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Redescription and taxonomic position of *Rodentolepis* (*sensu lato*) *asymmetrica* (Janicki, 1904), with the erection of *Kontrimavichusia* n. g. (Eucestoda: Hymenolepididae) from arvicoline rodents (Rodentia: Cricetidae)

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Abstract

Rodentolepis (*sensu lato*) *asymmetrica* (Janicki, 1904) is redescribed on the basis of materials from *Microtus agrestis*, *Microtus arvalis* and *Myodes glareolus* from Eastern Europe (Belarus, Lithuania, Latvia, Estonia, Ukraine and the north-eastern part of Russia). A new genus, *Kontrimavichusia* n. g., is proposed for it based on morphological and molecular evidence. The unique morphological diagnostic characters of this currently monotypic genus include the presence of an armature on the suckers, ventral osmoregulatory canals connected with irregularly spaced transverse anastomoses, an internal seminal vesicle with circular musculature and uterus with numerous diverticula, situated dorsally to the genital ducts, extending bilaterally beyond the longitudinal osmoregulatory canals. In addition, the new genus differs from morphologically related genera of the *Rodentolepis* clade by the structure of its vagina. The copulatory part of the vagina in specimens of *Kontrimavichusia* n. g. is surrounded by circular musculature and covered externally by a dense layer of intensely-stained cells; the conductive part of the vagina is clearly distinguishable from the seminal receptacle. Molecular analysis of the partial 28S rRNA gene fully supports the erection of *Kontrimavichusia* n. g. as a distinct lineage.

Introduction

The development of the taxonomy of the family Hymenolepididae is one of the most complex and confusing among cestodes. This is associated with the presence of a large number of species in the family and, on the other hand, with considerable morphological uniformity of its representatives. Difficulties have been further confounded by the inconsistency and brevity of morphological descriptions for many taxa (Mariaux *et al.*, 2017). Due to the intense development of molecular systematics, the taxonomic position of many species, established originally based on morphological criteria, requires now a re-evaluation as has been repeatedly demonstrated among the related groups of hymenolepidids (e.g. Haukisalmi *et al.*, 2010; Neov *et al.*, 2019; Haas *et al.*, 2020).

Among an assemblage of problematic species requiring clarification of generic affinities, *Rodentolepis* (*sensu lato*) *asymmetrica* (Janicki, 1904) is currently recognized as a cestode with a broad distribution in the western Palaearctic as a parasite in various arvicoline rodents. It was originally described from the common vole *Microtus arvalis* (Pallas) (syn: *Arvicola arvalis* Pallas) from Central Europe (Switzerland) and attributed to the genus *Hymenolepis* Weinland, 1858 (Janicki, 1904, 1906). The original description was very brief and based on specimens without scoleces. The relative position of female gonads was regarded as the most important distinctive character of. *Hymenolepis asymmetrica*; in this species, the vitellarium is shifted to the antiporal side of proglottis in relation to the ovary.

Using this feature, Baer (1932) attributed his material collected from *Chionomys nivalis* (Martins) (syn: *Microtus nivalis* Martins) from Switzerland to *H. asymmetrica*; he was the first to describe the scolex. According to Baer (1932), the scolex of this cestode is armed with 20–22 rostellar hooks, 19.2 µm in length; an illustration of rostellar hook was provided but no other morphological characters were illustrated. Furthermore, Baer (1932) recognized *Hymenolepis arvicolae* Galli-Valerio, 1930 from *M. arvalis* from Switzerland as a junior synonym of *H. asymmetrica*.

Joyeux & Baer (1936) reported this species in a both *M. arvalis* and *C. nivalis*; the presented metrical data were nearly identical to those reported by Baer (1932), with the exception of the larger cirrus-sac (160–170 vs. 170–220).

Skrjabin & Matevosyan (1948) repeated the morphological data for *H. asymmetrica* as originally reported by Janicki (1904, 1906) and Baer (1932).

Erhardová (1955) described *Hymenolepis ampla* Erhardová, 1955 from *C. nivalis* from Slovakia. Baer & Tenora (1970), based on morphological similarity, recognized this species as a synonym of *H. asymmetrica*.

Many authors provided descriptions and illustrations of the rostellar hooks and the anatomy of the proglottides of *H. asymmetrica* based on specimens from various arvicoline rodents from different regions of Europe (e.g. Žarnowski, 1955; Baer & Tenora, 1970; Tenora & Murai, 1972; Murai, 1974; Genov, 1984; Santalla *et al.*, 2002). All of these descriptions were in general agreement relative to shape, size and number of rostellar hooks as well as the antiporal position of the vitellarium in relation to the ovary.

Spassky (1954) proposed the specificity to definitive hosts as the major criterion for the taxonomic classification of hymenolepidids from small mammals at the generic level. The genus *Rodentolepis* Spassky, 1954 was erected for various hymenolepidids from rodents with scolex armed with rostellar hooks, including *R. asymmetrica*.

Subsequently, the validity of the genus *Rodentolepis* was questioned and *R. asymmetrica* was transferred again to *Hymenolepis* (e.g. Erhardová, 1955; Vaucher, 1967; Baer & Tenora, 1970; Murai, 1974; Genov, 1984) or to *Vampirolepis* Spassky, 1954 (e.g. Schmidt, 1986; Murai, 1989). After recognition of the independent status of *Rodentolepis* by Czaplinski & Vaucher (1994), *R. asymmetrica* has been considered as member of this genus (e.g. Santalla *et al.*, 2002).

Recent phylogenetic studies exploring relationships among hymenolepidids from rodents, insectivores and bats assigned to the *Rodentolepis* clade have demonstrated that the genus *Rodentolepis* (*sensu lato*) is a non-monophyletic taxon requiring thorough revision. Species of *Rodentolepis* (*sensu lato*), for which molecular data are available, are consistent in exhibiting a very high level of phylogenetic divergence from the type-species *Rodentolepis straminea* (Goeze, 1792) (Haukisalmi *et al.*, 2010; Greiman & Tkach, 2012; Makarikov *et al.*, 2015; Neov *et al.*, 2019). Some linages previously attributed to *Rodentolepis* (*sensu lato*) were later recognized as the genera *Pararodentolepis* Makarikov & Gulyaev, 2009 and *Nomadolepis* Makarikov, Gulyaev & Krivopalov, 2010 (Makarikov & Gulyaev, 2009; Makarikov *et al.*, 2010, 2015). Furthermore, it was shown that *R. asymmetrica* was not only phylogenetically unrelated to the type species of the genus but also was not included in the '*Rodentolepis* clade' (Haukisalmi *et al.*, 2010; Neov *et al.*, 2019) and thus having an uncertain generic allocation. Incomplete morphological data in the original description and the brief subsequent redescriptions of *R. asymmetrica* have also hindered a clear picture of the taxonomy of this species.

Specimens of *R. asymmetrica* from voles *Mi. arvalis*, *Mi. agrestis* (Linnaeus) and *Myodes glareolus* (Schreber) from Eastern Europe (Belarus, Estonia, Latvia, Lithuania, Ukraine and north-western Russia) were collected for the present study. In addition, voucher specimens from voles in France, Hungary, Spain and Switzerland, attributed to *R. asymmetrica* by various researchers and deposited in the helminthological collection of the Geneva Museum of Natural History, Switzerland (MHNG), have been studied for comparison.

The aim of the present article is to complete a detailed morphological redescription of *R. asymmetrica* and to analyse its relationships with other hymenolepidids from mammals based on partial sequences of the nuclear ribosomal 28S rRNA gene. The generic allocation of this species is clarified based on integration of morphological criteria and molecular phylogenetic analysis.

Materials and methods

Mounted specimens of *R. asymmetrica* used in the present study and some tissues stored in ethanol were taken from the research collection of the late Dr Vytautas L. Kontrimavichus supported by the Lithuanian State Science and Studies Foundation. Cestodes from *Mi. agrestis*, *Mi. arvalis* and *My. glareolus* were assembled from field surveys during 2007–2009 conducted in Belarus, Estonia, Latvia, Lithuania, Ukraine and north-western Russia. Sample collection sites and their geographical coordinates are presented in table 1.

Host specimens were dissected fresh. Cestodes were isolated, rinsed and relaxed in water, and preserved in 70% ethanol. Specimens were stained with Ehrlich's haematoxylin, dehydrated in an ethanol series, cleared in clove oil and mounted in Canada balsam. Some scoleces and fragments of strobila were mounted in Berlese's medium to facilitate detailed examination of the rostellar hooks, suckers, cirrus armature and structure of the eggs. Additional tissue was subsampled from some strobila and stored in 96% ethanol for molecular analyses. Specimens were studied using standard light and differential interference contrast microscopy. In the descriptions, measurements are given in micrometres except where otherwise stated; they are presented as the range followed by the mean and the number of the measurements (n) in parentheses. The voucher specimens of *R. asymmetrica* have been deposited in the collection of the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia and the Institute of Ecology of Nature Research Centre, Vilnius, Lithuania. Mammalian taxonomy follows Musser & Carelton (2005).

The type materials of *R. asymmetrica* are not available as those are not mentioned in the catalogues of the international collections of helminthes. With this regard, the following voucher specimens attributed to *R. asymmetrica* and deposited in the helminthological collection of the MHNG, were studied for comparison purposes:

(1) Vouchers of *R. asymmetrica*: MHNG-PLAT-17730 (C40/96), ex *Microtus arvalis*, Németbánya, Veszprém County, Hungary, 1973, collector E. Murai, description published by Murai (1974).
(2) Vouchers of *R. asymmetrica*: MHNG-PLAT-40927 (118/76-77), ex *Chionomys nivalis*, exact locality is not specified, collector F. Tenora.
(3) Vouchers of *R. asymmetrica*: MHNG-PLAT-40928 (118/78-80), ex *Microtus subterraneus*, exact locality is not specified, collector F. Tenora.
(4) Vouchers of *R. asymmetrica*: MHNG-PLAT-11779-11781 (C6/35-39), ex *Microtus* sp., Ramosch, Canton Grisons (Graubünden), Switzerland, 1971, collector A. Meylan, identified by C. Vaucher.

Table 1. Specimens of *Rodentolepis* (*sensu lato*) *asymmetrica* examined in the current study, including vouchers used for morphological redescription and DNA extraction.

