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Broadening diversity in the *Arostrilepis horrida* complex: *Arostrilepis kontrimavichusi* n. sp. (Cyclophyllidea: Hymenolepididae) in the western red-backed vole *Myodes californicus* (Merriam) (Cricetidae: Arvicolinae) from temperate latitudes of the Pacific Northwest, North America

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Abstract Specimens originally identified provisionally as *Hymenolepis horrida* (Linstow, 1901) [later *Arostrilepis horrida* (Linstow, 1901)] in *Myodes californicus* (Merriam) from near the Pacific coastal zone of southern Oregon are revised. Specimens in western red-backed voles represent an undescribed species of *Arostrilepis* Mas Coma & Tenora, 1997, contributing to recognition and resolution of a broadening complex encompassing cryptic diversity for these hymenolepidid tapeworms distributed across the Holarctic region. Consistent with recent studies defining diversity in the genus, the form, dimensions, and spination (pattern, shape and size) of the cirrus are diagnostic. Among 12 nominal congeners, specimens of *A. kontrimavichusi* n. sp. are further distinguished by the relative position and length of the cirrus-sac, arrangement of the testes and relative size of the external seminal vesicle and seminal receptacle. Specimens from Oregon voles represent the fifth

endemic hymenolepidid in this genus from the Nearctic. Host range for the North American assemblage of species includes Cricetidae (Arvicolinae and Neotominae), Heteromyidae, Geomyidae, and rarely Sciuridae.

Introduction

During much of the past century, *Arostrilepis horrida* (Linstow, 1901) [syns *Taenia horrida* Linstow, 1901; *Hymenolepis horrida* (Linstow, 1901)] was regarded as a morphologically hypervariable and geographically widespread species capable of infecting a broad assemblage of phylogenetically disparate rodent hosts across the Holarctic (e.g. Rausch, 1952, 1957; Schiller, 1952; Voge, 1952; Spassky, 1954; Ryzhikov et al., 1978; Fedorov, 1986). Recent morphological and molecular studies exploring species diversity within *Arostrilepis* Mas Coma & Tenora, 1997 have revealed a complex of cryptic species historically attributed to *A. horrida*. Remarkably, revision within this assemblage has led to the description of 12 nominal species and recognition of additional evolutionarily discrete lineages with characteristic distributions in the Palaearctic, Nearctic and Holarctic zones (Kontrimavichus & Smirnova, 1991; Gulyaev & Chechulin, 1997; Cook et al., 2005; Makarikov & Kontrimavichus, 2011; Makarikov et al., 2011, 2012, 2013; Hoberg et al., 2012; Galbreath et al., 2013).

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Among this assemblage, initial discovery of species endemic to the Nearctic was documented based on examination of specimens held in helminthological collections and museum archives from North America. *Arostrilepis mariettavogae* Makarikov, Gardner & Hoberg, 2012 was found in the U.S. National Parasite Collection (USNPC) among specimens in rodents including species of *Peromyscus* Gloger and *Perognathus* Wied-Neuwied from the central coastal zone of California, USA. Another species, *A. schilleri* Makarikov, Gardner & Hoberg, 2012 was described based on specimens in *Thomomys bulbivorus* (Richardson) a rodent of the family Geomyidae from west-central Oregon, USA, held in the Harold W. Manter Laboratory of Parasitology (HWML). In both instances, multiple lots of specimens had been attributed to *Hymenolepis horrida* (e.g. Voge, 1952; Gardner, 1985; Gardner & Schmidt, 1988). These and an extensive series of specimens of *Arostrilepis* spp. assembled through field collections and inventory in North America and eastern Siberia are now serving to change the picture for diversity among this considerable assemblage of rodents and tapeworm parasites (e.g. Cook et al., 2005; Hoberg et al., 2012; Makarikov & Kontrimavichus, 2011; Makarikov et al., 2011, 2012, 2013).

It is apparent that considerable diversity remains to be discovered and characterised among species attributable to *Arostrilepis*. Consistent with these observations, we re-examined cestode specimens identified as *H. horrida* in western red-backed voles, *Myodes californicus* (Merriam), collected in the early 1970's from five sites adjacent to the coastal zone of southern Oregon, USA. Specimens on permanent slides were from the Robert and Virginia Rausch Helminthological Collections (RHC), archived in the Division of Parasitology at the Museum Southwestern Biology, University of New Mexico (MSB). These specimens were originally collected by R.L. Rausch, but had not been the subject of any publications on rodent parasite diversity. Our examination indicated that these specimens in *M. californicus* represent an undescribed species of *Arostrilepis*, which is described herein.

