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TWO NEW SPECIES OF *HYMENOLEPIS* (CESTODA: HYMENOLEPIDIDAE) FROM MURID RODENTS (RODENTIA: MURIDAE) IN THE PHILIPPINES

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ABSTRACT: Two previously unrecognized species of the genus *Hymenolepis* are described based on specimens obtained from murid rodent species *Bullimus luzonicus*, *Apomys microdon*, and *Rattus everetti* collected on Luzon Island, Philippines. *Hymenolepis bicauda* n. sp. differs from all known *Hymenolepis* spp. in relative position of the poral dorsal and ventral osmoregulatory canals, gravid uterus occupying less than half the length of proglottid, relatively few eggs, and the highly characteristic longitudinal split of proglottids at the end of the gravid strobila. *Hymenolepis haukisalmii* n. sp. differs from all known *Hymenolepis* spp. in the relative position of both poral and aporal dorsal and ventral osmoregulatory canals and uterus lacking dorsal and ventral diverticula. The shift in the relative position of the dorsal and ventral osmoregulatory canals was not known in *Hymenolepis* from rodents in other regions of the world and is reminiscent of the situation observed in *Hymenolepis erinacei*, parasitic in hedgehogs, and members of the genus *Talpolepis*, parasitic in moles. The cosmopolitan species *Hymenolepis diminuta* was the only member of the genus previously reported from the Philippines.

The genus *Hymenolepis* Weinland, 1858, includes hymenolepidid cestodes with an unarmed scolex and rudimentary rostellar apparatus, parasitic primarily in rodents, with a few species known from bats and 1 from hedgehogs. Members of the genus have been reported from the Palearctic, Nearctic, Ethiopian, and Oriental regions (López-Neyra, 1942a, 1942b; Skrjabin and Matevosyan, 1948; Spassky, 1954; Yamaguti, 1959; Hunkeler, 1972; Ryzhikov et al., 1978; Genov, 1984; Gardner, 1985; Schmidt, 1986; Gardner and Schmidt, 1988; Czaplinski and Vaucher, 1994; Mas-Coma and Tenora, 1997; Sawada, 1997; Gulyaev and Melnikova, 2005; Makarikova et al., 2010; Makarikov and Tkach, 2013). To the best of our knowledge, *Hymenolepis diminuta* (Rudolphi, 1819) is the only species of *Hymenolepis* previously reported from the Philippines (Tubangui, 1931; Fedorko, 1999). As part of a biodiversity survey of terrestrial vertebrates and their parasites in the Philippines, we found hymenolepidid cestodes belonging to *Hymenolepis* in three species of murid rodents, namely, the large Luzon forest rat *Bullimus luzonicus* (Thomas, 1895), the small Luzon forest mouse *Apomys microdon* Hollister, 1913, and the Philippine forest rat *Rattus everetti* (Günther, 1879), collected in Aurora Province, Luzon Island. These 2 species of cestodes, described herein, are morphologically distinct from previously known *Hymenolepis* species.

MATERIALS AND METHODS

Rodents were collected in the summer of 2009 at several sites in Aurora Province, Luzon Island, Philippines, as a part of a biodiversity survey. Animals were trapped using live traps and pitfall traps. The two new species described in the present work were found in *B. luzonicus*, *A. microdon*, and *R. everetti* (see taxonomic summaries for geographic locations).

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 hematoxylin, dehydrated in an ethanol series, cleared in methyl salicilate (after Mayer's hematoxylin) or clove oil (after Ehrlich's hematoxylin), and mounted in Canada balsam. 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. 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).

The following type and voucher materials from previously described species deposited in the United States National Parasite Collection, Beltsville, Maryland (USNPC), and Geneva Museum of Natural History (MHNG) were studied for comparative analysis: syntypes and vouchers of *Hymenolepis uranomidis* Hunkeler, 1972 (MHNG INVE 18679, INVE 18680, INVE 1868, INVE 18685); holotype of *Hymenolepis tualatinensis* Gardner, 1985 (USNPC 078418), holotype of *Hymenolepis pitymi* Yarinsky, 1952 (USNPC 038261); voucher of *Hymenolepis citelli* (McLeod, 1933) (USNPC 044825).

Other examined materials included tapeworms from the collections of Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, representing specimens of *Hymenolepis* sp. from *Apodemus agrarius* (Pallas, 1771), *H. diminuta* (Rudolphi, 1819) from *Rattus norvegicus* (Berkenhout, 1769), *Hymenolepis megaloon* (von Linstow, 1901) from *Urocitellus undulatus* (Pallas, 1778), *Talpolepis peipingensis* (Hsü, 1935) from *Mogera robusta* Nehring, 1891, and *H. erinacei* (Gmelin, 1790) from *Erinaceus* spp. from the Altai Mountains, Siberia and the Russian Far East. Additionally we studied vouchers of *Hymenolepis sulcata* (von Linstow, 1879) from *Glis* (Linnaeus, 1766) from MHNG.

Measurements are given in micrometers except where otherwise stated.

DESCRIPTION

Hymenolepis bicauda n. sp.

(Figs. 1–3)

The paratype illustrated here (Figs. 1B–E, 2) was initially chosen for a holotype. After all the illustrations were finished, the cover slip moved slightly because the Canada balsam was not completely hardened. It resulted in some damage of that particular specimen (although the structures shown on the figures were preserved). We decided to change the holotype. It does not affect the description in any way (other than the measurements of the holotype) because there are practically no differences between these specimens.