Specimen identification number	Slides' deposition	Host species	Country	Date of collection	Geographical coordinates	Genetic data 28S rDNA
VK08-742[a]	Institute of Ecology of Nature Research Centre, Vilnius, Lithuania (IENRC)	*Myodes glareolus*	Vawkavysk District, Belarus	2008	N53°15′10″; E24° 29′2″	
VK08-898/4[a]	IENRC	*My. glareolus*	Vawkavysk District, Belarus	2008	N53°15′10″; E24° 29′2″	
VK08-1510	Institute of Systematics and Ecology of Animals, Novosibirsk, Russia (ISEA)	*Microtus agrestis*	Võru County, Estonia	5.08.2008	N57°55′06.5″; E027° 09′32.3″	
VK08-1510/1	ISEA	*Mi. agrestis*	Võru County, Estonia	5.08.2008	N57°55′06.5″; E027° 09′32.3″	
VK08-1510/4	ISEA	*Mi. agrestis*	Võru County, Estonia	5.08.2008	N57°55′06.5″; E027° 09′32.3″	
VK08-1520[a]	IENRC	*My. glareolus*	Võru County, Estonia	5.08.2008	N57°55′06.5″; E027° 09′32.3″	
VK08-1535/2	ISEA	*Mi. agrestis*	Tartu County, Estonia	6.08.2008	N58°34′54.6″; E027° 10′14.0″	
VK08-1537/1	ISEA	*Mi. agrestis*	Tartu County, Estonia	6.08.2008	N58°34′54.6″; E027° 10′14.0″	
VK08-1537/4	IENRC	*Mi. agrestis*	Tartu County, Estonia	6.08.2008	N58°34′54.6″; E027° 10′14.0″	
VK08-1537/7	ISEA	*Mi. agrestis*	Tartu County, Estonia	6.08.2008	N58°34′54.6″; E027° 10′14.0″	
VK08-1537/8	ISEA	*Mi. agrestis*	Tartu County, Estonia	6.08.2008	N58°34′54.6″; E027° 10′14.0″	
VK08-1544/0	ISEA	*Mi. agrestis*	Tartu County, Estonia	6.08.2008	N58°34′54.6″; E027° 10′14.0″	ON562542
VK08-1544/5	IENRC	*Mi. agrestis*	Tartu County, Estonia	6.08.2008	N58°34′54.6″; E027° 10′14.0″	
VK08-1550	ISEA	*Mi. agrestis*	Lääne-Viru County, Estonia	7.08.2008	N59°31′02.7″; E026° 27′30.0″	
VK08-1593	ISEA	*Mi. agrestis*	Lääne County, Estonia	8.08.2008	N59°08′01.6″; E023° 32′08.4″	
VK08-1593/3	ISEA	*Mi. agrestis*	Lääne County, Estonia	8.08.2008	N59°08′01.6″; E023° 32′08.4″	
VK08-1593/5	IENRC	*Mi. agrestis*	Lääne County, Estonia	8.08.2008	N59°08′01.6″; E023° 32′08.4″	
VK08-589/1	IENRC	*Mi. agrestis*	Aizkraukle Municipality, Latvia	02.08.2007	56°34′56.9″; E25° 29′36.5″	
VK07-589/2	ISEA	*Mi. agrestis*	Aizkraukle Municipality, Latvia	02.08.2007	56°34′56.9″; E25° 29′36.5″	
VK07-603	ISEA	*Mi. agrestis*	Aizkraukle Municipality, Latvia	02.08.2007	56°34′56.9″; E25° 29′36.5″	
VK07-604/3	IENRC	*Mi. arvalis*	Aizkraukle Municipality, Latvia	02.08.2007	56°34′56.9″; E25° 29′36.5″	ON562541
VK07-652	IENRC	*Mi. agrestis*	Aizkraukle Municipality, Latvia	06.08.2007	56°34′56.9″; E25° 29′36.5″	ON562540
VK08-30	IENRC	*Mi. agrestis*	Molėtai District Manucipality, Lithuania	2008	N55°8′45.24″; E25° 21′43.56″	ON562543
VK08-30/1	IENRC	*Mi. agrestis*	Molėtai District Manucipality, Lithuania	2008	N55°8′45.24″; E25° 21′43.56″	ON562544

(*Continued*)

Table 1. (*Continued.*)

Specimen identification number	Slides' deposition	Host species	Country	Date of collection	Geographical coordinates	Genetic data 28S rDNA
VK08-30/2	IENRC	*Mi. agrestis*	Molėtai District Manucipality, Lithuania	2008	N55°8′45.24″; E25° 21′43.56″	
VK08-140	IENRC	*Mi. agrestis*	Leningrad Oblast, Russia	20.08.2008	N59°14′22.9″; E34° 47′15.3″	
VK09-626/1[a]	ISEA	*My. glareolus*	Ivano-Frankivsk Oblast, Ukraine	2009	N48°26′10″; E24° 16′0″	
VK09-626/2[a]	ISEA	*My. glareolus*	Ivano-Frankivsk Oblast, Ukraine	2009	N48°26′10″; E24° 16′0″	

[a] Specimens of *Rodentolepis* (*sensu lato*) *asymmetrica* from *Myodes glareolus* from Belarus, Estonia and Ukraine used for morphological comparison but not included in the redescription.

(5) Vouchers of *R. asymmetrica*: MHNG-PLAT-18413 (C61/54), ex *Microtus agrestis*, Allanche, Auvergne region, France, 1993, collector A. de Chambrier, identified by C. Vaucher.
(6) Vouchers of *R. asymmetrica*: MHNG-PLAT-18399, 18502-18503 (C61/90-96), MHNG-PLAT-18156, 18165 (C56/43-45), ex *Microtus agrestis*, Le Lieu, Le Brasus, Canton Vaud, Switzerland, 1993-1994, collection and identification C. Vaucher.
(7) Vouchers of *R. asymmetrica*: MHNG-PLAT-18362 (C60/07-10), ex *C. nivalis*, Col de Bretolet, Canton Valais, Switzerland, 1968, collection and identification C. Vaucher.
(8) Vouchers of *R. asymmetrica*: MHNG-PLAT-18363 (C60/11), 30549 (C99/38) ex *Mi. agrestis*, La Praz, Canton Vaud, Switzerland, 1967, 1994, collection and identification C. Vaucher.
(9) Vouchers of *R. asymmetrica*: MHNG-PLAT-18364 (C60/12-14), ex *Mi. subterraneus*, Col de Bretolet, Canton Valais, Switzerland, 1968, collection and identification C. Vaucher.
(10) Vouchers of *R. asymmetrica*: MHNG-PLAT-18365 (C60/15), ex *Mi. arvalis*, Col de Bretolet, Canton Valais, Switzerland, 1968, collection and identification C. Vaucher.
(11) Vouchers of *R. asymmetrica*: MHNG-PLAT-17613 (C40/29-30), ex *Mi. agrestis*, Valangin, Canton Neuchâtel, Switzerland, 1966, collector C. Vaucher.
(12) Vouchers of *R. asymmetrica*: MHNG-PLAT-39304 (C53/3-6), ex *Myodes glareolus*, La Chaux-de-Fonds, Canton Neuchâtel, Switzerland, 1967, collection and identification W. Reichenbach.
(13) Vouchers of *R. asymmetrica*: MHNG-PLAT-32861 (C107/078), ex *My. glareolus*, Moulis, Oriental Pyrenees, France, 1997, collection and identification C. Feliu, description published by Santalla *et al.* (2002).
(14) Vouchers of *R. asymmetrica*: MHNG-PLAT-32862 (C107/079), ex *Microtus gerbei*, Eugi, Navarra, Spain, 1996, collection and identification C. Feliu, description published by Santalla *et al.* (2002).
(15) Vouchers of *R. asymmetrica*: MHNG-PLAT-32863 (C107/80), ex *Mi. arvalis*, Val d'Aran, Cataluña, Spain, 1997, collection and identification C. Feliu, description published by Santalla *et al.* (2002).
(16) Vouchers of *R. asymmetrica*: MHNG-PLAT-30668, 39413 (C54/45, 59), ex *Mi. subterraneus*, Bex, Montricher, Canton Vaud, Switzerland, 1973, collector A. Meylan, identified by C. Vaucher.
(17) Vouchers of *R. asymmetrica*: MHNG-PLAT-30533 (C99/4), ex *C. nivalis*, Arolla, Canton Valais, Switzerland, 1997, collector C. Vaucher & F. Catzeflis, identified by C. Vaucher.
(18) Vouchers of *R. asymmetrica*: MHNG-PLAT-30536-30539 (C99/7-12), ex *Mi. subterraneus, Microtus arvalis*, Ain, France, 1998, collector C. Vaucher & A. Meylan, identified by C. Vaucher.
(19) Vouchers of *R. asymmetrica*: MHNG-PLAT-19075, 19078, 19162-19165, 19181, 19183-19184, 19205-19206, 19663 (C82/14-27, 31, 39, 41; C99/37), ex *Mi. agrestis, Mi. arvalis*, Le Lieu, Canton Vaud, Switzerland, 1993, 1994, collection and identification C. Vaucher.
(20) Vouchers of *R. asymmetrica*: MHNG-PLAT-30668-30669, 30672-30673 (C99/78-84), ex *Microtus subterraneus*, Mont Tendre, Canton Vaud, Switzerland, 1973, collector A. Meylan, identified by C. Vaucher.
(21) Vouchers of *R. asymmetrica*: MHNG-PLAT-19321 (C82/40), MHNG-PLAT-19328 (C99/94), ex *Microtus subterraneus*, Piora Valley, Canton Ticino, Switzerland, 1994, collection and identification C. Vaucher.
(22) Vouchers of *R. asymmetrica*: MHNG-PLAT-40937 (11/72-73), ex *C. nivalis*, Zaté (Val d'Hérens), Switzerland, 1931, collection and identification J. Baer, description published by Baer (1932).

Genomic DNA for molecular phylogenetic analysis was extracted from specimens of *Rodentolepis* (*sensu lato*) *asymmetrica* collected from Estonia, Latvia and Lithuania. A fragment (1.5–2 mm long) of a single adult worm was used for each DNA extraction upon preliminary morphological identification. Scoleces and the remaining strobila have been mounted on slides. DNA was extracted using a standard phenol–chloroform protocol as described by Vainio *et al.* (1998) and Sambrook & Russell (2002). DNA fragments approximately 1080 base pairs (bp) long at the 5′ end of the nuclear large ribosomal subunit (28S) gene was amplified by polymerase chain reaction (PCR) on an Eppendorf EP Gradient thermal cycler using OneTaq Quick-load Mastermix from New England Biolabs (Ipswich, MA) according to the manufacturer's instructions. Forward primer 28S-5′ (5′-TAC CCG CTG AAC TTA AGC ATA T-3′) and reverse primer 28S-3′ (5′-CTC CTT GGT CCG TGT TTC AAG AC-3′) designed by Zehnder & Mariaux (1999) were used for amplification; the PCR protocol included 40 cycles with annealing temperature 53°C. Sequencing (from both sides) was carried out by Macrogen Inc. (Geumchun-gu Seoul 153-781, Korea) using the same primers. Sequences were aligned using BioEdit software, version 7.0.1. (Hall, 1999). Pairwise comparisons of sequences of *R. asymmetrica* were calculated using MEGA X (Kumar *et al.*, 2018). To build a phylogenetic tree and reconstruct relationships between the *R. asymmetrica* and other hymenolepidids, we used maximum likelihood with a general time reversible model as distance substitution. For phylogenetic analyses, we used 5 newly obtained nucleotide sequences of *R. asymmetrica* and those of hymenolepidids published in previous studies outlined in table 2 (Lockyer *et al.*, 2003; Waeschenbach *et al.*, 2007; Haukisalmi *et al.*, 2010; Greiman & Tkach, 2012; Tkach *et al.*, 2013; Widmer *et al.*, 2013; Makarikov *et al.*, 2015; Nkouawa *et al.*, 2016; Binkienė *et al.*, 2019; Haas *et al.*, 2020). *Dilepis undula* (Schrank, 1788) was used as an outgroup as proposed by Neov *et al.* (2019) for the phylogeny of Hymenolepididae. Bootstrap values were counted using MEGA as the percentage of 1000 replicates.

