A redescription of *Arostrilepis horrida* (Linstow, 1901) and descriptions of two new species from Palaearctic microtine rodents, *Arostrilepis macrocirrosa* sp. n. and *A. tenuicirrosa* sp. n. (Cestoda: Hymenolepididae)

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Abstract: The type species of the cestode genus *Arostrilepis* Mas-Coma et Tenora, 1997, *Arostrilepis horrida* (Linstow, 1901), is redescribed on the basis of the syntype material from the brown rat (*Rattus norvegicus*) deposited in the collection of the Museum für Naturkunde, Berlin. *Arostrilepis horrida* (sensu lato), reported from a wide range of rodents throughout the Holarctic Region, is shown to be a species complex. The proposed host range and geographical distribution of *A. horrida* (sensu stricto) are limited to the data reported in the original description. The previously proposed synonymy of *A. horrida* is examined and the following species are excluded from the list of its synonyms: *Hymenolepis procera* Janicki, 1904, *H. arvicolina* Cholodkowsky, 1913, *H. sciurina* Cholodkowsky, 1913 and *H. mathevossianae* Akhmyan, 1946; these are considered *species inquirendae*. Specimens previously identified as *A. horrida* from voles from the Asian part of Russia are revised and newly collected materials are worked out. Two new species, *A. macrocirrosa* sp. n. and *A. tenuicirrosa* sp. n., are described. The main differentiating characters used to distinguish *Arostrilepis* spp. are the form and size of cirrus and its armature as well as the type of arrangement for the testes. The new species can also be distinguished from one another on the basis of sequences of the ITS2 rRNA gene. The generic diagnosis of *Arostrilepis* is emended. *Hymenolepis neurotrichi* Rausch, 1962, which had been placed in *Arostrilepis* by Mas-Coma and Tenora (1997), does not correspond to the generic diagnosis and is considered a *species incertae sedis*.

Keywords: Cestoda, Hymenolepididae, *Arostrilepis horrida*, redescription, *Arostrilepis macrocirrosa*, *Arostrilepis tenuicirrosa*, new species, morphology, microtine rodents

The original description of *Arostrilepis horrida* (Linstow, 1901) [syn.: *Taenia horrida* Linstow, 1901; *Hymenolepis horrida* (Linstow, 1901)] from the brown rat *Rattus norvegicus* (Berkenhout) from Germany (Linstow 1901) is inadequate. As a consequence, nearly all hymenolepidid cestodes from rodents possessing an unarmed scolex and lacking a vestigial rostellar apparatus have been identified as *A. horrida* (see Baer 1932, Schiller 1952, Voge 1952, Spassky 1954, Żarnowski 1955, Rybicka 1959, Surkov and Nadochii 1970, Murai and Tenora 1973, Egorova and Nadochii 1975, Genov 1984, Fedorov 1986, Kontrimavichus and Smirnova 1991, Mas-Coma and Tenora 1997, Asakawa et al. 2002). Thus, the published data create the impression that *A. horrida* has a Holarctic distribution and occurs in a diverse assemblage of rodent definitive hosts (i.e., Sciuridae, Myoxidae, Zapodidae, Cricetidae, Gerbillinae and Muridae) (Ryzhikov et al. 1978, Mas-Coma et al. 1980). It has not been found in Muridae, including

the designated type host, since its original description. Furthermore, *A. horrida* (s. l.) holds a central role in this group of tapeworms as it was designated as the type species of the genus *Arostrilepis* Mas-Coma et Tenora, 1997 (see Mas-Coma and Tenora 1997).

Only recently, two additional species were reported in this genus. These were *A. beringiensis* (Kontrimavichus et Smirnova, 1991) Gulyaev et Chechulin, 1997 from lemmings in Chukotka (Kontrimavichus and Smirnova 1991) and *A. microtis* Gulyaev et Chechulin, 1997 from voles of the genus *Microtus* Schrank from the Altai Mts. and Western Siberia (Gulyaev and Chechulin 1997). The lack of clear species limits and a contemporary redescription of the type series of *A. horrida* hinder further studies of species diversity in this group.

Syntype material of *A. horrida* is preserved in the Helminthological Collection of the Museum für Naturkunde in Berlin, Germany. This allowed us to prepare a rede-

scription and to initiate extensive studies to resolve species diversity within the *Arostrilepis*-complex. During a survey of the helminth fauna of red-backed voles (*Myodes* Pallas) in the Sakhalin Region (Sakhalin and Kunashir Islands), we found two other species belonging to *Arostrilepis*. Further, examination of specimens from the collections of the Institute of Systematics and Ecology of Animals, Novosibirsk (ISEZH), indicated that hymenolepidid cestodes from microtine rodents, which had been identified as *A. horrida* and originated from the Altai Mts., Siberia and the Russian Far East, also belonged to these two new species. These species are specific parasites of red-backed voles and can be easily distinguished from the type species and from congeners, *A. microtis* and *A. beringiensis*, by the size and shape of suckers, the size and armature of the cirri and the topography of the internal organs. In this article, we provide a redescription of the type species of the genus *Arostrilepis* based on syntype specimens and describe two new species of the same genus from *Myodes* spp.

MATERIALS AND METHODS

Cestodes from rodents were collected during June 2005 in the Poronayskiy Reserve, near the town of Poronaysk on Sakhalin Island, and during July 2006 in the Kurilskiy Reserve located on Kunashir Island. Three species of *Myodes* were sampled: *M. rutilus* (Pallas) (17 specimens), *M. rufocanus* (Sundevall) (37 specimens) and *M. sikotanensis* (Tokuda) (9 specimens). Another series of cestodes from *M. glareolus* (Schreber) was collected from Yarkovskiy Rayon, Tyumenskaya Oblast' from July to August 2007.

Host specimens were dissected immediately after their death. Cestodes were isolated, washed and relaxed in water; they were then fixed in 70% ethanol. They were stained with Ehrlich's haematoxylin, differentiated in a 3% aqueous solution of ferric-ammonium sulphate 12-hydrate, dehydrated in an ethanol series, cleared in clove oil and mounted in Canada balsam. Some specimens were mounted in Berlese's medium to facilitate the examination of their copulatory apparatus. Tissue from 13 cestode individuals was stored in 70–96% ethanol for DNA analysis (Haukisalmi et al. 2007).