Diagnosis (based on 7 specimens; measurements of the holotype are followed by the range, mean values, and number of measured specimens in parentheses): Fully developed strobila 26 (26–29; n = 5) mm long, with maximum width at pregravid or gravid (but not terminal) proglottids, 0.99 (0.99–1.19; n = 5) mm. Strobila consisting of 175–193 craspedote proglottids. Scolex slightly flattened dorso-ventrally, 265 (260–288, 270, n = 5) wide, not clearly distinct from strobila (Fig. 1A, B). Suckers unarmed, round or oval, 95–99 × 83–87 (92–103 × 80–95, 97 × 86, n = 12), with thick muscular walls. Rhynchus unarmed, 37 × 5 (36–44 × 4–6, 39 × 5, n = 5), invaginated in rostellar pouch 75 × 52 (75–83 × 50–56, 79 × 53, n = 5); rostellum absent (Fig. 1A, B). Rostellar pouch with muscular walls,

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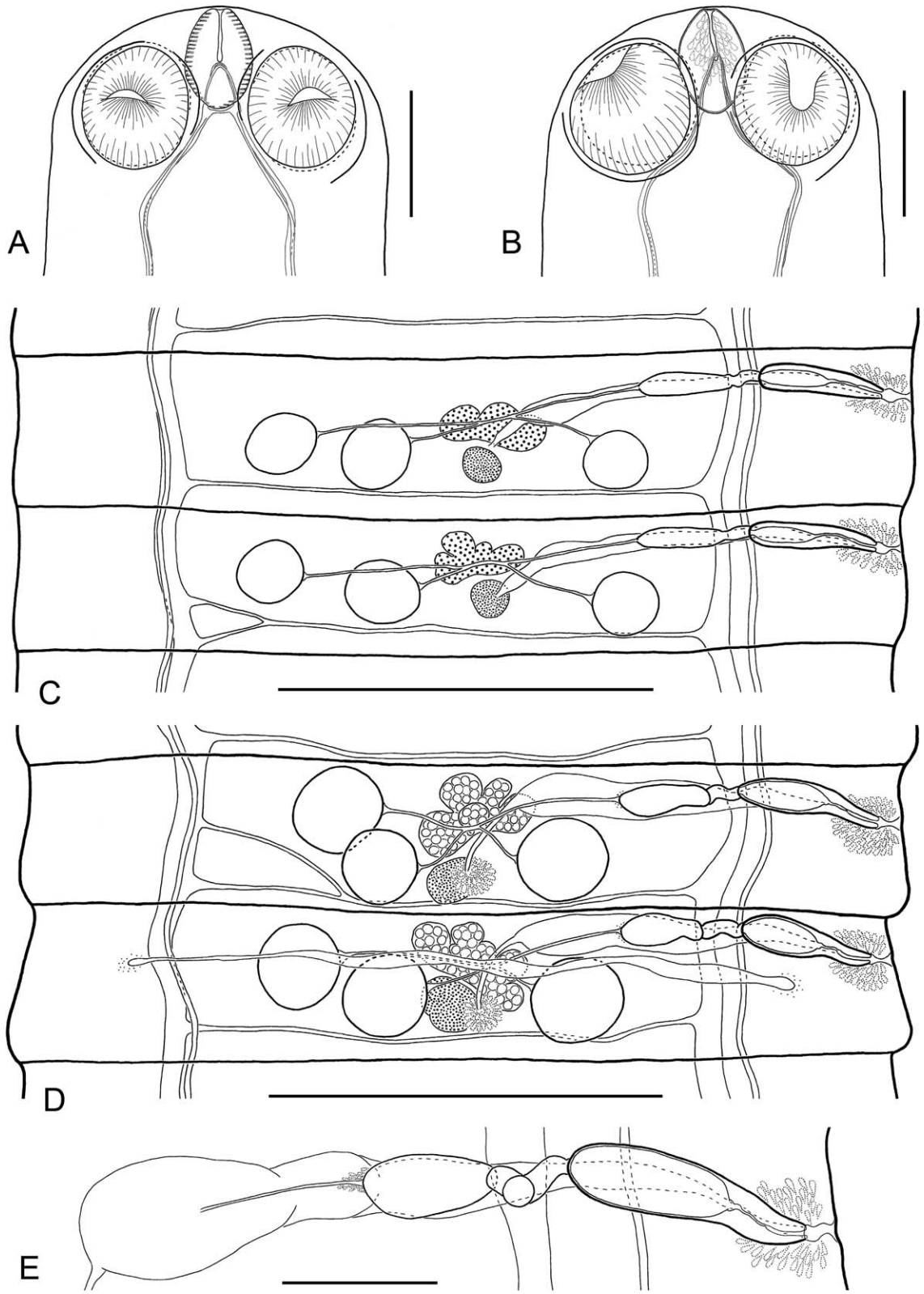

FIGURE 1. *Hymenolepis bicauda* n. sp. (**A**) Holotype, dorso-ventral view of scolex; (**B**) paratype, dorso-ventral view of scolex; (**C**) paratype, male mature proglottids; (**D**) paratype, hermaphroditic mature proglottids; (**E**) paratype, genital ducts. Scale bars: A, B, E = 100 μm; C, D = 400 μm.

