

Description of two new species of *Hymenolepis* Weinland, 1858 (Cestoda: Hymenolepididae) from rodents on Luzon Island, Philippines

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Abstract Our helminthological examination of murid rodents on Luzon Island, Philippines, revealed a remarkable diversity of *Hymenolepis* Weinland, 1858. Here we describe two new species based on specimens from murid rodents *Rattus everetti* (Günther) and *Apomys datae* (Meyer) collected from Luzon Island. *Hymenolepis alterna* n. sp. differs from all known species of *Hymenolepis* in having irregularly alternating genital pores. This feature has not been reported from any previously known member of *Hymenolepis*. Additionally, *Hymenolepis alterna* n. sp. also differs from other *Hymenolepis* spp. in the relative position of both poral and antiporal dorsal osmoregulatory canals which are shifted towards the middle of the proglottis in relation to the ventral canals on both sides of the proglottides, and in having curved or twisted external seminal vesicle, covered externally by a dense layer of intensely stained cells. *Hymenolepis bilateralis* n. sp. differs from all known species of

Hymenolepis in the relative position of both poral and antiporal dorsal osmoregulatory canals, which are shifted bilaterally towards the margins of proglottides in relation to the ventral canals, and in possession of testes situated in a triangle and eggs with very thin outer coat. A total of seven species of *Hymenolepis* are known from the Philippine archipelago. This total includes the cosmopolitan species *Hymenolepis diminuta* (Rudolphi, 1819), which was likely introduced to the island with invasive rats. Strikingly, all seven known species occur on the island of Luzon alone. By comparison, only six *Hymenolepis* spp. are known from the whole Palaearctic and seven from the Nearctic despite a much better level of knowledge of rodent helminths in these zoogeographical regions, as well as vast territories, diverse landscapes and very rich rodent fauna. This suggests that *Hymenolepis* spp. may have undergone an unusually active radiation in the Philippines. Possible explanations of this phenomenon are discussed.

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Introduction

Cestodes in the genus *Hymenolepis* Weinland, 1858 primarily parasitise rodents. A few species parasitise bats and one parasitises hedgehogs. Members of this genus share several morphological features such as: an unarmed scolex containing a rudimentary rostellar apparatus, ventral osmoregulatory canals connected by transverse anastomoses, cirrus-sac with well-

pronounced muscular walls, vagina surrounded by circular musculature, saccate uterus, and eggs with a thick outer coat (Mas-Coma & Tenora, 1997; Gulyaev & Mel'nikova, 2005; Makarikova et al., 2010; Makarikov & Tkach, 2013; Makarikov et al., 2013). A morphologically similar genus *Talpolepis* Gulyaev & Mel'nikova, 2005 was erected based largely on the presence of two distinct characters: dorsal osmoregulatory canals asymmetrically shifted relative to ventral canals, and thin cirrus-sac wall lacking obvious musculature. The distinction between *Hymenolepis* and *Talpolepis* is clouded by the recent discovery and description of two species from the Philippines that exhibit intermediate morphological characters. Although placed in the genus *Hymenolepis*, *H. bicauda* Makarikov, Tkach & Bush, 2013 and *H. haukisalmii* Makarikov, Tkach & Bush, 2013 have dorsal osmoregulatory canals shifted in relation to the ventral canals and cirrus-sac with muscular walls. With continued biotic surveys in the Philippines, we have discovered two more species with morphological characters that are intermediate between *Hymenolepis* and *Talpolepis*. Like *H. bicauda* and *H. haukisalmii* these two new species also have osmoregulatory canals shifted in relation to the ventral canals and cirrus-sac with muscular wall. Despite some similarities, these cestodes have unique morphological characters clearly differentiating them from all other previously described *Hymenolepis* species. Herein, we describe these two new species and discuss the validity of the morphological criteria used to define the genus *Talpolepis*.

Materials and methods

Rodents were collected in the summers of 2009 and 2011 at several sites on Luzon Island, Philippines, as a part of a biodiversity survey of terrestrial vertebrates and their parasites. The two new species described in the present work were found in the Philippine forest rat *Rattus everetti* (Günther) in the Aurora Province and the Luzon montane forest mouse, *Apomys datae* (Meyer) in the Cagayan Province.

Animals were trapped using live traps and pitfall traps. Cestodes were removed from the intestine, rinsed in saline, heat-killed in hot water, and preserved in 70% ethanol. They were stained with Mayer's or

Ehrlich's haematoxylin, dehydrated in an ethanol series, cleared in methyl salicylate (after Mayer's haematoxylin) or clove oil (after Ehrlich's haematoxylin) and mounted in Damar gum. Some specimens were mounted in Berlese's clearing medium to facilitate the examination of the cirrus armature and the organization of the eggs.

Type-material was deposited in the parasite collection of the Harold W. Manter Laboratory (HWML) of the University of Nebraska, Lincoln, Nebraska. The types were deposited at HWML with the understanding that some will ultimately be repatriated to collections in the Philippines. Hosts were deposited at the University of Kansas Natural History Museum, Lawrence, Kansas (KUMNH).

Syntypes and vouchers of *Hymenolepis uranomidis* Hunkeler, 1972 deposited in the Geneva Museum of Natural History (MHNG INVE 18679, INVE 18680, INVE 1868, INVE 18685) were studied for comparative purposes. Measurements are given in micrometres except where otherwise stated.

Hymenolepis alterna n. sp.

Type-host: Philippine forest rat *Rattus everetti* (Günther) (Rodentia: Muridae). The new cestode species was found in both specimens of *R. everetti* examined in the type-locality.

