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VERSITA

Two new species of *Hymenolepis* (Cestoda: Hymenolepididae) from Spalacidae and Muridae (Rodentia) from eastern Palearctic

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Abstract

Previously unrecognized species of the genus *Hymenolepis* are described based on specimens from spalacid and murid (Murinae) rodents. *Hymenolepis rymzhanovi* sp. nov. from the Siberian zokor, *Myospalax myospalax* (Laxmann), from East Kazakhstan, and *H. apodemi* sp. nov. from Eurasian field mice, *Apodemus peninsulae* (Thomas), *A. uralensis* (Pallas) and *A. agrarius* (Pallas), from the south of Russian Far East, western Siberia and south-eastern Kazakhstan are characterized. The new species differ from other species of the genus by the morphology of the scolex, the relative position and length of the cirrus-sac and the relative position and arrangement of the testes. Differential criteria of species of *Hymenolepis* (*sensu stricto*) are also discussed.

Keywords

Cestoda, *Hymenolepis* diagnosis, *Hymenolepis rymzhanovi* sp. nov., *Hymenolepis apodemi* sp. nov., eastern Palearctic, rodents, *Apodemus*, *Myospalax*

Introduction

The genus *Hymenolepis* Weinland, 1858 once was one of the largest cestode genera including more than 300 species parasitic in both mammalian and avian definitive hosts (Fuhrmann 1932; Hughes 1940; Lopez-Neyra 1942a, b). After numerous revisions, *Hymenolepis* (sensu stricto) currently includes hymenolepidid cestodes with an unarmed scolex which parasitize rodents (12–13 species), bats (about 4 species) and hedgehogs (1) and are distributed across the Palearctic, Nearctic, Ethiopian and Oriental regions (Lopez-Neyra 1942a, b; Skrjabin and Matevosyan 1948, Spassky 1954, 1963, Yamaguti 1959, Schmidt 1986, Czaplinski and Vaucher 1994, Mas-Coma and Tenora 1997, Gulyaev and Melnikova 2005). Mas-Coma and Tenora (1997) have erected a new genus *Arostrilepis* Mas-Coma et Tenora, 1997 for the members of *Hymenolepis* lacking a rudimentary rostellum. At the same time, they proposed several new important differentiating criteria for the genus *Hymenolepis* (*sensu stricto*), namely the unarmed scolex having a rudimentary rostellar apparatus, ventral osmoregulatory canals connected by transverse anastomoses, testes situated in one row, saccate uterus, and eggs with a thick outer coat. However, these authors did not provide a formal emended diagnosis of the genus Hymenolepis (*sensu stricto*). The situation has not changed since.

Recent studies suggest that this genus contains several species complexes that may include a number of yet undescribed species. For example, *Hymenolepis diminuta* (Rudolphi, 1819) originally described from *Rattus norvegicus* (Berkenhout) and subsequently reported in a diverse assemblage of rodent definitive hosts (i.e., Sciuridae, Gliridae, Dipodidae, Cricetidae, Muridae and Gerbillinae) (Ryzhikov *et al*. 1978) is now thought to include a complex of cryptic species (Haukisalmi *et al*. 2010). Four species of the rodent genus *Apodemus* Kaup, namely i.e. *A. agrarius* (Pallas), *A. peninsulae* (Thomas), *A. uralensis* (Pallas) and *A. flavicollis* (Melchior), were listed among definitive hosts of *H. diminuta* (Rudolphi, 1819) from the former Soviet Union, (Ryzhikov *et al*. 1978). Recent studies suggested that the true *H. diminuta* is mainly a parasite of rodents of the genus *Rattus* Fischer-Waldheim, whereas *Apodemus* hosts two other species of *Hymenolepis*. These are *H. hibernia* Montgomery, Montgomery et Dunn, 1986 found in *A. sylvaticus* (Linnaeus) from Europe and *H. pseudodiminuta* Tenora, Asakawa et Kamiya, 1994 described from *A. speciosus* (Temminck) and *A. argenteus* (Temminck) from Japan (Montgomery *et al*. 1986, Tenora *et al*.

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1994). These two *Hymenolepis* species have not been detected outside their type territories since their original descriptions.

During our survey of the helminth fauna of rodents from the southern part of the Russian Far East, western Siberia and south-eastern Kazakhstan we found two new hymenolepidid species attributable to *Hymenolepis*. One of them was found in East Kazakhstan Province (Tarbagatai Mts.) in the Siberian zokor, *Myospalax myospalax* (Laxmann). Our new species is the first record of a *Hymenolepis* or any tapeworm, from this rodent endemic to Eastern Kazakhstan and the southern part of the West Siberian Plains. The other new species was found in Eurasian field mice (*Apodemus* spp.) in the Russian Far East, western Siberia and south-eastern Kazakhstan.

In addition, our comparative studies of the type species, *H. diminuta* and other congeners, namely *H. uranomidi*s Hunkeler, 1972, *H. tualatinensis* Gardner, 1985, *H. pitymi* Yarinsky, 1952, *H. citelli* (McLeod, 1933), *H. megaloon* (Linstow, 1901) and *H. erinacei* (Gmelin, 1790), revealed new morphological features of these cestodes that could be used as additional differentiating characters of the genus *Hymenolepis*.

Therefore, we describe herein two new species of *Hymenolepis* from spalacid and murid rodents in Russian Far East, western Siberia and south-eastern Kazakhstan and propose an emended generic diagnosis of *Hymenolepis*.

Materials and methods

Cestodes from *A. peninsulae* were collected by Yulia Melnikova from the Bol'shekhekhtsirskiy Nature Reserve, Khabarovskiy Kray (48°16′N, 134°45′E) during July to August 2003 and in Lazovsky Reserve, Primorskiy Kray, Russia during June 2005. Another series of cestodes from *A. uralensis* and *M. myospalax* were collected by us from the Tarbagatai Mts., Kazakhstan (47°14′N, 81°43′E, h 1080 m) in May of 2007 and from *A. peninsulae* and *A. agrarius* in the Ussuriiskiy Nature Reserve (ca., 43°38′N, 132°20′E) and suburbs of the city of Vladivostok (ca., 43°11′N, 131°55′E), Primorskiy Kray, Russia during July-September 2007.

Cestodes were isolated, rinsed and relaxed in water, and preserved in 70% ethanol. They were stained with Ehrlich's haematoxylin, dehydrated in an ethanol series, cleared in clove oil and mounted in Canada balsam. Some specimens were mounted in Berlese's clearing medium to facilitate the examination of the cirrus (general structure and spination) and the morphology of the eggs and the embryophore. The type and voucher specimens of the two new species have been deposited in the Zoological Museum at the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia (ISEA) and the Natural History Museum, Geneva, Switzerland (MHNG).

The following type materials from previously described species were studied: syntypes and vouchers of *H. uranomidis* Hunkeler, 1972 (MHNG INVE 18679, INVE 18680, INVE 1868, INVE 18685); holotype of *H. tualatinensis* (USNPC 078418), holotype of *H. pitymi* (USNPC 038261); voucher of *H. citelli* (USNPC 044825) from U.S. National Parasite Collection, Beltsville.