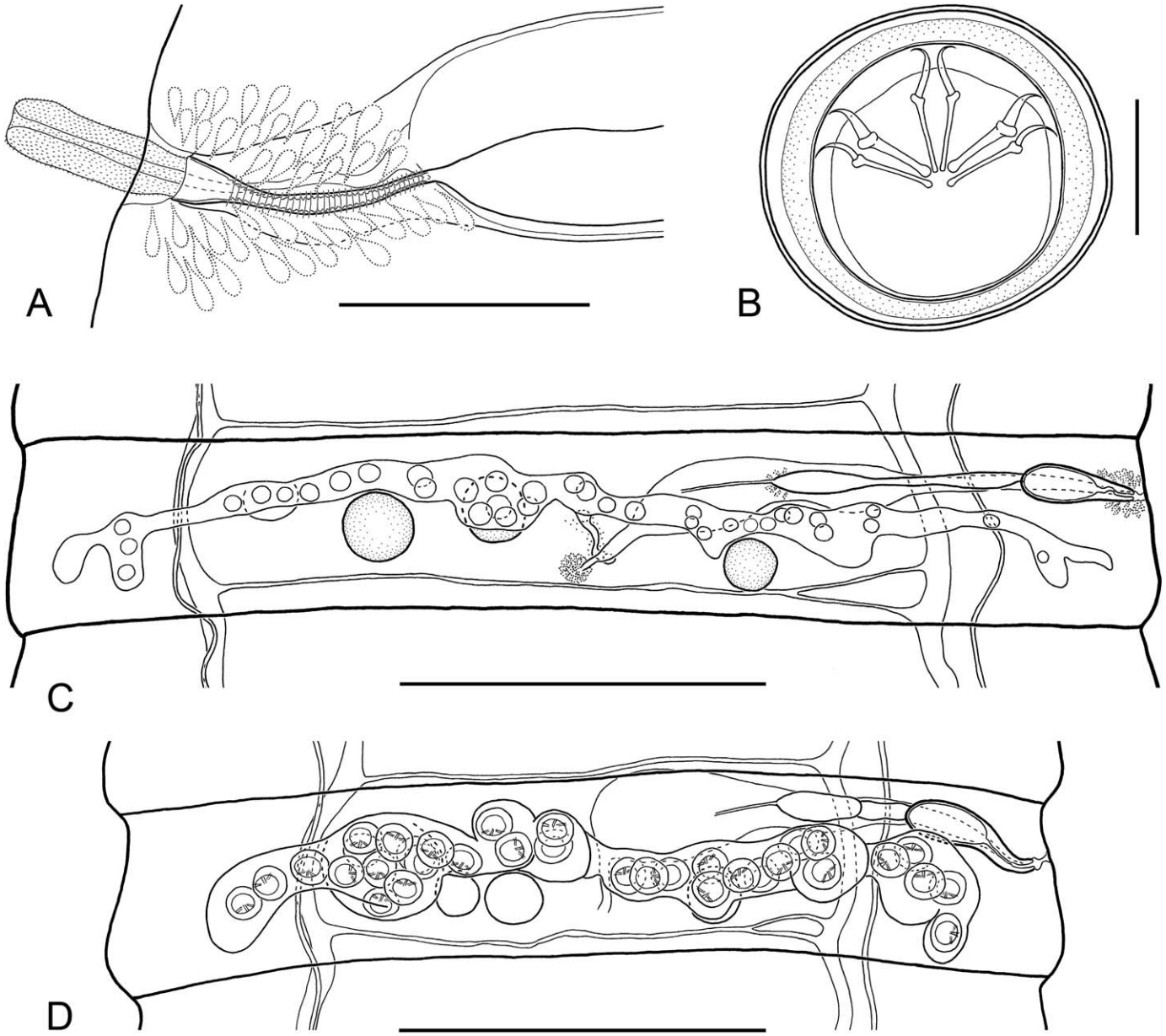

FIGURE 2. *Hymenolepis bicauda* n. sp. (**A**) Paratype, cirrus and vagina; (**B**) paratype, egg; (**C**) paratype, pregravid proglottid, showing uterus development; (**D**) paratype, gravid proglottid. Scale bars: A = 50 μm; B = 20 μm; C, D = 400 μm.

osmoregulatory canals penetrate through rostellar pouch wall. Neck wider than scolex, 270 (268–410; n = 4).

Ventral osmoregulatory canals 12–23 (12–38, 22, n = 14) wide, connected by transverse anastomoses. Dorsal osmoregulatory canal 6–7 (5–8, 6, n = 14) wide, usually situated directly above ventral canal in antiporal side of proglottids, while on the poral side of proglottids, the dorsal canal always shifted towards margin of proglottid in relation to poral ventral canal. Genital pores unilateral, dextral. Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals (Fig. 1C–E). Development of proglottids gradual, protandrous. External segmentation becomes evident at level of premature part of strobila.

Mature proglottids 165–180 × 890–990 (150–200 × 880–1,020, 171 × 956, n = 14), transversely elongate, trapezoid (Fig. 1C, D). Testes relatively small, usually 3, almost equal in size, 70–90 × 66–78 (70–103 × 65–100, 84 × 80, n = 21), round or oval, normally situated in 1 row; poral testis separated from 2 antiporal testes by female gonads. Cirrus-sac elongate, relatively short, 142–163 × 35–39 (140–166 × 35–45, 149 × 39, n = 10), with thin muscular walls. Antiporal part of cirrus-sac usually reaching the dorsal osmoregulatory canal or slightly crossing it, but commonly does not reach ventral longitudinal canal (Fig. 1D, E). Genital atrium simple, infundibular, deep, situated approximately in middle of lateral proglottid margin. Cirrus 41–48 × 10 (35–48 × 10–12, 39 × 11, n = 11), cylindrical, armed with minuscule (<1 long) spines (Fig. 2A). Internal seminal vesicle oval, 85–105 × 28–33 (77–105 × 28–37, 89 × 33, n = 10), more than half of cirrus-sac length (Fig. 1E). External seminal vesicle elongate 93–102 × 36–45 (82–111 × 28–45, 95 × 36, n = 10), clearly distinguishable from vas deferens, distinctly smaller than seminal receptacle.