Results

Morphological study of *R. asymmetrica* specimens revealed the presence of a set of unique morphological features of supraspecific level that distinguish this species from other genera of mammalian hymenolepidids, and this clearly indicated the need to erect a new genus for this cestode.

Family Hymenolepididae Perrier, 1987

Genus *Kontrimavichusia* n. g.

Diagnosis

Hymenolepididae of medium size. Development of proglottides gradual. Proglottides numerous, transversely elongate, craspedote. Rostellar apparatus well developed. Rhynchus armed with one row of small cricetoid-like hooks; number of rostellar hooks more than 10 and less 40. Suckers muscular, not prominent, armed along its entire surface with minute spines. Dorsal and ventral osmoregulatory canals located on same sagittal plane. Ventral canals connected by irregularly spaced transverse anastomoses. Genital pores unilateral, dextral; genital ducts pass dorsally to osmoregulatory canals. Testes, usually three, as exception four to five, situated in one row or antiporal testes lie on top of each other; poral testis separated from two antiporal testes by female gonads. Cirrus-sac does not reach median line of proglottis. Cirrus armed with minuscule spines. External and internal seminal vesicles present. Internal seminal vesicle with circular musculature. Ovary median, transversely elongate, fan-shaped. Vitellarium postovarian, median or slightly shifted to lateral side of proglottis, slightly lobed. Vagina with two distinct parts: copulatory part surrounded by circular musculature and covered externally by dense layer of intensely-stained cells; and conductive part thin-walled, clearly distinguishable from seminal receptacle. Uterus, initially transversely elongated stripe, situated dorsally to genital ducts and extending laterally beyond longitudinal osmoregulatory canals. Fully developed uterus labyrinthine, extending beyond osmoregulatory canals into both lateral fields, situated dorsally to osmoregulatory canals and genital ducts. Eggs numerous, subspherical, with thin outer coat. Embryophore subspherical, without polar filaments. Parasites of voles (Rodentia, Arvicolinae) in western Palaearctic.

Type species: *Kontrimavichusia asymmetrica* (Janicki, 1904) n. comb.

ZooBank registration: To comply with the regulations set out in Article 8.5 of the amended version of the International Code of Zoological Nomenclature (ICZN, 2012), details of the new genus have been submitted to ZooBank. The Life Science Identifier for *Kontrimavichusia* n. g. is urn:lsid:-zoobank.org:act:CCA8465A-4DDF-4500-B82B-D2B6CB8B928C.

Etymology: This species has been named in honour of the late Dr Vytautas L. Kontrimavichus, in recognition of his seminal and critical studies of parasites of vertebrates, helminth systematics, biogeography, ecology and evolution.

Remarks

Kontrimavichusia n. g. is most similar to other genera of hymenolepidids from mammals in having a scolex armed with rostellar hooks. These genera are *Armadolepis* Spassky, 1954, *Arvicolepis* Makarikov, Gulyaev & Chechulin, 2005, *Nomadolepis* Makarikov, Gulyaev & Krivopalov, 2010, *Pararodentolepis* Makarikov & Gulyaev, 2009, *Relictolepis* Gulyaev & Makarikov, 2007 and *Rodentolepis* Spassky, 1954 from rodents, *Staphylocystis* Villot, 1877 from shrews and *Vampirolepis* Spassky, 1954 from bats. The new genus is consistently distinguished from these taxa by a complex of unique characters such as the presence of armament on suckers, vagina subdivided into copulatory part and conductive part, copulatory part of vagina surrounded by circular musculature and enveloped in a dense sleeve of intensely-stained cells and by the presence of musculature on the internal seminal vesicle.

In specimens of *Kontrimavichusia* n. g., the apex of rostellum is invaginable and blades of retracted hooks are directed anteriorly. In contrast, all members of the *Rodentolepis* clade with an armed scolex, *Armadolepis*, *Nomadolepis*, *Pararodentolepis*, *Rodentolepis*, *Staphylocystis* and *Vampirolepis*, have a rostellum with non-invaginable apex; when rostellar apparatus is retracted, the blades of the hooks are directed posteriorly. *Kontrimavichusia* n. g. also differs from the majority of hymenolepidids from mammals by the presence of irregularly spaced transverse anastomoses between the ventral osmoregulatory canals; so far this character has also been noted in some species of *Nomadolepis* (Makarikov *et al.*, 2010).

Kontrimavichusia asymmetrica n. comb. differs from morphologically related taxa in uterine position and structure. When gravid, the fully-developed uterus is labyrinthine in shape, extending beyond the osmoregulatory canals into both lateral fields and is situated dorsally to osmoregulatory canals and genital ducts. These characters could be used as additional features to distinguish the new genus from other morphologically related genera from mammals. As exemplified, *Rodentolepis* (*sensu stricto*) and its type species *R. straminea* as well as species of *Armadolepis*, *Nomadolepis*, *Relictolepis* and *Pararodentolepis* have the uterus situated dorsally to the osmoregulatory canals and ventrally to genital ducts. The gravid uterus of these genera (*Nomadolepis*, *Pararodentolepis*, some species of *Staphylocystis* and *Vampirolepis*) is a bilobed sac not extending laterally beyond the osmoregulatory canals.

Kontrimavichusia asymmetrica (Janicki, 1904) n. comb.

Synonyms: *Hymenolepis asymmetrica* Janicki, 1904; *Rodentolepis asymmetrica* (Janicki, 1904) Spassky, 1954; *Vampirolepis asymmetrica* (Janicki, 1904) Schmidt, 1986; *Hymenolepis arvicolae* Galli-Valerio, 1930; and *Hymenolepis ampla* Erhardová, 1955.

Type host: *Microtus arvalis* (Pallas) (Rodentia: Cricetidae).

Other hosts: *Chionomys nivalis* (Martins), *Microtus agrestis* (Linnaeus, 1761), *Mi. subterraneus* (de Sélys-Longchamps, 1836), *Myodes glareolus* (Schreber) (Rodentia: Cricetidae).

Type locality: suburbs of Basel, Switzerland.

Redescription (figs 1–4)

(Based on 18 specimens from *Microtus agrestis* and *Mi. arvalis* from north-eastern Europe). Fully developed strobila 98–160

Table 2. Published sequences of 28S rDNA of cestodes deposited in GenBank included in the present phylogenetic analysis.

Cestode species	GenBank accession number	Host species	Host order	Country	Source
Armadolepis dryomi	MG025955	*Dryomys nitedula*	Rodentia	Russia (Rostovskaya Oblast')	Makarikov *et al.* (2018)
Armadolepis tenorai	MG025953	*Dryomys nitedula*	Rodentia	Kazakhstan	Makarikov *et al.* (2018)
Arostrilepis macrocirrosa	MN723792	*Microtus oeconomus*	Rodentia	United States	Haas *et al.* (2020)
Arostrilepis tenuicirrosa	MN723817	*Myodes rufocanus*	Rodentia	Russia	Haas *et al.* (2020)
Hymenolepis diminuta	AY157181	*Rattus_norvegicus*	Rodentia	Denmark	Lockyer *et al.* (2003)
Hymenolepis hibernia	KT148842	*Apodemus flavicollis*	Rodentia	Croatia	Nkouawa *et al.* (2016)
H. hibernia	KT148845	*Apodemus agrarius*	Rodentia	South Korea	Nkouawa *et al.* (2016)
Hymenolepis weldensis	GU166230	*Geomys bursarius*	Rodentia	United States (Indiana)	Haukisalmi *et al.* (2010)
Nomadolepis fareasta	KT161962	*Cricetulus barabensis*	Rodentia	Russia (Amurskskaya Oblast')	Makarikov *et al.* (2015)
Nomadolepis shiloi	KT161963	*Micromys minutus*	Rodentia	Russia (Novosibirskaya Oblast')	Makarikov *et al.* (2015)
Rodentolepis asymmetrica	GU166231	*Chionomys nivalis*	Rodentia	France	Haukisalmi *et al.* (2010)
R. asymmetrica	GU166232	*Microtus agrestis*	Rodentia	Sweden	Haukisalmi *et al.* (2010)
R. asymmetrica	GU166233	*Dinaromys bogdanovi*	Rodentia	Bosnia	Haukisalmi *et al.* (2010)
R. asymmetrica	GU166234	*Microtus majori*	Rodentia	Turkey	Haukisalmi *et al.* (2010)
R. asymmetrica	HM138528	*Mi. agrestis*	Rodentia	United Kingdom	Haukisalmi *et al.* (unpublished GenBank submission)
Rodentolepis evaginata	GU166245	*Ondatra zibethicus*	Rodentia	United States (Alaska)	Haukisalmi *et al.* (2010)
Rodentolepis fraterna	GU166268	*Mus domesticus*	Rodentia	Spain	Haukisalmi *et al.* (2010)
Rodentolepis microstoma	GU166278	*M. domesticus*	Rodentia	Spain	Haukisalmi *et al.* (2010)
Rodentolepis straminea	GU166238	*Apodemus agrarius*	Rodentia	Croatia	Haukisalmi *et al.* (2010)
Ditestolepis sp.	GU166261	*Sorex isodon*	Eulipotyphla	Finland	Haukisalmi *et al.* (2010)
Ditestolepis diaphana	GU166253	*Sorex araneus*	Eulipotyphla	Finland	Haukisalmi *et al.* (2010)
Hymenolepis erinacei	KX928757	*Erinaceus roumanicus*	Eulipotyphla	Lithuania	Binkienė *et al.* (2019)
Lineolepis scutigera	GU166250	*S. araneus*	Eulipotyphla	Finland	Haukisalmi *et al.* (2010)
Neoskrjabinolepis schaldybini	GU166248	*S. araneus*	Eulipotyphla	Finland	Haukisalmi *et al.* (2010)
Gulyaevilepis tripartita	GU166255	*S. araneus*	Eulipotyphla	Finland	Haukisalmi *et al.* (2010)
Pararodentolepis gnoskei	JQ260806	*Suncus varilla*	Eulipotyphla	Malawi	Greiman & Tkach (2012)
Soricinia infirma	GU166260	*S. araneus*	Eulipotyphla	Finland	Haukisalmi *et al.* (2010)
Spasskylepis ovaluteri	GU166262	*S. caecutiens*	Eulipotyphla	Finland	Haukisalmi *et al.* (2010)
Staphylocystis brusatae	JQ260805	*Crocidura suaveolens*	Eulipotyphla	Ukraine	Greiman & Tkach (2012)
Staphylocystis furcata	KF257897	*S. araneus*	Eulipotyphla	Ukraine	Tkach *et al.* (2013)
Staphylocystis schilleri	KF257896	*Sorex palustris*	Eulipotyphla	United States (Montana)	Tkach *et al.* (2013)

(*Continued*)

Table 2. (*Continued.*)

Cestode species	GenBank accession number	Host species	Host order	Country	Source
Staphylocystoides gulyaevi	KC789835	*Sorex monticolus*	Eulipotyphla	United States (Alaska)	Greiman *et al.* (2013)
Vampirolepis sp.	GU969051	*Eptesicus nilssoni*	Chiroptera	Finland	Haukisalmi *et al.* (2010)
Vampirolepis sp.	JQ260802	*Scotomanes ornatus*	Chiroptera	China	Greiman & Tkach (2012)
Dilepis undula	AF286915	*Turdus merula*	Passeriformes	United Kingdom	Waeschenbach *et al.* (2007)
Microsomacanthus sp.	JQ950693	*Stachyris nigriceps*	Passeriformes	Malaysia	Widmer *et al.* (2013)
Microsomacanthus passeris	JQ950692	*Pycnonotus leucotis*	Passeriformes	Iran	Widmer *et al.* (2013)