Type-locality: IDC Forestry land, Barangay Casapsipan, Municipality of Casiguran, Aurora Province, Luzon Island, Philippines (N 16.293, E 122.186; 1 m a. s. l.).

Site in host: Small intestine.

Type-material: Holotype, HWML-75062 (one specimen on two slides; field number P.2902#1A, 1B, host KUMNH # 167932), labelled: ex. *Rattus everetti*, IDC Forestry land, Barangay Casapsipan, Municipality of Casiguran, Aurora Province, Luzon Island, Philippines, 1.vii.2009, coll. V. Tkach. Paratypes, HWML-75063 (one specimen on two slides; field number P.2902#2A, 2B); HWML-75063 (one specimen on two slides; field number P.2902 slide1, slide2) and HWML-75063 (field number P.2904, host KUMNH # 167933) (all labelled identical to the holotype).

Etymology: The species name refers to the very distinctive morphological feature of the species, namely the irregularly alternating genital pores, which is unique among species of *Hymenolepis*.

Description (Figs. 1–2)

[Based on 5 specimens; measurements of the holotype are followed by the range, mean values and number of measured specimens in parentheses]. Fully developed strobila 165 (165–170; $n = 2$) mm long, with maximum width at pregravid or gravid proglottides, 2.9–3.8 mm. Strobila consisting of 390–421 craspedote proglottides. Scolex slightly flattened dorsoventrally, 380 (380–410; 389; $n = 3$) wide, not clearly distinct from strobila (Fig. 1A, B). Suckers unarmed, round or oval, 160–170 \times 130–141 (154–189 \times

130–144; 169 \times 137; $n = 12$), with thick muscular walls, not reaching lateral margins of scolex. Rhynchus unarmed, 49 \times 7 (39–49 \times 4–7; 45 \times 5; $n = 3$), invaginated in rostellar pouch 152 \times 85 (152–175 \times 82–90; 162 \times 85; $n = 3$); rostellum absent (Fig. 1A, B). Rostellar pouch with muscular wall, osmoregulatory canals penetrate through rostellar pouch wall. Neck 347 (295–347; $n = 3$) wide.

Ventral osmoregulatory canals 107–172 (105–172; 135; $n = 13$) wide, connected by transverse anastomoses. Dorsal osmoregulatory canals 25–41 (20–41; 31; $n = 13$) wide, shifted on both sides towards middle

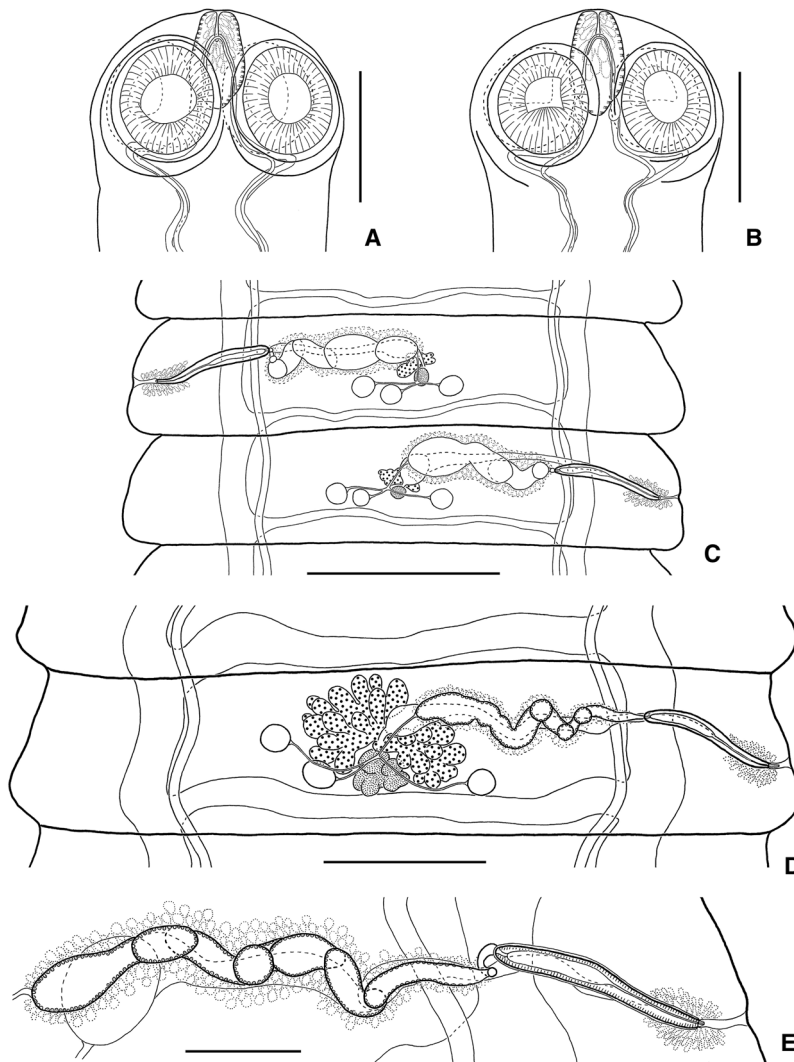


Fig. 1 *Hymenolepis alterna* n. sp. A, Holotype (HWML-75062), dorsoventral view of scolex; B, Paratype (HWML-75063, P.2902#2B), dorsoventral view of scolex; C, Holotype, male mature proglottides; D, Holotype, hermaphroditic mature proglottides; E, Holotype, genital ducts, dorsal view. Scale-bars: A, B, E, 200 μ m; C, D, 500 μ m