Ovary 114–129 (108–140, 125, n = 10) wide, median, lobed, fan-shaped, ventral to male genital organs, occupying less than quarter of median field width, usually not overlapping testes (Fig. 1D). Vitellarium 40–44 × 57–60 (38–55 × 50–65, 47 × 57, n = 10), postovarian, median, compact, entire. Copulatory part of vagina 47–53 × 4–6 (47–65 × 4–8, 53 × 5, n = 7), tubular, clearly distinct from seminal receptacle; ventral to cirrus-sac. Vagina surrounded by circular musculature and covered externally by

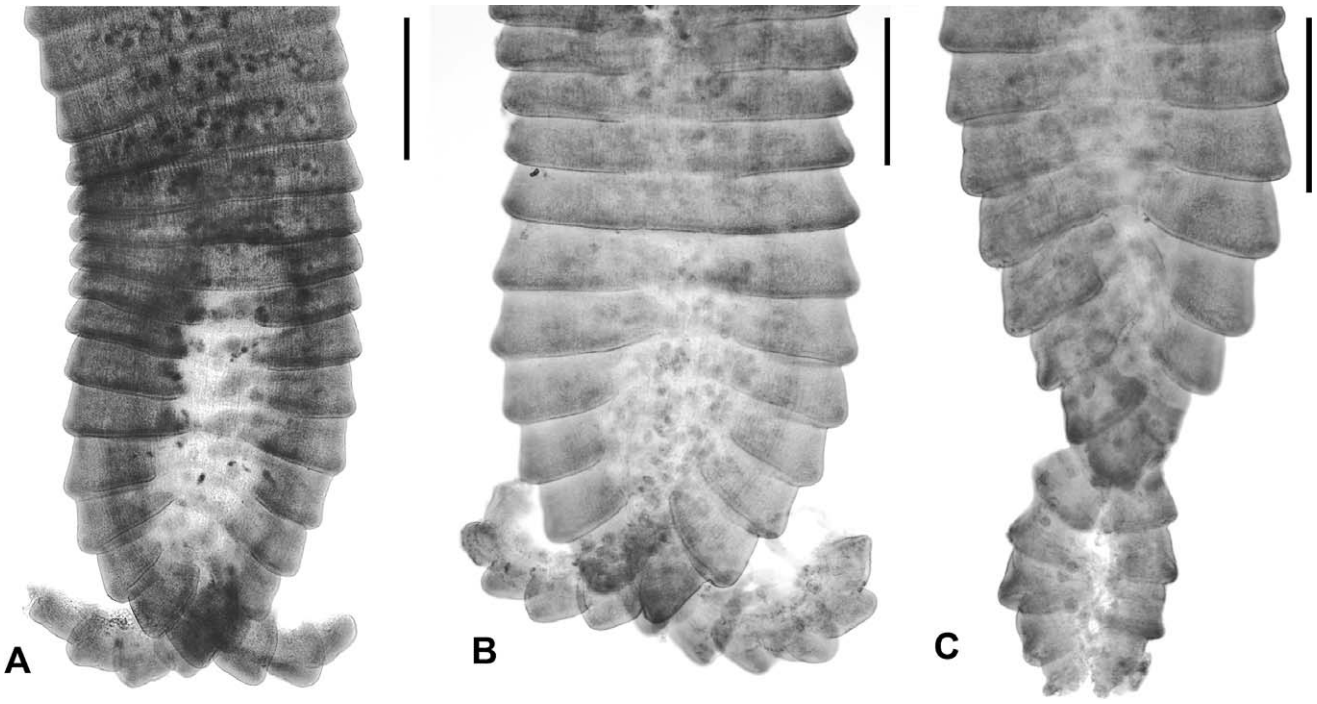

FIGURE 3. *Hymenolepis bicauda* n. sp. Microphotographs of posterior ends of strobila in three paratypes showing terminal gravid proglottids splitting in the middle to form two tail-like structures. Note eggs in the region of proglottid rupture. Scale bars: A, B, C = 500 μm.

dense layer of intensely stained cells (Fig. 2A). Seminal receptacle relatively large, 265–298 × 50–54 (265–340 × 40–75, 307 × 52, n = 9), pear-shaped (Fig. 1D, E).

Uterus first appears as transversely elongated tube, situated dorsally to other organs and extending laterally beyond longitudinal osmoregulatory canals (Figs. 1D, 2C). With proglottid development, uterus forms few (2–4) diverticula predominantly on ventral side of strobola (Fig. 2D). Testes cirrus-sac and vagina persist in gravid proglottids. Gravid proglottids transversely elongate, 150–165 × 970–990 (150–255 × 970–1,185, 207 × 1,077, n = 13). Fully developed uterus occupying no more than half of median field and extending laterally beyond longitudinal osmoregulatory canals, saccate, with diverticula, lateral sides of gravid uterus usually not perforated (Fig. 2E). Uterus contains small number of eggs (up to 30–45). Eggs 46–54 × 50–60, subspherical, with relatively thin outer coat (up to 1); oncosphere 27–33 × 31–38 (Fig. 2B). Embryophore subspherical, thin, 32–38 × 37–44. Embryonic hooks 17.5–19 long. Dissemination of eggs apparently occurs through the break in middle of gravid proglottids, resulting in a split of several terminal gravid proglottids forming a swallow tail–like structure (Fig. 3). Empty proglottids not immediately separated from the strobila.

Taxonomic summary

Type host: Apomys microdon Hollister, 1913 (Rodentia: Muridae).

Symbiotype: KUMNH KU167624

Site in the host: Small intestine.

Type locality: Aurora Memorial National Park, near Sitio Dimani, Barangay Villa Aurora, Municipality of Maria, Aurora Province, Luzon Island, Philippines (500 m; 15.685°N, 121.341°E).

Type specimens: Holotype, HWML 49780 (labeled: ex. *Apomys microdon*, Aurora Memorial National Park, near Sitio Dimani, Barangay Villa Aurora, Municipality of Maria, Aurora Province, Luzon Island, Philippines, 25 May 2009, coll. V. Tkach). Paratypes, HWML 49779 (9 slides; labeled: identical to holotype).