(122, $n = 7$) mm long, with maximum width 2.5–4.45 (3.1, $n = 7$) mm at level pregravid or gravid proglottides. Strobila flat, consisting of 780–940 craspedote proglottides. Scolex slightly compressed dorso-ventrally, 245–325 wide (280, $n = 7$), not clearly distinct from neck. Suckers small, thick-walled, rounded or oval, cup-shaped, 120–144 × 105–125 (134 × 111; $n = 22$), usually reaching lateral margins of scolex, armed with minute (less than 1 mm long) spines; spines covering entire sucker surface (figs 1A, B and 4A). Rostellar pouch 168–185 × 83–115 (175 × 100; $n = 7$), with muscular walls, its bottom reaching or slightly extending beyond level of posterior margin of suckers. Rostellum 113–135 × 42–81 (120 × 64; $n = 7$), sac-like, muscular, apex invaginable; when rostellar apparatus retracted, rostellar hooks with blades directed anteriorly (fig. 4B). Rhynchus 65–80 long and 45–84 wide, with well-developed circular musculature, armed with single crown of 18–23 ($n = 12$) rostellar hooks of cricetoid-like type (figs 1C and 3A–G). Rostellar hooks with relatively short handle and straight blade; axis of blade situated to the axis of guard at an acute angle; guard narrow in anterior surface; handle and blade slightly shorter or equal in length with guard. Hook measurements: total length 20–22.5 (21.1; $n = 20$); handle 7.5–9 (7.9; $n = 20$); blade 7.5–9 (8.1; $n = 20$); and guard 8–9.5 (8.7; $n = 20$). Neck 240–320 ($n = 7$), approximately equal in width with scolex (fig. 1A, B).

Ventral osmoregulatory canals 65–165 (118; $n = 21$) wide, connected by irregularly spaced transverse anastomoses (in 9–28% proglottides) (fig. 1D). Dorsal osmoregulatory canals very thin, 7–12 (9; $n = 21$) wide at level of hermaphroditic proglottides, usually situated directly dorsal (not shifted left or right) to ventral canals. Genital pores unilateral, dextral (fig. 1D, E). Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals. Development of proglottides gradual, protandrous.

Mature proglottides 150–200 × 1450–1950 (176 × 1711; $n = 18$), transversely elongate, trapezoid (fig. 1D, E). Testes 3, relatively large, almost equal in size, 155–215 × 110–168 (183 × 138; $n = 30$), round or oval, most often situated in one row or, rarely, in triangle with flat angle (anterior antiporal testis shifted to lateral side of proglottis in relation to posterior antiporal testis), poral testis separated from two antiporal testes by female gonads. Number of testes usually constant, variation with four testes per proglottis infrequent. Cirrus-sac relatively short, 215–270 × 48–66 (243 × 54; $n = 28$), with thick muscular walls. Antiporal part of cirrus-sac reaching ventral osmoregulatory canal, rarely overlapping or slightly crossing it (fig. 1E, F). Genital atrium simple, cup-shaped, opens laterally, approximately in middle of lateral proglottis margin. Cirrus large, 105–166 × 25–36 (143 × 28; $n = 32$), cylindrical, armed with very small (up to 1.0–1.5 long), needle-shaped spines; distal part of fully-evaginated cirrus unarmed (fig. 2A). Internal seminal vesicle with circular musculature, ovoid, 126–164 × 42–56 (148 × 49; $n = 30$), occupying less than half of cirrus-sac length (fig. 1E, F). External seminal vesicle, 75–152 × 70–105 (104 × 82; $n = 20$), round or oval, clearly distinguishable from vas deferens, distinctly smaller than seminal receptacle.

Ovary 410–690 (543; $n = 20$) wide, median, transversely elongate, fan-shaped, irregularly lobed, ventral to male genital organs, occupying substantial part of median field, overlapping testes (fig. 1E). Vitellarium 70–105 × 192–276 (81 × 220 $n = 20$), postovarian, slightly shifted to lateral side of proglottis, slightly lobed. Vagina tubular, clearly distinct from seminal receptacle; ventral to cirrus-sac. Copulatory part of vagina 67–90 × 10–22 (76 × 15; $n = 15$), shorter than cirrus, thick-walled, surrounded by circular musculature and covered externally by dense layer of intensely stained cells; proximal part of vagina infundibular (figs 1F and 2A). Conductive part of vagina 145–190 × 9–18 (175 × 13; $n = 15$), thin-walled. Seminal receptacle relatively large, transversely elongate, 240–445 × 80–110 (346 × 92; $n = 20$).

Uterus appears as perforated, transversely-elongate stripe, situated dorsally to testes, genital ducts and osmoregulatory canals and extending laterally beyond longitudinal osmoregulatory canals. With proglottis development, uterus forms numerous diverticula on ventral side and becomes labyrinthine in terminal postmature proglottides. Testes persist in postmature proglottides; cirrus-sac and vagina persist in gravid proglottides (fig. 2B). Gravid proglottides transversely elongate, 320–480 × 2350–4450 (392 × 2966; $n = 20$). Fully developed uterus labyrinthine, occupying entire median field, extending bilaterally, dorsally, beyond longitudinal osmoregulatory canals (fig. 2C). Uterus contains numerous (up to 2000–2300) small eggs. Eggs 42–50 × 47–54, subspherical, with very thin outer coat (up to 0.8–1 thick); oncospheres 18–21 × 20–25 (fig. 2D). Embryophores very thin, 22–26 × 25–32, without polar filaments. Embryonic hooks small, antero-lateral hooks 9.0–9.5, much more robust than slender postero-lateral (9.0–9.5) and median (10.0–10.5) hooks (fig. 2E).

Molecular phylogenetic analysis

The length of the alignment after trimming was 975 nucleotides. All sequences of *K. asymmetrica* n. comb. from Eastern Europe

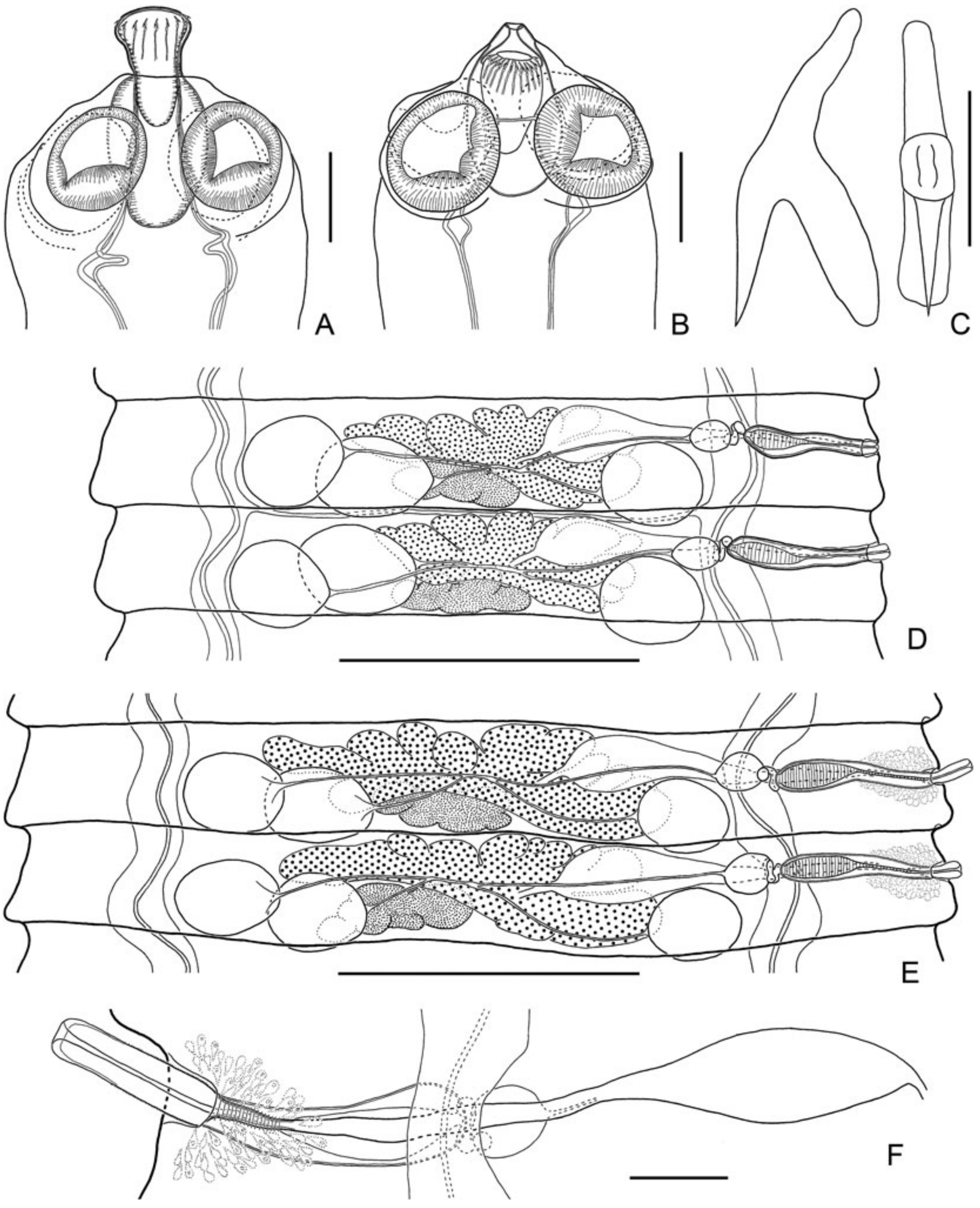

Fig. 1. *Kontrimavichusia asymmetrica* (Janicki, 1904) n. comb. (A) voucher (VK08-1593/3, ex *Microtus agrestis*, Estonia), dorso-ventral view of scolex; (B) voucher (VK08-1537/8, ex *M. agrestis*, Estonia), dorso-ventral view of scolex; (C) voucher (VK08-1537/7, ex *M. agrestis*, Estonia), rostellar hooks in profile and frontal view (note narrow hook guard); (D) voucher (VK08-1535/2, ex *M. agrestis*, Estonia), male mature proglottides, dorsal view; (E) voucher (VK08-1535/2, ex *M. agrestis*, Estonia), hermaphroditic mature proglottis, dorsal view; and (F) voucher (VK08-1537/8, ex *M. agrestis*, Estonia), genital ducts, ventral view. Scale bars: (A, B) 100 μm; (C) 10 μm; (D, E) 600 μm; (F) 60 μm.

including specimens from *Mi. agrestis* (GenBank: ON562541), and *Mi. arvalis* (GenBank: ON562540, ON562542–ON562544) obtained in the present study were identical and form one well-supported clade with those previously deposited in GenBank that were attributed to this species (table 2). It should be noted that the intraspecific differences between all available sequences of putative *K. asymmetrica* reach up to 1–6 bp (table 3).