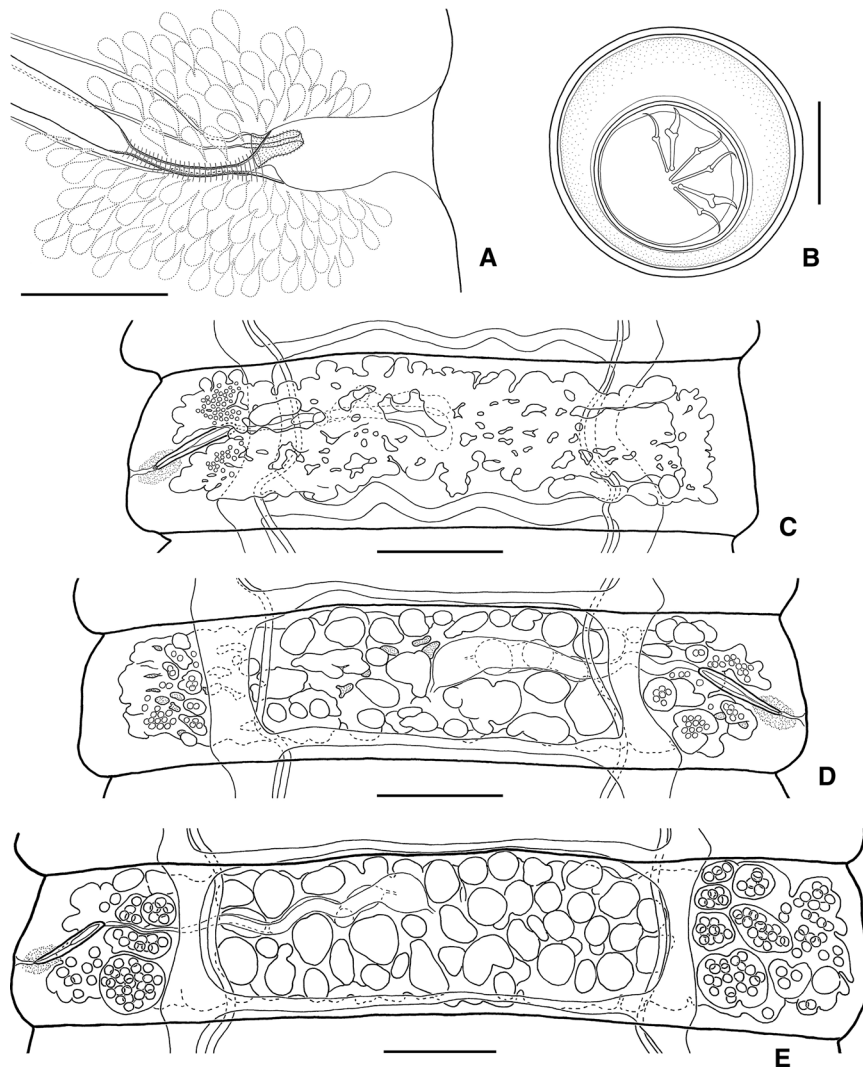


Fig. 2 *Hymenolepis alterna* n. sp. A, Paratype (HWML-75063, P.2904), cirrus and vagina, ventral view; B, Paratype (HWML-75063, P.2902#2A), egg; C, Holotype (HWML-75062), postmature proglottides from dorsal side, showing uterine development; D, Paratype (HWML-75063, P.2902#2B), pregravid proglottides from ventral side, showing appearance of ventral uterine diverticula; E, Paratype (HWML-75063, P.2902#2B), gravid proglottis from ventral side, showing saccate uterus with ventral uterine diverticula. Scale-bars: A, 50 μ m; B, 20 μ m; C–E, 500 μ m

of proglottis in relation to ventral canals. Genital pores unilateral, irregularly alternating (Fig. 1C). Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals (Fig. 1C, D, E). Development of proglottides gradual, protandrous. External segmentation becomes evident at level of premature part of strobila.

Mature proglottides 480–525 \times 2,230–2,440 (300–525 \times 2,100–2,440; 422 \times 2,275; n = 12), transversely elongate, trapezoid (Fig. 1C, D). Testes

relatively small, usually 3, almost equal in size, 83–111 \times 72–91 (72–111 \times 65–91; 93 \times 78; n = 16), round or oval, most often situated in 1 row, sometimes in shallow triangle; poral testis separated from 2 antiporal testes by female gonads. Cirrus-sac elongate, relatively short, 365–390 \times 40–52 (350–395 \times 40–54; 373 \times 46; n = 12), with thick muscular wall. Antiporal part of cirrus-sac rarely overlapping ventral longitudinal canal, but commonly does not reach dorsal osmoregulatory canal (Fig. 1D, E). Genital atrium

simple, tubular, very deep, situated approximately in middle of or slightly posterior to lateral proglottis margin. Cirrus (32–47 × 7–10; 37 × 8; n = 10) cylindrical in basal region, armed with minuscule (less than 1 long) spines (Fig. 2A); fully evaginated cirrus not observed. Internal seminal vesicle oval, 172–205 × 24–35 (169–205 × 23–37; 181 × 27; n = 12), no longer than half of cirrus-sac length (Fig. 1E). External seminal vesicle 630–790 × 90–110 (620–790 × 55–110; 698 × 84; n = 10), elongate, usually curved or twisted, with size approximately equal to, or slightly smaller than seminal receptacle, covered externally by dense layer of intensely stained cells; internal surface of external seminal vesicle lined by layer of epithelial cells.