The type specimens of the two new species were deposited into the collections of the Zoological Museum at the Institute of Systematics and Ecology of Animals, Novosibirsk (ISEZH), the Natural History Museum, Geneva, Switzerland (MHNG) and the Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic (IPCAS).

The following type materials from previously described species were studied: a syntype of *A. horrida*, No. 3640-Q, Museum für Naturkunde, Berlin, Germany, loaned by Dr. Birger Neuhaus; *A. beringiensis*, No. 646 (holotype), No. 647 (paratype), Centre of Parasitology of the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia; *A. microtis*, No. C 751 (holotype), No. C 752–761 (paratypes), Zoological Museum of ISEZH, Novosibirsk, Russia; *A. neurotrichi* No. 59813 (holotype), US National Parasite Collection, ARS, USDA, Beltsville, MD, USA loaned by Dr. Eric P. Hoberg.

The collections of the Zoological Museum of ISEZH, Novosibirsk included more than 650 slides of cestodes of the genus *Arostrilepis* from microtine rodents from the Altai Mts., Siberia and the Russian Far East. They were also examined in the course of the present study.

Measurements are given in micrometres except where otherwise stated. Metrical data for the holotypes are followed by those for paratypes in parentheses.

Tissue samples (c. 1.5–2 mm long) from cestodes were used for total DNA extraction. They were dried, and then placed in SET-buffer. The DNA was extracted using a standard phenol-chloroform protocol as described by Vainio et al. (1998) and Sambrook and Russell (2002). A fragment of the ITS2 region of the rRNA was amplified using the following primers: Proteo 1 F (5'-CGG TGG ATC ACT CGG CTC-3') and Proteo 2 R (5'-TCC TCC GCT TAT TGA TAT GC-3') (Škeřiková et al. 2001, Bean et al. 2007). The cycling profile consisted of an initial denaturation for 2:30 min at 95°C, 35 cycles of 45 s at 95°C, 45 s at 53°C, 1 min at 72°C and a final extension at 72°C for 10 min. The amplification was evaluated by running 3 µl of the final PCR product on a 2% agarose gel. Sequencing (from both sides) was carried out by MacroGen Inc. (Geumchun-gu Seoul 153-781, Korea) using the same primers.

Sequences were assembled using Sequencher 4.7 (Gene Codes Corporation); they were edited by visual inspection. Consensus sequences were aligned in Clustal W (Thompson et al. 1994) using BioEdit (Hall 2005). We used the MEGA software package (Version 4) to construct a neighbour-joining (NJ) tree with a Kimura 2-parameter distance substitution model (Kumar et al. 2004). For construction of the phylogenetic tree, we used 13 newly obtained sequences (deposited in GenBank). Two sequences of *Hymenolepis diminuta* (Rudolphi, 1819) and *Hymenolepis* (s. l.) *nana* (Siebold, 1852) were downloaded from GenBank (Okamoto et al. 1997) and were used as an outgroup. Bootstrap values were counted using MEGA as the percentage of 1,000 replicates.

RESULTS

Arostrilepis horrida (Linstow, 1901) Mas-Coma et Tenora, 1997 Fig. 1

Syns.: *Taenia horrida* Linstow, 1901; *Hymenolepis horrida* (Linstow, 1901).

Redescription. Total length and number of proglottides cannot be described. Maximum width at posterior part of strobila, 1.87–1.93 mm. Strobila flat, proglottides craspedote. Scolex slightly compressed dorso-ventrally, 270–300 wide, clearly wider than neck. Suckers unarmed, with ovoid outlines, 133–145 × 128–134, prominent, with thin walls (Fig. 1A). Rhynchus and rostellar apparatus absent. Neck relatively long and narrow, 16–17 wide.

Development of proglottides gradual, protandrous. Strobilar part containing juvenile proglottides without external segmentation; proglottides become externally distinct at level of premature part of strobila. Genital pores unilateral, dextral.

Mature proglottides transversely elongate, trapezoid, 90–130 × 1840–1930 (Fig. 1C, D). Testes relatively large,

Fig. 1. *Arostrilepis horrida* (Linstow, 1901) (syntype). **A** – scolex; **B** – egg; **C** – male mature proglottides; **D** – hermaphroditic mature proglottides; **E** – genital ducts; **F** – cirrus. Scale bars: A, E = 200 μ m; C, D = 500 μ m; B, F = 20 μ m.

usually three in number, of almost equal size, 220–290 $\times$ 50–70, pear-shaped, situated in triangle; poral testis separated from two antiporal testes by female genital glands. Cirrus-sac relatively short, 240–270 $\times$ 30–40, with well-developed external muscle layers, its antiporal end typically not reaching poral testis (Fig. 1E). Genital atrium simple, cup-shaped, deep, opens in anterior half of lateral proglottis margin. No evaginated cirrus in material studied. Invaginated cirrus 88–94 $\times$ 6–10, armed along its entire length with relatively large rosethorn-shaped spines (up to 4.5 long) (Fig. 1F). Internal seminal vesicle ovoid, 100–120 $\times$ 30–34, shorter than half of cirrus-sac length. External seminal vesicle elongate, 130–170 $\times$ 40–50, clearly outlined from vas deferens, distinctly smaller than seminal receptacle.

Ovary 620–690 wide, median, fan-shaped, irregularly lobed, ventral to testes, occupying substantial part of median field; overlapping testes (Fig. 1D). Vitellarium 35–44

$\times$ 240–270, postovarian, median, scarcely lobed. Vagina tubular, clearly distinct from seminal receptacle; ventral to cirrus-sac. Seminal receptacle transversely elongate, 250–370 $\times$ 37–55.

Postmature, pregravid and gravid proglottides lacking in material studied. Single egg available among strobilar fragments. Egg 30 $\times$ 53, elliptic, with thin outer coat; oncosphere 10 $\times$ 13 (Fig. 1B). Embryophore fusiform, 40 $\times$ 11, with recurved (S-shaped) polar processes.

Type host: The brown rat *Rattus norvegicus* (Berkenhout), syn.: *Mus decumanus* Pallas.

Type locality: Lower Saxony (Niedersachsen), Germany.

