboratory using beetles, *Tenebrio molitor* (L.), as intermediate hosts, and pocket gophers of three genera (*Geomys*, *Thomomys*, and *Pappogeomys*) as definitive hosts. Development of *H. weldensis* did not occur in laboratory rats, *Rattus norvegicus* (Berkenhout). Morphologic relationships four species of *Hymenolepis* (*H. diminuta*, *H. tualatinensis*, *H. weldensis*, and *H. geomydis*) were analyzed using multiple discriminant function analysis, which clearly allocated individual cestodes to the respective groups and discriminated species.

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Des cestodes représentant des espèces encore inconnues d'*Hymenolepis* sensu stricto (Yamaguti 1959) ont été trouvés chez des Gaufres bruns, *Geomys bursarius*, dans le nord-est du Colorado. ***Hymenolepis weldensis*** n.sp. et ***Hymenolepis geomydis*** n.sp. quoique ne parasitant jamais ensemble le même hôte, ont été retrouvés chez 3 et 8% des gaufres examinés. Le cycle complet d'*H. weldensis* a été obtenu en laboratoire : le ténébrion *Tenebrio molitor* (L.) a servi d'hôte intermédiaire et des gaufres appartenant à trois genres (*Geomys*, *Thomomys* et *Pappogeomys*), d'hôtes terminaux. Le développement d'*H. weldensis* n'a pu être rendu à terme chez des rats de laboratoire *Rattus norvegicus* (Berkenhout). Une analyse discriminante multiple a servi à établir des relations morphologiques entre quatre espèces d'*Hymenolepis* (*H. diminuta*, *H. tualatinensis*, *H. weldensis*, *H. geomydis*). L'analyse permettait de classifier un individu dans un groupe particulier et de distinguer les espèces.

[Traduit par la revue]

Introduction

Cestodes representing the genus *Hymenolepis* Weinland, 1858 (sensu Yamaguti 1959) occur primarily in rodents and insectivores, and have been reported from these mammals in most biogeographic regions of the world (Burt 1980). Approximately 21 species have been assigned to this genus, with 5 occurring in both rodents and insectivores exclusively in the Nearctic region (Mas-Coma *et al.* 1980). Gardner (1985) indicated that there is considerable diversity in numbers of species of the genus *Hymenolepis* in rodents of the family Geomyidae. This paper reports the results of studies concerning morphological characteristics and life cycle in cestodes of the genus *Hymenolepis* from *Geomys bursarius* (Shaw) and *Thomomys bulbivorus* (Richardson) from northeastern Colorado and western Oregon, respectively.

The helminth parasites of *Thomomys bulbivorus*, a species endemic to the Willamette Valley of Oregon, have been studied more intensively than other species of parasites in the genus *Thomomys* (see Gardner 1985). Cestodes of the genus *Hymenolepis* s.str. have been commonly encountered in several species of the genus *Thomomys*. Table 1 provides a complete list of records reporting *Hymenolepis* from pocket gophers.

Pocket gophers have a Nearctic distribution, with representatives of five extant genera occurring in suitable habitats from about latitude 54° N in western Canada south to southern Panama (Hall 1981; Maser *et al.* 1981). Members of the genus *Thomomys* Wied-Neuwied, which currently includes about nine species (Thaeler 1980; Russell 1968) occur from southwest and south-central Canada throughout the western part of the United States to Oaxaca and Vera Cruz states in southern Mexico (Hall 1981).

Geomys bursarius (Shaw) reaches the western limit of its range in Colorado, and in general the range is essentially co-extensive with the central North American grassland, which extends east of the Rocky Mountains from southern Manitoba south to the Gulf of Mexico (Armstrong 1972; Hall 1981). Cestodes of the genus *Hymenolepis* have been encountered by investigators less frequently in members of the genus *Geomys* than in *Thomomys* (Table 1).

Materials and methods

Most material used in the following descriptions was collected (by S.L.G.) between May 1980 and June 1983. In northeastern Colorado, specimens of *G. bursarius* were collected from two populations, occupying wetland–saltgrass (*Distichlis spicata*) and cropland–alfalfa (*Medicago sativa*) habitat types. In these areas, wetland–saltgrass habitats were characterized by relatively small, isolated areas with soils consisting primarily of sand with small amounts of organic

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TABLE 1. References reporting *Hymenolepis* s.str. from rodents of the family Geomyidae

Host	Species of *Hymenolepis*	Geographic locality	Reference
Thomomys bottae (Eydoux and Gervais)	*H. citelli* (Mcleod, 1933)	California	Voge 1955
	Hymenolepis sp.	California	Voge 1955
	H. horrida (von Linstow, 1901)	California	Schiller 1952
Thomomys bulbivorus (Richardson)	*H. tualatinensis* Gardner, 1985	Oregon	Gardner 1985
Thomomys monticola	*H. horrida*	California	Howard and Childs 1959
Thomomys talpoides (Richardson)	*H. horrida*	Utah	Grundmann *et al.* 1976
	H. diminuta	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	Colorado	This study
	H. geomydis	Colorado	This study
	Hymenolepis sp.	Texas	English 1932
Geomys spp.	*Hymenolepis* spp.	Midwestern United States	Douthitt 1915

material present in the upper layers. The cropland–alfalfa habitat was a distinct area surrounded by cropland and wetland. In this area, the dominant species of plant was alfalfa (*M. sativa*), present in monoculture. Sixty specimens of *G. bursarius* were collected from the two habitat types.