Materials and methods

Specimens of *Arostrilepis* described in present study were derived from field collections and materials previously deposited in the Museum Southwestern

Biology, Division of Parasites, University of New Mexico, Albuquerque, New Mexico, USA. Cestodes in *Myodes californicus* were assembled from field surveys conducted by Robert L. Rausch (RLR) during the early 1970's at five field sites distributed across south-western Oregon, USA: (i) 4 voles (all with cestodes) near Bandon, Coos County; and (ii) single voles (all with cestodes) near Brookings, Curry County, an additional unspecified locality in Curry County, near Blue River, Lane County, and near Gardiner, Douglas County. Other rodents collected adjacent to Bandon during November and December 1971, not found to be infected with cestodes, included three specimens of *Peromyscus maniculatus* (Wagner), two *Microtus townsendii* (Bachman), and a single *Tamiasciurus douglasii* (Bachman) (see host and parasite records hosted in the Arctos database system- <http://arctos.database.museum>). Across additional sites in Oregon specimens of other small rodents were examined by RLR but hymenolepidids were not encountered: (i) species of *Microtus* Schrank (12 specimens, including *M. oregoni* (Bachman), *M. townsendii*, and *Microtus* sp.); (ii) species of *Thomomys* Wied-Neuwied [five specimens including *T. talpoides* (Richardson)]; and (iii) species of *Tamias* Illiger (two specimens).

Arvicoline rodents were collected by snap-traps (Museum Special). Cestodes were collected at necropsy, allowed to relax in water, and fixed in neutral 10% formalin. Individual specimens were stained in Semichon's acetic carmine, destained in 70% ethanol and HCl, dehydrated through an ethanol series, cleared in xylene and mounted in Permount. All available specimens, with the exception of three designated vouchers, were examined as a basis for the description. Some specimens on slides with crystallised Permount were rehabilitated and remounted in Canada balsam. All measurements are in micrometres except where otherwise stated and are presented as the range, followed by the mean and sample size (n) in parentheses. Nomenclature for mammals follows Patton (2005) and Musser & Carleton (2005).

Hymenolepididae Perrier, 1897

Arostrilepis Mas Coma & Tenora, 1997

Arostrilepis kontrimavichusi n. sp.

Type-host: Western red-backed vole *Myodes californicus* (Merriam) (Rodentia: Cricetidae: Arvicolinae).

Type-locality: Adjacent to Bandon, Coos County, Oregon, USA (4 miles southeast, *c.*43°03'N, 124°20'W) on 18.xii.1971.

Other localities: in western Oregon, USA: (i) adjacent to Brookings, Curry County (10 miles east, *c.*42°03'N, 124°07'W) on 7.xii.1971; (ii) an unspecified locality in Curry County on 25.ix.1970; (iii) adjacent to Blue River, Lane County, (5.5. miles north, *c.*44°14'N, 122°20'W) on 22.i.1972. (iv) adjacent to Gardiner, Douglas County (9 miles north, *c.*43°54'N, 124°06'W) on 28.ii.1972.

Type-material: Holotype: MSB Parasitology 19007 (RHC field collection - 39755) in the type-host and locality by RLR on 18.xii.1971. Paratypes from the type-locality and type-host species: 2 specimens on separate slides under MSB 19007 (RHC-39755) on 18.xii.1971; 2 specimens on separate slides under MSB 19008 (RHC-39758) on 21.xii.1971; 2 specimens on separate slides under MSB 19012 (RHC-39759) on 19.xii.1971. Additional paratypes in the type-host but from other localities: 1 specimen MSB 19009 (RHC-39009), Brookings, Curry County, Oregon, USA on 7.xii.1971; 1 specimen MSB 19010 (RHC-39906), Blue River, Lane County, Oregon, USA on 22.i.1972; 1 specimen MSB 19011 (RHC-39916), Gardiner, Douglas County, Oregon, USA on 28.ii.1972.

Voucher material: Confirmed vouchers included: 2 specimens from the type-locality on separate slides under MSB 24565 (RHC-39777) on 28.xi.1971; 1 specimen under MSB 24566 (RHC-38582) from an unspecified site in Curry County, OR on 25.ix.1970.

Symbiotype: Host specimen not archived; identification based on observation (MSB 15404) in <http://arctos.database.museum>.

Etymology: This species has been named in honour of our friend, mentor and prominent parasitologist, Dr. Vytautas L. Kontrimavichus, in recognition of his contributions to the taxonomy and systematics of the genus *Arostrilepis*.

Description (Figs. 1–2)

[Based on 10 specimens.] Fully developed strobila up to 65–100 (*n* = 3) mm long, with maximum width at pregravid or gravid (but not terminal) proglottides, 0.75–1.0 (0.904; *n* = 3) mm. Strobila flat, consisting of about 400–500 craspedote proglottides. Scolex slightly compressed dorso-ventrally, 173–275 (223;

n = 5) wide, clearly wider than neck (Fig. 1A, B). Suckers unarmed, ovoid in surface view, 110–140 × 77–118 (121 × 95; *n* = 14), with thin walls, prominent. Rhynchus and rostellar apparatus absent. Neck relatively long and narrow, 90–170 (138; *n* = 6) wide.