Kontrimavichusia n. g. is placed as the putative sister for species of *Hymenolepis* (*sensu stricto*), with the latter characterized by an unarmed scolex, rudimentary rostellar apparatus consisting of a partly reduced rostellar pouch and rhynchus and a fully reduced rostellum (fig. 5). Topology is consistent with that presented for these taxa in the analyses by Haukisalmi *et al.* (2010) and Neov *et al.* (2019). The monophyly of each of the two clades corresponding to *Kontrimavichusia* and *Hymenolepis* is well supported (1.0 and 0.99 posterior probability, respectively) but the support of the basal branching of the *Hymenolepis* clade is poorly supported. In the current analysis, the relationship of the *Hymenolepis* clade constituting *Kontrimavichusia* n. g. and *Hymenolepis* remains in a polytomy with certain species of

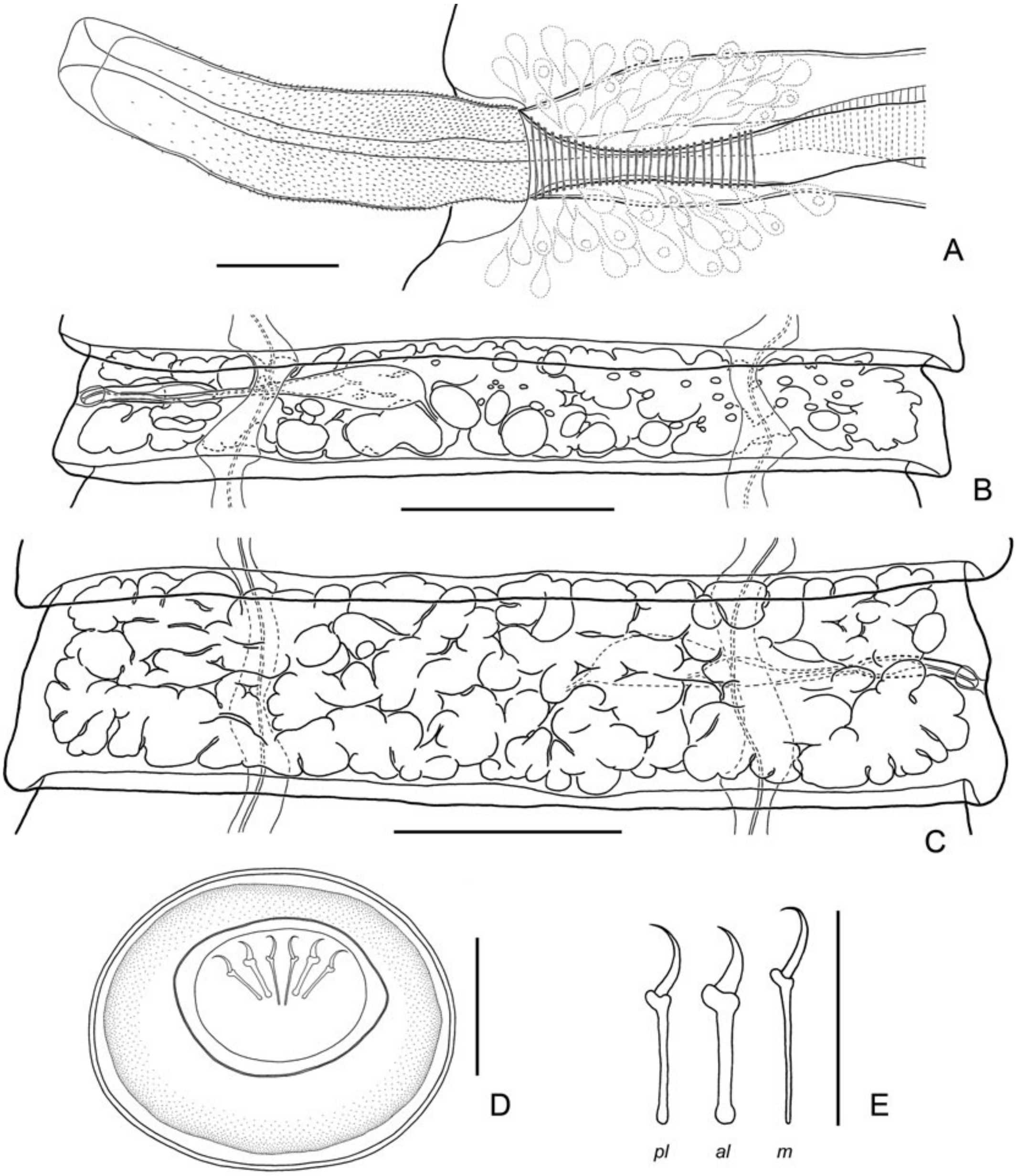

Fig. 2. *Kontrimavichusia asymmetrica* (Janicki, 1904) n. comb. (A) voucher (VK08-1537/8, ex *Microtus agrestis*, Estonia), cirrus and vagina, ventral view; (B) voucher (VK08-1535/2, ex *M. agrestis*, Estonia), pregravid proglottis, showing appearance of uterine diverticula, ventral view; (C) voucher (VK08-1593/5, ex *M. agrestis*, Estonia), gravid proglottis, showing labyrinthine uterus, dorsal view; (D) voucher (VK08-1510, ex *M. agrestis*, Estonia), egg; and (E) voucher (VK08-1510, ex *M. agrestis*, Estonia), embryonic hooks (m, median; al, anterolateral; pl, postero-lateral);. Scale bars: (A) 30 µm; (B, C) 500 µm; (D) 20 µm; (E) 10 µm.

Microsomacanthus from passerine birds and *Rodentolepis* (*sensu lato*) *evaginata* (Barker & Andrews, 1915) from muskrat.

Notably the majority of other hymenolepidids from mammals (Rodentia, Insectivora and Chiroptera), considered in our partial analyses, have variable levels of support and the overall topology is poorly resolved. These encompass taxa having scoleces armed with cricetoid or fraternoid hooks, including the type species of *Rodentolepis* (*R. straminea*) from the *Rodentolepis* clade *sensu* Haukisalmi *et al.* (2010). Although *Kontrimavichusia* n. g. and members of the *Rodentolepis* clade have rostellar hooks of similar shape, these taxa are not related. The closest to the *Hymenolepis* clade is the *Arostrilepis* clade, which would unite cestodes from rodents and insectivores having a fully reduced rostellar apparatus or normally well-developed armed rostellum with rostellar hooks (fig. 5). The *Ditestolepis* clade herein, including only cestodes with a rudimentary rostellar apparatus, a fully reduced rostellar pouch and partly reduced rostellum, forms the poorly supported as a sister-group for other hymenolepidids from mammals. Overall, instability in topology across these taxa may reflect limited taxon sampling and insufficient genetic diversity in a single 28S dataset.

Discussion

There have been a number of redescriptions of *K. asymmetrica* n. comb. based on specimens from various arvicoline hosts from multiple regions and field collections across Europe (Janicki, 1906; Baer, 1932; Žarnowski, 1955; Baer & Tenora,

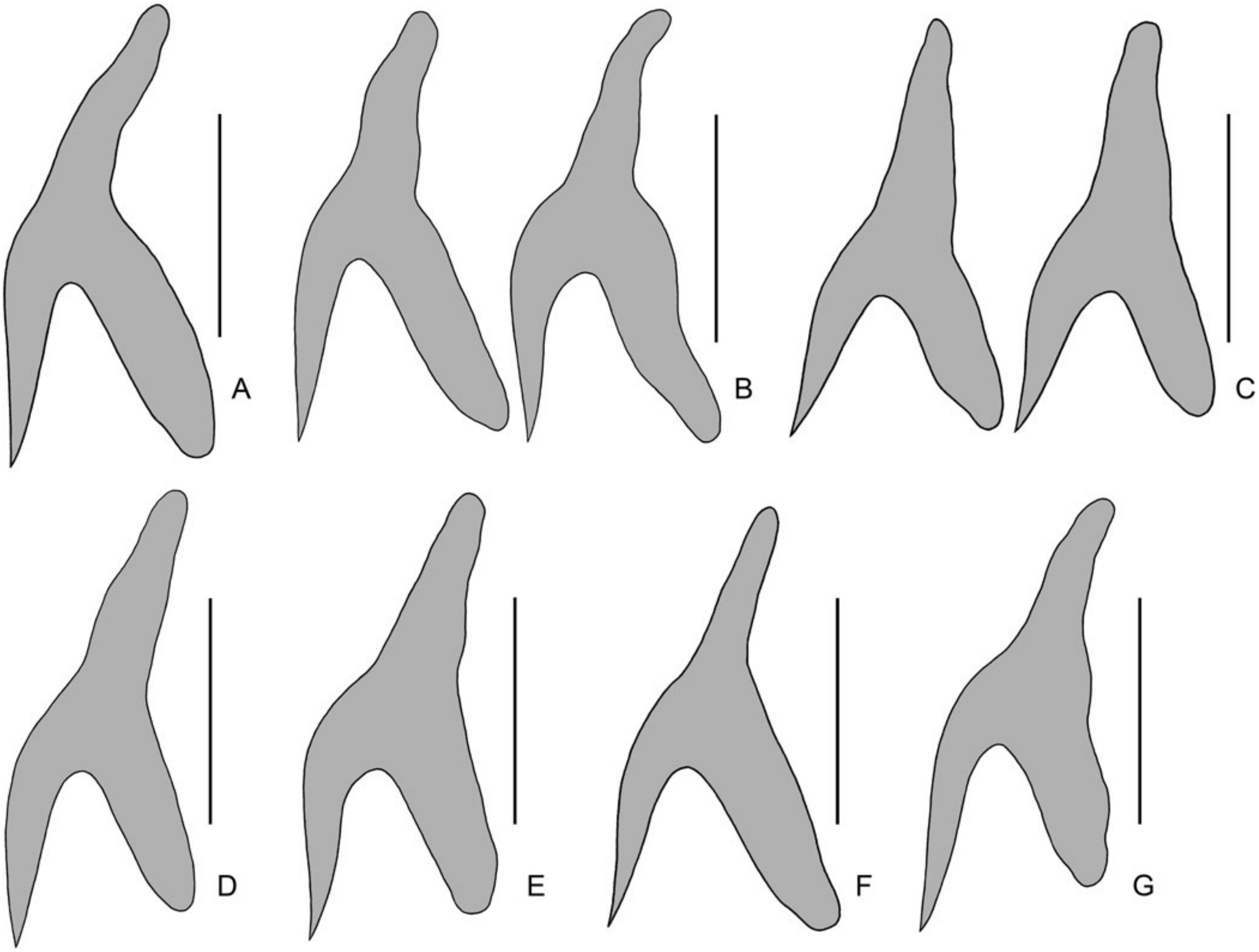

Fig. 3. *Kontrimavichusia asymmetrica* (Janicki, 1904) n. comb. (A–G) rostellar hooks, showing variation in hooks shape between specimens. (A) voucher VK08-1537/7, ex *Microtus agrestis*, Estonia; (B) voucher MHNG-PLAT-18363 ex *M. agrestis*, Switzerland; (C) voucher MHNG-PLAT-40937 ex *Chionomys nivalis*, Switzerland; (D) voucher MHNG-PLAT-30668 ex *M. subterraneus*, Switzerland; (E) voucher MHNG-PLAT-11781, ex *Microtus* sp., Switzerland; (F) voucher 626/2, ex *Myodes glareolus*, Ukraine; and (G) voucher MHNG-PLAT-39304, ex *Myodes glareolus*, Switzerland. Scale bars: (A–G), 10 µm.