Specimens of *H. tualatinensis* were obtained from *T. bulbivorus* from two different areas of the Willamette Valley in Oregon (Gardner 1985). *Hymenolepis diminuta* was obtained from *Rattus norvegicus* (Berkenhout), purchased from Carolina Biological Supply Co.

Gophers were trapped using either Victor–Macabee or Cinch gopher traps. All specimens were necropsied as soon as possible after collection to minimize postmortem changes in the parasites. Maximum time to necropsy after death was about 3 h for gophers recovered dead in the traps and less than 5 min for gophers recovered alive. Contents of each organ of the gastrointestinal system were examined separately for helminths, using a dissecting microscope.

All cestodes found were placed in distilled water for approximately 20 min to allow the strobila to relax, fixed in hot 10% (v/v) aqueous formalin solution, stained with Ehrlich's acid hematoxylin or Semichon's acetic carmine, dehydrated in ethanol, cleared in terpineol and xylene, and mounted permanently in Canada balsam.

The life cycles of those species of *Hymenolepis* recovered during this study were investigated using beetles of the following species as experimental intermediate hosts: *Tenebrio molitor* (Linnaeus), *Tribolium castaneum* Herbst, and *Tribolium confusum* du Val. Individual gravid segments of each cestode recovered from pocket gophers captured in the field were fed to adult specimens of *T. molitor* while the beetles were held on their backs. All beetles had moisture (carrots) withheld for 24 h before feeding. An estimate of the number of eggs each beetle ingested was made by counting the average number of eggs per segment of cestode and presenting the beetle with a known number of segments. By observing the beetles with a dissecting microscope it was possible to determine if most of the eggs were ingested. This procedure allows an estimate to be made of the susceptibility of beetles as intermediate hosts (see Results). All beetles used for experimental infections were the same age and were maintained under identical conditions. Adults of *T. molitor* were kept in a large glass dish filled with wheat bran; carrots were provided for moisture. Individuals of both species of *Tribolium* were exposed to eggs following the method of Heyneman (1958). Approximately 25 days postexposure, beetles were dissected and examined for cysticercoids. Any cysticercoids found were fed to hosts via stomach tube. Less than 10 cysticercoids were given to each animal to minimize the effects of crowding on the morphological characteristics of the strobilae of adult cestodes.

The following species of rodents were used as experimental definitive hosts: *Thomomys mazama* (Richardson), *T. talpoides* (Richardson), *Pappogeomys castanops* (Biard), and *Rattus norvegicus*. All pocket gophers used as experimental hosts were captured in the field and were determined to be free of cestodes by fecal examination via zinc sulfate centrifugation. *Rattus norvegicus* were obtained from a cestode-free laboratory stock maintained at the University of Northern Colorado. Experimental animals were maintained according to the regulations established by the Canadian Council of Animal Care.

Starting 10 days postinfection, fecal samples from experimentally infected rodents were examined daily for the presence of cestode eggs. When cestode eggs were detected in the feces, the gopher was killed and necropsied. All cestodes were processed as outlined above. Posterior segments of selected specimens were removed and used to perpetuate the cestodes.

All measurements of *H. diminuta* used for the following comparisons were taken from individuals grown experimentally in *R. norvegicus* and three species of pocket gophers (*P. castanops*, *T. talpoides*, and *T. mazama*).

Statistical methods

Discriminant analysis of four species of *Hymenolepis* was performed using the following methods. The statistical package BIOSTAT II (Pimentel and Smith 1985) was used for all multivariate procedures. All measurements except for variable No. 3 (number of segments) were scaled to similar units (micrometres) before analysis (see Table 2). Levels of statistical significance were set before analysis at $p \leq 0.05$. Determination of possible deviations from normality was made by calculating confidence intervals of skewness and kurtosis (multigroup discriminant function analysis MDA) of BIOSTAT. Because the distributions of some variables did not conform to normality, data were log transformed ($\log_{10}$) and checked again for normality. Subsequent analyses were then performed on the log-transformed data. To examine detailed relationships between character variables, Student–Newman–Keuls (SNK) multiple-range tests of equality of means between each species pair were performed. Canonical variates analysis (= multigroup discriminant function analysis; MDA) was performed on 17 character variables and 27 individual cestodes representing four species of *Hymenolepis* (see Table 2).

Following are descriptions of two new species of *Hymenolepis* s.str. from *Geomys bursarius*. Measurements are given in micrometres unless otherwise indicated. *N* is the number of individual structures examined; mean ± SD are given in parentheses. Measurements of organs in mature segments were taken from the segments immediately anterior to segments in which eggs begin to appear in the developing uterus.