Osmoregulatory canals 2 pairs, without transverse anastomoses. Dorsal osmoregulatory canals thin, 0.5–2.5 (1.4; *n* = 9) wide, situated predominantly in same sagittal plane as ventral canals. Ventral osmoregulatory canals 30–55 (42; *n* = 20) wide. Position of dorsal osmoregulatory canals not always constant; loops may be situated laterally to ventral canals. Genital pores unilateral, dextral (Figs. 1C, D, 2C). Genital ducts usually pass dorsally to longitudinal osmoregulatory canals; position of genital ducts between osmoregulatory canals within the same strobila was not observed in the present material. 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 145–190 × 590–795 (167 × 716; *n* = 24), transversely elongate, trapeziform (Fig. 1D). Testes 3, relatively large, almost of equal size, 110–175 × 85–116 (131 × 96; *n* = 30), round or oval, normally arranged in triangle of varying configuration; poral testis separated from two antiporal testes by female gonads. No variation in testes number observed at present material (Fig. 1C, D). Cirrus-sac relatively short, 148–184 × 31–45 (163 × 37; *n* = 25), with well-developed external muscular layers belonging to wall of cirrus-sac. Antiporal part of cirrus-sac commonly extends across ventral longitudinal canal (Figs. 1D, 2C). Genital atrium simple, infundibular, deep, opens laterally about middle of lateral proglottis margin. Cirrus, 49–65 × 11.5–14 (56 × 12; *n* = 31) cylindrical; armed along its entire length with relatively large (up to 2.8–3.3 long) rosethorn-shaped spines (Fig. 2A). Internal seminal vesicle with circular musculature, ovoid, 74–108 × 28–38 (87 × 32; *n* = 24), slightly longer than half of cirrus-sac length (Figs. 1D, 2C). External seminal vesicle transversely elongate, 115–190 × 54–80 (141 × 61; *n* = 18), clearly outlined from vas deferens, distinctly larger than seminal receptacle.

Ovary 185–310 (238; *n* = 18) wide, median, fan-shaped, irregularly lobed, ventral to male genital organs, occupying less than half of median field,