Ovary median, 506–525 (395–525; 461; n = 10) wide, lobed, fan-shaped, ventral to male genital organs, occupies less than half of median field width, usually not overlapping testes (Fig. 1D). Vitellarium 105–157 × 145–205 (90–165 × 125–205; 128 × 160; n = 10), post-ovarian, median, slightly lobed. Copulatory part of vagina tubular (50–57 × 3–6; 54 × 4; n = 7), clearly distinct from seminal receptacle; ventral to cirrus-sac (Fig. 2A). Vagina surrounded by circular musculature and covered externally by dense layer of intensely stained cells. Seminal receptacle 770 × 110 (765–900 × 68–123; 860 × 104; n = 8), elongate, usually not curved (Fig. 1D, E).

Uterus first appears as perforated transversely elongate sac, situated dorsally to other organs and extending laterally beyond longitudinal osmoregulatory canals (Fig. 2C). With proglottis development, uterus forms numerous diverticula on both dorsal and ventral sides (Fig. 2D). Testes persist in postmature proglottides; cirrus-sac and vagina persist in gravid proglottides. Gravid proglottides transversely elongate (670–750 × 3,300–3,800; 707 × 3,650; n = 7). Fully developed uterus occupying entire median field and extending laterally beyond longitudinal osmoregulatory canals, saccate, with numerous ventral and dorsal diverticula, lateral sides of gravid uterus usually not perforated (Fig. 2E). Uterus contains numerous (up to 5,000–6,000) small eggs. Eggs 48–51 × 49–53, subspherical, with relatively thick outer coat (up to 2) and rough surface; oncosphere 23–26 × 25–27 (Fig. 2B). Embryophore subspherical, thin, 27–29 × 29–33. Embryonic hooks small, 12.3–14 long.

Remarks

Hymenolepis alterna n. sp. has morphological characters typical of *Hymenolepis* (*s. str.*), namely scolex with rudimentary rostellar apparatus, unarmed rhynchus invaginated in rostellar pouch, ventral canals with transverse anastomoses, testes situated in one row, cirrus-sac with muscular walls, vagina surrounded by circular musculature, saccate uterus with ventral and dorsal diverticula and spherical eggs with thick outer coat. However, unlike in other known *Hymenolepis* spp., both dorsal osmoregulatory canals in *H. alterna* n. sp. are shifted towards middle of proglottis in relation to ventral canals. The external seminal vesicle in the new species is covered externally by a dense layer of intensely stained cells while its internal surface is lined with a layer of epithelial cells. A similar structure of external seminal vesicle was observed only in *H. uranomidis* from *Uranomys ruddi* Dollman from West Africa (Hunkeler, 1972; our observations from the type-series). However, in the latter species the external seminal vesicle is compact and significantly smaller than the seminal receptacle, whereas in the new species it is curved or twisted and is of approximately equal size as the seminal receptacle. Additionally, genital pores in the new species are irregularly alternating. The latter character is unique not only among members of *Hymenolepis* but also among other hymenolepidids from mammals.

Due to the morphological peculiarity of the new species and its geographic isolation in the Philippines we do not provide differentiation of *H. alterna* n. sp. from the Eurasian and north American congeners based on morphometric data. The new species is readily distinguishable from the sympatric species *H. bicauda* and *H. haukisalmii* by the significantly wider strobila and scolex, larger suckers, rostellar pouch, longer cirrus-sac and seminal receptacle and wider ovary. Furthermore, the number of eggs in the new species is considerably higher than in its congeners from Luzon Island (see Table 1).

Hymenolepis bilateralis n. sp.

Type-host: Luzon montane forest mouse, *Apomys datae* (Meyer) (Rodentia: Muridae).

Table 1 Main morphometric data distinguishing *Hymenolepis* spp. from the Luzon Island, Philippines (measurements in μm except where otherwise stated)

Characters/ Species	<i>H. bicauda</i> ^a	<i>H. haukisalmii</i> ^a	<i>H. alterna</i> n. sp.	<i>H. bilateralis</i> n. sp.
Strobila length	26–29 mm	up to 132 mm	165–170 mm	86 mm
Strobila width	0.99–1.19 mm	2.4 mm	2.9–3.8 mm	1.5–2.5 mm
Scolex width	260–288	240–265	380–410	347–400
Sucker size	92–103 × 80–95	83–105 × 81–93	154–189 × 130–144	110–150 × 105–120
Rostellar pouch size	75–83 × 50–56	88–94 × 50–60	152–175 × 82–90	90–98 × 45–56
Hermaphroditic mature proglottid size	150–200 × 880–1,020	245–270 × 1,820–2,080	300–525 × 2,100–2,440	180–282 × 950–1,195
Testes size	70–103 × 65–100	116–160 × 85–157	72–111 × 65–91	92–126 × 75–106
Testes arrangement	Linear	Linear	Most often linear	Triangular
Cirrus-sac size	140–166 × 35–45	234–289 × 34–44	350–395 × 40–54	170–200 × 40–54
Cirrus size	35–48 × 10–12	43–56 × 9–14	32–47 × 7–10	55–66 × 12–16
Ovary width	108–140	193–208	506–525	190–230
Vitellarium size	38–55 × 50–65	61–83 × 80–125	90–165 × 125–205	70–85 × 80–115
Seminal receptacle size	265–340 × 40–75	595–779 × 137–172	765–900 × 68–123	310–395 × 42–80
Egg number	up to 30–45	up to 360–450	up to 5,000–6,000	120–280
Egg size	46–54 × 50–60	29–34 × 37–46	48–51 × 49–53	67–90 × 71–103
Oncosphere size	27–33 × 31–38	15–17 × 18–20	23–26 × 25–27	35–45 × 37–48
Embryonic hook size	17.5–19	11–13	12.3–14	17–19.1

^a Measurements from Makarikov et al. (2013)

Type-locality: Mt. Cagua, Barangay Magrafil, Gonzaga City, Cagayan Province, Luzon Island, Philippines; (18.236°N; 122.104°E; 680 m a. s. l.).