TABLE 2. Range of measurements of Nearctic species of *Hymenolepis* s.str. occurring in rodents

	H. tualatinensis	*H. diminuta*	*H. pitymi*	*H. weldensis*	*H. geomydis*
Strobila length (mm)	23.9–210	128–328	19.6	111.9–165.2	72.26–168.41
Maximum width (mm)	0.385–1.54	1.44–2.94	0.750	1.87–2.29	1.98–3.30
No. of segments	247–602	1025–1188	350	821–943	456–697
Mature segments, *L/W*	0.18–0.36	0.9–0.12	0.25	0.11–0.19	0.11–0.22
Gravid segments, *L/W*	0.43–0.69	0.11–0.24	—	0.16–0.23	0.14–0.20
Cirrus sac length	56–150	202–388	79	149–194	83–160
Internal seminal vesicle length	41–80	105–256	51–70	87–159	40–177
External seminal vesicle length	28–134	141–247	77	63–183	45–202
Seminal receptacle length	48–169	71–540	155–241	175–552	99–369
Ovary width	96–126	108–133	97–116	90–293	180–484
Vitelline gland width	37–172	47–99	30	54–106	101–209
Egg length	57–89	67–83	28	70–81	76–85
Egg width	42–68	61–77	31	67–77	72–83
Embryo length	23–49	36–42	23	38–45	38–50
Embryo width	19–49	31–36	20	38–40	34–43
Medial hook length	17–20	14–19	—	13–16	16–20
Medial hook width at guard	2–3	2	—	2	2–3

NOTE: All data used for comparisons with present material taken from Gardner (1985). Measurements in micrometres unless otherwise indicated. *L*, length; *W*, width.

Results

Hymenolepis weldensis n.sp.
(Figs. 1–3)

DESCRIPTION: Scolex (Fig. 1), $N = 4$, 140–254 (210 ± 44) long by 126–288 (220 ± 81) wide. Apical organ present, unarmed. Neck, $N = 5$, 990–3120 (2074 ± 907) long by 107–229 (164 ± 50) wide. Strobila, $N = 6$, 111.9–165.2 mm (143.6 ± 18.2 mm) long, with 821–943 (892 ± 56) segments; maximum width 1875–2290 (2026 ± 149), attained early in gravid segments. Strobilar margins serrate, with intersegmental boundaries well defined in mature and gravid segments. Segments wider than long (Fig. 2). Strobila attenuated anteriorly, with increase in relative length beginning in mature segments; length:width ratio of mature and gravid segments 0.11–0.19 ($N = 32$) and 0.16–0.23 ($N = 32$), respectively. Genital pores unilateral, sinistral. Genital ducts passing dorsally across longitudinal excretory canals. Ventral excretory canals, $N = 21$, 43–137 (78 ± 24) wide, connected by narrow transverse ducts. Dorsal canals, $N = 19$, 4–8 (6 ± 1.0) wide, passing under genital ducts porally, and maintaining position directly over ventral canal aporally, through length of mature segments. Cirrus sac elongate, piriform, $N = 31$, 149–194 (171 ± 15) long by 34–51 (43 ± 9) in maximum width, directed anteriad with aporal end always overlapping longitudinal excretory canals. Cirrus with minute spines. Internal seminal vesicle fusiform, $N = 30$, 87–159 (123 ± 23) long by 20–48 (37 ± 8) in maximum width. External seminal vesicle, $N = 25$, 63–183 (144 ± 73) long by 20–78 (52 ± 19) in maximum width, situated dorsally to vagina and anterior to poral testis. Testes subspherical, $N = 30$, 92–166 (124 ± 16) wide, usually with one poral and two aporal in segment. Aporal testes situated lateral to ovary, sometimes pressing ovary into a smaller field, usually one testis anterior and one posterior in segment. Seminal receptacle, $N = 30$, 175–552 (369 ± 117) long by 43–148 (100 ± 27) in maximum width, extending porally, anterior to ovary. Ovary lobate, globular, $N = 32$, 90–149 (120 ± 18) in maximum length by 90–293 (206 ± 53) in maximum width. Vitelline gland with smooth margins, $N = 31$, 50–112 (71 ± 13) in maximum length by 54–106 (80 ± 15) in maximum width, situated in posterior margin of segment near midline, ventral and posterior to ovary. Gravid uterus (Fig. 3) saccular, usually filling whole segment, always overlapping longitudinal excretory canals dorsally. Genital ducts persisting in gravid segments; seminal receptacle usually prominent. Eggs subspherical with thin outer shell, $N = 20$, 70–81 (75 ± 3) long by 67–77 (70 ± 3) wide. Embryo oval, $N = 20$, 38–45 (43 ± 2) long by 38–40 (39 ± 1) wide. Measurements of embryo hooks as follows: larger hooks of first and third pairs, $N = 16$, 14–16 (16) long by 4 wide at guard; smaller hooks of first and third pairs, $N = 15$, 15–16 by 2–3 wide at guard; middle pair of hooks identical in morphologic characteristics, $N = 10$, 13–16 long by 2 wide at guard.