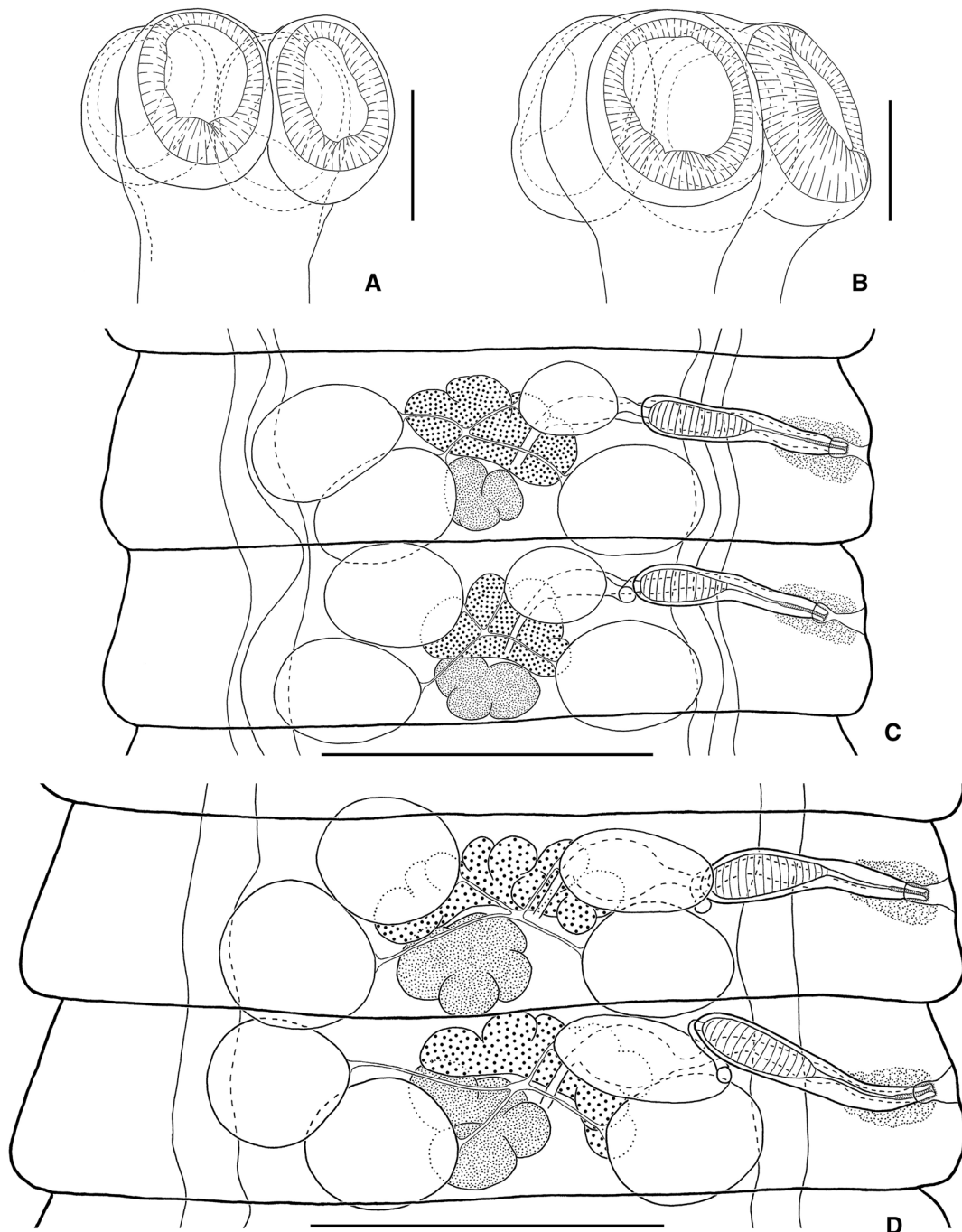


Fig. 1 *Arostrilepis kontrimavichusi* n. sp. ex *Myodes californicus*. A, Paratype (MSB 19012), dorsoventral view of scolex; B, Paratype (MSB 19008), sublateral view of scolex; C, Holotype, male mature proglottides from dorsal side; D, Holotype, hermaphroditic mature proglottides from dorsal side. Scale-bars: A, B, 100 μ m; C, D, 300 μ m

overlapping testes (Fig. 1D). Vitellarium 74–120 \times 116–153 (85 \times 129; n = 20), postovarian, median or slightly shifted antiporally, weakly lobed. Vagina

tubular, clearly distinct from seminal receptacle; ventral to cirrus-sac (Fig. 2C). Copulatory part of vagina 70–91 \times 8–14 (78 \times 11; n = 27), thick-