Other materials examined by us included tapeworms from the ISEA collection, representing specimens of *Hymenolepis* sp. from *A. agrarius*, *H. diminuta* from *R. norvegicus*, *H. megaloon* from *Urocitellus undulatus* (Pallas), *Talpolepis peipingensis* (Hsü, 1935) from *Mogera robusta* Pomel and *H. erinacei* (Gmelin, 1790) from *Erinaceus* spp. from the Altai Mts., Siberia and the Russian Far East. Additionally we studied vouchers of *H. sulcata* (Linstow, 1879) from *Glis glis* (Linnaeus) from MHNG.

Measurements are given in micrometres except where otherwise stated.

Results

Hymenolepis rymzhanovi sp. nov. (Figs 1 and 2)

Description (based on 1 specimen): Fully developed strobila 88 mm long, with maximum width at pregravid or gravid proglottids, 1.63 mm. Strobila consisting of 628 craspedote proglottids. Scolex slightly flattened dorso-ventrally, 235 wide. Border between scolex and neck distinct. Suckers unarmed, oval, 119–125 × 77–91 (122 × 82, n = 4), oriented antero-laterally, with thick walls (Fig. 1A). Rhynchus unarmed (41 × 11), invaginated in rostellar pouch (101 × 65); rostellum absent (Fig. 1A, B). Rostellar pouch with muscular walls, osmoregulatory canals penetrate through rostellar pouch wall. Neck 250 wide.

Ventral osmoregulatory canals 37–50 (45, n = 5) wide, connected by transverse anastomoses. Dorsal osmoregulatory canals 16–25 (19, n = 5) wide, approximately half as thin as ventral canals. Dorsal osmoregulatory canals usually situated directly above ventral canals although in some proglottids their loops may be situated lateral to ventral canals. Genital pores unilateral, dextral. Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals (Fig. 1C, D). Development of proglottids gradual, protandrous. External segmentation becomes evident at level of premature part of strobila.

Mature proglottids 170–193 × 790–910 (185 × 942, n = 8), transversely elongate, trapezoid (Fig. 1C, D). Testes relatively small, usually three, almost equal in size, 63–80 × 70–83 (72 × 77, n = 13), round or oval, normally situated in one row; poral testis separated from two antiporal testes by female gonads. Cirrus-sac elongate, relatively short, 165–190 × 31–37 (178 × 34, n = 6), with well-developed muscular walls. Antiporal part of cirrus-sac usually overlapping ventral longitudinal canal (Fig. 1D, E). Genital atrium simple, infundibular, deep, situated approximately in middle of lateral proglottid margin. Cirrus 35–48 × 6–9 (42 × 7, n = 11), cylindrical, armed with minuscule (less than 1 long) spines (Fig. 2A). Internal seminal vesicle oval, 85–100 × 19–28 (91

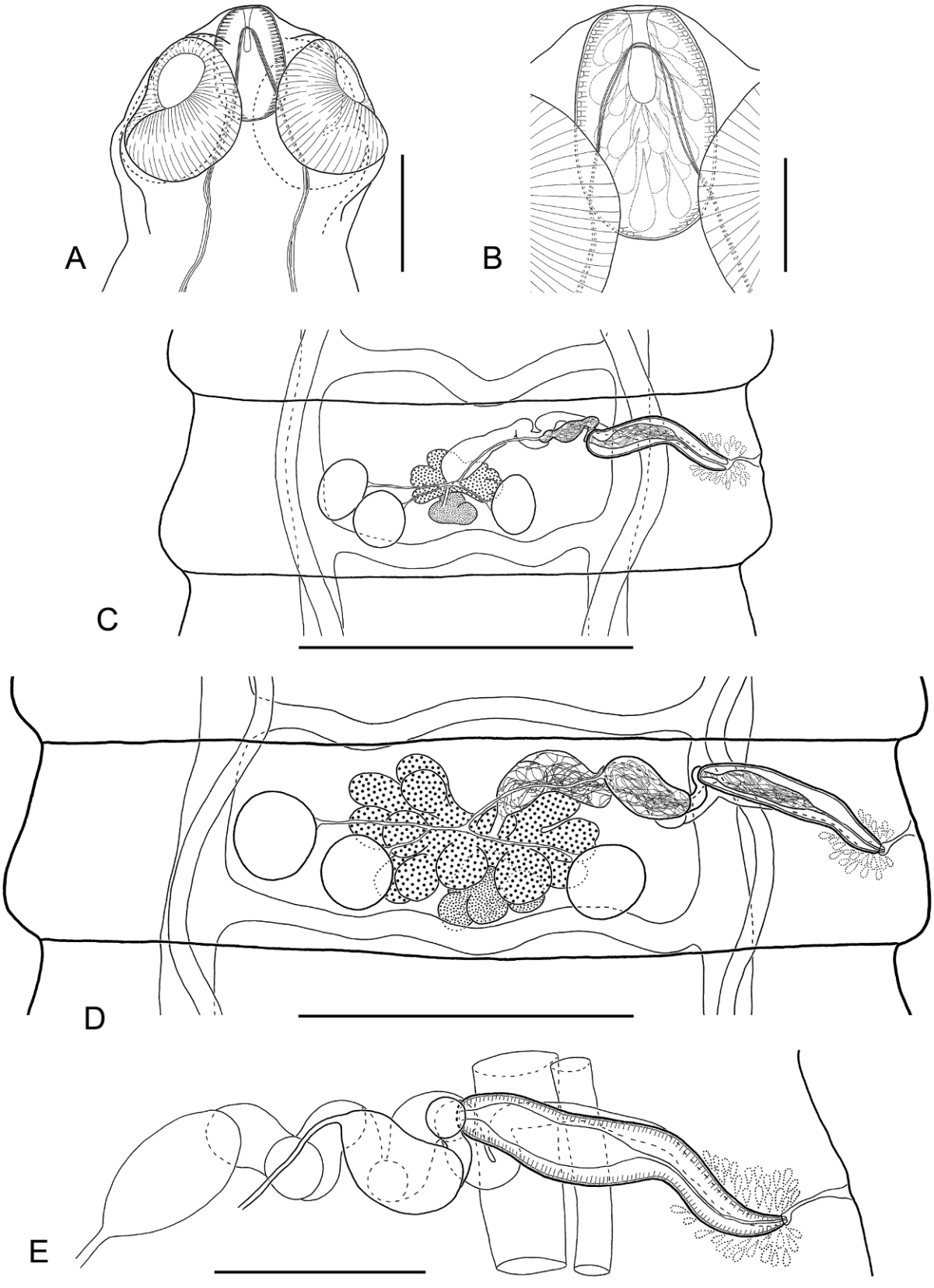

Fig. 1. *Hymenolepis rymzhanovi* sp. nov. **A** – holotype, dorsoventral view of scolex; **B** – holotype, rostellar pouch; **C** – holotype, male mature proglottid; **D** – holotype, hermaphroditic mature proglottid; **E** – holotype, genital ducts. Scale bars: A, E = 100 μm; B = 50 μm; C, D = 300 μm

× 23, n = 8), not longer than about half of cirrus-sac length (Fig. 1E). External seminal vesicle elongate 67–82 × 34–48 (73 × 38, n = 6), clearly distinguishable from vas deferens, distinctly smaller than seminal receptacle.