TYPE HOST: *Geomys bursarius* (Shaw)

SITE OF INFECTION: Small intestine, duodenum

TYPE LOCALITY: Weld County, Colorado, 1.6 km SE of Kersey (40°22′ N, 104°33′ W)

HOLOTYPE: USNM Helm. Coll. No. 79842

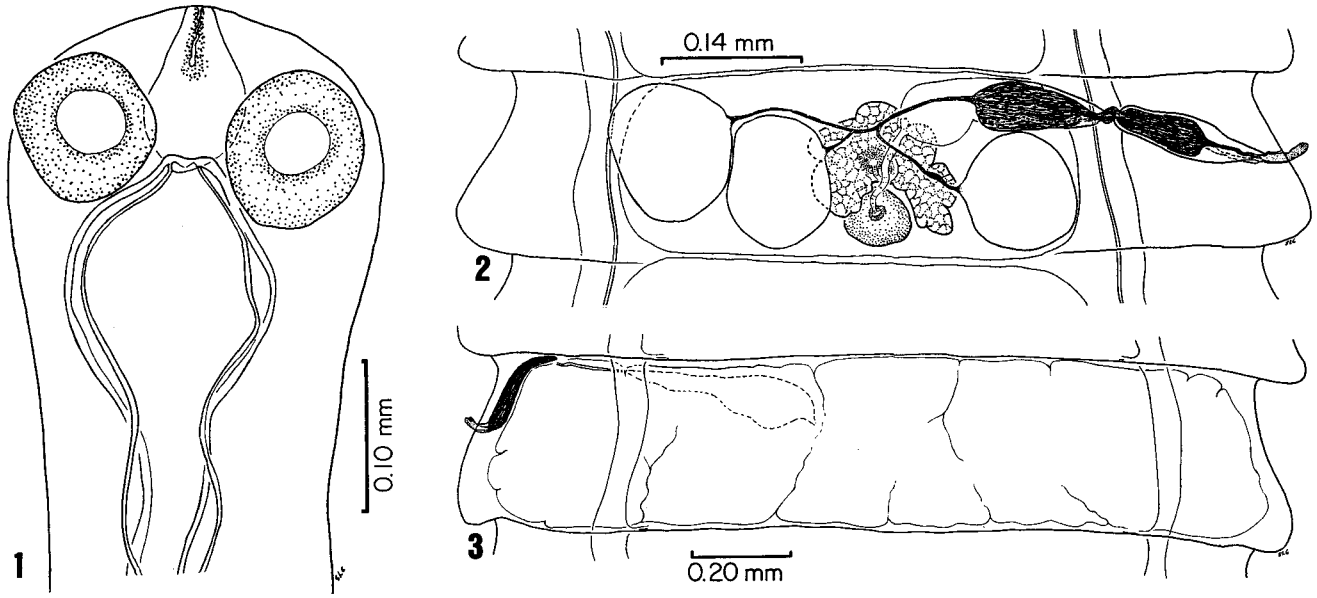
PARATYPE: USNM Helm. Coll. Nos. 79843, 79844

Life cycle

Viable cysticercoids of *H. weldensis* were recovered from the hemocoel of individuals of *T. molitor* as early as 17 days postinfection. The metacestodes resembled those of *H. diminuta* in general structure. Only 22% of the beetles exposed to *H. weldensis* became infected, and an average of three cysticercoids was recovered from each infected beetle. The number of eggs per gravid proglottid of *H. weldensis* was estimated to be about 800; therefore the rate of experimental infection of eggs of *H. weldensis* was approximately 0.4%. This was considerably lower than the results obtained from the same experimental infections with *H. diminuta*, in which the number of beetles becoming infected after experimental feeding of eggs was 100%, with a large number of cysticercoids (>50) being recovered from each infected beetle. All of 5 pocket gophers exposed to *H. weldensis* became infected. None of 5 laboratory rats and 2 laboratory gerbils, *Meriones unguiculatus* (Milne-Edwards), similarly exposed became infected.

Comparisons

The genus *Hymenolepis* s.str. contains about 21 species, of which 18 occur in rodents and 3 in insectivores. The actual



FIGS. 1–3. *Hymenolepis weldensis* n.sp. Fig. 1. Scolex. Fig. 2. Dorsal view of mature segment. Fig. 3. Ventral view of gravid segment.

TABLE 3. Variables compared using the Student–Newman–Keuls multiple-range test for equality of means

Variable	Pairwise comparisons of sample groups					
	W–D	W–T	W–G	D–T	D–G	T–G
1. Total length	*	*	ns	*	ns	*
2. Maximum strobila width	ns	*	ns	*	*	*
3. No. of segments	*	*	*	*	*	*
4. Cirrus sac length	*	*	*	*	*	*
5. Cirrus sac width	*	*	*	*	*	*
6. Internal seminal vesicle length	*	*	*	*	*	*
7. Internal seminal vesicle width	*	ns	ns	ns	*	*
8. External seminal vesicle length	*	ns	ns	ns	*	*
9. External seminal vesicle width	ns	*	ns	*	*	*
10. Testes, length	*	ns	*	*	ns	ns
11. Testes, width	ns	*	ns	*	*	*
12. Seminal receptacle length	ns	*	*	*	ns	*
13. Seminal receptacle width	*	*	ns	*	ns	*
14. Ovary length	ns	*	ns	ns	*	*
15. Ovary width	ns	*	*	*	ns	*
16. Vitelline gland length	*	ns	*	ns	*	*
17. Vitelline gland width	ns	ns	ns	*	*	*

NOTE: W, *H. weldensis*; D, *H. diminuta*; T, *H. tualatinensis*; G, *H. geomydis*. *, significantly different at the $p \leq 0.05$ level; ns, no significance difference. Sample sizes unequal.