1970; Tenora & Murai, 1972; Murai, 1974; Genov, 1984; Santalla *et al.*, 2002). Although in general agreement, none of these contain complete information about the morphology of this species. Additionally, we documented several discrepancies in this range of published descriptions addressing some morphological features for this cestode. We address a variety of intraspecific morphological features and apparent host specificity of *K. asymmetrica* n. comb. based on specimens collected from voles from Eastern Europe, materials deposited at MHNG and published data outlined below. Furthermore, we discuss the taxonomic significance of supraspecific characteristics for the justification of *Kontrimavichusia* n. g.

Morphological analysis of specimens

Scolex

The morphology of the scolex has always been an essential characteristic in the division of cestodes at higher taxonomic levels (Mas-Coma & Galan-Puchades, 1991; Mariaux *et al.*, 2017).

Rostellum: Hymenolepidids with either an invaginable or non-invaginable apex of rostellum reflect a long-standing differentiation of ontogenetic development of metacestodes in relatively distant taxa and thus the morphology of rostellar apparatus can be used in generic and suprageneric taxonomy (Gulyaev, 2000). For instance, the orientation of retracted rostellar hooks is a major character for distinguishing of the family Gryporhynchidae from Dilepididae (Mariaux *et al.*, 2017). This feature clearly distinguishes *Kontrimavichusia* from members of the *Rodentolepis* clade, in which the apex of the rostellum is non-invaginable. In fig. 1B, the rostellar hooks of the specimen from Estonia show the blades directed posteriorly as the rostellar apparatus is not fully retracted. Other specimens from Eastern Europe, with a fully retracted rostellar apparatus and blades of hooks directed anteriorly, were mounted in Berlese's medium. Furthermore, in all specimens from MHNG (MHNG-PLAT 11779; MHNG-PLAT 18502 – two specimens; MHNG-PLAT 18165; MHNG-PLAT 19162–19164) having a fully retracted rostellar apparatus, the blades of hooks are also directed anteriorly (fig. 4B).

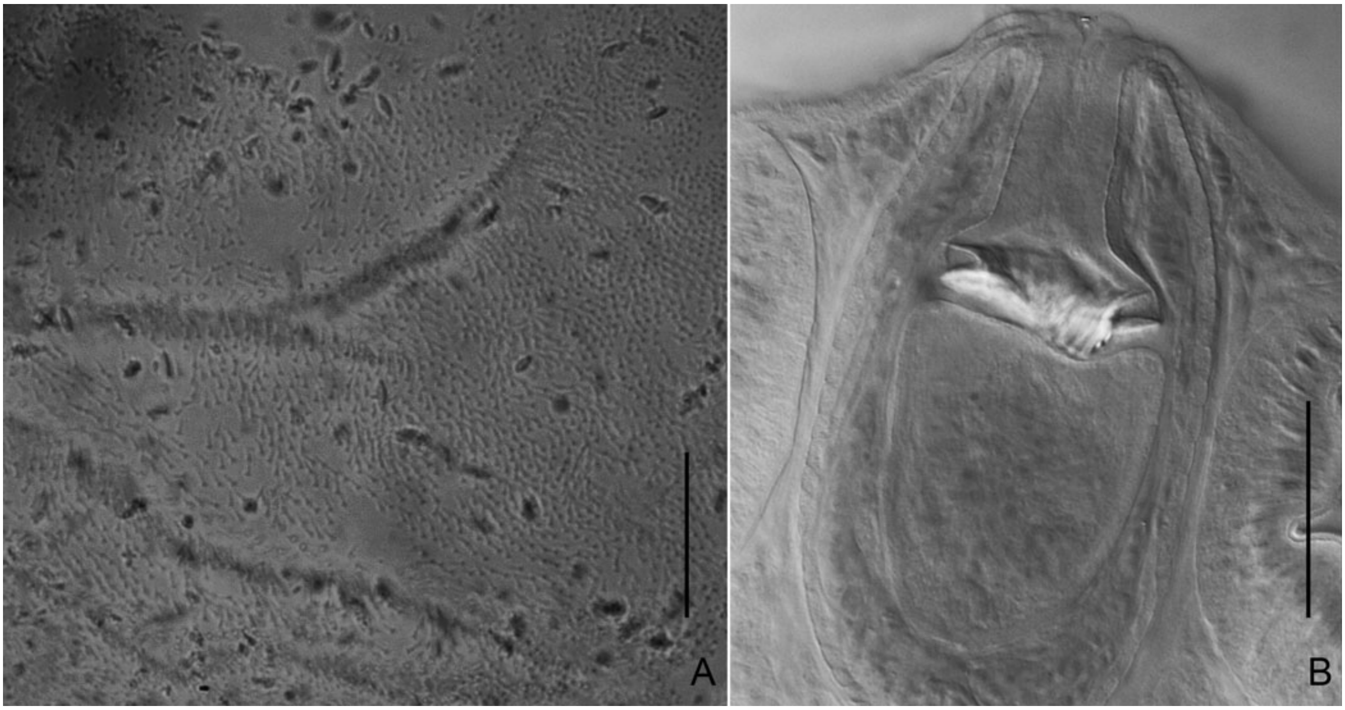

Fig. 4. *Kontrimavichusia asymmetrica* (Janicki, 1904) n. comb. (A) sucker surface of the scolex mounted in Berlese's medium, showing presence of armature; (B) fully retracted rostellar apparatus, showing blades of hooks directed anteriorly. *Scale bars*: (A) 20 µm; (B) 50 µm.

Rostellar hooks: The number, size and shape of rostellar hooks are traditionally among the most important characteristics for the identification of species with an armed scolex. Based on the published descriptions of *K. asymmetrica*, the number of hooks in this cestode varies from 18 to 26 (table 4). Material on this species from Eastern Europe is in the middle of this range. No distinct differences among specimens from different hosts and regions were noted. Also, an examination of voucher specimens of *K. asymmetrica* deposited in MHNG showed the most common number of rostellar hooks is in the range between 18 and 22 (18–3; 19–3; 20–5; 21–1; 22–3; 23–1; 23–1; 24–2; 25–1; 26–1).

The size of rostellar hooks usually varies between 18 and 23 micrometres. No distinct differences between specimens from different hosts and regions were noted (table 4). At the same time the hooks length presented by Santalla *et al.* (2002) is notably different from the specimens examined in our study and the data published by other authors, and extends intraspecific limits. Possible reasons for these differences can be both errors in measurements and, less likely, presence of more than one species in this material. In any case, these data from Santalla *et al.* (2002) cannot be used for subsequent comparisons. We had the opportunity to examine several vouchers of *K. asymmetrica* from Santalla *et al.* (2002) deposited at MHNG (MHNG-PLAT-32861–32863). There were no scoleces mounted in Berlese's medium and only one stained specimen retained the scolex, with the hooks in the crown laid very compact, which made it impossible to count and measure them correctly.

It should be noted that specimens attributable to *K. asymmetrica* examined in the present study demonstrate a relatively high variation in hook shape that has not been observed in other mammalian hymenolepidids (fig. 3). As it was described above, the most common hook shape of this species is the cricetoid type, characterized by a relatively short handle equal or shorter in length with the guard and straight, a blade shorter than former two structures (fig. 3A, B). There is also a variety of hook shape with guard shorter than blade and handle; however, this modification appears relatively rarely and is most likely intraspecific (fig. 3D, G). The dependence of the shape of the hooks on the species of the host was not noticed in the present study and the same specimen can have hooks with both aforementioned shapes. At the same time, the most peculiar shape of hooks was found in the material from *Chionomys nivalis*, which was used by Baer (1932) for the first description of the scolex morphology of this species (MHNG-PLAT-40937); hooks are characterized by a relatively short blade and guard, and both structures are shorter than the handle (fig. 3C). Such a modification is not found in cestodes from other hosts including the type. However, there is not enough data to state that if this shape of hook is associated with this host or not; in addition, other specimens from hosts of the genus *Chionomys* Miller (MHNG-PLAT-18362; MHNG-PLAT-30533) have hooks in similar shape to cestodes from *Microtus* spp.

Suckers: The suckers armed with minute hooks were previously noted in *Hymenolepis myoxi* (Rudolphi, 1819) *sensu* Baer (1932) from glirid rodents. This single character was used by Spassky (1954) to erect the genus *Armadolepis* Spassky, 1954, although, this feature subsequently was rejected in this taxon (Makarikov, 2017). Based on a current understanding of diversity, the presence of armature on suckers in *Kontrimavichusia* is a unique character, which is not known in any other hymenolepidids from mammals. There are also some hymenolepidids from birds, which have suckers armed with spines (e.g. *Anatinella* Spassky & Spasskaja, 1954; *Diorchis* Clerc, 1903; *Echinolepis* Spassky & Spasskaja, 1954; *Gastrotaenia* Wolffhügel, 1938; *Skrjabinoparaksis* Krotov, 1949). All these genera have completely different strobilar morphology and are unrelated, thus suggesting

Table 3. Pairwise uncorrected genetic distances (below diagonal) and total nucleotide differences (above diagonal) in sequences of 28S rDNA between putative *Kontrimavichusia asymmetrica* specimens.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. ON562540 *Microtus agrestis*, Latvia	–	0	0	0	0	1	1	4	4	6
2. ON562541 *Microtus arvalis*, Latvia	0.0000	–	0	0	0	1	1	4	4	6
3. ON562542 *Mi. agrestis*, Estonia	0.0000	0.0000	–	0	0	1	1	4	4	6
4. ON562543 *Mi. agrestis*, Lithuania	0.0000	0.0000	0.0000	–	0	1	1	4	4	6
5. ON562544 *Mi. agrestis*, Lithuania	0.0000	0.0000	0.0000	0.0000	–	1	1	4	4	6
6. GU166232 *Mi. agrestis*, Sweden	0.0010	0.0010	0.0010	0.0010	0.0010	–	0	3	3	5
7. HM138528 *Mi. agrestis*, United Kingdom	0.0010	0.0010	0.0010	0.0010	0.0010	0.0000	–	3	3	5
8. GU166231 *Chionomys nivalis*, France	0.0038	0.0038	0.0038	0.0038	0.0038	0.0029	0.0029	–	6	8
9. GU166233 *Dinaromys bogdanovi*, Bosnia	0.0038	0.0038	0.0038	0.0038	0.0038	0.0029	0.0029	0.0058	–	4
10. GU166234 *Microtus majori*, Turkey	0.0058	0.0058	0.0058	0.0058	0.0058	0.0048	0.0048	0.0077	0.0038	–

the independent origin of armament on suckers in different hymenolepidid taxa.

It should be noted that the spines on the suckers in *Kontrimavichusia* are usually poorly visible in stained specimens under light microscopy but become well distinguished on scoleces mounted in Berlese's medium (fig. 4A). The nature and chemical composition of these structures is not yet clear. In any case, it was repeatedly noted that the presence and pattern of the distribution of armature on suckers is a diagnostic character of genera (Skrjabin & Matevosyan, 1948; Spassky, 1954; Mas-Coma & Galan-Puchades, 1991; Czaplinski & Vaucher, 1994).