Ovary 225–250 (236, n = 8) wide, median, fan-shaped, irregularly lobed, ventral to male genital organs, occupying substantial part of median field, usually overlapping testes (Fig. 1D). Vitellarium 67–85 × 95–120 (74 × 104, n = 6), postovarian, median, scarcely lobed. Copulatory part of vagina 63–75 × 7–12 (67 × 9, 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; internal surface of vagina lined by microvilli (Fig. 2A). Seminal receptacle relatively large, 330–363 × 38–46 (350 × 41, n = 5), usually curved or twisted (Fig. 1D, E).

Uterus first appears as perforated transversely elongated sac, situated dorsally to other organs and extending laterally beyond longitudinal osmoregulatory canals (Fig. 2C). With proglottid development, uterus forms numerous diverticula on dorsal and ventral sides (Fig. 2D). Testes still visible in postmature proglottids; cirrus-sac and vagina persist in gravid proglottids. Gravid proglottids transversely elongate, 265–295 × 1420–1630 (278 × 1528, n = 5). Fully developed uterus occupying entire median field and extending laterally beyond longitudinal osmoregulatory canals, saccate, with ventral and dorsal diverticula commonly arranged in two rows, lateral sides of gravid uterus usually deeply folded or perforated (Fig. 2E). Uterus contains numerous (up to 600–800) small eggs. Eggs 47–51 × 49–56, subspherical or oval, with relatively thick outer coat (up to 1.7), egg surface rough; oncosphere 28–32 × 30–36 (Fig. 2B). Embryophore subspherical, thin, 36–39 × 37–41. Embryonic hooks 15–16.5 long.

Taxonomic summary

Site in the host: small intestine.

Type host: *Myospalax myospalax* (Laxmann) (Rodentia: Spalacidae).

Symbiotype: Female subadult, skull and skin, collection No. 59531. ISEA collection of vertebrate animals.

Type locality: Tarbagatai Mts., Urzhar District, East Kazakhstan Province; ca. 47°14′N, 81°43′E, h 1080 m.

Type specimens: Holotype, two slides, MHNG INVE 82286, labelled Tarbagatai Mts., Urzhar District, East Kazakhstan Province, 21 May 2007, coll. A.A. Makarikov.

Etymology: This species has been named in honor of Dr. Tleubeck Rymzhanov, a prominent Kazakh malacologist who helped one of the authors (AAM) during his field work in East Kazakhstan.

Remarks

Hymenolepis rymzhanovi sp. nov. 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 one row, cirrus-sac with muscular walls, saccate uterus with ventral and dorsal diverticula, spherical or oval eggs with thick outer coat.

Hymenolepis rymzhanovi sp. nov. is readily distinguishable from *H. pitymi* from *Microtus pinetorum* (Le Conte) (syn.: *Pitymys pinetorum* (Le Conte)), *H. vogeae* Singh, 1956 from *Mus booduga* (Gray) (in original description *Mus buduga* Thomas) from India, *H. geomydis* Gardner et Schmidt, 1988 and *H. tualatinensis* from Nearctic Geomyidae, all of which have testes arranged in a triangle while in the new species the testes arrangement is linear.

Hymenolepis rymzhanovi is morphologically similar to *H. diminuta*. The new species can be distinguished from *H. diminuta* by the significantly smaller strobila and narrower scolex (see Table I). The cirrus-sac in *H. rymzhanovi* is shorter than that of *H. diminuta*. Furthermore, in the new species testes are overlapping ovary while in *H. diminuta* they do not. The new species differs from *H. uranomidis* from *Uranomys ruddi* Dollman from West Africa by the shorter cirrus-sac and smaller testes (Hunkeler 1972, our observations). Besides, eggs and embryonic hooks of *H. rymzhanovi* are larger than those of *H. uranomidis*. In addition, the external seminal vesicle of *H. uranomidis* is surrounded by a dense layer of intensely stained cells (likely of glandular nature) which is lacking in the new species.

Hymenolepis rymzhanovi differs from *H. hibernia* described from *A. sylvaticus* in Europe by smaller strobila, larger cirrus-sac and smaller ovary. Furthermore, both poral and first aporal testes in new species overlap the ovary while in *H. hibernia* only the first aporal testis overlaps the ovary.

New species is distinguished from *H. pseudodiminuta* known from *Apodemus* spp. in Japan by the significantly smaller strobila, narrower scolex, shorter cirrus-sac and larger embryonic hooks. In addition, the testes in *H. rymzhanovi* overlap the ovary while in *H. pseudodiminuta* they do not.

Hymenolepis rymzhanovi can be distinguished from *H. weldensis* Gardner et Schmidt, 1988 parasitic in Nearctic Geomyidae in having a broader strobila, smaller testes and eggs. Furthermore, the cirrus-sac in the new species is elongate and usually crosses the ventral longitudinal canal while in *H. weldensis* the cirrus-sac is pyriform and only reaches or rarely crosses the longitudinal osmoregulatory canals.

Hymenolepis rymzhanovi differs from *H. megaloon*, a parasite of *Spermophilus* spp. in the Palaearctic by a significantly wider ovary, smaller eggs and embryonic hooks. Testes of *H. rymzhanovi* in mature proglottids usually overlap the ovary, while in *H. megaloon* they do not reach the ovary. Furthermore, the uterus of *H. rymzhanovi* extends beyond the longitudinal osmoregulatory canals and has numerous ventral and dorsal diverticula while in *H. megaloon* the uterus does not extend beyond the longitudinal osmoregulatory canals and lacks diverticula.

The new species is distinguished from *H. citelli* parasitic in *Spermophilus* spp. in the Nearctic in having a narrower strobila and scolex, as well as smaller testes and larger cirrus-sac and ovary. In addition, the cirrus-sac in the new species is elongate and usually crosses the ventral longitudinal canal while in *H. citelli* the cirrus-sac is pyriform and only reaches or rarely crosses the longitudinal osmoregulatory canals.