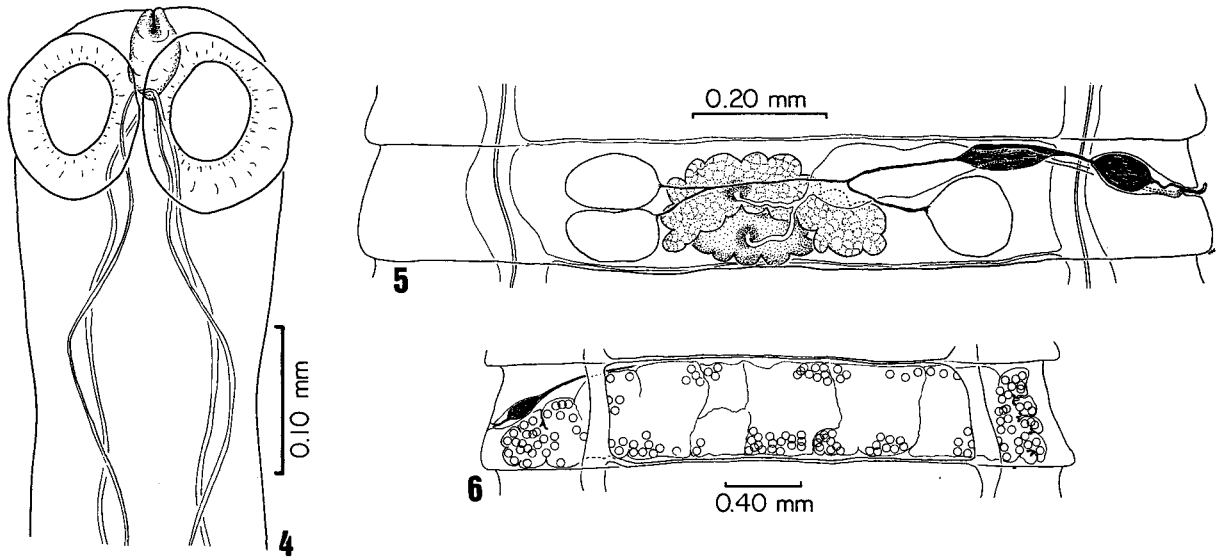
number of valid species in the genus is uncertain, as some descriptions are not detailed enough to permit adequate comparisons. The following comparisons will be restricted to those species of *Hymenolepis* that occur in rodents, with emphasis on Nearctic forms (Table 1).

Mas-Coma *et al.* (1980) separated species of *Hymenolepis* s.str. into two groups, based on the presence or absence of an apical organ on the scolex. Additionally, Mas-Coma (1982) established a new family, Arostrilepididae, for those species lacking an apical organ. However, no diagnosis of the family was provided. We therefore retain both morphological groups in the family Hymenolepididae but compare *H. weldensis* only with those species possessing an apical organ. Mas-Coma *et al.* (1980) and Mas-Coma (1982) listed all known species lacking an apical organ.

Comparisons with Nearctic forms

Hymenolepis weldensis was compared directly with the type specimen of *Hymenolepis pitymi* Yarinsky, 1952 (USNM Helm. Coll. No. 38261) from the pine vole, *Pitymys pinetorum* Le Conte. The description by Yarinsky (1952) is in good agreement with the type specimen. *Hymenolepis weldensis* differs from *H. pitymi* by possessing a much longer strobila, larger eggs, and an ovary that is lobate, complete, and not divided.

Hymenolepis weldensis can be differentiated from *H. diminuta* on the basis of the life cycle (see below) and can also be separated from this species by several easily discernible quantitative characters: shorter strobila, fewer segments, and smaller cirrus sac and internal seminal vesicle (see Table 2). Statistically significant differences in the means of 10 of 17



FIGS. 4–6. *Hymenolepis geomydis* n.sp. Fig. 4. Scolex. Fig. 5. Dorsal view of mature segment. Fig. 6. Ventral view of gravid segment; some eggs have been drawn to scale for reference.

quantitative variables (using the SNK test) are also evident (Table 3).

Voge (1969) provided some evidence that *H. citelli* and *H. diminuta* are distinct; others have not been able to demonstrate morphological differences in the strobilar stage (Rausch and Tiner 1948; Hansen 1950). Therefore, characters that serve to distinguish *H. diminuta* from other species will also suffice to distinguish *H. citelli*.