Excretory system

The presence of transverse anastomoses between the ventral osmoregulatory canals was indicated in the original description of *K. asymmetrica*: 'Von den 2 Exkretionsgefäßpaaren ist das eine außerordentlich stark entwickelt; es bildet Queranastomosen' (Janicki, 1904). Furthermore, this character has been later redescribed and illustrated by the author of this species: 'Von den zwei Paaren der Exkretionsgefäße fällt das eine durch seine ungewöhnlich starke Entwicklung auf, namentlich in jüngeren Gliedern (vgl. Taf. XXII, fig. 42 und 43 Text fig. 11); es verläuft unter starker Schlängelung und bildet in einer jeden Proglottis Queranastomosen' (Janicki, 1906). In all subsequent redescriptions of this species by other authors this feature was completely ignored (Baer, 1932; Žarnowski, 1955; Baer & Tenora, 1970; Tenora & Murai, 1972; Murai, 1974; Genov, 1984; Santalla *et al.*, 2002). The ventral osmoregulatory canals connected with transverse anastomoses is among the generic characters of *Hymenolepis* (*sensu stricto*) (Makarikov & Tkach, 2013). In contrast to *Hymenolepis*, in *Kontrimavichusia*, transverse anastomoses are not located in every proglottis; those are randomly spaced throughout the strobila. Furthermore, in the proglottis anastomoses can pass terminally, medially or anteriorly, and in this, their irregularity is manifested. Irregular transverse anastomoses between ventral osmoregulatory canals also have been observed among some species of *Nomadolepis* and this feature is used among generic characters (Makarikov *et al.*, 2010), which can also be applied to the genus *Kontrimavichusia*.

Mature proglottides

Testes: No distinct variations in number and arrangement of the testes were observed in the material examined in the present study. Specimens are generally uniform in the distribution of testes, which usually are situated as noted in the redescription: in transverse line, one poral and two antiporal, separated by female gonads. At the same time, the following modifications in number and arrangement were noted: two poral testes and one antiporal testis (2–9 cases of 100 proglottides); triangular arrangement of the testes (1–8 cases of 100 proglottides); and four testes per proglottis (0–2 cases of 100 proglottides). The geometric arrangement of testes in hymenolepidids is used as a feature both for differentiation between species and between genera (Mas-Coma & Galan-Puchades, 1991; Czaplinski & Vaucher, 1994). Since *Kontrimavichusia* is currently a monotypic genus, there is no possibility to assess its systematic significance for this taxon.

Cirrus: Baer (1932) gave initial information on the cirrus of this species and considered that this structure was unarmed (table 4). Subsequently, all the authors who redescribed the cirrus of *K. asymmetrica* were unanimous in reporting the presence of the armature (Žarnowski, 1955; Baer & Tenora, 1970; Tenora & Murai, 1972; Murai, 1974; Genov, 1984). We found that the armature of the cirrus is present although not evenly distributed; the distal part of the fully evaginated cirrus lacks spines (fig. 2A). Although in some groups of cestodes the patterns of spination are used to differentiate between species (Kornienko *et al.*, 2006; Makarikov *et al.*, 2013), we believe that in this case this feature would not have taxonomic significance, since it is likely that the tiny spines in distal part of the cirrus may have been partially lost due to fixation and/or staining.

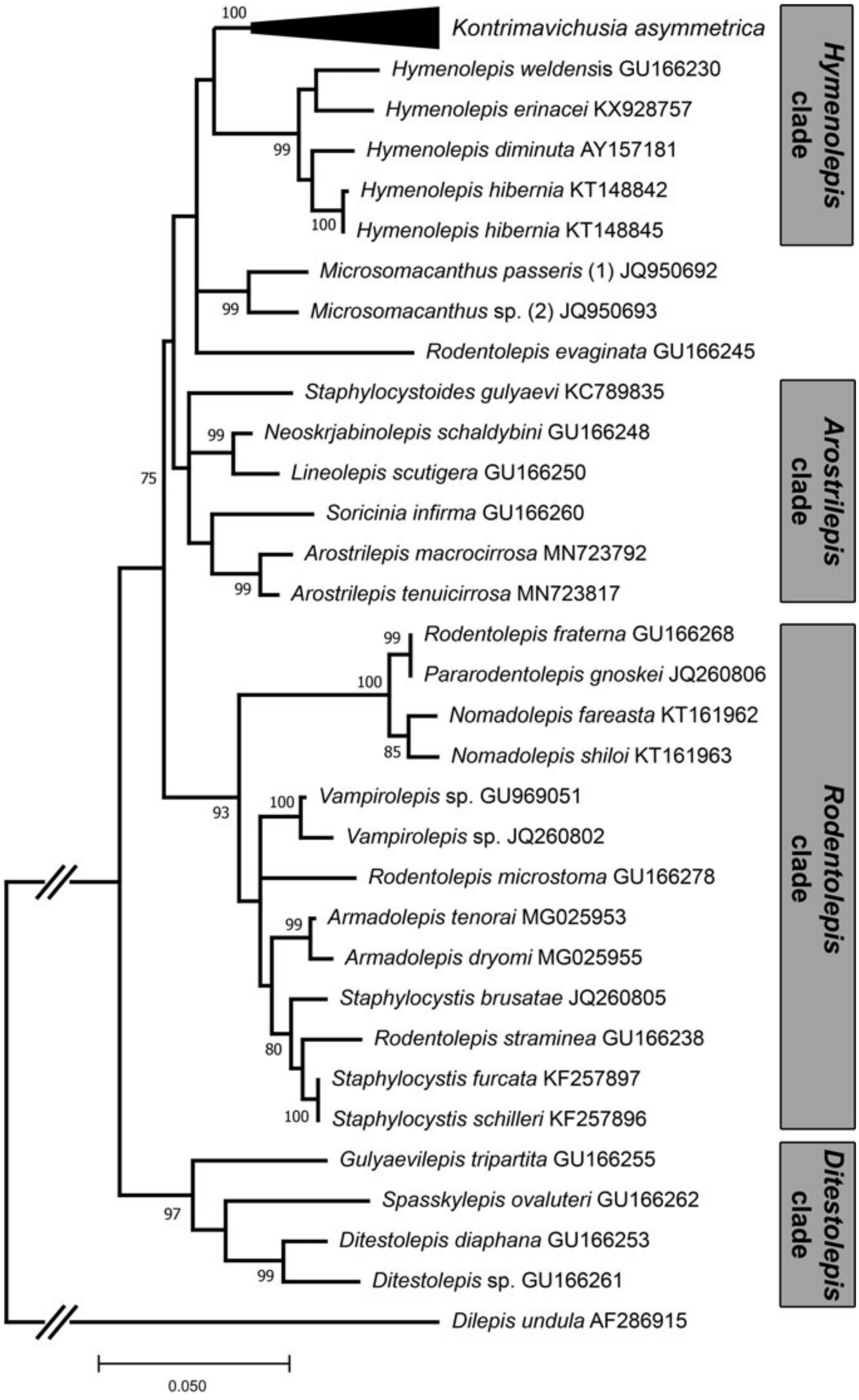

Fig. 5. Maximum likelihood phylogenetic tree of hymenolepidids based on analysis of partial sequences of the 28S rRNA gene. Bootstrap support given for maximum likelihood analysis based on 1000 replicates. Bootstrap support values lower than 70% are not shown.

Vagina: A detailed description of the female genital ducts in *K. asymmetrica* was fully neglected as well as in the most other hymenolepidids from mammals. However, the position of the vagina in relation to the cirrus sac and its morphology are used for generic differentiation of avian hymenolepidids (Mas-Coma & Galan-Puchades, 1991). Similarly, we believe that peculiarities in vaginal structure of this species can be useful for exploring characters at the generic level. In *Kontrimavichusia*, this primarily refers to the division of the vagina into distinct parts; the copulatory part of the vagina is surrounded by circular musculature and covered externally by a dense layer of intensely stained cells, while the conductive part thin-walled is clearly distinguishable from the seminal receptacle (figs 1F and 2A). Structurally, this is markedly different from representatives of the *Rodentolepis* clade, in which the copulatory part of the vagina is simply organized without additional structures and the conductive part is indistinguishable (Makarikov *et al.*, 2015, 2018).

Relative position of female gonads: The shifted position of the vitellarium to the lateral side of the proglottis in relation to the ovary was the key feature in initial differentiation of this species (Baer, 1932; Joyeux & Baer, 1936; Skrjabin & Matevosyan, 1948). Apparently this character cannot be considered as reliable,

Table 4. Comparative morphometric data of *Rodentolepis* (*sensu lato*) *asymmetrica* by various authors and the present study (measurements in micrometres except where otherwise stated).

Source	Janicki (1904, 1906)	Baer (1932)	Žarnowski (1955)	Baer & Tenora (1970)	Tenora & Murai (1972)	Murai (1974)	Genov (1984)	Santalla *et al.* (2002)	Present study
host species	*Microtus arvalis*	*Chionomys nivalis*	*Microtus arvalis*	*Microtus agrestis*, *Mi. arvalis*, *Mi. subterraneus*, *Myodes glareolus*, *Chionomys nivalis*	*Microtus agrestis*, *Mi. arvalis*, *Mi. subterraneus*	*Microtus agrestis*, *Mi. arvalis*, *Mi. subterraneus*, *Myodes glareolus*	*Microtus arvalis*, *Mi. subterraneus*, *Myodes glareolus*	*Microtus agrestis*, *Mi. arvalis*, *Mi. gerbei*, *Myodes glareolus*[a]	*Microtus agrestis*, *Mi. arvalis*
country	Switzerland	Switzerland	Poland	Switzerland, former Czechoslovakia, Poland	Hungary	Hungary	Bulgaria	Spain	Estonia, Latvia, Lithuania
strobila length (mm)	60 mm	30–40	129–177	30–118	50–135	50–135	51–106 mm	–	98–160 mm
strobila width (mm)	4 mm	2 mm	3.46–4.18 mm	1–4 mm	2–4 mm	2–4 mm	1.9–2.6 mm	–	2.5–4.45 mm
scolex width	–	310	–	270–412	220–300	220–300	272–320	192–286	245–325
suckers size	–	130 × 100	–	102 × 135	90 × 120	85 × 120	144–160 × 116–124	87 × 166	120–144 × 105–125
rostellar pouch size	–	83 × 84	–	–	–	–	158–180 × 84–100	97–240 × 58–151	168–185 × 83–115
rostellum size	–	–	–	–	42–60	–	–	38–84 × 23–76	113–135 × 42–81
rostellar hooks number	–	20–22	20	20–26	18–21	18–21	19–21	20–25	18–23
rostellar hooks size	–	19.2	16–18	21–26	18–20	18–20	20–23	12.8–20.5	20–22.5
testes size	100	95	110 × 132	228	120 × 200	–	152–180 × 104–148	73–176 × 49–128	155–215 × 110–168
cirrus-sac size	200	160–170 × 60	162–200	125–228	150–330 × 60	200–330 × 60	280–320 × 50–62	184–238 × 30–56	225–270 × 48–66
cirrus: size	–	–	–	–	100–120 × 30–33	100 × 30	–	–	110–166 × 25–36
cirrus spines: presence	–	unarmed	armed	armed	armed	armed	armed	–	armed
external seminal vesicle size	94	–	–	151 × 27	–	–	–	64–138 × 51–84	75–152 × 70–105
ovary width	–	–	–	158–457	220–400	200–400	208–296	102–550	410–690
vitellarium size	–	–	–	87 × 205	–	–	56 × 152–154	43–90 × 128–205	70–105 × 192–276
seminal receptacle size	–	–	–	274 × 82	280–360 × 90–123	350 × 100	–	77–307 × 51–84	240–445 × 80–110

egg size	40	40	40 × 57	45 × 78	42 × 67	45 × 67	63–65 × 44–48	45–51 × 36–46	42–50 × 47–54
oncosphere size	20	–	20 × 27	20 × 56	20 × 30	20 × 30	23 × 30	20–30 × 16–22	18–21 × 20–25
embryonic hooks size	–	–	–	6.8–10.8	8.5–9	8.5–9	10–11	8.4–10.1	9.0–10.5

[a]Measurements by Santalla *et al.* (2002) are presented only from specimens originated from *Microtus agrestis* and *Mi. arvalis*.

since different groups of hymenolepidids also show a varying degree of shifting of the vitellarium to the antiporal side of the proglottis in relation to the ovary.