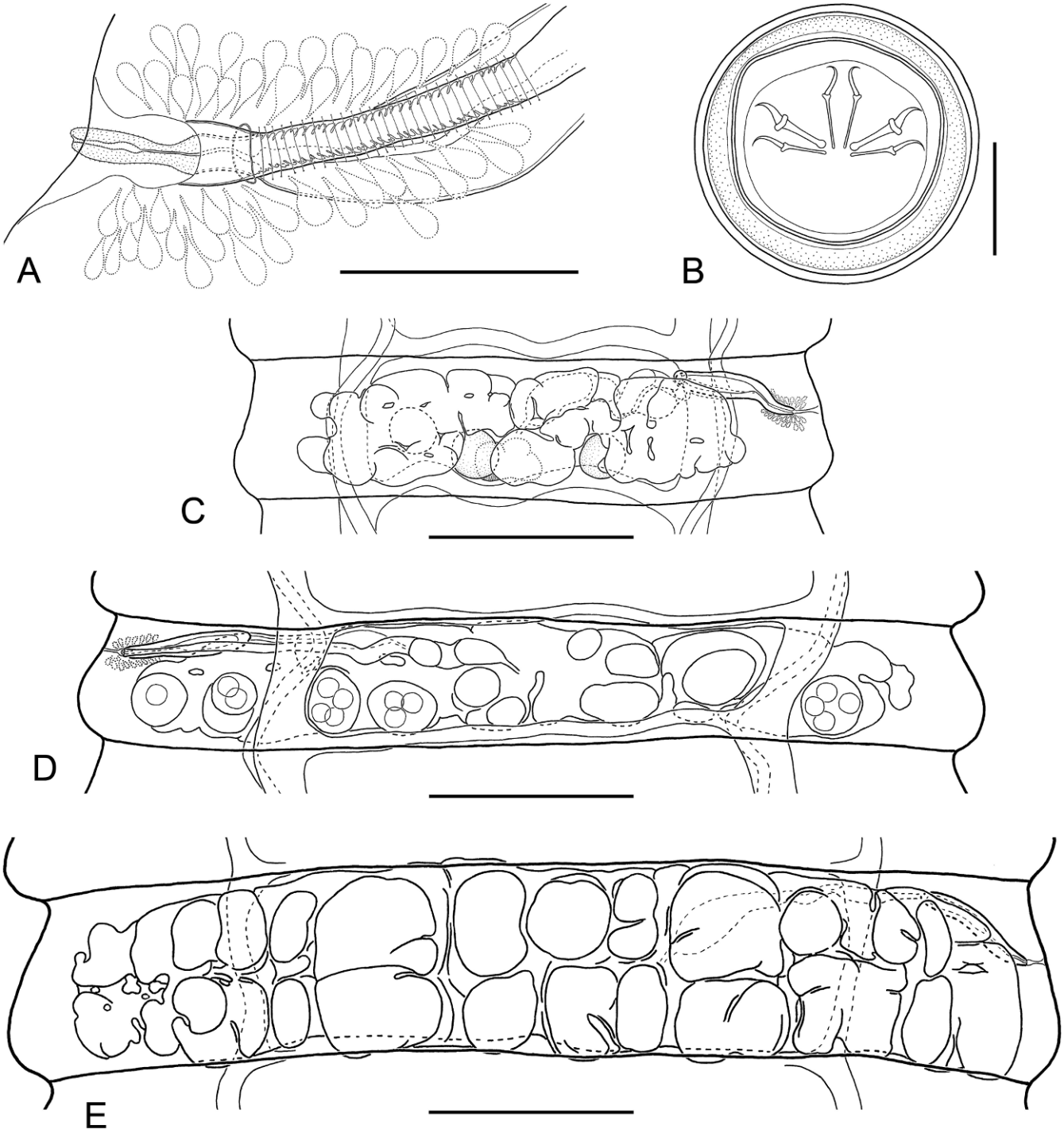

Fig. 2. *Hymenolepis rymzhanovi* sp. nov. **A** – holotype, cirrus and vagina; **B** – holotype, egg; **C** – holotype, postmature proglottid from dorsal side, showing uterus development; **D** –holotype, pregravid proglottid from ventral side, showing appearance of dorsal uterine diverticula; **E** – gravid proglottid from dorsal side, showing saccate uterus with dorsal uterine diverticula. Scale bars: A = 50 μm; B = 20 μm; C, D, E = 300 μm

Table I. Main morphometric data distinguishing *Hymenolepis* spp. (measurements in micrometres except where otherwise stated)

Characters	*H. diminuta*[1]	*H. citelli*[2]	*H. megaloon*[1]	*H. uranomidis*[3]	*H. hibernia*[4]	*H. pseudo-diminuta*[5]	*H. vogeae*[6]	*H. tualatinensis*[7]	*H. weldensis*[8]	*H. geomydis*[8]	*H. rymzhanovi* sp. nov.	*H. apodemi* sp. nov.
Strobila length	183 mm	150 mm	38–72 mm	100–105 mm	169 mm	80–110 mm	120–140 mm	24–210 mm	111–165 mm	72–168 mm	88 mm	105–165
Strobila width	2.38–2.56 mm	2.8 mm	2–2.28 mm	1.5–4 mm	2.9 mm	2–2.9 mm	0.89–0.93 mm	1.75 mm	0.82–0.94 mm	1.98–3.3 mm	1.63 mm	2.4–3.8 mm
Scolex width	286–296	245	276–307	210–300	213–231	288–370	203–332	92–167	126–288	194–245	235	280–390
Sucker size	96–108	113×87	88–112× 78–118	97–116	79–94×84–92	93–124	–		–	92–124× 65–94	119–125 ×77–91	110–140× 100–128
Rostellar pouch size	94–108× 44–52		128–152× 63–78	80–110× 50–60	85–89×43–48	93–103	–	51–61	–	–	101×65	120–145× 60–72
Hermaphroditic mature proglottid size	–	–	–	–	84–06× 1315–1635	86–98× 900–1200	224×819	–	–	–	170– 193×790–910	140–160× 1710–2170
Testes size	118–220× 40–48	143×113	63–118× 69–120	–	87–122× 55–78	72	–	63–141× 54–141	92–166	55–180× 81–180	63–80×70–83	139–193× 125–170
Cirrus-sac size	240–300× 28–48	157	118–200× 36–48	180–230× 35–64	127–143× 39–43	200–280×50	156–195× 51–66	56–150× 26–49	149–194× 34–51	80–160× 36–67	165–190× 31–37	216–250× 37–55
Cirrus size	38–47*	–	–	–	36–43	–	59–66×23	-	-	-	35–48×6–9	60–76×12–16
Cirrus armature	minute spines*	–	–	–	–	unarmed	unarmed	minute spines	minute spines	minute spines	minute spines	minute spines
Ovary width	345–402	–	56–88	–	401–442	300	156–273	96–216	90–293	180–494	225–250	300–470
Vitellarium size	–	–	–	–	48–59× 113–145	25–40	163	34–109× 37–132	50–112× 54–106	61–137× 101–209	67–85× 95–120	60–115× 95–145
Seminal receptacle size	–	–	–	–	–	–	242–83× 117–164	48–169× 23–70	175–552× 43–148	99–369× 59–108	330–363× 38–46	780–920× 125–184
Egg size	56–60×63–66	59–65×78–86	98–117× 111–127	36–39×43–47	51–63	52–62	27	57–89×42–68	70–81×67–77	76–85×72–83	47–51×49–56	61–75×63–77
Oncosphere size	23–25×28–31	–	39×55	20–21×25–28	–	31–37	7	23–49	38–45×38–40	38–50×34–43	28–32×30–36	27–33×34–38
Embryonic hook size	14–15	–	22–24	13–14,5	–	14	–	17–20	13–16	16–20	15–16.5	15.5–17.5

[1]Measurements from Genov (1984); [2]measurements from McLeod 1933; [3]measurements from Hunkeler, 1972; [4]measurements from Montgomery et al. (1986); [5]measurements from Tenora et al. 1994; [6]measurements from Singh, 1956; [7]measurements from Gardner, 1985; [8]measurements from Gardner and Schmidt, 1988; *characters and measurements were taken in present study.

Allocation of *H. ognewi* Skrjabin, 1924 from *Rhombomys opimus* (Lichtenstein) from Kazakhstan in *Hymenolepis* (*sensu stricto*) is questionable because of the inadequacy of its original description. Nevertheless *H. rymzhanovi* can be distinguished from *H. ognewi* by the larger ovary and vitellarum which overlaps the testes. In addition, the cirrus-sac in *H. rymzhanovi* usually crosses the ventral longitudinal canal while in *H. ognewi* the cirrus-sac does not reach the ventral longitudinal canal.