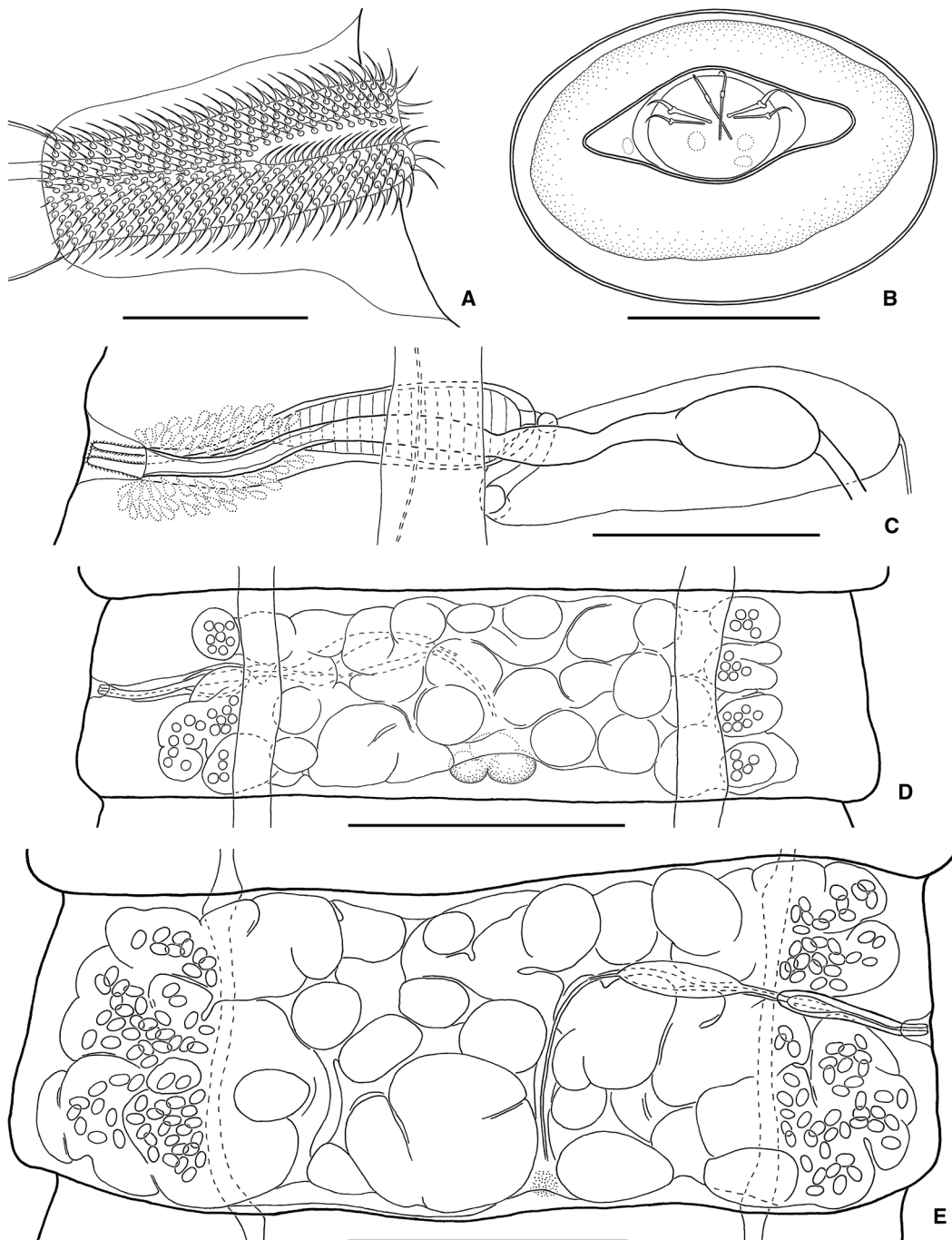


Fig. 2 *Arostrilepis kontrimavichusi* n. sp. ex *Myodes californicus*. A, Holotype, evaginated cirrus; B, Holotype, egg; C, Holotype, copulatory part of the vagina, ventral view; D, Holotype, pregravid proglottis from ventral side (immature eggs are illustrated only on the lateral sides of the uterus); E, Holotype, gravid proglottis from dorsal side (mature eggs are illustrated only on the lateral sides of the uterus). Scale-bars: A, B, 20 μ m; C, 100 μ m; D, E, 300 μ m

walled, covered externally by dense layer of small intensely stained cells; proximal part of vagina infundibular. Conductive part of vagina

80–164 \times 9–25 (120 \times 16; n = 17), thin-walled, vastly varying in diameter depending on degree of filling with sperm. Seminal receptacle relatively small,

transversely elongate, 50–115 × 35–55 (77 × 41; n = 18).

Uterus appears as complex of fine-walled anastomosing tubes of varying length and diameter, positioned ventrally to testes and genital ducts, but dorsally to ovary, vitellarium, and osmoregulatory canals. With development of proglottides, tubular structures increase in width and uterus becomes labyrinthine (Fig. 2D). Testes remain in postmature and pregravid proglottides; cirrus-sac and vagina persist in gravid proglottides. Gravid proglottides transversely elongate, 320–435 × 770–1000 (394 × 910, n = 18). Fully developed uterus labyrinthine, occupying entire median field, extending bilaterally beyond longitudinal osmoregulatory canals dorsally to them (Fig. 2E). Uterus contains numerous (up to 850) small eggs. Eggs 26–31 × 39–45 (28 × 41, n = 10), elliptic (Fig. 2B), with very thin, easily deformed outer coat (less than 1); oncosphere 10–11 × 12–15 (10 × 13, n = 10). Embryophore fusiform, 11–14 × 25–31 (12 × 27, n = 10), with straight polar processes. Embryonic hooks small, length of anterolateral, slender postero-lateral, and median hooks 6.5–7.5.

Remarks

Following the description of *Arostrilepis kontrimavichusi* n. sp., the genus *Arostrilepis* currently includes 13 nominal species (Makarikov et al., 2013; present study). Among species of this assemblage, specimens of *A. kontrimavichusi* are readily distinguished from seven congeners by the cylindrical shape of the cirrus. Structurally these specimens contrast with those attributed to *A. cooki* Makarikov, Galbreath & Hoberg, 2013; *A. macrocirrosa* Makarikov, Gulyaev & Kontrimavichus, 2011; *A. mariettavogae*; and *A. rauschorum* Makarikov, Galbreath & Hoberg, 2013, all characterised by a conical cirrus; and *A. gulyaevi* Makarikov, Galbreath & Hoberg, 2013; *A. microtis* Gulyaev & Chechulin, 1997; and *A. tenuicirrosa* Makarikov, Gulyaev & Kontrimavichus, 2011, in which the cirrus has a conical basal region and cylindrical distal region. Furthermore, *A. kontrimavichusi* differs from these species by the relative position of the cirrus-sac and arrangement of the testes. The previously unrecognised species can be distinguished from *A. microtis*, *A. mariettavogae* and *A. rauschorum* as the testes are arranged in a

triangle, whereas in the latter three species, the testes are situated in one row. The antiporal end of the cirrus-sac substantially crosses the poral osmoregulatory canal in *A. kontrimavichusi*, whereas in *A. gulyaevi*, *A. microtis*, *A. mariettavogae*, *A. rauschorum* and *A. tenuicirrosa* the cirrus-sac does not reach or rarely overlaps but does not cross the ventral longitudinal canal.