Hymenolepis weldensis differs from *H. tualatinensis* in several ways: 12 of 17 morphologic variables had significantly different mean values (SNK test) (Table 3) and the middle pair of embryonic hooks of *H. weldensis* were significantly shorter than those of *H. tualatinensis* (Student's *t*-test). The characteristics of their life cycles also serve to separate these species. *Hymenolepis weldensis* develops in *Tenebrio molitor* whereas *H. tualatinensis* does not develop in any of the three species of tenebrionid beetles used for experimental infections (Gardner 1985). (See Table 2 for comparative measurements.)

Comparisons with Old World forms

Hymenolepis weldensis can be distinguished from the following three species by the larger size of its strobila, and by the fact that these three are restricted to Old World rodents: *Hymenolepis sulcata* (von Linstow, 1879), described from *Glis glis* (L.) in Europe and found again in the same host in Hungary (Murai and Tenora 1977); *Hymenolepis uranomidis* Hunkeler, 1972, which occurs in five species of west African rodents (Hunkeler 1974); and *Hymenolepis pennanti* Nama, 1974, a parasite of the squirrel *Funambulus pennanti* Wroughton, in Jodhpur, India (Nama 1974).

Hymenolepis weldensis can be separated from *H. ognewi* Skrjabin, 1924 in possessing a shorter cirrus sac. *Hymenolepis ognewi*, a species with a Palearctic distribution, was described from *Rhombomys opimus* Lichtenstein and also has been reported in *Meriones tamaricinus* (Pallas) and *M. meridianus* Pallas (Ryzhikov *et al.* 1978; Mas-Coma *et al.* 1980). Joyeux and Foley (1930) recognized that *H. ognewi* may be a synonym of *H. diminuta*; however, it appears that *H. ognewi* is host-specific for Palearctic cricetids (Mas-Coma *et al.* 1980).

Hymenolepis weldensis can be separated from *H. vogeae* Singh, 1956 in possessing a larger strobila, an armed cirrus, and larger eggs. *Hymenolepis vogeae*, described originally from *Mus buduga* Thomas in India, was recently redescribed by Mikhail and Fahmy (1976) from *Meriones libycus* Lichtenstein in Egypt. It is doubtful, however, that the specimens of *Hymenolepis* described by Mikhail and Fahmy (1976) are in fact *H. vogeae*, primarily because of the great geographic and phylogenetic distance between the hosts; *M. buduga*, a murid, occurs only in India, and *Meriones libycus*, a cricetid, occurs only in the northern Ethiopian region.

Hymenolepis procera von Janicki, 1904, a species lacking an apical organ on the scolex, was described originally from the water vole, *Arvicola amphibius* L., in Europe. Baer (1932) considered *H. procera* to be a synonym of *H. horrida*, a species lacking an apical organ on the scolex. However, Joyeux and Foley (1930) published a redescription of *H. procera* from material recovered from *Meriones shawi* Rozet in Egypt, but indicated that their specimens possessed a rostellum. Mas-Coma *et al.* (1980) considered that the specimens determined to be *H. procera* by Joyeux and Foley (1930) were probably identical with the specimens described as *H. vogeae* by Mikhail and Fahmy (1976).

Hymenolepis geomydis n.sp.
(Figs. 4–6)

DESCRIPTION: Scolex (Fig. 4), $N = 4$, 189–252 (208 ± 30) long by 194–245 (216 ± 24) in maximum width. Suckers, $N = 15$, 92–124 (110 ± 13) long by 65–94 (78 ± 9) wide. Apical organ (rostellum) unarmed, small. Neck, $N = 5$, 528–1824 (1046 ± 503) long by 158–221 (186 ± 32) in maximum width. Strobila, $N = 7$, 72.26–168.41 mm (129 ± 32.76 mm) long, with 456–697 (640 ± 99) segments; maximum width, $N = 9$, 1.98–3.30 mm (2.79 ± 0.439 mm), attained late in gravid segments. Strobilar margins serrate, with intersegmental boundaries well defined in mature segments. Segments (Fig. 5) wider than long; strobila attenuated anteriorly, with increase in relative length beginning in mature segments; length:width ratio of mature and gravid segments 0.11–0.22 ($N = 30$) and 0.14–0.20 ($N = 30$), respectively.