In addition to the above, hymenolepidids with an unarmed scolex and rudimentary rostellum from moles also bear some morphological similarity to the new species. These species include *Talpolepis peipingensis* (Hsü, 1935) in moles of China and Russian Far East, *T. scalopi* (Schultz, 1939) in *Scalopus aquaticus intermedius* (Elliot) from North America, *T. dymecodontis* (Sawada et Harada, 1990) from *Urotrichus pilirostris* True and *Scaptonyx moschatus* Milne-Edwards from Japan and China and *T. mogerae* (Sawada et Koyasu, 1991) from *Mogera kobeae* Thomas from Japan (Gulyaev and Melnikova 2005). However, all of them have significant morphological differences that separate them from *Hymenolepis* (*sensu stricto*), among them the dorsal longitudinal osmoregulatory canals clearly shifted porally in relation to the ventral canals. Another feature characteristic of *Talpolepis* is the cirrus-sac lacking external muscular layers. They were allocated into a separate genus *Talpolepis* Gulyaev et Melnikova, 2005 (Gulyaev and Melnikova 2005), therefore, we do not provide here a detailed differentiation of the new species from these cestodes.

The differentiation of *H. rymzhanowi* sp. nov. from *H. apodemi* sp. nov. is provided below.

Some additional morphological characteristics of *H. rymzhanovi* such as relatively wide dorsal osmoregulatory canals and curved or twisted seminal receptacle, can be potentially valuable or even unique. However, these features cannot be used for differentiation at this point because the majority of previous descriptions are not detailed enough for adequate comparison.

***Hymenolepis apodemi* sp. nov.** (Figs 3 and 4)

Description (based on 11 specimens): Fully developed strobila 105–165 mm long, with maximum width 2.4–3.8 mm at level of pregravid or gravid proglottids. Strobila consisting of 700–950 craspedote proglottids. Scolex retractable, slightly flattened dorso-ventrally, 280–390 (315, n = 5) wide, not clearly distinct from strobila (Fig. 3A, B). Suckers unarmed, oval, 110–140 × 100–128 (126 × 113, n = 16), thick-walled. Rhynchus unarmed, 20–30 × 12–15 (26 × 13, n = 5), invaginated in rostellar pouch 120–145 × 60–72 (128 × 66, n = 8); rostellum absent (Fig. 3A, B). Rostellar pouch with muscular walls, osmoregulatory canals penetrate through rostellar pouch wall (Fig. 3C). Neck wider than scolex, 290–450.

Ventral osmoregulatory canals 45–95 (59, n = 10) wide, connected by transverse anastomoses. Dorsal osmoregulatory canals thin, 6–14 (9, n = 10) wide, usually situated above ventral canals. Genital pores unilateral, dextral. Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals (Fig. 3D, E). Development of proglottids gradual, protandrous. External segmentation becomes evident at level of premature part of strobila.

Mature proglottids 140–160 × 1710–2170 (149 × 1944, n = 12), transversely elongate, trapezoid (Fig. 3D, E). Testes relatively small, usually three, almost equal in size, 139–193 × 125–170 (171 × 143, n = 22), round or oval, normally situated in one row; poral testis separated from two antiporal testes by female gonads. Cirrus-sac pyriform, relatively short, 216–250 × 37–55 (231 × 42, n = 22), with well-developed muscular walls. Antiporal part of cirrus-sac commonly does not reach ventral longitudinal canal (Fig. 3E, F). Genital atrium simple, infundibular, deep, opens laterally in about middle of lateral proglottid margin. Cirrus 60–76 × 12–16 (65 × 12, n = 11), cylindrical, armed with minuscule (less than 1 long) spines (Fig. 3G). Internal seminal vesicle ovoid, 132–170 × 28–44 (149 × 34, n = 10), more than half of cirrus-sac length (Fig. 3F). External seminal vesicle elongate 165–220 × 50–115 (183 × 76, n = 12), clearly distinguishable from vas deferens, distinctly smaller than seminal receptacle.

Ovary 300–470 (361, n = 21) wide, median, fan-shaped, irregularly lobed, ventral to male genital organs, occupying less than half of median field, usually not overlapping testes or rarely slightly overlapping median aporal testis (Fig. 3E). Vitellarium 60–115 × 95–145 (77 × 123, n = 17), postovarian, median, scarcely lobed. Copulatory part of vagina 60–75 × 6–10 (63 × 8, n = 8), 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; internal surface of vagina lined by microvilli (Fig. 3H). Seminal receptacle relatively large, 780–920 × 125–184 (840 × 169, n = 10) (Fig. 3E).

Uterus first appears as perforated transversely elongated sac, situated dorsally to other organs and extending laterally beyond longitudinal osmoregulatory canals (Fig. 4A). With proglottid development, uterus forms numerous diverticula on dorsal and ventral side (Fig. 4B, C). Testes remain in postmature proglottids; cirrus-sac and vagina persist in gravid proglottids. Gravid proglottids transversely elongate, 360–460 × 1650–3160 (396 × 2754, n = 10). Fully developed uterus occupying entire median field and extending laterally beyond longitudinal osmoregulatory canals, saccate, with ventral and dorsal diverticula, commonly arranged in two rows, lateral sides of gravid uterus usually deeply folded or perforated (Fig. 4D). Uterus contains numerous (more than 1000) small eggs. Eggs 61–75 × 63–77, subspherical or oval, with relatively thick outer coat (up to 2.5–4); oncosphere 27–33 × 34–38 (Fig. 4E). Embryophore subspherical, thin, 32–38 × 39–42. Embryonic hooks 15.5–17.5 long (Fig. 4F).

Taxonomic summary

Site in the host: small intestine.

Type host: *Apodemus peninsulae* (Thomas) (Rodentia: Muridae).