Etymology: The species name refers to the very characteristic morphological feature of the species, namely, the posterior segments splitting into two "tails" (Fig. 3).

Remarks

Hymenolepis bicauda n. sp. has morphological characters typical of *Hymenolepis*, namely, the scolex with rudimentary rostellar apparatus, unarmed rhynchus invaginated in rostellar pouch, ventral canals with transverse anastomoses, testes situated in 1 row, cirrus-sac with muscular walls, and vagina surrounded by circular musculature. However, morphological comparison of *H. bicauda* n. sp. with type and voucher materials of numerous species of hymenolepids parasitic in rodents and insectivores (see Materials and Methods), as well as published descriptions, has revealed several features unique to the new species. Unlike other known *Hymenolepis* species from rodents, the poral dorsal osmoregulatory canal in *H. bicauda* n. sp. is shifted towards the margin of the proglottid in relation to the poral ventral canal. The developing uterus in the new species is tubular, eggs are few (no more than 45), and the egg outer coat is very thin. In other members of *Hymenolepis* that were described in sufficient detail, the developing uterus is an elongated, perforated sac, eggs are very numerous, and eggs have a relatively thick outer coat. Moreover, the splitting of the terminal proglottids into 2 "tails" (Fig. 3) is not known in any other *Hymenolepis*. Examination of multiple specimens has shown that this is a stable feature present in all complete gravid specimens.

The similar relative position of the osmoregulatory canals is found in *H. erinacei* from hedgehogs in Europe. *Hymenolepis bicauda* is readily distinguishable from *H. erinacei* in having a shorter cirrus-sac, which usually does not reach the ventral osmoregulatory canal, while in *H. erinacei* specimens, the cirrus-sac usually crosses the ventral osmoregulatory canal. Furthermore, in the new species, the fully developed uterus is narrow (not reaching anterior and posterior margins of the proglottid) and extends laterally beyond longitudinal osmoregulatory canals on either side, while in *H. erinacei*, the uterus fills the entire median field and does not extend beyond longitudinal canals (Genov, 1984; Gulyaev and Melnikova, 2005; A. Makarikov, pers. obs.).

In addition, the new species bears some morphological similarity to cestodes of the genus *Talpolepis* Gulyaev et Melnikova, 2005, from moles, which also have a rudimentary rostellum and poral dorsal osmoregulatory canal shifted in relation to the poral ventral canal. However, the antiporal dorsal canal in *Talpolepis* is also shifted towards the middle part of

proglottids with regard to the ventral canal, whereas in *Hymenolepis bicauda*, the antiporal dorsal osmoregulatory canal is situated directly above the ventral canal.

Hymenolepis haukisalmii n. sp.
(Figs. 4, 5)

Diagnosis (based on 3 specimens; measurements of the holotype are followed by the range, mean values, and number of measured specimens in parentheses): Fully developed strobila up to 132 mm long, with maximum width at pregravid or gravid proglottids, up to 2.4 mm. Strobila consisting of about 820 craspedote proglottids. Scolex slightly flattened dorsoventrally, 255 (240–265, 253, n = 3) wide, not clearly distinct from neck (Fig. 4A, B). Suckers unarmed, round or oval, 83–105 × 81–88 (83–105 × 81–93, 98 × 88, n = 12), with thick walls. Rhynchus unarmed, 39 × 5 (37–40 × 5–8, 38 × 6, n = 3), invaginated in rostellar pouch 88 × 55 (88–94 × 50–60, 91 × 55, n = 3); rostellum absent (Fig. 4A, B). Rostellar pouch with muscular walls; osmoregulatory canals penetrate through rostellar pouch wall. Neck wider than scolex, 270 (215–287; n = 3).

Ventral osmoregulatory canals 55–62 (39–65, 57, n = 10) wide, connected by transverse anastomoses. Dorsal osmoregulatory canals 11–15 (10–15, 12, n = 10) wide. Poral dorsal canal shifted lateral relative to poral ventral canal, whereas antiporal dorsal canal shifted towards middle part of proglottid relative to ventral canal. Genital pores unilateral, dextral. Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals (Fig. 4C, D). Development of proglottids gradual, protandrous. External segmentation becomes evident at level of premature part of strobila.

Mature proglottids 246–270 × 1,850–2,080 (245–270 × 1,820–2,080, 260 × 1,942, n = 6), transversely elongate, trapezoid (Fig. 4C, D). Testes relatively small, normally 3, almost equal in size, 116–160 × 105–157 (116–160 × 85–157, 136 × 118, n = 13), round or oval, normally situated in 1 row; poral testis separated from 2 antiporal testes by female gonads. Cirrus-sac elongate, relatively short, 259–289 × 39–44 (234–289 × 34–44, 265 × 39, n = 9), with thick muscular walls. Antiporal part of cirrus-sac usually does not reach ventral longitudinal canals (Fig. 4D, E). Genital atrium simple, infundibular, deep, situated approximately in middle of lateral proglottid margin. Cirrus 43–45 × 9–14 (43–56 × 9–14, 47 × 11, n = 10), cylindrical, armed with minuscule (less than 1 long) spines (Fig. 5A). Internal seminal vesicle oval, 195–216 × 30–34 (175–217 × 26–34, 199 × 30, n = 10), more than half of cirrus-sac length (Fig. 4E). External seminal vesicle elongate 204–242 × 45–60 (204–242 × 27–60, 222 × 48, n = 7), clearly distinguishable from vas deferens, distinctly smaller than seminal receptacle.