Type material: Syntype of *Hymenolepis horrida* (Linstow, 1901) (*Taenia horrida* Linstow, 1901), slide No. 3640-Q from the Museum für Naturkunde, Berlin, Germany. The type material is represented by the single slide. The slide is in bad condition and contains only fragments of hymenolepidid specimens that are compressed, macerated, poorly stained

Fig. 2. *Arostrilepis macrocirrosa* sp. n. **A, B** – scolex; **C** – male mature proglottis; **D** – hermaphroditic mature proglottis. Scale bars: A, B = 200 μ m; C, D = 500 μ m.

(probably with carmine) and with damaged tegument. In addition, a tube with dry cestode fragments is available (No. 4421-E), which is not informative for re-examination purposes.

Remarks. Despite the fact that the original description of *A. horrida* is incomplete and the type material is inadequate as a result of its poor condition, the available specimens remain recognisable and distinct. Further, we do not consider *A. horrida* as *species inquirenda* in order to preserve the nomenclatural stability of this group.

Mas-Coma and Tenora (1997) designated *A. horrida* (s. l.) as the type species of the genus *Arostrilepis* but consistent with Johri (1956) suggested that it represented a constituent of a larger poorly differentiated complex of hymenolepidid cestodes across the Holarctic. Confusion over the identity of *A. horrida* has been exemplified by

assumptions about considerable morphological variation and by numerous and widespread records for this species among microtine rodents (e.g., Schiller 1952). For example in their paper, Mas-Coma and Tenora (1997) presented drawings of a hymenolepidid cestode from *Microtus subterraneus* (Microtinae) from Hungary, which had been identified as *A. horrida*. They did not, however, describe these specimens, nor make direct comparisons with the type series for *A. horrida*. Based on comparisons to the type material in the present study, *A. horrida* sensu Mas-Coma et Tenora, 1997 clearly differs in the width of the strobila (twice narrower than that of the type specimens) and in having a twice smaller cirrus, cirrus-sac and ovary than those of the type specimens (Table 1). We suggest that the type materials of *A. horrida* and *A. horrida* sensu Mas-Coma et Tenora, 1997 belong to different species

Fig. 3. *Arostrilepis macrocirrosa* sp. n. **A** – cirrus; **B** – egg; **C** – copulatory part of the vagina; **D** – gravid proglottis. Scale bars: A = 20 μ m; B = 25 μ m; C = 100 μ m; D = 500 μ m.

of the same genus and highlights what may be a general problem for taxonomy and recognition of species limits in the genus.

***Arostrilepis macrocirrosa* sp. n.**

Figs. 2, 3

Description (based on 12 specimens). Fully developed strobila 129 (116–170) mm long, with maximum width at pregravid or gravid proglottides, 1.0–1.10 (0.90–1.60) mm. Strobila flat, consisting of 610–900 craspedote proglottides. Scolex slightly compressed dorso-ventrally, 300 (290–320) wide, clearly wider than neck. Suckers un-

armed, ovoid in surface view, 180 $\times$ 160 (160–200 $\times$ 140–170), prominent, with thick walls (Fig. 2A, B). Rhynchus and rostellar apparatus absent. Neck relatively long and narrow, 170 (150–190) wide.

Two pairs of osmoregulatory canals, without transverse anastomoses. Dorsal osmoregulatory canals thin, 2–3 (2–4) wide, situated predominantly in same sagittal plane as ventral canals. Ventral osmoregulatory canals 60–90 (50–130) wide. Position of dorsal osmoregulatory canals not always constant; their loops may be situated laterally to ventral canals. Genital pores unilateral, dextral. Genital ducts may pass dorsally or between longitudinal osmo-

regulatory canals within same strobila; intersegmental variation does not show any regularity (Fig. 2C, D). Development of proglottides gradual, protandrous. Strobilar part containing juvenile proglottides without external segmentation; proglottides become externally distinct at level of premature part of strobila.

Mature proglottides $220\text{--}250 \times 800\text{--}830$ ($190\text{--}250 \times 780\text{--}1160$), transversely elongate, trapeziform (Fig. 2C, D). Testes relatively large, usually three in number, almost of equal size, $120\text{--}130 \times 90\text{--}100$ ($110\text{--}170 \times 80\text{--}130$), round or oval, situated in triangle; poral testis separated from two antiporal testes by female gonads. Arrangement of testes may vary. Cirrus-sac relatively short, $205\text{--}214 \times 42\text{--}45$ ($195\text{--}230 \times 35\text{--}45$), with well-developed external muscular layers, commonly overlapping ventral longitudinal canal (Fig. 2D). Genital atrium simple, cup-shaped, deep, opens laterally about middle of lateral proglottis margin. Cirrus large, $107\text{--}118 \times 28\text{--}32$ ($100\text{--}128 \times 27\text{--}34$), conical, armed along its entire length with relatively large (up to 3.5–4 long) rosethorn-shaped spines (Fig. 3A). Internal seminal vesicle with circular musculature, ovoid, $80\text{--}100 \times 30\text{--}32$ ($70\text{--}120 \times 30\text{--}38$), shorter than half of cirrus-sac length (Fig. 2D). External seminal vesicle transversely elongate, $120\text{--}160 \times 65\text{--}75$ ($120\text{--}190 \times 60\text{--}80$), clearly outlined from vas deferens, with size approximately equal to that of seminal receptacle.

Ovary $250\text{--}330$ ($250\text{--}430$) wide, median, fan-shaped, irregularly lobed, ventral to male genital organs, occupying substantial part of median field, overlapping testes (Fig. 2D). Vitellarium $75\text{--}83 \times 120\text{--}140$ ($73\text{--}86 \times 120\text{--}190$), postovarian, median, scarcely lobed. Vagina tubular, clearly distinct from seminal receptacle; ventral to cirrus-sac. Copulatory part of vagina $120\text{--}140 \times 15\text{--}18$ ($100\text{--}140 \times 12\text{--}20$), thick-walled, covered externally by dense layer of small intensely stained cells; proximal part of vagina infundibular (Fig. 3C). Conductive part of vagina $40\text{--}55 \times 12\text{--}22$ ($40\text{--}75 \times 10\text{--}30$), thin-walled, vastly varying in diameter depending on degree of filling with sperm. Seminal receptacle relatively small, transversely elongate, $120\text{--}145 \times 55\text{--}63$ ($120\text{--}190 \times 55\text{--}78$).