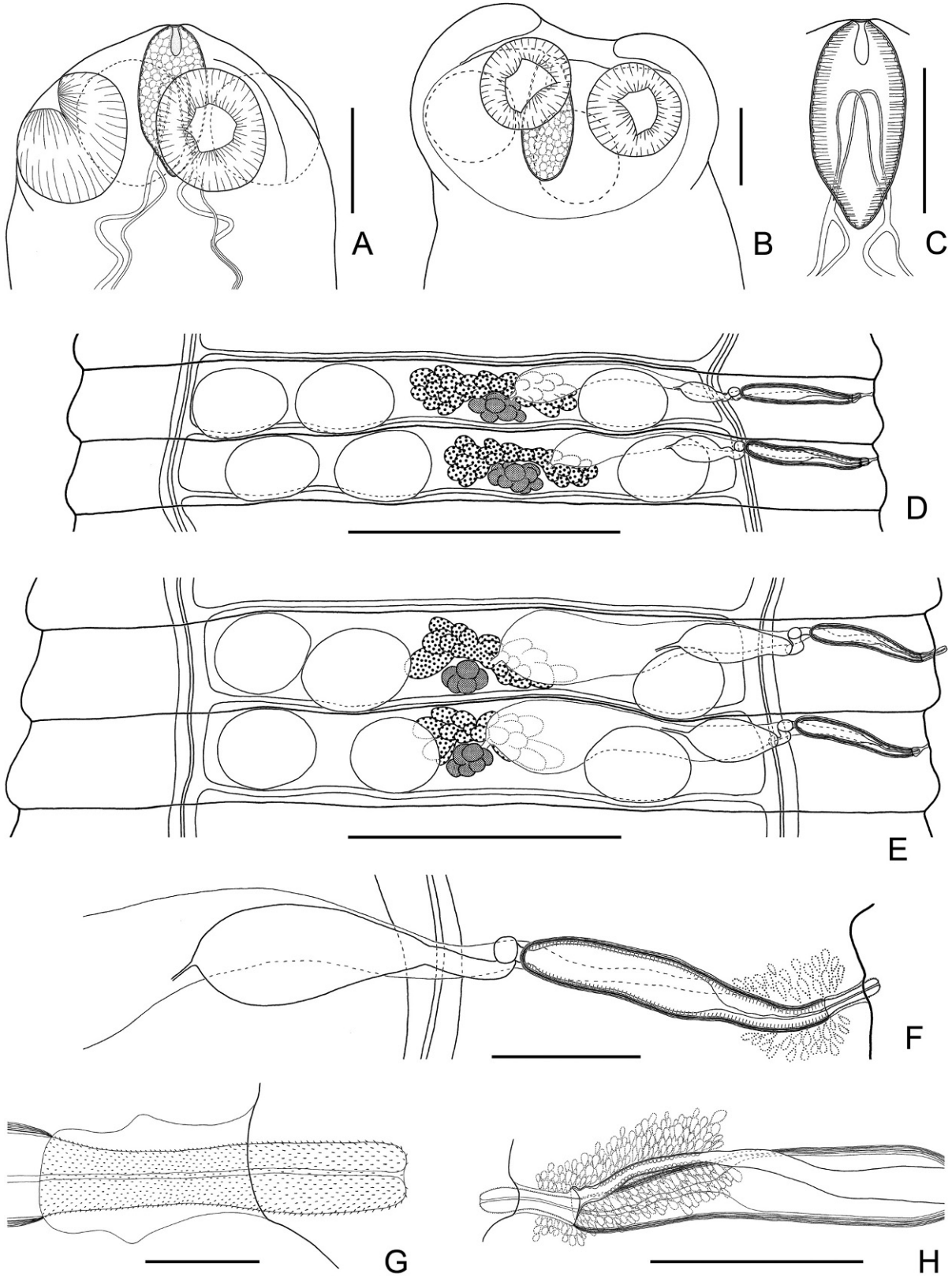

Fig. 3. *Hymenolepis apodemi* sp. nov. **A** – holotype, dorsoventral view of scolex; **B** - paratype 18.31.4.30, dorsoventral view of retracted scolex; **C** – holotype, rostellar pouch; **D** – paratype 18.31.4.30, male mature proglottids; **E** – holotype, hermaphroditic mature proglottids; **F** –holotype, genital ducts; **G** – holotype, cirrus; **H** – vagina. Scale bars: A, B, C, F, H = 100 μm; D, E = 500 μm; G = 20 μm

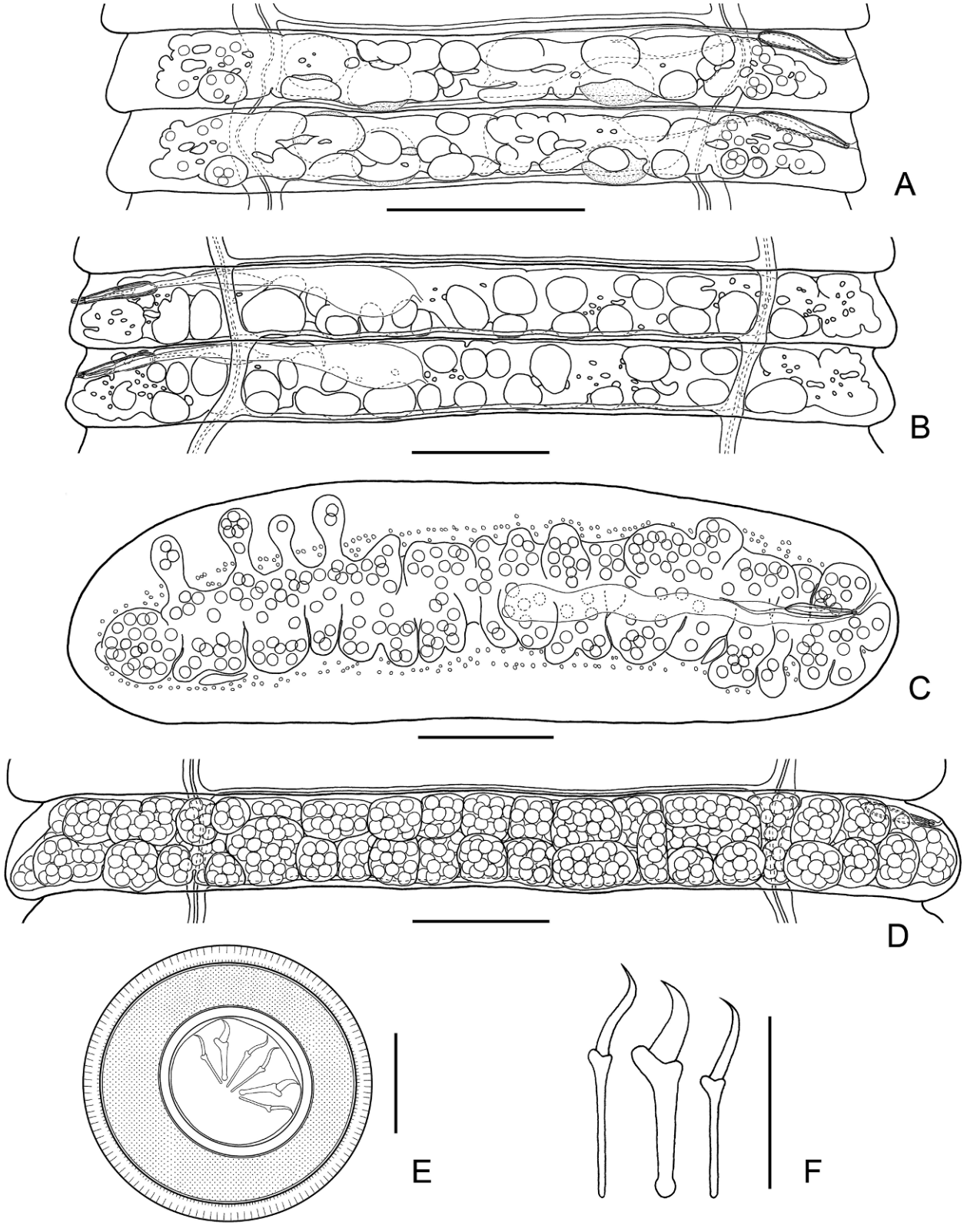

Fig. 4. *Hymenolepis apodemi* sp. nov. **A** – holotype, postmature proglottids from dorsal side, showing uterus development; **B** – paratype 18.31.4.30, pregravid proglottids from ventral side, showing appearance of dorsal uterine diverticula; **C** – voucher 18.31.4.70, cross-section showing dorsal and ventral uterine diverticula; **D** – paratype 18.31.4.30, gravid proglottid from dorsal side, showing saccate uterus with dorsal uterine diverticula; **E** – paratype 18.31.4.30, egg; **F** – paratype 18.31.4.30, embryonic hooks. Scale bars: A, B, C, D = 500 μm; E = 25 μm; F = 15 μm

Other hosts*: A. uralensis* (Pallas), *A. agrarius* (Pallas).

Type locality: Lazovsky Reserve, Primorskiy Kray, Russia (exact coordinates unknown).