Site in host: Small intestine.

Type-material: Holotype, HWML-75064 (field number P.4655#2, KUMNH host collector # JAC106), labelled: ex. *Apomys datae*, intestine, Mt. Cagua, Barangay Magrafil, Gonzaga City, Cagayan Province, Luzon Island, Philippines, 20.vii.2011, coll. S. Villa. Paratypes, HWML-75065 (field number P.4655); HWML-75065 (one specimen on two slides; field number P.4655#1A, 1B) and HWML-75065 (field number P.4655#3) (all labelled identical to the holotype).

Etymology: The species name refers to a distinctive morphological feature of the species, namely the dorsal osmoregulatory canals shifted bilaterally towards the lateral margins of proglottis in relation to the ventral canals (Fig. 3C, D).

Description (Figs. 3–4)

[Based on 4 specimens; measurements of the holotype are followed by the range, mean values and number of

measured specimens in parentheses.] Fully developed strobila 86 mm long, with maximum width at pregravid or gravid proglottides, 1.5 (1.5–2.5) mm. Strobila consisting of 395 craspedote proglottides. Scolex slightly flattened dorsoventrally, 347 (347–400; 373; n = 3) wide, not clearly distinct from strobila (Fig. 3A, B). Suckers unarmed, round or oval, 127–150 × 106–111 (110–150 × 105–120; 122 × 112; n = 10), with thick muscular walls, not reaching lateral margins of scolex. Rhynchus unarmed, 35 × 5 (27–35 × 5–8; 30 × 6; n = 3), invaginated in rostellar pouch 92 × 54 (90–98 × 45–56; 93 × 51; n = 3); rostellum absent (Fig. 3A, B). Rostellar pouch with muscular wall, osmoregulatory canals penetrate through rostellar pouch wall. Neck 310 (310–390; n = 3) wider than scolex.

Ventral osmoregulatory canals 29–47 (22–47; 33; n = 17) wide, connected by transverse anastomoses. Dorsal osmoregulatory canals 7–9 (5–9; 6; n = 14) wide, shifted bilaterally towards lateral margins of proglottis in relation to ventral canals. Genital pores unilateral, dextral. Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals (Fig. 3C–E). Development of proglottides gradual,

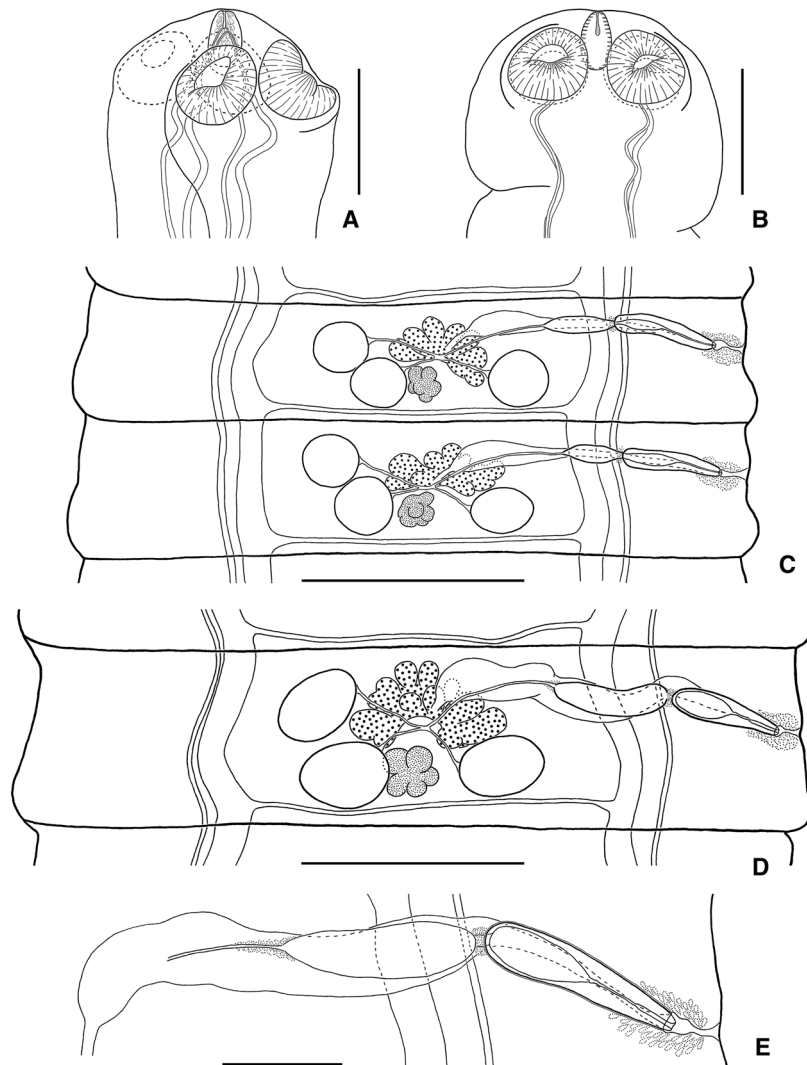


Fig. 3 *Hymenolepis bilateralis* n. sp. A, Holotype (HWML-75064), sublateral view of scolex; B, Paratype (HWML-75065, P.4655#3), dorsoventral view of scolex; C, Holotype, male mature proglottides; D, Holotype, hermaphroditic mature proglottides; E, Holotype, genital ducts, dorsal view. Scale-bars: A, B, 200 μ m; C, D, 300 μ m; E, 100 μ m

protandrous. External segmentation becomes evident at level of premature part of strobila.