Uterus appears as complex of fine-walled anastomosing tubes of varying length and diameter, positioned ventrally to other organs. With development of proglottides, tubular structures increase in width and uterus becomes labyrinthine. Testes remain in postmature and pregravid proglottides; cirrus-sac and vagina persist in gravid proglottides. Gravid proglottides increase in length and may become slightly wider than long, $500\text{--}550 \times 900\text{--}1100$ ($440\text{--}750 \times 700\text{--}1500$). Fully developed uterus labyrinthine, occupying entire median field and extending bilaterally beyond longitudinal osmoregulatory canals (Fig. 3D). Uterus contains numerous (up to 700–1100) small eggs. Eggs $33\text{--}45 \times 52\text{--}63$, elliptic, with thin outer coat (Fig. 3B); oncosphere $17\text{--}20 \times 25\text{--}32$. Embryophore fusiform, $20\text{--}24 \times 40\text{--}45$, with straight polar processes. Embryonic hooks small, 8–8.5 long.

Type host: *Myodes rutilus* (Pallas) (Rodentia: Cricetidae).

Other hosts: *Myodes rufocanus* (Sundevall); *M. glareolus* (Schreber); rarely *Microtus maximowiczii* Schrank and *M. oeconomus* Pallas.

Type locality: Poronayskiy Reserve, Sakhalin Island, Russia.

Other localities (from the collection of ISEZH): Yarkovskiy Rayon, Tyumenskaya Oblast'; Village of Ust'-Urgul'ka, suburbs of the city of Novosibirsk, Novosibirskaya Oblast'; Artybash, Altay Mts.; Bauntovskiy Rayon, River Bol'shoy Amalot, Republic of Buryatia, Russia; Hantaiskoe Reservoir, River Turmakit, Taymyr Peninsula; Sredne-Kolymskiy Rayon, Verkhoyan'e, River Tuostakh, Yakutia; Nyukzha River, Dyeltulakskiy Rayon, Amurskaya Oblast'; River Amgun', Khabarovskiy Kray, Russia.

Site of infection: Intestine.

Type material: Holotype: ISEZH No. 18.28.3.6, ex *M. rutilus*, Poronayskiy Reserve, 30.07.2005. Paratypes: No. 18.28.3.1, ex *M. rutilus*, 25.07.2005; No. 18.28.3.2, ex *M. rutilus*, 27.07.2005; No. 18.28.3.3, ex *M. rutilus*, 30.07.2005; No. 18.28.3.7, ex *M. rutilus*, 31.07.2005; No. 18.28.3.8, ex *M. rutilus*, 31.07.2005; No. C-579, ex *M. rutilus*, 31.07.2005; INVE 74207, ex *M. rutilus*, 30.07.2005. All paratypes are from the Poronayskiy Reserve and are deposited in ISEZH except INVE 74207 deposited in MHNG and C-579 deposited in IPCAS.

Etymology: This species has been named in reference to the size of its cirrus, which is the largest one among those of its congeners.

Remarks. *Arostrilepis macrocirrosa* is distinguished from congeners based on exceptionally large conical cirrus armed with relatively large rosethorn-shaped spines. The cirrus-sac of *A. macrocirrosa* is shorter than that in the syntype material of *A. horrida* but larger than in *A. beringiensis*. The ovary is smaller relative to those in *A. horrida* and *A. microtis* (Table 2). Furthermore, this species is characterized by the arrangement of its testes in a triangle. In addition, the cirrus-sac overlaps the ventral longitudinal osmoregulatory canal, the gravid proglottides may become slightly wider than long (in complete strobila) and the polar processes of the embryophore are straight.

Arostrilepis tenuicirrosa sp. n.

Figs. 4, 5

Description (based on 10 specimens). Fully developed strobila 120 (120–200) mm long, with maximum width at pregravid or gravid proglottides, 1.7–1.85 (1.7–2.3) mm. Strobila flat, consisting of 650–1100 craspedote proglottides. Scolex slightly compressed dorso-ventrally, 360 (280–360) wide, clearly wider than neck. Suckers unarmed, ovoid, 170×130 ($150\text{--}180 \times 110\text{--}140$), prominent, with thick walls (Fig. 4A, B). Rhynchus and rostellar apparatus absent. Neck relatively long and narrow, 210 (160–210) wide.

Two pairs of osmoregulatory canals, without transverse anastomoses. Ventral osmoregulatory canals 80–130 (50–130). Dorsal osmoregulatory canals very thin, 2–4 wide,

Fig. 4. *Arostrilepis tenuicirrosa* sp. n. **A, B** – scolex; **C** – male mature proglottides; **D** – hermaphroditic mature proglottis. Scale bars: A, B = 200 μ m; C, D = 500 μ m.

located mainly in same plane with ventral osmoregulatory canals. Position of dorsal osmoregulatory canals not constant, their loops may be situated laterally to ventral osmoregulatory canals. Genital pores unilateral, dextral. Genital ducts may pass dorsally or between longitudinal osmoregulatory canals within same individual; intersegmental variation does not show any regularity (Fig. 4C). Development of proglottides gradual, protandrous. Strobilar part containing juvenile proglottides without external segmentation; proglottides become externally distinct at level of premature part of strobila.

Mature proglottides 230–260 $\times$ 1200–1370 (210–270 $\times$ 1200–1700), transversely elongate, trapeziform (Fig. 4C, D). Testes relatively large, usually three, almost of equal size, 210–230 $\times$ 140–150 (200–300 $\times$ 140–170), pear-shaped, usually situated in triangle; poral testis separated from two antiporal testes by female gonads. Arrangement of testes often not constant. Cirrus-sac relatively short,

175–200 $\times$ 35–39 (175–225 $\times$ 35–45), with well-developed external muscular layers. Antiporal part of cirrus-sac reaching ventral longitudinal canal, rarely overlapping or slightly crossing it (Fig. 4D). Genital atrium simple, infundibular, deep, opens at about middle of lateral proglottis margin. Cirrus 66–69 $\times$ 6–11 (64–71 $\times$ 5–12), with relatively wide conical basal region and narrow cylindrical distal region; armed along its entire length with 5–10 rows of small needle-shaped spines (up to 2–2.5 long) (Fig. 5A). Internal seminal vesicle with circular muscle, ovoid, 80–90 $\times$ 28–32 (75–95 $\times$ 28–35), shorter than half of cirrus-sac length (Fig. 4D). External seminal vesicle transversely elongated, 200–240 $\times$ 55–65 (170–240 $\times$ 40–68), clearly outlined from vas deferens, slightly smaller than seminal receptacle.