Other localities: Village of Ust'-Urgul'ka (ca., 56°19′N, 77°47′E), suburbs of the city of Novosibirsk (ca., 54°49′N, 83°05′E), Novosibirskaya Oblast'; Bol'shekhekhtsirskiy Nature Reserve, Khabarovskiy Kray (ca., 48°16′N, 134°45′E); Ussuriiskiy Nature Reserve (ca., 43°38′N, 132°20′E), suburbs of the city of Vladivostok (ca., 43°11′N, 131°55′E), Primorskiy Kray, Russia; Tarbagatai Mts., Urzhar District, East Kazakhstan region, Kazakhstan (ca. 47°14′N, 81°43′E, h 1080 m).

Type specimens: Holotype, ISEA 18.31.4.27 from type host species and locality, 16.06.05. Paratypes INVE 82284 (ISEA 18.31.4.26) from type host species and locality, 16.06.05; INVE 82285 (ISEA 18.31.4.28) from type host species and locality, 16.06.05; ISEA 18.31.4.30 from type host species and locality, 17.06.05; ISEA 18.31.4.31 from type host species and locality, 16.06.05 (Berlese's medium); ISEA 18.31.4.32 from type host species and locality, 16.06.05; ISEA 18.31.4.45 ex *A. agrarius*, suburbs of the city of Vladivostok, 07.09.2007; ISEA 18.31.4.46 ex *A. agrarius*, suburbs of the city of Vladivostok, 11.09.2007; ISEA 18.31.4.54 ex *A. agrarius*, suburbs of the city of Vladivostok, 07.09.2007. Vouchers ISEA 294 *A. agrarius*, Village of Ust'-Urgul'ka, 1997; ISEA 1422 *A. agrarius*, Village of Ust'-Urgul'ka, 1984; ISEA 2205 *A. agrarius*, Village of Ust'-Urgul'ka, 1984; ISEA 68/561 *A. agrarius*, suburbs of the city of Novosibirsk, 1994; ISEA 68/561 *A. agrarius*, suburbs of the city of Novosibirsk, 1995; ISEA 18.31.4.11 ex *A. penninsulae*, Bol'shekhekhtsirskiy Nature Reserve, 14.07.2003; ISEA 18.31.4.70 *A. uralensis*, Tarbagatai Mts., 19.05.2007; ISEA 18.31.4.71 *A. uralensis*, Tarbagatai Mts., 21.05.2007; ISEA 18.31.4.72 *A. uralensis*, Tarbagatai Mts., 21.05.2007.

Etymology: The species name refers to the name of its definitive host.

Remarks

Hymenolepis apodemi sp. nov. 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 one row, cirrus-sac with muscular walls, saccate uterus with ventral and dorsal diverticula, subspherical eggs with thick outer coat.

Hymenolepis apodemi is readily distinguishable from *H. pitymi*, *H. vogeae*, *H. geomydis* and *H. tualatinensis*, all of which have testes arranged in a triangle while in the new species the testes arrangement is linear.

Hymenolepis apodemi is morphologically similar to *H. diminuta*. The new species can be distinguished from *H. diminuta* by the longer cirrus (see Table I) and pyriform cirrus-sac usually not reaching ventral longitudinal osmoregulatory canal while *H. diminuta* has elongate cirrus-sac crossing poral osmoregulatory canals.

Hymenolepis apodemi differs from *H. pseudodiminuta* by a longer rostellar pouch, larger eggs and embryonic hooks. In addition, the cirrus-sac of *H. apodemi* usually does not reach the poral osmoregulatory canals while in *H. pseudodiminuta* it always crosses the poral osmoregulatory canals. Furthermore, *H. apodemi* is characterized by a retractable scolex. To the best of our knowledge a retractable scolex has not been reported in any other member of *Hymenolepis*.

The new species is distinguished from *H. hibernia* by having a larger cirrus-sac and cirrus, and somewhat larger eggs. In addition, the cirrus-sac of *H. apodemi* usually does not reach the ventral longitudinal canal and the poral testis in the new species does not overlap ovary. In contrast, the cirrus-sac in *H. hibernia* overlaps the poral osmoregulatory canals and its poral testis overlaps the ovary.

Hymenolepis apodemi differs from *H. uranomidis* by larger eggs and embryonic hooks (Hunkeler 1972, our observations). Furthermore, the cirrus-sac of *H. apodemi* usually does not reach the ventral longitudinal canal and the poral testis in the new species does not overlap the ovary while in *H. uranomidis* the cirrus-sac overlaps the poral osmoregulatory canals and the poral testis overlaps the ovary.

The new species can be distinguished from *H. citelli* by the larger cirrus-sac which does not reach the ventral longitudinal canal (overlaps ventral canal in *H. citelli*) and eggs with a thick outer coat (thin in *H. citelli*).

Hymenolepis apodemi can be distinguished from *H. megaloon* by a larger cirrus-sac and ovary and smaller eggs and embryonic hooks (Genov 1984, our observations). Furthermore, the uterus of *H. apodemi* extends beyond the longitudinal osmoregulatory canals and has ventral and dorsal diverticula while in *H. megaloon* the uterus does not extend beyond the longitudinal osmoregulatory canals and lacks diverticula.

Hymenolepis apodemi differs from *H. weldensis* in having a broader strobila, longer cirrus-sac and wider ovary. In addition, the cirrus-sac of the new species normally does not reach the ventral longitudinal canal while in *H. weldensis* the cirrus-sac overlaps the poral osmoregulatory canals.

Hymenolepis apodemi can be differentiated from *H. ognewi* by a longer cirrus-sac and a fan-shaped, multi-lobed ovary vs compact scarcely lobed ovary in *H. ognewi*.

Hymenolepis apodemi differs from *H. rymzhanovi* by a longer cirrus-sac and cirrus. Furthermore, the cirrus-sac of the new species normally does not reach the ventral longitudinal canal (overlapping canals in *H. rymzhanovi*) and the poral testis does not overlap the ovary (overlaps in *H. rymzhanovi*).

Discussion

To date, only *H. megaloon* from *Spermophilus* spp. and *H. diminuta* from several rodent families are known from the eastern Palaearctic (Ryzhikov *et al*. 1978). We add two additional species to the list. It can be safely predicted that various

groups of rodents in the region harbour additional yet undescribed species of this genus.

Currently, little is known about the helminth fauna of the Siberian zokor. Before our study, only the nematodes *Heligmoptera sibirica* (Shakhmatova, 1990) and larvae of *Echinococcus multilocularis* (Leuckart, 1963) have been reported from this rodent endemic to Eastern Kazakhstan and the south of the West Siberian Plain (Ryzhikov *et al*. 1978, Shaikenov 1981, Shakhmatova 1990). Our description of *H. rymzhanovi* is the first record of an adult tapeworm from this species or any member of the Myospalacinae (Nadtochii 1970, Shakhmatova 1990, Ganzorig *et al*. 1999, Elias *et al*. 2002, Tinnin *et al*. 2011). Interestingly, Shaikenov (1981) has examined 449 specimens of the Siberian zokor in Kalbinsky Mountains and 130 specimens from the Tarbagatai mountain ridge and detected only *E. multilocularis* infection. The absence of other helminths in Siberian zokors studied by Shaikenov (1981) may be attributed to either seasonal changes or patchy distribution of parasites. We have dissected only a single Siberian zokor from the type locality of *H. rymzhanovi* and it was infected with the cestode. We collected our material in May, while Shaikenov conducted his research in the late summer.