Gravid proglottides

Uterus: The shape of the uterus through different stages of strobilar development as well as its relative position to the other internal organs and extent of the fully developed uterus relative to the osmoregulatory canals are considered to be useful for generic classification of hymenolepidids (Mas-Coma & Galan-Puchades, 1991; Mariaux *et al.*, 2017). Characteristics of the uterus both in the original description as well as in its subsequent redescriptions for *K. asymmetrica* were incomplete. We stated that the shape and topography of the uterus in *K. asymmetrica* is more consistent with the genus *Hymenolepis* (*sensu stricto*) rather than with representatives of the *Rodentolepis* clade. The uterine morphology of *K. asymmetrica* and *Hymenolepis* has the following common features: the presence of numerous diverticula and the position dorsally to genital ducts, extending bilaterally beyond the longitudinal osmoregulatory canals. Thus, the structure of the uterus may also confirm the putative molecular–phylogenetic relationship of these taxa.

Eggs: Details of egg morphology could be also considered as additional distinctive characters at the supraspecific level. For instance, the presence of polar filaments on the embryophore is a generic character in some members of the *Rodentolepis* clade (Makarikov *et al.*, 2010, 2015). Homologous structures are absent in *Kontrimavichusia*.

Thus, the discovered complex of peculiar morphological features in specimens of *K. asymmetrica* clearly justifies the need for erection of a distinct genus for this species.

Host range and specificity

The common vole *Microtus arvalis* is the type host of *K. asymmetrica*. This species was also found in other arvicoline rodents of the genera *Microtus* Schrank, *Myodes* Pallas, *Chionomys* Miller and *Dinaromys* Kretzoi (Baer & Tenora, 1970; Tenora & Murai, 1972; Santalla *et al.*, 2002) and even in Muridae rodents of the genera *Apodemus* Kaup, *Micromys* Dehne and *Mus* Clerck (Erhardová, 1958; Ryzhikov *et al.*, 1978). At the same time, the overwhelming majority of specimens of this species from Central Europe deposited in MHNG originate from *Mi. agrestis*; while there are only a few slides from the type host, such a small number of specimens were also found in other vole species. Furthermore, no confirmed specimens outside of Arvicolinae in MHNG were detected. This is also consistent with the present collection of this species from Eastern Europe, where both *Mi. agrestis* and *Mi. arvalis* live in sympatry but *K. asymmetrica* was found more often in the former host. For instance, in on our study, specimens of *K. asymmetrica* in Estonia were found in seven out of 31 specimens of *Mi. agrestis* (prevalence 22.5%) and in one out of 26 specimens of *My. glareolus* (prevalence 0.3%), while none of the 16 specimens of *Mi. arvalis* were of infected with this cestode. In Latvia, *K. asymmetrica* was found in four specimens of *Mi. agrestis* and in only one individual of *Mi. arvalis*. In Belarus, specimens of *K. asymmetrica* were found in one out of 56 individuals of *My. glareolus* (prevalence 1.8%) while no specimens of *Mi. agrestis* and *Mi. arvalis* were studied there. A similar result on host specificity of *K. asymmetrica* was obtained by Tenora & Murai (1972) from Hungary where *Mi. agrestis* is the dominant host for this cestode (prevalence 60%); in contrast, in *Mi.*

arvalis and *Mi. subterraneus* (de Selys-Longchamps) (syn.: *Pitymys subterraneus* (de Selys-Longchamps)), it is much less common, with prevalence 4% and 10%, respectively. Santalla *et al.* (2002) also showed that in the Pyrenean Mountains (Spain and France), among voles, the highest values of the prevalence with this cestode were in *Mi. agrestis* and *Mi. arvalis* (12.5–29.4% and 13.8–26.0%, respectively), less in *Mi. gerbei* (Gerbe) (5.2–17.7%) and the lowest in *My. glareolus* (1.2–4.0%).

All these data suggest that the genus *Microtus* and particularly *Mi. agrestis* is the most optimal host for the circulation of this parasite. The observed specimens from voles *Chionomys nivalis*, *Mi. subterraneus* and *My. glareolus* morphologically correspond to those from the type host and can be considered as additional hosts for this species. The detection of *K. asymmetrica* in *Dinaromys bogdanovi* (Martino) and *Mi. majori* (Thomas) requires confirmation since the morphology of these cestodes is unknown and the genetic distances of these specimens (discussed below) from cestodes from the type host extend beyond the limits of one species (Haukisalmi *et al.*, 2010). Similarly, the same applies to the specimens from *Mi. gerbei* from Spain (Santalla *et al.*, 2002) whose metrical data differ from those in cestodes from the type host. In addition, it is obvious that reports of this cestode from other hosts outside of the subfamily Arvicolinae are likely to be incorrect identifications of other hymenolepidids (Erhardová, 1958; Ryzhikov *et al.*, 1978).

Phylogeny

All our new as well as GenBank available *K. asymmetrica* sequences form one well supported subclade within the *Hymenolepis* clade (fig. 5). However, it should be noted that some of the inner lineages of *Kontrimavichusia* demonstrate interspecific variability (table 3). One of these lineages is represented by the specimens from *Mi. arvalis* and *Mi. agrestis* included in GenBank (GU166232 and HM138528) and those from the present study. Unlike previously published sequences from GenBank, the vouchers of the latter specimens are available and those are morphologically fully consistent with the materials from the type host deposited in museum collections, thus apparently representing true *K. asymmetrica*. The other lineages published in GenBank originated from various arvicoline rodents that are phylogenetically distant from specimens from the type host. One of these represents sequence from *C. nivalis* from France (GU166231). The pairwise distances between this lineage and putative true *K. asymmetrica* reach up to 0.38% (4 bp). The two other lineages are from *D. bogdanovi* from Bosnia (GU166233) and in *Mi. majori* from Turkey (GU166234); they differ from *K. asymmetrica* up to 0.38% (4 bp) and 0.58% (6 bp), respectively. These data exceed the limits of intraspecific variability in this relatively conservative region of the rDNA. For instance, the proposed values of interspecific variability of the 28S gene among hymenolepidids from small mammals are in the range of 0–7 bp (Greiman & Tkach, 2012; Greiman *et al.*, 2013; Tkach *et al.*, 2013; Makarikov *et al.*, 2015).

The presence of superspecific lineages within the *Kontrimavichusia* subclade suggests that this taxon may include a complex of cryptic species. Lack of morphological vouchers for the sequences from GenBank makes it difficult to further study species diversity within the genus. In this regard, the examination of specimens, assumed to be *K. asymmetrica*, originating from rodents that are phylogenetically distant from the genus *Microtus*, is of great interest.

Since the erection of the genus *Rodentolepis*, *K. asymmetrica* has been considered a member of this genus and the taxonomic position of the species has never been challenged by authors who followed the revision of mammalian hymenolepidids of Spassky (1954). In this regard, the first molecular data on this species revealed unexpected insights (Haukisalmi *et al.*, 2010). This species is excluded from the *Rodentolepis* clade *sensu* Haukisalmi *et al.* (2010), which unites the majority of hymenolepidids from mammals having a scolex armed with cricetoid or fraternoid rostellar hooks, including the type of *Rodentolepis*, *R. straminea*. The emergence of an inclusive clade with *K. asymmetrica* and representatives of the genus *Hymenolepis* (*sensu stricto*) having unarmed scolex with rudimentary rostellar apparatus was among the most confusing contradictions of that initial phylogenetic study. Furthermore, this association was also confirmed by Neov *et al.* (2019) and the present study. Relatively recent and an even more unusual example was discovered during examination of species diversity within *Armadolepis*. Those analyses showed that the same genus of hymenolepidids includes both species having a normally developed rostellar apparatus with a rhynchus armed by hooks as well as species having an unarmed and rudimentary rostellar apparatus (Makarikov, 2017; Makarikov *et al.*, 2018). Meanwhile, in addition to the morphology of the scolex, we found that the anatomy of the strobila of *Kontrimavichusia* specimens is more similar to the genus *Hymenolepis* rather than to the representatives of the *Rodentolepis* clade. The first two groups are united by such characters as presence of transverse anastomoses between ventral osmoregulatory canals, the structure of the vagina, the shape of the uterus and its relative position to the genital ducts. Thus, the similarity in morphology partly confirms this phylogenetic linkage of *K. asymmetrica* with the genus *Hymenolepis* (*sensu stricto*).

So far, only in the *Ditestolepis* clade, all known representatives have an unarmed scolex, while the other clades include cestodes with both armed and unarmed scoleces. Such a distribution indicates that, in different lineages of mammalian hymenolepidids, an independent reduction of the rostellar apparatus has occurred (Spassky, 1992; Haukisalmi *et al.*, 2010). The structure of the rostellar apparatus of the ancestral forms of *Hymenolepis* is unknown but, given the great importance of this feature for suprageneric phylogeny and similarity in morphology of strobila, it can be speculated that it could resemble that of *Kontrimavichusia*. Data confirming or refuting this assumption have not yet been collected. In addition, all representatives of *Hymenolepis* have unarmed suckers, and now there is no possibility to establish if the ancestral forms of these cestodes used to have an armature on suckers and then lost this in the course of historical development or not. The presence of an armature on suckers and an invaginating apex of the rostellum may probably indicate that *Kontrimavichusia* originated from some avian cestodes having similar morphological characters as a result of colonization of rodents and adaptation of these hymenolepidids to a new host. A similar origin from avian hymenolepidids that adapted to parasitize rodents was supposed for *Arvicolepis transfuga* (Spassky & Merkusheva, 1967) from voles; this form also has an invaginating apex of the rostellum (Makarikov *et al.*, 2005). However, the present phylogeny and discovered phylogenetic affinity of the *Hymenolepis* clade with *Microsomacanthus* spp. from passerine birds cannot be unambiguously interpreted as a confirmation of this assumption. As only a small part of avian hymenolepidid taxa were included in phylogenetic studies, it is difficult to further study the relationships among these cestodes.

In conclusion, the present morphological analyses of specimens of *K. asymmetrica* is in agreement with results of phylogenetic studies performed by Haukisalmi *et al.* (2010), Neov *et al.* (2019) and the results obtained in the present study. Integrated data from comparative morphology and molecular phylogenetic analysis fully support the erection of a new genus for this species. *Kontrimavichusia* is currently a monotypic genus and includes only *K. asymmetrica*. Given the presence of interspecific lineages within this cluster, species diversity in this group of cestodes requires further study.

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