Ovary 400–430 (400–570) wide, median, fan-shaped, irregularly lobed, ventral to male genital organs, occupying substantial part of median field and overlapping testes

Fig. 5. *Arostrilepis tenuicirrosa* sp. n. **A** – cirrus; **B** – egg; **C** – copulatory part of the vagina; **D** – gravid proglottis. Scale bars: A = 20 μ m; B = 25 μ m; C = 100 μ m; D = 500 μ m.

(Fig. 4D). Vitellarium 90–110 $\times$ 140–160 (80–110 $\times$ 140–200), postovarian, median, scarcely lobed. Vagina tubular, clearly distinct from seminal receptacle; ventral to cirrus-sac. Copulatory part of vagina 74–80 $\times$ 7–10 (72–83 $\times$ 6–10), thick-walled, covered externally by dense layer of small, intensely-stained cells, with infundibular proximal part (Fig. 5C). Conductive part of vagina 120–126 $\times$ 25–32 (115–130 $\times$ 22–34), thin-walled, varying in diameter depending on degree of filling with sperm. Seminal receptacle relatively small, transversely elongate, 175–185 $\times$ 35–43 (175–290 $\times$ 35–50).

Uterus appears as complex of fine-walled anastomosing tubes of various length and diameter; positioned ventrally to other organs. With development of proglottides, tubular structures increase in width and uterus becomes labyrinthine. Testes remain in postmature and pregravid proglottides; cirrus-sac and vagina persist in gravid proglotti-

des. Gravid proglottides transversely elongate, 320–370 $\times$ 1500–1750 (250–380 $\times$ 1500–2000). Fully-developed uterus with labyrinthine aspect, occupying entire median field and extending bilaterally beyond longitudinal osmoregulatory canals (Fig. 5D). Uterus containing large number (up to 800–1000) of small eggs. Eggs 30–34 $\times$ 50–57, elliptic, with thin outer coats (Fig. 5B); oncosphere 14–17 $\times$ 18–22. Embryophore fusiform, with straight polar processes, 18–22 $\times$ 35–44. Embryonic hooks small, 7–8 long.

Type host: *Myodes rutilus* (Pallas) (Rodentia: Cricetidae).

Other hosts: *Myodes rufocanus* (Sundevall); *M. glareolus* (Schreber); *M. sikotanensis* (Tokuda); rarely *Microtus oeconomus* Pallas.

Type locality: Poronayskiy Reserve, Sakhalin Island, Russia.

Other localities (from the collection of ISEZH): Yarkovskiy Rayon, Tyumenskaya Oblast'; suburbs of the city of

Novosibirsk, Novosibirskaya Oblast'; Artybash, Altay Mts.; Bauntovskiy Rayon, River Bol'shoi Amalot, Baikal'skiy Reserve, Republic of Buryatia; suburbs of the town of Nosok, Taymir Peninsula; Gorniy Rayon, Sredne-Kolymskiy Rayon, Yakutia; River Nyukzha, Dyeltulakskiy Rayon, Amurskaya Oblast'; River Amgun', Khabarovskiy Kray; Lake Azabach'e, Kamchatka Peninsula; Kurilskiy Reserve, Kunashir Island, Russia.

Site of infection: Intestine.

Type material: Holotype: ISEZH No. 18.28.4.21, ex *M. rutilus*, Poronayskiy Reserve, 30.07.2005. Paratypes: No. 18.28.4.10, ex *M. rutilus*, 31.07.2005; No. 18.28.4.53, ex *M. sikotanensis*, 14.07.2006; No. 18.28.4.55, ex *M. rufocanus*, 14.07.2006; No. 18.28.4.56, ex *M. rufocanus*, 14.07.2006; No. C-578, ex *M. sikotanensis*, 16.07.2006; INVE 74210, ex *M. sikotanensis*, 16.07.2006. All paratypes are from the Kurilskiy Reserve except No. 18.28.4.10, which is from the Poronayskiy Reserve. All the type specimens are deposited in ISEZH except INVE 74210 in MHNG and C-578 deposited in IPCAS.

Etymology: The name of this species refers to the shape of its cirrus, which has a narrow cylindrical distal region that is a unique character among its congeners.

Remarks. *Arostrilepis tenuicirrosa* is distinguished from *A. macrocirrosa*, *A. horrida*, *A. microtis* and *A. beringiensis* by the length and shape of the cirrus. In specimens of *A. tenuicirrosa* the cirrus is smaller relative to those in *A. macrocirrosa*, *A. horrida* and *A. microtis*, but longer in comparison to *A. beringiensis*. The cirrus is armed with relatively small needle-shaped spines and has a unique form, with a conical basal region and a very narrow cylindrical distal region; these features distinguish *A. tenuicirrosa* from all other *Arostrilepis* species. The cirrus-sac is shorter than in *A. horrida*, *A. macrocirrosa* and *A. microtis* but longer than in *A. beringiensis*. The ovary is smaller than in the syntype of *A. horrida* and in *A. microtis* (see Table 2). The antiporal end of the cirrus-sac reaches the ventral longitudinal canal but rarely overlaps it. This species can be distinguished from *A. beringiensis* as its testes are arranged in a triangle; in the latter species, the testes form a flat angle or are situated in one row. Similarly, the testes form one row in *A. microtis*. Furthermore, the gravid proglottides are transversely elongate and the polar processes of the embryophore are straight in *A. tenuicirrosa*.