Mature proglottides 265–282 \times 1,050–1,145 (180–282 \times 950–1,195; 245 \times 1,076; n = 14), transversely elongate, trapezoid (Fig. 3C, D). Testes relatively small, usually 3, almost equal in size, 100–120 \times 80–93 (92–126 \times 75–106; 108 \times 87; n = 25), round or oval, normally arranged in triangle of varying configuration; poral testis separated from 2 antiporal testes by female gonads. Cirrus-sac pyriform, relatively short, 187–200 \times 41–54 (170–200 \times 40–54; 185 \times 43; n = 14), with thin muscular walls.

Antiporal part of cirrus-sac usually does not reach dorsal osmoregulatory canal or rarely slightly crosses it, but commonly does not reach ventral longitudinal canal (Fig. 3D, E). Genital atrium simple, infundibular, deep, situated approximately in middle of or slightly anterior to lateral proglottis margin. Cirrus 56–65 \times 12–16 (55–66 \times 12–16; 60 \times 14; n = 13), cylindrical in basal region, armed with minuscule (less than 1 long) spines (Fig. 4A); fully evaginated cirrus not observed. Internal seminal vesicle oval, 85–107 \times 34–43 (75–110 \times 32–43; 91 \times 36; n = 14), no longer than half of cirrus-sac length (Fig. 3E). External

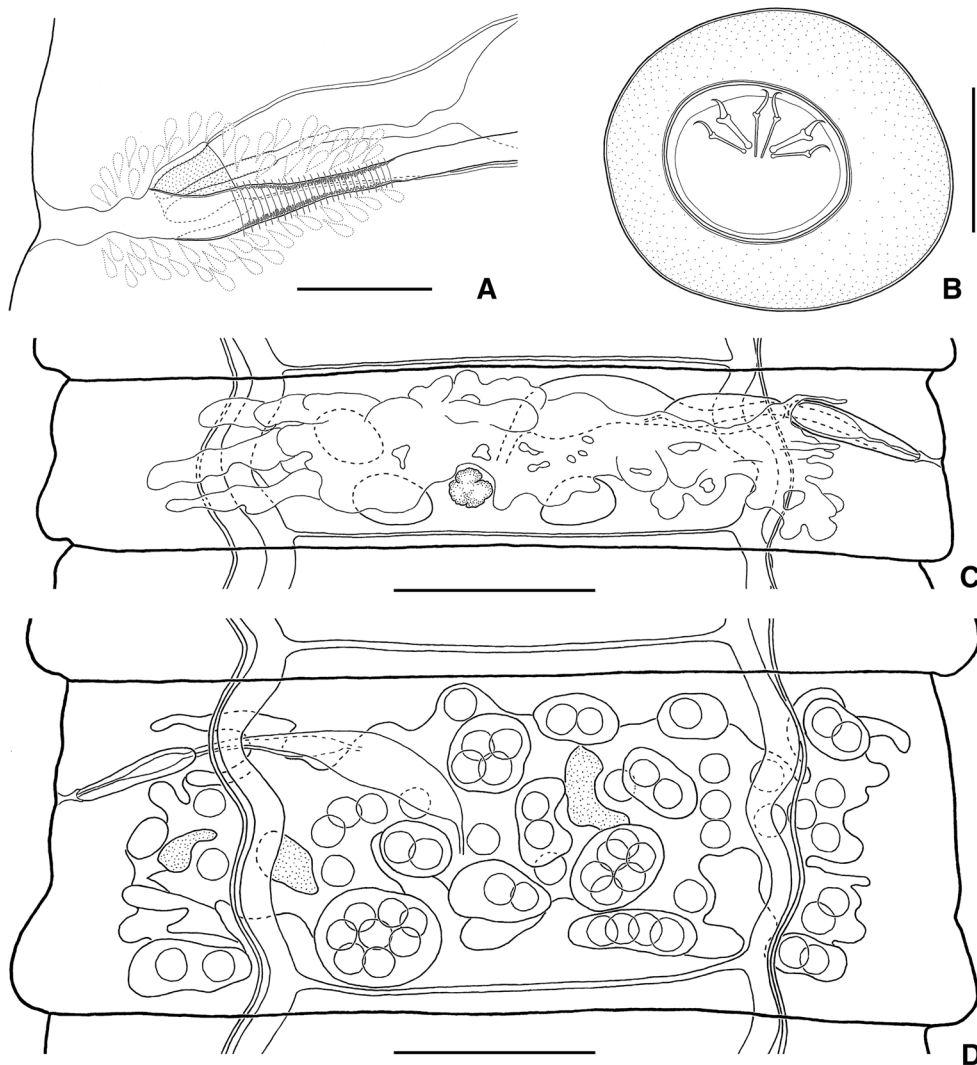


Fig. 4 *Hymenolepis bilaterala* n. sp. A, Holotype (HWML-75064), cirrus and vagina, ventral view; B, Paratype (HWML-75065, P.4655#1A), egg; C, Holotype, pregravid proglottis from dorsal side, showing uterus development; D, Holotype, gravid proglottis from ventral side, showing uterine diverticula. Scale-bars: A, B, 40 μ m; C, D, 300 μ m

seminal vesicle elongate, oval, clearly distinguishable from vas deferens, distinctly smaller than seminal receptacle, 135–173 \times 42–50 (130–175 \times 40–65; 154 \times 50; n = 10).