Ovary relatively small, 193–202 (193–208, 200, n = 8) wide, median, fan-shaped, irregularly lobed, ventral to male genital organs, occupying less than one-fifth of median field, usually not overlapping testes (Fig. 4D). Vitellarium 61–82 × 80–109 (61–83 × 80–125, 74 × 99, n = 8), postovarian, median, entire or slightly lobed. Copulatory part of vagina 57–63 × 6–14 (44–63 × 4–14, 51 × 7, n = 6), tubular, clearly distinct from seminal receptacle; ventral to cirrus-sac. Vagina surrounded by circular musculature and covered externally by dense layer of intensely stained cells (Fig. 5A). Seminal receptacle relatively large, 635–779 × 158–172 (595–779 × 137–172, 692 × 158, n = 7), pear-shaped (Fig. 4D, E).

Uterus first appears as slightly perforated transversely elongated sac, situated dorsally to other organs and extending laterally beyond longitudinal osmoregulatory canals. Uterus does not form dorsal or ventral pockets during maturation (Fig. 5C). Testes remain in postmature proglottids; cirrus-sac and vagina persist in gravid proglottids. Gravid proglottids transversely elongate, 365–490 × 2,050–2,380 (419 × 2,265, n = 8). Fully developed uterus occupying entire median field and extending laterally beyond longitudinal osmoregulatory canals, saccate, without ventral or dorsal pockets. Lateral sides of gravid uterus usually have invaginations (Fig. 5D). Uterus contains numerous (up to 360–450) small eggs. Eggs 29–34 × 37–46, oval or subspherical, with relatively thin outer coat (up to 1); oncosphere 15–17 × 18–20 (Fig. 5B). Embryophore thin, subspherical, 21–24 × 24–31. Embryonic hooks 11–13 long.

Taxonomic summary

Type host: Bullimus luzonicus (Thomas, 1895) (Rodentia: Muridae).

Site in the host: Small intestine.

Type locality: Aurora Memorial National Park, near Sitio Dimani, Barangay Villa Aurora, Municipality of Maria, Aurora Province, Luzon Island, Philippines (500 m; 15.685°N, 121.341°E).

Type specimens: Holotype, HWML 49776 (labeled: ex. *Bullimus luzonicus*, Aurora Memorial National Park, near Sitio Dimani, Barangay Villa Aurora, Municipality of Maria, Aurora Province, Luzon Island, Philippines, 24 May 2009, coll. V. Tkach). Paratypes, HWML 49777 (labeled: identical to holotype); HWML 49778 (labeled: ex. *Rattus everetti* Aurora Memorial National Park, near Sitio Dimani, Barangay Villa Aurora, Municipality of Maria, Aurora Province, Luzon Island, Philippines, 25 May 2009, coll. V. Tkach).

Etymology: The species is named for Dr. Voitto Haukisalmi, in recognition of his contributions to the taxonomy, systematics, and phylogenetics of cestodes of small mammals.

Remarks

Hymenolepis haukisalmii n. sp. has morphological characters typical of *Hymenolepis*, namely, the scolex with rudimentary rostellar apparatus, unarmed rhynchus invaginated in rostellar pouch, ventral canals with transverse anastomoses, testes situated in 1 row, cirrus-sac with muscular walls, and vagina surrounded by circular musculature. However, unlike the majority of other *Hymenolepis* species, its uterus lacks ventral and dorsal diverticula. The poral dorsal osmoregulatory canal in the new species is situated lateral to the poral ventral canal, while the antiporal dorsal canal is shifted towards the middle of the proglottid relative to the ventral canal. The latter character is unique among species of *Hymenolepis* from rodents.

H. bicauda sp. nov. (see previous description) and *H. erinacei* also have poral dorsal osmoregulatory canal situated lateral relative to the poral ventral canal, but their antiporal dorsal canals are situated directly above the ventral canals. *Hymenolepis haukisalmii* n. sp. is a much larger cestode than *H. bicauda* n. sp., and its terminal proglottids do not split.

Among other hymenolepidids of mammals with unarmed scolex and rudimentary rostellum, members of *Talpolepis* from moles also show some similarity with the new species in the relative position of osmoregulatory canals (Gulyaev and Melnikova, 2005). Among other characters, *Hymenolepis haukisalmii* n. sp. can be readily distinguished from species of *Talpolepis* by having a cirrus-sac with thick muscular walls, while species of *Talpolepis* have cirrus-sac with thin walls lacking pronounced musculature. The new species is also separated from the members of *Talpolepis* by the host specificity and geographic isolation because moles are absent in the Philippines.

DISCUSSION

Only 2 previous publications mentioned *Hymenolepis* (s. str.) from the Philippines; both of them reported the cosmopolitan species *Hymenolepis diminuta*. Tubangui (1931) found this species in 64% of introduced Norway rats *Rattus norvegicus* (*Mus norvegicus* in the paper) in Manila, Luzon Island. Fedorko (1999) reported 18.75% prevalence of *H. diminuta* in Philippine rice rats *Rattus rattus mindanensis* (Mearns, 1905) in Leyte Province, Leyte Island. In the present work, we describe 2 new species, both found in native Philippine rodents trapped in natural habitats. Considering the relatively diverse rodent fauna of the Philippines and the large number of islands comprising the archipelago, we anticipate that future studies will reveal additional species of *Hymenolepis* and other cestodes in Philippine rodents.

One of the 2 species described herein, namely, *Hymenolepis bicauda* n. sp., possesses a unique feature not found in other members of *Hymenolepis* or any other hymenolepidids of rodents. Its gravid proglottids, containing fully formed eggs, break in the middle, resulting in the split of the terminal part of the strobila into 2 "tails" observed in complete, gravid specimens (Fig. 3). The most obvious explanation of this unique feature is that it allows eggs to leave the otherwise closed uterus and more efficiently disperse in the environment, thus increasing the probability of being ingested by an intermediate host, most likely a beetle.