Specimens of *A. kontrimavichusi* could not be differentiated from the remaining five species of *Arostrilepis* based on the shape of the cirrus [i.e. *A. horrida*; *A. beringiensis* (Kontrimavichus & Smirnova, 1991); *A. intermedia* Makarikov & Kontrimavichus, 2011; *A. janickii* Makarikov & Kontrimavichus, 2011 and *A. schilleri*]. Separation of this group of species based on morphological criteria requires a more detailed differential diagnosis (see Table 1).

Arostrilepis kontrimavichusi can be distinguished from *A. beringiensis*, a parasite of lemmings from the Holarctic, by a longer cirrus and cirrus-sac, larger spines of the cirrus, substantially narrower strobila and smaller, eggs. In addition, the antiporal end of the cirrus-sac substantially crosses the poral osmoregulatory canal in *A. kontrimavichusi*, whereas in *A. beringiensis* the cirrus-sac does not reach the ventral longitudinal canal.

The new species differs from *A. horrida* described in *Rattus norvegicus* (Berkenhout) from Europe and *A. intermedia*, a parasite of red-backed voles from the eastern Palaearctic, by smaller dimensions of the cirrus, spines of cirrus, cirrus-sac, eggs, and embryophore and substantially narrower strobila. In addition, the antiporal end of the cirrus-sac substantially crosses the poral osmoregulatory canal in *A. kontrimavichusi*, whereas in *A. intermedia* the cirrus-sac rarely overlaps but does not cross the ventral longitudinal canal.

Arostrilepis kontrimavichusi is distinguished from *A. janickii* known in voles of the genera *Arvicola* Lacépède, *Microtus*, and *Chionomys* Miller from Europe in having smaller spines of the cirrus, a smaller embryophore and narrower strobila. In addition, the antiporal end of cirrus-sac substantially crosses the poral osmoregulatory canal in *A. kontrimavichusi*, whereas in *A. janickii* the cirrus-sac rarely overlaps but does not cross the ventral longitudinal canal.

The new species is distinguished from *A. schilleri* parasitic in Nearctic Geomyidae by a longer cirrus-

Table 1 Primary morphometric data distinguishing species of *Arostrilepis* (measurements in micrometres except where otherwise stated)

Character/ Species	<i>A. beringsis</i> (Kontrimavichus & Smirnova, 1991)	<i>A. janickii</i> Makarikov & Kontrimavichus, 2011	<i>A. intermedia</i> Makarikov & Kontrimavichus, 2011	<i>A. schilleri</i> Makarikov, Gardner & Hoberg, 2012 n. sp.
Host genus	<i>Rattus</i>	<i>Arvicola</i> , <i>Microtus</i> and <i>Chionomys</i>	<i>Myodes</i>	<i>Thomomys</i> <i>Myodes</i>
Distribution	western Palaearctic ^a north-western Nearctic ^b	western Palaearctic ^b	eastern Palaearctic ^b	western Nearctic ^c western Nearctic
Strobila length (mm)	100–125	50–80	100–150	67
Strobila width (mm)	1.4–1.6	1.00–2.00	1.35–1.80	0.90–0.98
Scolex width	230–320	190–240	290–320	230–250
Suckers	133–145 × 128–134	170–270 × 120–160	200–250 × 130–150	140–176 × 115–140
Testes	220–290 × 50–70	100–185 × 80–142	145–210 × 70–140	110–183 × 70–112
Cirrus-sac	240–270 × 30–40	95–140 × 25–36	180–210 × 28–40	95–123 × 22–31
Cirrus	88–94 × 6–10	33–44 × 10–12	80–98 × 14–20	61–74 × 17–21
Spines	up to 4.5	3.5–4.3	3.5–4.0	3.4–3.7
Ovary width	620–690	230–415	300–460	210–310
Vitellarium	35–44 × 240–270	45–80 × 95–185	65–88 × 130–200	45–70 × 80–125
Seminal receptacle	250–370 × 37–55	100–180 × 30–40	110–175 × 35–65	75–105 × 25–42
Egg	30 × 53	27–36 × 43–52	36–42 × 60–65	24–31 × 40–48
Oncosphere	10 × 13	10–11 × 14–15	15–20 × 20–25	9–13 × 10–15
Embryophore	11 × 40	11–15 × 34–40	18–22 × 42–45	12–16 × 23–31

^a Measurements from Makarikov et al. (2011); ^b measurements from Makarikov & Kontrimavichus (2011); ^c measurements from Makarikov et al. (2012)

sac. The length of the cirrus in *A. kontrimavichusi* is very close to that in *A. schilleri*, but in the former species the cirrus is distinctly narrower. In addition, the antiporal end of the cirrus-sac substantially crosses the poral osmoregulatory canal in *A. kontrimavichusi*, whereas in *A. schilleri* the cirrus-sac rarely overlaps but does not cross the ventral longitudinal canal.