Genetic distances between *A. macrocirrosa* and *A. tenuicirrosa*

We obtained sequences for the ITS2 rRNA gene (587–630 bp) from multiple specimens of *A. macrocirrosa* and *A. tenuicirrosa*; sequence length did not show significant differences among specimens or species. Comparable data or specimens suitable for sequencing for other species of *Arostrilepis* were not available. A neighbour-joining (NJ) tree based on ITS2 sequences, rooted with two other hymenolepidids (*Hymenolepis* (s. l.) *nana* and *H. diminuta*),

Fig. 6. Neighbour-joining tree of 13 ITS2 gene lineages of two *Arostrilepis* species; *Hymenolepis diminuta* and *H. (s. l.) nana* are used as outgroup species. Numbers indicate bootstrap support based on 1,000 replicates. GenBank accession numbers of sequences are given after species names. Closely related lineages (intraspecific genetic distance of $\leq 1.4\%$) which belong to *A. macrocirrosa* (A.m.) and *A. tenuicirrosa* (A.t.) are marked by bars A and B, respectively.

was used to establish a phylogenetic diagnosis for *A. macrocirrosa* and *A. tenuicirrosa*. The taxonomically limited NJ analysis demonstrated reciprocal monophyly (100% bootstrap) for lineages representing *A. macrocirrosa* and *A. tenuicirrosa*. Assessment of pairwise distances revealed significant genetic divergence (5.6–7.2%) between lineages and specimens representing *A. macrocirrosa* (7 specimens, clade A) and *A. tenuicirrosa* (6 specimens, clade B) (Fig. 6). Intraspecific sequence diversity within *A. macrocirrosa* and *A. tenuicirrosa* was $< 1.4\%$ and $< 0.5\%$, respectively. Genetic data corroborate the clear morphological differences that distinguish *A. macrocirrosa* and *A. tenuicirrosa*.

Arostrilepis Mas-Coma et Tenora, 1997

Emended generic diagnosis (after Mas-Coma and Tenora 1997, with modifications): Hymenolepididae of medium size. Development of proglottides gradual. Proglottides numerous, transversely elongate, craspedote. Scolex unarmed, without vestigial rostellar apparatus. Suckers unarmed, prominent. Dorsal and ventral osmoregulatory canals located on same sagittal plane. Ventral canals without transverse anastomoses. Genital pores unilateral, dextral. Genital ducts may pass either dorsally or between osmoregulatory canals within same strobila. Three testes situated in triangle or in one row; poral testis separated from two antiporal testes by female gonads. Cirrus-sac does not reach median line of proglottis. Cirrus armed. External and internal seminal vesicles present. Internal seminal vesicle with circular muscle. Ovary fan-shaped, median, lobed. Vitellarium postovarian, median, slightly

Table 1. Comparison of measurements of *Arostrilepis horrida* from its original description and redescrptions (measurements in micrometres except where otherwise stated).

	Linstow 1901	Present study	Mas-Coma and Tenora 1997*
Strobila: length	80 mm	–	–
Strobila: width	2,14 mm	1.87–1.93 mm	0.84–1.01 mm
Scolex: width	250	270–300	183–229
Suckers: size	120	133–145 × 128–134	125–158 × 80–125
Hermaphroditic mature proglottis: size	180 × 1540 (middle part of strobila)	90–130 × 1840–1930	108–124 × 560–735
Testes: size	88 × 160	50–70 × 220–290	45–62 × 85–104
Cirrus-sac: size	240	240–270 × 30–40	159 × 35
Cirrus: size	78 × 10	88–94 × 6–10	44
Internal seminal vesicle: size	–	100–120 × 30–34	64 × 28
External seminal vesicle: size	89 × 35	130–170 × 40–50	143 × 32
Ovary: width	–	620–690	155–245
Vitellarium: size	–	35–44 × 240–270	53–55 × 95–110
Seminal receptacle: size	440	250–370 × 37–55	133 × 63
Gravid proglottis: size	260 × 2140 (posterior part of strobila)	–	225–438 × 727–1010
Egg: size	34 × 68	30 × 53	22–26 × 47–50
Oncosphere: size	10 × 15	10 × 13	10–11 × 13–14
Embryophore: size	–	11 × 40	11–12 × 36–39
Embryonic hooks: size	10	–	10

*Measurements were taken from the illustrations in Mas-Coma and Tenora (1997).

Table 2. Main morphometric data distinguishing species of *Arostrilepis* (measurements in micrometres except where otherwise stated).

	<i>A. horrida</i> ¹	<i>A. macrocirrosa</i> sp. n.	<i>A. tenuicirrosa</i> sp. n.	<i>A. beringiensis</i> ¹	<i>A. microtis</i> ²
Strobila: width	1.87–1.93 mm	0.9–1.7 mm	1.7–2.3 mm	1.4–1.6 mm	3.0–3.65 mm
Suckers: size	133–145 × 128–134	160–200 × 140–170	150–180 × 110–140	170–270 × 120–160	160–190 × 120–150
Hermaphroditic mature proglottis: size	90–130 × 1840–1930	190–250 × 780–1160	210–270 × 1200–1700	200–280 × 750–1200	150–270 × 1350–2000
Testes: size	220–290 × 50–70	110–170 × 80–130	200–300 × 140–170	100–185 × 80–142	160–190 × 180–220
Cirrus-sac: size	240–270 × 30–40	195–230 × 35–45	175–225 × 35–45	95–140 × 25–36	220–250 × 45–55
Cirrus: size	88–94 × 6–10	100–128 × 27–34	64–71 × 5–12	33–44 × 10–12	75–85 × 20–22
Spines: size	up to 4.5	3.5–4	2–2.5	2.2–2.7	3–4
Ovary: width	620–690	250–430	400–570	280–380	450–620
Vitellarium: size	35–44 × 240–270	73–86 × 120–190	80–110 × 140–200	60–100 × 130–180	80–110 × 160–230
Copulative part of vagina: size	–	100–140 × 12–20	72–83 × 6–10	55–84 × 7–22	100–110
Seminal receptacle: size	250–370 × 37–55	120–190 × 55–78	175–290 × 35–50	100–180 × 30–40	550–840 × 60–85
Gravid proglottis: size	–	440–750 × 700–1500	250–380 × 1500–2000	300–430 × 1250–1600	310–370 × 2000–3600
Egg: size	30 × 53	33–45 × 52–63	30–34 × 50–57	30–36 × 48–56	22–25 × 45–48
Oncosphere: size	10 × 13	17–20 × 25–32	14–17 × 18–22	8–10 × 13–15	7.5–8.5 × 14–15
Embryophore: size	11 × 40	20–24 × 40–45	18–22 × 35–44	10–14 × 31–36	–

¹Measurements were taken in present study; ²measurements from Gulyaev and Chechulin (1997).