Ovary 200–225 (190–230; 207; n = 14) wide, median, lobed, fan-shaped, ventral to male genital organs, occupying less than half of median field width, usually not overlapping testes (Fig. 3D). Vitellarium 78–80 \times 80–94 (70–85 \times 80–115; 76 \times 94; n = 14), postovarian, slightly shifted antiporally or rarely median, lobed. Copulatory part of vagina 64–73 \times 6–16 (57–73 \times 5–16; 66 \times 9; n = 8), tubular, clearly

distinct from seminal receptacle; ventral to cirrus-sac (Fig. 4A). Vagina surrounded by circular musculature and covered externally by dense layer of intensely stained cells. Seminal receptacle 336–386 \times 50–78 (310–395 \times 42–80; 345 \times 62; n = 7), elongate, usually not curved (Fig. 3D, E).

Uterus first appears as perforated transversely elongate sac, situated dorsally to other organs and extending laterally beyond longitudinal osmoregulatory canals (Fig. 4C). With proglottis development, uterus forms numerous diverticula on dorsal and ventral side of strobila (Fig. 4D). Testes remain in

postmature proglottides; cirrus-sac and vagina persist in gravid proglottides. Gravid proglottides transversely elongate, 504–540 × 1,300–1,450 (430–540 × 1,300–2,430; 493 × 1,681; n = 8). Fully developed uterus occupying entire median field and extending laterally beyond longitudinal osmoregulatory canals, saccate, with ventral and dorsal diverticula, slightly perforated (Fig. 2D). Uterus contains relatively small number (up to 120–280) large eggs. Eggs 67–90 × 71–103, subspherical, with very thin outer coat (less than 1), egg surface rough; oncosphere 35–45 × 37–48 (Fig. 4B). Embryophore subspherical, thin, 40–51 × 42–54. Embryonic hooks relatively large, 17–19.1 long.

Remarks

Hymenolepis bilaterala n. sp. has morphological characters typical of *Hymenolepis* (*s. str.*), namely coxlex with rudimentary rostellar apparatus, unarmed rhynchus invaginated in rostellar pouch, ventral canals with transverse anastomoses, cirrus-sac with muscular walls, vagina surrounded by circular musculature, saccate uterus with ventral and dorsal diverticula, and spherical eggs. However, unlike other known species of *Hymenolepis*, the dorsal osmoregulatory canals in *H. bilaterala* n. sp. are shifted bilaterally towards the lateral margins of proglottis in relation to ventral canals and the fully developed eggs in the new species have very thin outer coat. There are only three species of *Hymenolepis* from rodents with shifted dorsal osmoregulatory canals relative to the ventral canals, all of them from the Philippines. These are *H. bicauda*, *H. haukisalmii* and *H. alterna* n. sp. (Makarikov et al., 2013; this publication). However, each of these exhibits a unique combination of the relative position of osmoregulatory canals. In *H. bicauda* the poral dorsal osmoregulatory canal is situated lateral relative to the poral ventral canal, but its antiporal dorsal canal is situated directly above the ventral canal. In *H. haukisalmii* the poral dorsal osmoregulatory canal is situated lateral to the poral ventral canal while the antiporal dorsal canal is shifted towards the middle of the proglottis relative to the antiporal ventral canal. Finally, in *H. alterna* n. sp. both dorsal osmoregulatory canals are shifted towards the middle of proglottis in relation to the corresponding ventral canals. The characteristic arrangement of the osmoregulatory canals is stable within the observed samples from

each species. Furthermore, all three species have testes that are most commonly situated in one row, while in *H. bilaterala* n. sp. the testes are situated in triangle.

Similarly to the first new species described herein, *H. bilaterala* n. sp. has morphological peculiarities and geographic isolation in the Philippines, so we differentiate the new species from congeners only from Luzon Island. The cirrus-sac of *H. bilaterala* n. sp. is smaller compared with those in *H. haukisalmii* and *H. alterna* n. sp. but larger than in *H. bicauda*. The ovary of the new species is wider in comparison with *H. bicauda* but narrower than in *H. alterna* n. sp. The eggs of *H. bilaterala* n. sp. are larger relative to those in *H. bicauda*, *H. haukisalmii* and *H. alterna* n. sp. The embryonic hooks of *H. bilaterala* n. sp. are larger in comparison with *H. haukisalmii* and *H. alterna* n. sp. Furthermore, the egg number in the new species is considerably larger than in *H. bicauda* but smaller than in *H. haukisalmii* and *H. alterna* n. sp. (see Table 1).

Discussion

There are four named species of *Hymenolepis* (*s. str.*) that are currently known to occur on Luzon Island including two described in the present work. Additionally, immature specimens we collected from rodents in the northern Luzon Island indicate the presence of at least two more species of *Hymenolepis*. Unfortunately, adults have not yet been collected, which prevents us from providing formal descriptions at this time. In addition to the native species of *Hymenolepis*, the cosmopolitan *Hymenolepis diminuta* (Rudolphi, 1819) parasitic in Norway rats *Rattus norvegicus* (Berkenhout) was reported in Manila (Tubangui, 1931; the Norway rat is referred to as *Mus norvegicus* by Tubangui).