Furthermore, in *A. kontrimavichusi*, the external seminal vesicle is distinctly larger than the seminal receptacle; in contrast, most congeners are characterised by a smaller external seminal vesicle relative to the seminal receptacle or these structures have near equal dimensions.

Discussion

Prior reports on the parasite fauna of western red-backed voles have not been presented in the literature. Our description of *A. kontrimavichusi* n. sp. is, apparently, the first record of a helminth species in this arvicoline rodent that has a limited endemic distribution along the west coast of North America (western Oregon and north-western California, USA). Further, these collections represent the second species of *Arostrilepis* to be recognised among rodents from Oregon. At least two congeners have potential to be sympatric with *A. kontrimavichusi* across a broader range in the temperate zone adjacent to the north-western coast of North America although neither has been demonstrated among arvicoline (Makarikov et al., 2012). *Arostrilepis mariettavogae* was described in species of *Peromyscus* and *Perognathus* from the central California coast and *A. schilleri* in pocket gophers [*Thomomys bulbivorous* (Richardson)] from the Willamette Valley of western Oregon. These are among five species in total which are considered endemic in north-western North America, including *A. rauschorum* among species of *Microtus* and *A. cooki* known only in *Myodes gapperi* (Vigors) (see Makarikov et al., 2013). The eight remaining species are distributed either in the Palaearctic (five species) or have Holarctic distributions determined across Beringia (three species) (Makarikov et al., 2013).

Differentiation among species of *Arostrilepis* has been based on comparative morphology (Kontrimavichus & Smirnova, 1991; Gulyaev & Chechulin, 1997; Makarikov & Kontrimavichus, 2011; Makarikov et al., 2011, 2012) or on an integrated approach

which uses structural attributes in combination with diagnostic molecular data, primarily derived from sequences of the cytochrome *b* gene of mitochondrial DNA (Makarikov et al., 2013; Galbreath et al., 2013). Among the 13 nominal taxa, four have been characterised morphologically (including *A. kontrimavichusi* n. sp.), whereas recent descriptions and re-descriptions among nine species have applied broad-based datasets. The shape, dimensions, structure and spination of the cirrus have generally provided an unequivocal basis for separation among the currently recognised species, although a more extensive suite of characters may increasingly be required as the limits for diversity in this species complex are explored (Makarikov et al., 2013). Where molecular data are available, it is apparent that discrete genetic lineages directly correspond to and complement a suite of structural attributes that distinguish currently recognised diversity in the genus.

Specimens within the type-series for *A. kontrimavichusi* n. sp. were not suitable for molecular analyses, and additional material will be required to concurrently examine morphological and sequence variation based on sampling from single cestodes. Recent field collections of hymenolepidids from localities in Oregon, however, have through sequence-based and phylogenetic comparisons demonstrated the presence of a discrete lineage of *Arostrilepis* in *M. californicus* which may represent *A. kontrimavichusi*; immediate confirmation based on morphology is limited by availability of suitable specimens (K.E. Galbreath, G. Haas, V. Haukisalmi, E.P. Hoberg, A. Makarikov, unpublished data). These data highlight the complex nature of the *Arostrilepis* spp. assemblage of western North America and serve to indicate the limits on our understanding of the diversity at latitudes previously south of the Laurentide-Cordillera glaciers during the Quaternary (e.g. Hoberg et al., 2012). At temperate latitudes of Oregon, additional sequence-based lineages for these cestodes are also observed in species of *Microtus*, *Peromyscus* and *Thomomys* (K.E. Galbreath, G. Haas, V. Haukisalmi, E.P. Hoberg, A. Makarikov, unpublished data). These may represent previously unknown taxa or may be attributable to *A. mariettavogae* and *A. schilleri* described in the absence of sequence data from localities in California and Oregon, USA (Makarikov et al., 2012).

Recent studies based on geographically extensive field collections and inventories for host and parasite