Table 3. Cestode specimens included in the present analysis of ITS2 sequences.

Cestode species	Host species	Region, locality	Total alignment (bp)	GenBank Acc. No.
<i>Arostrilepis macrocirrosa</i> sp. n.	<i>Myodes glareolus</i>	Tyumenskaya Oblast'	586	HM561417
<i>A. macrocirrosa</i>	<i>M. glareolus</i>	Tyumenskaya Oblast'	597	HM561418
<i>A. macrocirrosa</i>	<i>M. glareolus</i>	Tyumenskaya Oblast'	587	HM561419
<i>A. macrocirrosa</i>	<i>M. glareolus</i>	Tyumenskaya Oblast'	591	HM561420
<i>A. macrocirrosa</i>	<i>M. glareolus</i>	Tyumenskaya Oblast'	617	HM561421
<i>A. macrocirrosa</i>	<i>Myodes rutilus</i>	Sakhalin Island	597	HM561422
<i>A. macrocirrosa</i>	<i>M. rutilus</i>	Sakhalin Island	618	HM561423
<i>Arostrilepis tenuicirrosa</i> sp. n.	<i>M. glareolus</i>	Tyumenskaya Oblast'	588	HQ174772
<i>A. tenuicirrosa</i>	<i>M. glareolus</i>	Tyumenskaya Oblast'	603	HQ174773
<i>A. tenuicirrosa</i>	<i>Myodes sikotanensis</i>	Kunashir Island	623	HQ174774
<i>A. tenuicirrosa</i>	<i>M. sikotanensis</i>	Kunashir Island	630	HQ174775
<i>A. tenuicirrosa</i>	<i>M. glareolus</i>	Tyumenskaya Oblast'	608	HQ174776
<i>A. tenuicirrosa</i>	<i>Myodes rufocanus</i>	Kunashir Island	601	HQ174777
<i>Hymenolepis diminuta</i>	<i>Rattus norvegicus</i>	Japan: Hokkaido	724	AB494475
<i>Hymenolepis</i> (s. l.) <i>nana</i>	<i>Mus musculus</i>	Japan: Tokyo	702	AB494476

lobed. Fully developed uterus has labyrinthine aspect, extending bilaterally beyond longitudinal osmoregulatory canals. Eggs numerous, with thin outer coat. Embryophore fusiform, with polar processes. Parasites of cricetid (Cricetidae) and sciurid (Sciuridae) rodents in the Holarctic. Type species: *A. horrida* (Linstow, 1901).

Remarks. The generic name *Arostrilepis* was initially proposed by Mas-Coma (1982) but without sufficient data to be considered available in the terms of the International Code of Zoological Nomenclature. Subsequently, the genus *Arostrilepis* was erected properly (Mas-Coma and Tenora 1997) and *A. horrida* (s. l.) was designated its type species on the basis of a description of specimens from the European pine vole (*Microtus subterraneus* Selys-Longchamps) collected in Hungary. Establishing limits for diversity within *Arostrilepis* has been complicated.

Several incompletely described species have been reduced to synonymy under *A. horrida*. Baer (1932) considered *Hymenolepis procera* Janicki, 1904 and *H. arvicolina* Cholodkowsky, 1913 both from voles as synonyms of *A. horrida*. Spassky (1954) recognised voles (Microtinae) as the main definitive hosts of *H. horrida* and added *H. sciurina* Cholodkowsky, 1913 from squirrels (Sciuridae) to its synonyms on the basis of the similarity of their egg morphology (embryophore with pointed ends) and the presence of armed cirrus. Later, *H. mathevossianae* Akhumian, 1946 from the Turkish hamster, *Mesocricetus brandti* (Nehring) from Armenia was also placed among the synonyms of *H. horrida* (see Rybicka 1959). However, *H. arvicolina* has characteristics of the genus *Hymenolepis* (s. str.) (for the current generic definition, see Czaplinski and Vaucher 1994) as its scolex has a rostellar pouch, its suckers do not exceed the margins of the scolex and its testes are situated in one row. In the description of *H. sciurina*, the only measurements presented are those of the total length, the width of the strobila and the size of the ovary; the illustrations are schematic (Cholodkowsky 1913). Therefore, the description is inadequate and does not allow comparisons with the species of the genus *Arostrilepis*. Although the type series of *H. arvicolina* and *H. sciurina* are mentioned in the collection catalogue of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), they are not currently registered and are considered lost. For this reason, we regard them as *species inquirendae*.

Hymenolepis procera can be distinguished from *A. horrida* and from other species of *Arostrilepis* by its very short strobila (28–40 mm), the arrangement of its testes in one row and its significantly smaller cirrus-sac size (130) (see Table 2). *Hymenolepis mathevossianae* differs from the species of the genus *Arostrilepis* by its cup-shaped suckers, the arrangement of the testes in one row, its very small cirrus-sac (80 × 50) and the occurrence in hamsters. The affiliation of this species to the genus *Arostrilepis* is not obvious as it has saccate uterus and its eggs have never been described. Unfortunately, the type

series of these species are also lost and the original descriptions are poor. For this reason, we consider them as *species inquirendae*.

Therefore, the validity and the generic allocation of *H. procera*, *H. arvicolina*, *H. sciurina* and *H. mathevossianae* require further study. However, we cannot accept their placement as synonyms of *A. horrida* as this generic affiliation has not been based on reliable morphological comparisons. Furthermore, it affects both generic concept of *Arostrilepis* and host range of its type species.

Mas-Coma and Tenora (1997) placed *A. neurotrichi* (Rausch, 1962) from North-American moles in the genus *Arostrilepis*. Earlier, Mas-Coma (1982) had chosen this cestode as a type species of the invalid genus *Corderolepis* Mas-Coma, 1982, which we consider as *nomen nudum*. Due to its tubular seminal receptacle, testes not separated by female genital glands and uterus situated in median field of proglottis, this hymenolepidid species appreciably differs from any species of *Arostrilepis*, and as such it is excluded from the genus.