Despite the fact that both new species have been collected in the same locality, *H. bicauda* n. sp. was found only in *A. microdon*,

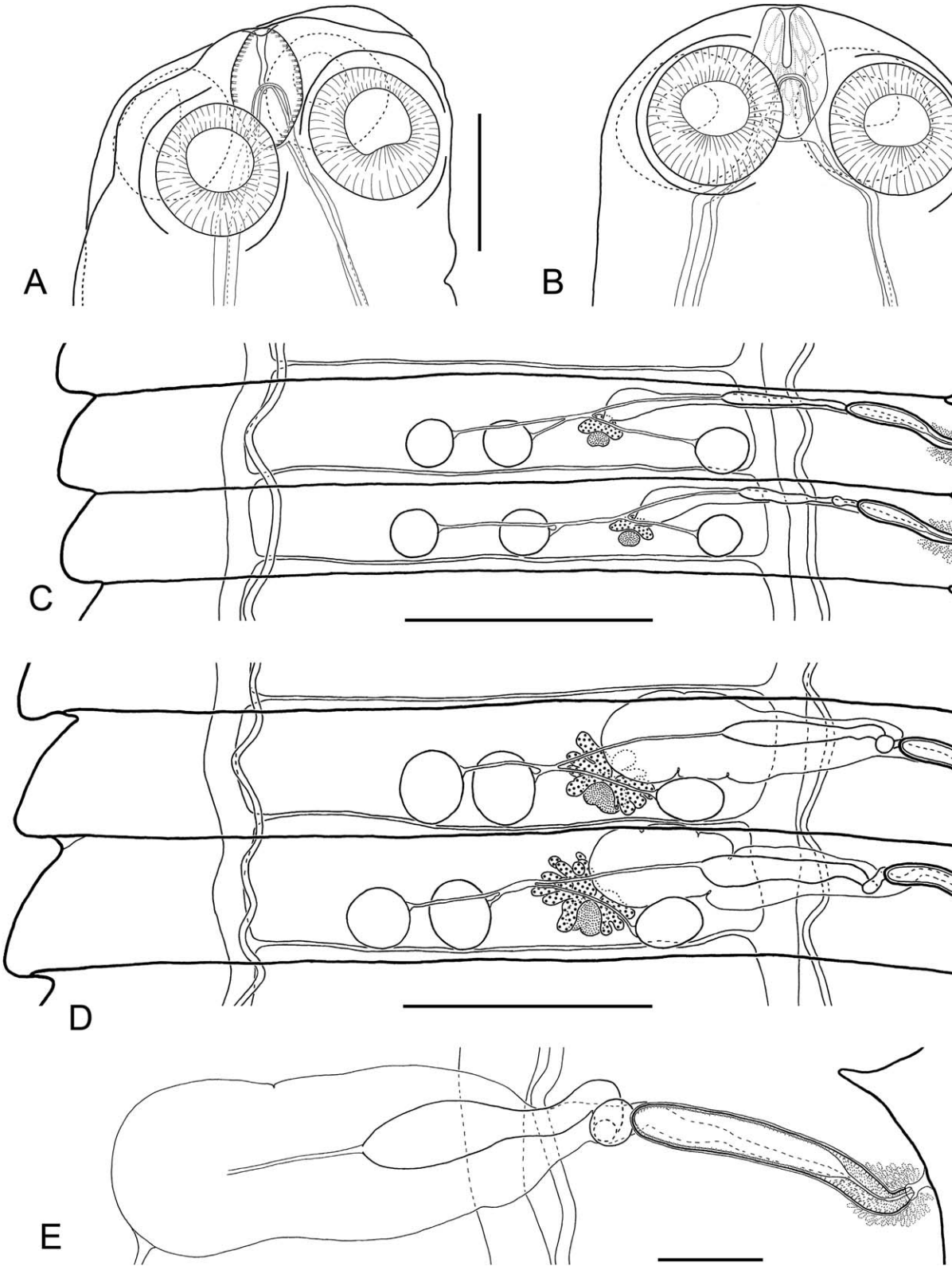

FIGURE 4. *Hymenolepis haukisalmii* n. sp. (**A**) Holotype, dorso-ventral view of scolex; (**B**) paratype, dorso-ventral view of scolex; (**C**) holotype, male mature proglottids; (**D**) holotype, hermaphroditic mature proglottids; (**E**) holotype, genital ducts. Scale bars: A, B, E = 100 μm; C, D = 500 μm.