diversity among a diverse assemblage of small mammals centered on Beringia and adjacent regions linking the eastern Palaearctic and western Nearctic, have indicated that species of *Arostrilepis* are largely limited in distribution to particular arvicoline genera (Cook et al., 2005; Hoberg et al., 2012; Makarikov et al., 2013). Exceptions to this association are observed for *A. schilleri* in pocket gophers (*Thomomys*, Geomyidae), and *A. mariettavogae* in deer mice (*Peromyscus*, Neotominae) and pocket mice (*Perognathus*, Heteromyidae) (Makarikov et al., 2012). Characteristic distributions relative to particular host groups within the Arvicolinae, however, tentatively may be informative in distinguishing among congeners (Makarikov & Kontrimavichus, 2011; Makarikov et al., 2013). Such patterns are apparent for distributions of *A. beringiensis* among true lemmings (*Lemmus* Link, *Myopus* Miller and *Synaptomys* Baird), *A. microtis* and *A. janickii* among *Microtus*, *Arvicola*, and *Chionomys* spp. voles and *A. rauschorum* in *Microtus* spp. voles. However, most of the known species of the genus are considered as specific parasites of red-backed voles (*Myodes* Pallas). These species include *A. cooki* in *M. gapperi*; *A. gulyaevi* in *M. rufocanus* (Sundevall); *A. intermedia* in *M. rutilus* (Pallas) and *M. rufocanus*; *A. macrocirrosa* in *M. rutilus*, *M. glareolus* (Schreber), and *M. rufocanus* and *A. tenuicirrosa* in *M. rutilus*, *M. glareolus*, *M. rex* (Imaizumi) [syn. *M. sikotanensis* (Tokuda)] and *M. rufocanus*. An additional species in *Myodes* is described in present study (i.e. *A. kontrimavichusi* in *M. californicus*). Although apparent specificity among host groups is observed, the history for diversification within the assemblage of cestodes can be attributed in large part to processes for geographical and host colonisation within the context of episodic climate variation and biotic expansion and isolation during the Quaternary (e.g. Hoberg et al., 2012; Galbreath & Hoberg, 2015).

Hypotheses for a complex history of diversification emerge from an examination of distributions among species of *Arostrilepis* that are often incongruent relative to hosts and geography. For instance, *A. macrocirrosa*, *A. intermedia* and *A. tenuicirrosa* occur in *M. rutilus*, although, only the former species is distributed in Palaearctic and Nearctic populations of this host and others are restricted to the Palaearctic (Makarikov et al., 2013). Furthermore, *M. rutilus* is dominant host for *A. macrocirrosa* in the Nearctic

(Alaska) and Palaearctic (e.g. Shantar Island), and *A. cooki* is documented only in *M. gapperi* and *A. gulyaevi* occurs in *M. rufocanus*, but not apparently among other species of *Myodes* in sympatry (Makarikov et al., 2013; Kornienko et al., 2014). In parallel to these observations for recognised species and host associations, specimens of *A. kontrimavichusi* n. sp. were found only in *M. californicus*. Other species of Arvicolinae, as well as Sciuridae and Geomyidae examined by RLR from Oregon (species and number of examined specimens are listed in the Materials and methods section) were not infected with *A. kontrimavichusi*.

It is possible that, at least for these four species of *Arostrilepis*, only one species of *Myodes* is an optimal host, and this pattern may represent a generality among other arvicoline genera for these tapeworms. This is reflected in the understanding that not all recognised hosts are equivalent or optimal, and thus may represent different contributions to the maintenance and persistence of parasites among sympatric and multi-species assemblages (Fenton et al., 2015). Maintenance of parasite populations in multi-host assemblages is complex, and faunal structure, including ecological similarity and degrees of sympatry, determine the dynamics for transmission and outcomes for persistence in evolutionary and ecological time (Dobson, 2004; Fenton et al., 2015; Hoberg & Brooks, 2013; Hoberg & Zarlenga, 2016). Occurrence of species of *Arostrilepis* reflects this interaction, where associations may be established and maintained through events of historical and contemporary geographical and host colonisation (see Hoberg & Brooks, 2008, 2015; Agosta et al., 2010; Araujo et al., 2015; Galbreath & Hoberg, 2015).

Alternating episodes of expansion and isolation, and patterns of host colonisation across Beringia and within western North America, would be consistent with processes of ecological fitting represented by phylogenetically conserved capacities by parasites to use a varying spectrum of hosts (and host-based resources) in zones of sympatry or secondary contact (Erwin, 1985; Halas et al., 2005; Agosta et al., 2010; Galbreath & Hoberg, 2015). These dynamics are further consistent with an integrated view of the origins and maintenance of complexity in the biosphere, as exemplified in the recently articulated Stockholm Paradigm (e.g. Hoberg & Brooks, 2015; Araujo et al., 2015; Galbreath & Hoberg, 2015). It is

apparent, based on the host distributions for species in other Muridae (Neotominae) Heteromyidae, Geomyidae, and occasionally among Sciuridae, that events of host colonisation have been involved in the broader history of diversification in the genus (Makarikov et al., 2012). To verify this assumption, additional research is needed using material from different habitats and regions explored in a phylogenetic/historical context in combination with direct comparisons of prevalence and intensity of infection that reveal the dynamics for transmission in space and time. In any case, the present geographic distributions and apparent host associations for species of *Arostrilepis* reflect a deep history with Arvicolinae rodents extending into the Pliocene and Pleistocene of Eurasia and North America (Musser & Carleton, 2005; Hoberg et al., 2012; Makarikov et al., 2013; Galbreath et al., 2013).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

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