DISCUSSION

The long list of definitive hosts of *Arostrilepis horrida* is a consequence of incorrect identifications (see above). The original description of *Taenia horrida*, which was illustrated with a cross-sectioned mature proglottis (Linstow 1901), was not a reliable basis for subsequent comparisons. This resulted in a series of erroneous identifications and various hymenolepidid cestodes from rodents without rostellar apparatus were reported as *A. horrida*. Among others, *A. horrida* sensu Mas-Coma and Tenora, 1997 from *Microtus subterraneus*, which has been used as a basis for the original generic diagnosis of *Arostrilepis* (see Mas-Coma and Tenora 1997), is not conspecific with the type series of *A. horrida*. In the extensive collections of hymenolepidids from rodents from the Asian part of Russia, deposited at ISEZH, we did not find cestodes with morphology corresponding to the type series of *A. horrida*. Therefore, the only reliable record of the host and geographical range of the type species of *Arostrilepis* is that contained within its original description (Linstow 1901). In addition, as discussed above, *Hymenolepis neurotrichi* from Nearctic moles, does not belong to the genus *Arostrilepis*, contrary to the opinion of Mas-Coma and Tenora (1997).

As revealed by the present study, the main differentiating characters for species of *Arostrilepis* are the form and size of the cirrus. The other characters may vary and overlap substantially among the species within the genus. Furthermore, variations in some morphometrical characters are due to the compression and (or) maceration of specimens. For this reason, we do not compare the two new species described here with the incomplete descriptions of *A. horrida* (s. l.) by other authors (Schiller 1952, Voge 1952, Żarnowski 1955, Rybicka 1959, Murai and Tenora 1973, Egorova and Nadtochii 1975, Mas-Coma

and Tenora 1997, Asakawa et al. 2002), which were based on specimens from various hosts and regions. Their identifications require additional studies. Special emphasis should be placed on integrated methods using molecular and morphological criteria and evaluation of the structural characters which have been shown to be reliable in the course of the present study.

There are further questions related to the morphology of the type species *A. horrida*. Unfortunately, the type series re-examined in the current study does not contain pregravid and gravid proglottides. In addition, the identification of the type host remains doubtful. As mentioned above, *A. horrida* had not been recorded in *Rattus norvegicus* after the original description. Therefore, it is possible that this is either associated with a record of accidental parasitism or the original description contains an erroneous host identification.

In summary, there are five species in the genus *Arostrilepis* now recognised from the Palaearctic Region: *A. horrida*, *A. beringiensis*, *A. microtis*, *A. macrocirrosa*, and *A. tenuicirrosa*. These species can be clearly distinguished by the shape and size of the cirrus, the position of the testes and host specificity. New distinctive generic-level characters for *Arostrilepis* have been detected: i.e., the irregular position of the genital ducts relative to the longitudinal osmoregulatory canals within the same strobila and the presence of circular musculature in the wall of the internal seminal vesicle. The level of intraspecific divergence among ITS2 sequences in *A. macrocirrosa* attains 1.4%, which may be high for this DNA region. Unfortunately, no comparable data on the intraspecific differences in the ITS2 sequences of other hymenolepidid tapeworms exist. Previously, it was shown that ITS2 sequence similarity may vary within a single species, e.g., 93.8–99.1% in *Bothriocephalus acheilognathi* Yamaguti, 1934 (see Bean et al. 2007). In *Diphyllbothrium dendriticum* (Nitzsch, 1824) and *D. ditremum* (Creplin, 1825), the variation is 97.0–98.0% and 98.2–99.9%, respectively (Škeřiková et al. 2006). These values correspond to the variation recorded within a single species in the present study. Our data confirm the interspecific differences and reciprocal monophyly between *A. macrocirrosa* and *A. tenuicirrosa*

and demonstrate that additional molecular studies will be useful for improving the taxonomy of *Arostrilepis*.

It should be noted that cestodes of the genus *Arostrilepis* from both sides of Beringia were studied based on morphological and molecular methods (Hoberg et al. 2003, Cook et al. 2005). Across the amphiberingian region, 10 distinct genetic lineages of *Arostrilepis* were recognised among various genera of the Microtinae that may deserve to be considered as distinct species (including five lineages from *Myodes*). These observations support the growing recognition of *A. horrida* as a widespread complex of cryptic species (e.g., Hoberg, et al. 2003, Cook et al. 2005). Within this complex, the resolution of identity of *A. horrida* (s. l.) relative to a diverse assemblage of congeners depends in part on new collections from the type locality. Descriptions of two new species of *Arostrilepis* from *Myodes* spp. from the Eastern Palaearctic serve in part to corroborate a geographically complex assemblage of tapeworms among microtine hosts.

Acknowledgements. We are grateful to Konstantin Feodorov, Nikolai Dokuchaev, Aleksandr Chechulin, Sergey Karpenko and Marina Malkova for making cestode specimens from rodents from Western and Eastern Siberia, North-Eastern Altai and the Russian Far East available for this study. Dr. Eric P. Hoberg kindly discussed results of ongoing work on microtine tapeworm faunas under the Beringian Coevolution Project and provided some editorial assistance on this paper. We wish to thank the curators of the cestode collections, Dr. Birger Neuhaus (Museum für Naturkunde, Berlin), Dr. Larisa Filimonova (Centre of Parasitology, A.N. Severtsov Institute of Ecology and Evolution, RAS, Moscow) and Dr. Eric P. Hoberg and Ms. Patricia Pilit (US National Parasite Collection, ARS, USDA, Beltsville) for loaning type materials. We also thank the staff of the Poronayskiy Reserve and the Kurilskiy Reserve, who kindly helped in collecting of materials. A substantial portion of the work was funded by the Russian Fund of Fundamental Research (grants 05-04-49010, 08-04-00342 and 06-04-63137). Postdoctoral fellowship of A.A. Makarikov is being funded by European Union Structural Funds project “Postdoctoral Fellowship Implementation in Lithuania” within the framework of the Measure for Enhancing Mobility of Scholars and Other Researchers and the Promotion of Student Research (VP1-3.1-ŠMM-01) of the Program of Human Resources Development Action Plan.

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Received 2 August 2010

Accepted 6 October 2010