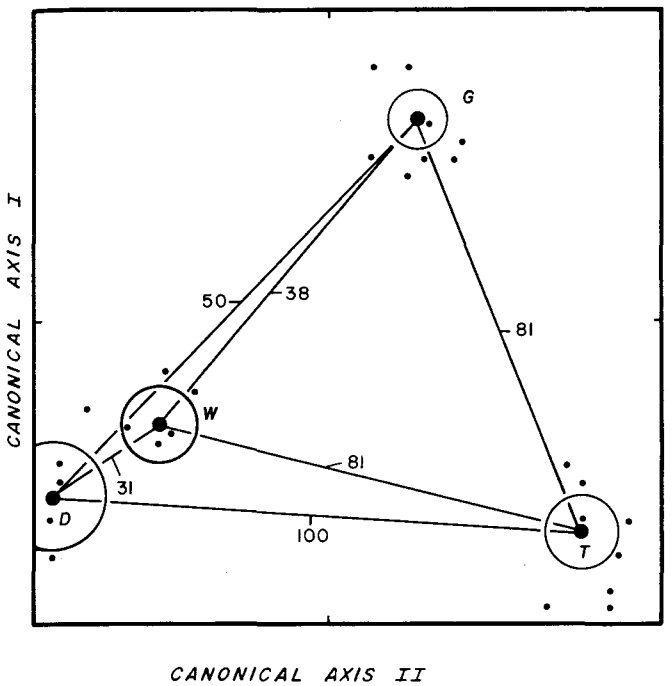


FIG. 7. Plot of canonical axes I and II; G, *H. geomydis*; W, *H. weldensis*; T, *H. tualatinensis*; D, *H. diminuta*. The centroid of each group is indicated by a large black dot; small dots represent the scatter of individuals around the centroids; circles represent 1 SD around the centroid of each species group. Relative euclidian (taxonomic) distances between groups are provided adjacent to lines connecting all centroids. Numbers represent degree of phenetic similarity (size and shape) between species pairs (pair with highest value is least similar).

Genital atrium, $N = 43$, 20–45 (27 ± 6) deep. Genital pores unilateral, sinistral. Genital ducts passing dorsally across longitudinal excretory canals. Ventral canals, $N = 36$, 23–90 (60 ± 16) wide, connected by narrow transverse ducts. Dorsal canal sometimes indistinct, $N = 5$, 3–5 (4 ± 1) wide. Cirrus sac elongate, pyriform, $N = 46$, 83–160 (119 ± 23) in maximum length by 36–67 (52 ± 7) in maximum width, directed slightly anteriad, in mature segments aporal end usually overlapping ventral excretory canals. Cirrus armed with minute spines. Internal seminal vesicle, $N = 43$, 40–117 (70 ± 16) in maximum length by 32–70 (44 ± 9) in maximum width. External seminal vesicle elongate, piriform, $N = 44$, 45–202 (125 ± 39) long by 27–130 (47 ± 44) in maximum width. Testes subspherical, $N = 45$, 55–180 (132 ± 60) long by 81–180 (139 ± 77) wide, one poral and two aporal. Aporal testes situated lateral to and not overlapping ovary; usually one anterior and one posterior in segment. From one to four testes per segment not unusual. Seminal receptacle, $N = 34$, 99–369 (226 ± 73) long by 59–108 (75 ± 17) in maximum width, extending porad, anterior to ovary. Ovary lobed, $N = 46$, 99–178 (137 ± 24) in maximum length by 180–484 (435 ± 61) in maximum width, situated medially in segment. In last mature segments (Fig. 5), vitelline gland lobate, with many small lobes, expanded laterally, situated ventrally and posterior to ovary, $N = 46$, 101–209 (144 ± 35) wide by 61–137 (87 ± 23) in maximum length. Ovary sometimes overlapping vitelline gland anteriorly. Gravid uterus filling whole segment. Genital ducts persisting in gravid segments. Posterior segments apolytic. Eggs subspherical with thin outer shell, $N = 20$, 76–85 (77 ± 16) long by 72–83 (73 ± 16) wide. Embryo surrounded by thin embryonic membrane, small inclusion bodies present, located next to inner layer of shell. Embryo oval, $N = 20$, 38–50 (40 ± 13) long by 34–43 (36 ± 7) wide. Larger hooks of first and third pairs, $N = 30$, 15–18 (17) long by 2–4 (4) wide at guard; smaller hooks of first and third pairs, $N = 28$, 15–19 (17) long by 2–4 (2) wide at guard; middle pair of hooks identical in morphological characteristics, $N = 16$, 16–20 (18) long by 2–3 (2) wide at guard.

TYPE HOST: *Geomys bursarius* (Shaw)

SITE OF INFECTION: Small intestine, duodenum

TYPE LOCALITY: Weld County, Colorado, 5 km SE of Kersey (40°22′ N, 104°33′ W)

HOLOTYPE: USNM Helm. Coll. No. 79840

PARATYPE: USNM Helm. Coll. No. 79841

Comparisons

Hymenolepis geomydis n.sp. can be differentiated from those congeners occurring in rodents of the Palearctic and Ethiopian regions on the same phylogenetic and biogeographic grounds as presented above for *H. weldensis*. This species is distinct from the four members of the genus *Hymenolepis* s.str. that occur in rodents in the Nearctic, as indicated in the following (see also Table 2).

Hymenolepis geomydis differs from *H. pitymi* by possessing a longer strobila, an ovary of different form, and larger eggs. Only one specimen of *H. pitymi* was available for study, so statistical significance in these differences could not be assessed.

Sixteen of 17 characters tested (SNK test) of *Hymenolepis geomydis* n.sp. differed significantly in their means from those of *H. tualatinensis* (Table 3) and the middle pair of embryonic hooks of *H. geomydis* was significantly shorter (Student's *t*-test).

Twelve of 17 characters tested (SNK test) between *H. diminuta* and *H. geomydis* were significantly different (Table 3). *Hymenolepis geomydis* also had statistically different mean sizes of eggs, embryos, and embryonic hooks (Student's *t*-test) and also differed from *H. diminuta* in the biological characteristics of the life cycle. Development of metacestodes of *H. geomydis* did not occur in the three species of tenebrionid beetles used for experimental infection (see Materials and methods).