One of the interesting morphological characters of *H. apodemi* is its ability to retract the scolex into the neck region. To the best of our knowledge this is unique among *Hymenolepis* and is somewhat reminiscent of the condition found in the genus *Coronacanthus* Spassky, 1954 that includes parasites of water shrews, genus *Neomys* Kaup. The latter type of scolex organization was named "tulip-like" by Vaucher (1982).

We have found *H. apodemi* in several geographically distant regions. The most distant localities (between Village of Ust'-Urgul'ka and suburbs of the city of Vladivostok) are situated 4040 km from each other. Nevertheless, we could not find any meaningful morphological differences among specimens from all these localities which suggests it is a broadly distributed species specific to mice of the genus *Apodemus*.

It is not rare when cestodes previously considered to be a single broadly distributed species prove to consist of a complex of cryptic species. We cannot exclude that the situation with *H. apodemi* may be similar to what was recently demonstrated for another broadly distributed hymenolepidid with unarmed scolex parasitic in rodents, namely *Arostrilepis horrida* (Linstow, 1901). The latter species was long regarded as a single morphologically variable species occurring in a diverse assemblage of rodent definitive hosts across an extensive geographic range encompassing the Holarctic region. However, combined molecular and morphological analysis has revealed that *A. horrida* represents a complex of 12 distinct species (Cook *et al*. 2005; Makarikov and Kontrimavichus 2011; Makarikov *et al*. 2011, 2012; Makarikov *et al*. unpublished data). Detailed molecular studies are necessary to explore the species boundaries, geographic ranges and host specificity among the members of *Hymenolepis* including *H. apodemi*. It is clear that the currently known species of *Hymenolepis* represent only a portion of the true diversity of this broadly distributed genus. At present, we have identified at least one undescribed species of *Hymenolepis* from rodents in Eastern Asia, four species in Southeast Asia and one in North America (Makarikov and Tkach unpublished data, Makarikov et *al*. unpublished data). There is little doubt that examination of not yet studied hosts from various regions of the world will increase the number of species in this genus.

Based on the data available in the literature and our observations, it can be cautiously suggested that associations with different rodent hosts may be informative in distinguishing among species of *Hymenolepis* and may represent an auxiliary criterion in outlining and identification of *Hymenolepis* species. This is true at least for the distribution of *H. diminuta* among species of rats (*Rattus*), *H. pseudodiminuta*, *H. hibernia* and *H. apodemi* among species of Eurasian field mice (*Apodemus*), *H. tualatinensis*, *H. weldensis* and *H. geomydis* in pocket gophers (Geomyidae), and *H. megaloon* and *H. citelli* among ground squirrels (*Spermophilus* spp.). Therefore, we suppose that some of the records of *H. diminut*a listed by Ryzhikov *et al*. (1978) from *Apodemus* in different parts of the former Soviet Union may in fact represent *H. apodemi* described in the present work. This suggestion is indirectly supported by the patterns of host specificity observed in some other rodent hymenolepidids. Among the best examples are the species of *Arostrilepis* which are largely specific to certain arvicoline genera (Makarikov and Kontrimavichus 2011; Makarikov *et al*. 2011, 2012; Makarikov *et al*. unpublished data).

Based on our examination of the type species, *H. diminuta* and other congeners (*H. megaloon*, *H. erinacei*, *H. uranomidis*, *H. tualatinensis*, *H. pitymi*, *H. citelli*, *H. rymzhanovi* sp. nov. and *H. apodemi* sp. nov.) we discovered additional distinctive generic-level characters of the genus *Hymenolepis*: osmoregulatory canals penetrating into interior of rostellar pouch (Figs 1A, B; 3A, C), cirrus-sac and vagina with well-defined muscular walls (Figs 1E; 2A; 3F, H) the latter covered externally by a dense layer of intensely stained cells (Figs 2A; 3H), cirrus armed with minuscule (less than 1 μm long) spines (Figs 2A, 3G) and uterus with ventral and dorsal diverticula (Figs 2E, 4C). Specimens of *H. diminuta* from *R. norvegicus* examined in the current study had the cirrus armed with minuscule (less than 1 long) spines. The same situation was found in *H. megaloon*, *H. uranomidis*, *H. tualatinensis*, *H. weldensis*, *H. geomydis*, *H. rymzhanovi* and *H. apodemi*. The spination of the cirrus in those species is highly visible in specimens mounted in Berlese's medium whereas in stained specimens cirri appear smooth. We assume that an armed cirrus is characteristic for all species of *Hymenolepis*, but due to the extremely small size of the spines they were usually overlooked in descriptions. In order to include these and other characters we provide an emended generic diagnosis of the genus.

Hymenolepis Weinland, 1858

Diagnosis (after Czaplinski and Vaucher 1994, Mas-Coma and Tenora 1997, modified): Hymenolepididae of medium size. Development of proglottids gradual. Proglottids numerous, transversely elongate, craspedote. Scolex with rudimentary rostellar apparatus; unarmed rhynchus invaginated in rostellar pouch. Osmoregulatory canals penetrate into interior of rostellar pouch. Suckers unarmed, sometimes with weak musculature. Dorsal and ventral osmoregulatory canals located in same sagittal plane. Ventral canals with transverse anastomoses. Genital pores unilateral, dextral, genital ducts pass dorsally to osmoregulatory canals. Three testes arranged in one row or in triangle; poral testis separated from two antiporal testes by female gonads. Cirrus-sac with muscular wall, not reaching median line of proglottid. Cirrus armed with minute spines. External and internal seminal vesicles present. Ovary fan-shaped or bilobed, median. Vitellarium postovarian, median, slightly lobed. Vagina with muscular walls and covered externally by a dense layer of intensely stained cells. Fully developed uterus saccate, with ventral and dorsal diverticula, extending bilaterally beyond longitudinal osmoregulatory canals, situated dorsally to other organs. Eggs spherical or subspherical, numerous, with thick outer coat. Embryophore subspherical. Parasites of rodents, bats and hedgehogs in the Holarctic, Afrotropical and Indomalayan regions. Type species: *H. diminuta* (Rudolphi, 1819).

Currently, 11 valid species from rodents could be attributable to the genus *Hymenolepis* (sensu stricto) (see Mas-Coma and Tenora 1997, Gulyaev and Melnikova 2005). These are *H. diminuta*, *H. megaloon*, *H. citelli*, *H. pitymi*, *H. vogeae*, *H. uranomidis*, *H. tualatinensis*, *H. hibernia*, *H. weldensis*, *H. geomydis* and *H. pseudodiminuta*. Generic position of *H. ognewi* requires additional study. Similarly, the generic placement of *H. sulcata* from European glirids (Gliridae) in *Hymenolepis* (sensu stricto) is doubtful since this species lacks transverse anastomoses between ventral osmoregulatory canals and the uterus does not extend beyond the longitudinal osmoregulatory canals and lacks diverticula (Murai and Tenora 1977, our observations). In addition to *Hymenolepis* spp. from rodents, there is one species parasitic in hedgehogs, namely *H. erinacei* and at least 4 species parasitic in bats (Sawada 1997, Makarikova *et al*. 2010). However, the situation with *Hymenolepis* in bats is much less clear and requires significant revisionary work due to very superficial descriptions of the majority of known species with an unarmed scolex, especially from the Eastern Palearctic and the Oriental region.

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