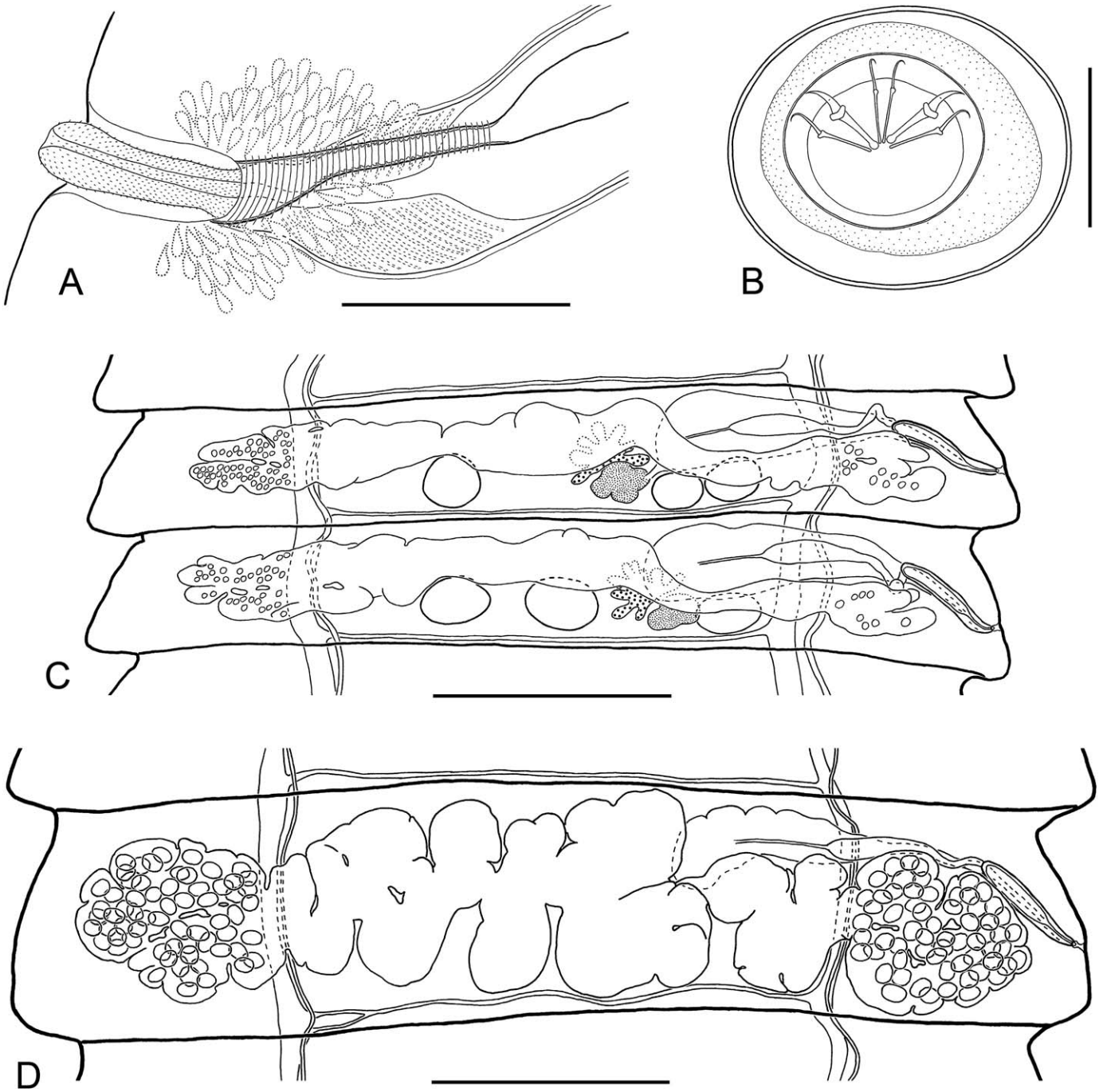

FIGURE 5. *Hymenolepis haukisalmii* n. sp. (**A**) Holotype, cirrus and vagina; (**B**) holotype, egg; (**C**) holotype, pregravid proglottids, showing uterus development; (**D**) holotype, gravid proglottid. Scale bars: A = 50 μm; B = 20 μm; C, D = 500 μm.

while *H. haukisalmii* n. sp. was found in all 3 species of murid rodents collected from the site. It is premature, however, to make conclusions regarding the host specificity of these cestodes due to the insufficient number of examined mammals. Only 4 specimens of *B. luzonicus* and a single specimen each of *A. microdon* and *R. everetti* were examined from the site. Examination of a greater number of rodents over a broader area will provide the data needed to more adequately address the issue of host-parasite associations among *Hymenolepis* and their rodent hosts in the Philippines.

Spassky (1992) considered hymenolepidids with unarmed scolex parasitic in mammals to be paraphyletic. Recent molecular phylogenetic studies (Haukisalmi et al., 2010; Greiman and Tkach, 2012) confirmed this suggestion and demonstrated that the loss of rostellum and/or rostellar armature occurred independently in several lineages of mammalian hymenolepidids.

Gulyaev and Melnikova (2005) transferred 4 *Hymenolepis* species described from moles in eastern and southeastern Asia and North America to the new genus *Talpolepis* Gulyaev and

Melnikova, 2005. *Talpolepis* was established mainly due to 2 distinctive characters, namely, the dorsal osmoregulatory canals asymmetrically shifted relative to the ventral canals and the difference in the cirrus-sac wall structure (thick and muscular in *Hymenolepis* and thin and lacking obvious musculature in *Talpolepis*). Concurrently, Gulyaev and Melnikova (2005) suggested that *H. erinacei* from hedgehogs should be also removed from *Hymenolepis* and placed in a separate genus due to several differences between *H. erinacei* and the type-species *H. diminuta*. These differences included the poral dorsal canal situated laterally to the poral ventral canal and saccate uterus without diverticula not extending beyond longitudinal canals. However, Gulyaev and Melnikova (2005) did not establish a new genus for *H. erinacei* at the time.

The 2 new species from Philippine rodents described in the present work are characterized by a set of morphological characters that is intermediate among *Hymenolepis*, *Talpolepis*, and *H. erinacei*. If one accepts the generic level characters proposed by Gulyaev and Melnikova (2005), i.e., relative position of osmoregulatory canals and absence or presence of distinct muscular walls of the cirrus-sac, then *H. bicauda* n. sp. and *H. haukisalmii* n. sp. should be placed in 2 new genera because each of them has a unique combination of these features. However, the systematic value of the characters used by Gulyaev and Melnikova (2005) should be considered with some caution due to the lack of detailed phylogenetic studies within this lineage of mammalian hymenolepidids. Very few *Hymenolepis* species from rodents and no *Hymenolepis* species from bats or former *Hymenolepis* species from moles have been included in molecular phylogenetic studies (Haukisalmi et al., 2010; Greiman and Tkach, 2012). Future phylogenetic studies incorporating a greater number of species from different hosts will allow us to better understand the evolution of this globally distributed lineage of hymenolepidid cestodes and re-evaluate the morphological characters currently used in their systematic arrangement. Until then, we refrain from proposing new genera or subgenera for the species described herein.

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