Hymenolepis geomydis can be separated from *H. weldensis* on the basis of the life cycle; *H. geomydis* did not develop in individuals of *T. molitor* despite repeated attempts to infect these beetles. Means of 17 characters were tested for significant differences between *H. geomydis* and *H. weldensis* (using SNK test); of these, 8 were significantly different (see Table 3). In addition, significant differences were present in the mean size of eggs, embryos, and embryonic hooks (Student's *t*-test), and discrimination by MDA (Fig. 7) showed good separation of individuals of *H. geomydis* into a discrete group, distinctly separate from individuals of the other three species.

Discussion

Multivariate analysis

Seventeen character variables were selected that should have allowed discrimination of the four groups (i.e., species; Table 3). Measurements of these characters were all taken from stained, mounted specimens. Characters of the scolex

TABLE 4. Character loadings, canonical vectors, and percent trace for 17 variables used in multigroup discriminant function analysis of four species of *Hymenolepis*, and percentage of variance of each variable in each canonical vector

Variable	Character loading		% variance of variable	
	CV I	CV II	CV I	CV II
1. Total length	0.151	−0.088	84.75	13.68
2. Maximum width	−0.124	0.145	60.51	38.97
3. Number of segments	−0.603	0.270	89.59	8.46
4. Cirrus sac length	−0.215	−0.356	1.42	53.14
5. Cirrus sac width	−0.554	0.685	58.14	41.72
6. Internal seminal vesicle length	−0.328	0.037	96.59	0.58
7. Internal seminal vesicle width	0.101	−0.072	52.93	12.62
8. External seminal vesicle length	−0.117	0.040	91.65	5.11
9. External seminal vesicle width	−0.048	0.115	25.40	67.98
10. Testes length	−0.001	0.073	0.03	73.14
11. Testes width	0.130	−0.040	74.64	3.33
12. Seminal receptacle length	−0.158	−0.105	70.19	14.41
13. Seminal receptacle width	0.183	0.151	72.27	23.14
14. Ovary length	0.047	0.203	9.47	83.43
15. Ovary width	0.050	0.333	4.48	93.93
16. Vitelline gland length	0.173	0.105	83.90	14.70
17. Vitelline gland width	0.031	−0.279	2.60	96.79
% trace	66.08	31.09		

NOTE: Percent trace is the amount of among-group differences extracted by each canonical axis. Percentage of variance of variable indicates the participation of each variable on each axis; the greater the percentage of variance attributable to each character variable in each canonical vector, the more the variable is involved in discrimination. CV, canonical vector.

were not used for the multivariate analysis because of the small numbers of scoleces measured. Characters of the eggs were not included because of possible distortion of the egg shell and embryo by reagents and because it is usually necessary to use fresh material for analysis of these characters. The characters chosen are easily identifiable and measurable in other groups of cestodes, and the analysis can be applied to morphologic measurements of preserved material; therefore the techniques may be applied to other groups with relative ease.

For multiple discriminant analysis, centroids of each group (species), defined *a priori* by classical methods, were determined to be significantly different ($F = 6.80$, df = 51,21). This is required for the results of MDA to be valid. The relative contribution of each individual character variable can be determined from Table 4. Variables 1, 3, 6, 8, and 16 are all measurements of length, and contribute most to the discrimination of canonical vector I. Canonical vector II has four variables, 9, 14, 15, and 17 (primarily measurements of width), contributing maximally to discrimination between groups. Thus, the horizontal axis (canonical axis I) in Fig. 7 is determined primarily by length of characters, and canonical axis II can be considered to be influenced by width of characters. Canonical vectors I and II contribute 66.08 and 31.09%, respectively, of the discrimination between groups (Table 4), therefore other vectors were not analyzed further. Figure 7 is a plot of canonical axes I vs. II; confidence limits were calculated for each group (Pimentel 1979, p. 224) and represent one standard deviation around the centroid. No confidence circles overlap; thus all species groups are considered significantly different from each other. Phenetic similarity among groups is indicated by taxonomic distances. *Hymenolepis diminuta* and *H. weldensis* are most similar phenetically (morphologically), and *H. diminuta* and *H. tualatinensis* are most dissimilar.

It is evident that members of the genus *Hymenolepis* s.str. occur commonly in the genera *Thomomys* and *Geomys*. Although several species of *Hymenolepis* have been reported from other Nearctic mammals (Mas-Coma *et al.* 1980; Gardner 1985), it appears that in the Nearctic region, the greatest diversity of species of this genus occurs in rodents of the family Geomyidae, specifically the genera *Thomomys* and *Geomys*. However, few complete helminthological surveys of other genera of pocket gophers have been conducted (Gardner 1985), and data on the parasite fauna of the genera *Orthogeomys* Merriam and *Zygogeomys* Merriam are needed. These genera include species that occur in the southern Nearctic and extreme northern Neotropics, and little is known of their natural history or systematic relationships.

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