In all, there are seven species of *Hymenolepis* known from Luzon Island, Philippines. By comparison, only six species of *Hymenolepis* (*s. str.*) are currently known from the whole Palaearctic, i.e. *H. apodemi* Makarikov & Tkach, 2013; *H. diminuta*; *H. hibernia* Montgomery, Montgomery & Dunn, 1986; *H. megaloon* (Linstow, 1901); *H. pseudodiminuta* Tenora, Asakawa & Kamiya, 1994 and *H. rymzhanovi* Makarikov & Tkach, 2013, and seven species are known from the Nearctic, i.e. *H. citelli* (McLeod, 1933); *H. diminuta*; *H. geomydis* Gardner & Schmidt, 1988; *H. pitymi* Yarinsky, 1952; *H. tualatinensis*

Gardner, 1985; *H. weldensis* Gardner & Schmidt, 1988 and *H. robertrauschi* Gardner, Luedders & Duszynski, 2014. Intriguingly, the intestinal parasites of mammals in both the Palaearctic and Nearctic are relatively well studied, whereas relatively few of the Philippine mammals have been examined for intestinal parasites. The recent discovery of several new species, despite a relatively small sample size of mammals from a small geographic region, suggests that *Hymenolepis* spp. have undergone an active radiation in the Philippines. It is safe to assume that a more thorough survey of the intestinal helminths of mammals from other parts of Luzon and other islands in the archipelago will likely result in the discovery of additional new species.

Remarkably, all species of *Hymenolepis* described so far from the Philippines have some very distinctive features and can be readily distinguished morphologically. The levels of species richness and morphological diversity of *Hymenolepis* in the Philippines may have several explanations. The most obvious of them is the intensive speciation and extremely high level of endemism among rodents on the Philippine islands. The archipelago is a hotspot of mammalian diversity with an extremely high level of endemism. Over 60% of the Philippine mammal species are endemic (Wilson & Reeder, 2005 and subsequent publications containing descriptions of new species; http://archive.fieldmuseum.org/philippine_mammals/introduction.asp). The levels of endemism are particularly high among the native murid rodents, which host all of the native Philippine *Hymenolepis* spp. Sixteen of 22 genera of murid rodents (73%) are endemic, and endemism at the species level is even higher: 68 out of 71 murid species (96%) are endemic to the archipelago (Heaney et al., 2011). The ability of rodents to disperse among islands and across complex landscapes is likely to be quite limited; thus, restricted gene flow across island habitats may be one driver of the unusually high diversity of mammals and *Hymenolepis* spp. in the Philippines.

It is likely that *Hymenolepis* spp. arrived in the Philippines with their murid hosts. Murid rodents experienced two waves of immigration into the archipelago, one in the middle Miocene (15 Mya), and another wave in the late Miocene or early Pliocene (3 to 7 Mya) (Jansa et al., 2006). Alternatively, chiropteran hosts may have carried this cestode genus across stretches of open ocean. As of yet, no *Hymenolepis*

spp. have been recovered from Philippine bats, but few bats have been surveyed. The geographic expansion of hymenolepidids by bats is not a new idea. Bats have been implicated in the geographic expansion of *Poterolepis* Spassky, 1994, a genus of tapeworms that typically parasitises the marsupials of Australia and New Guinea (Makarikova & Makarikov, 2012). Rigorous evidence that would support or refute this hypothesis has not yet been collected.

The presence of asymmetrically shifted dorsal osmoregulatory canals relative to the ventral canals is among two morphological features used for differentiation and erection of the genus *Talpolepis* (see Gulyaev & Mel'nikova, 2005). However, each of the four described species of *Hymenolepis* from the Philippines have unique relative positioning of the dorsal and ventral osmoregulatory canals that is intermediate between *Hymenolepis s. str.* and *Talpolepis*. For instance, the dorsal osmoregulatory canals in *H. bilateralis* n. sp. are shifted bilaterally towards the lateral margins of proglottis in relation to the poral ventral canals; in *H. bicauda* only the poral dorsal osmoregulatory canal is shifted towards the margin of proglottis in relation to the poral ventral canal while the antiporal canals are situated directly above each other; in *H. haukisalmii* the poral dorsal osmoregulatory canal is situated lateral to the poral ventral canal while the antiporal dorsal canal is shifted towards the middle of proglottis in relation to the ventral canal; finally, in *H. alterna* n. sp. the dorsal osmoregulatory canals are shifted bilaterally towards middle of proglottis in relation to ventral canals.

This variable intermediate morphology among the Philippine *Hymenolepis* spp. casts doubt on the value of the relative position of the osmoregulatory canals as a generic level character. We feel that this variable morphological trait is most useful as a species level character. However, due to the lack of detailed phylogenetic studies within this lineage of mammalian hymenolepidids (Haukisalmi et al., 2010; Greiman & Tkach, 2012) we refrain from synonymising *Talpolepis* with *Hymenolepis* at this time.

One of the two species described herein, namely *H. alterna* n. sp., possesses a unique feature not known in other members of *Hymenolepis* or any other hymenolepidid from mammals, namely the irregularly alternating genital pores (Fig. 1C). In other cyclophyllidean families (e. g., Anoplocephalidae, Dilepididae, Paruterinidae etc.) the presence of irregularly or regularly

alternating genital pores is considered an important feature distinctive among genera. However, the taxonomic significance of this character is not known in the Hymenolepididae. Conservatively, we place *H. alterna* n. sp. in *Hymenolepis*. In the future, studies taking a molecular approach, as well as studies that include a greater sampling of species from the Philippine archipelago will provide insights about synapomorphic and convergent morphological characters used in the systematic arrangement of this globally distributed lineage of hymenolepidid cestodes.

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