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Systematic relationships of *Mosgovoyia* Spasskii, 1951 (Cestoda: Anoplocephalidae) and related genera inferred from mitochondrial and nuclear sequence data

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Abstract The present study evaluates the phylogenetic position and systematic relationships of two species of *Mosgovoyia* Spasskii, 1951 and related genera (Cestoda: Anoplocephalidae) based on sequences of 28S ribosomal RNA and mitochondrial NADH dehydrogenase subunit 1 (Nad1) genes. Both molecular data-sets show that *M. pectinata* (Goeze, 1782) and *Schizorchis caballeroi* Rausch, 1960 are sister species and that they are phylogenetically independent from *M. ctenoides* (Railliet, 1890). This shows unambiguously that *Mosgovoyia* [*sensu* Beveridge (1978)] is a non-monophyletic assemblage, supporting the validity of *Neoctenotaenia* Tenora, 1976, erected for *M. ctenoides*. The results also show that the morphologically related *Ctenotaenia marmotae* (Fröhlich, 1802) is the sister species of *Andrya rhopalocephala* (Riehm, 1881) and therefore represents a more derived lineage. Modified diagnoses are provided for *Mosgovoyia* and *Neoctenotaenia*.

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Introduction

Mosgovoyia Spasskii, 1951 (Cestoda: Anoplocephalidae) was proposed for *Cittotaenia pectinata* (Goeze, 1782) (type-species) from hares and rabbits (Lagomorpha: Leporidae) and two other species from leporids and chincillid rodents, respectively (Spasskii, 1951). In his comprehensive taxonomic revision, Beveridge (1978) significantly modified the diagnosis of *Mosgovoyia*, including in it only three species from leporids, i.e. *M. pectinata*, *M. ctenoides* (Railliet, 1890) and *M. variabilis* (Stiles, 1895). Previously, these three species had been variously assigned to *Mosgovoyia*, *Ctenotaenia* Railliet, 1893, *Cittotaenia* Riehm, 1881 and *Neoctenotaenia* Tenora, 1976 (see Beveridge, 1978).

The systematic relationships of *Mosgovoyia* spp. and related cestodes have not been analysed comprehensively using explicit phylogenetic methods. The existing phylogenetic data suggest that *M. pectinata* and *Schizorchis caballeroi* Rausch, 1960 from a pika (an ochotonid lagomorph) are sister taxa, which have a basal, unresolved position among anoplocephaline cestodes of mammals (Wickström et al., 2005). However, the analysis of Wickström et al. (2005) did not include other species of *Mosgovoyia*, of which *M. ctenoides* has been assigned to *Neoctenotaenia* as its type-species (Tenora, 1976)

The present study provides new molecular data for *M. pectinata*, *M. ctenoides, S. caballeroi* and *Ctenotaenia marmotae* (Fröhlich, 1802) in order to evaluate their systematic relationships and phylogenetic position among anoplocephaline cestodes of mammals.

Materials and methods

Several new 28S ribosomal RNA and mitochondrial NADH dehydrogenase subunit 1 (Nad1) sequences were obtained for *Mosgovoyia pectinata*, *M. ctenoides*, *Schizorchis caballeroi* and *Ctenotaenia marmotae,* and analysed together with published sequences of these and other anoplocephaline cestodes (Table 1). Previously, no 28S sequences were available for *M. ctenoides* and *C. marmotae*, and no published Nad1 sequences existed for anoplocephalid cestodes. Attempts to amplify DNA of *Cittotaenia denticulata* (Rudolphi, 1804) using 28S and Nad1 primers were unsuccessful. Material from East Siberia and Alaska were collected in connection with the Beringian Coevolution Project (Cook et al., 2005).

Tissue samples fixed and preserved in 70–100% ethanol were extracted using E.Z.N.A.™ Tissue Kit (OMEGA Bio-Tek). For 28S rRNA (D1–D3), DNA was amplified using three alternative pairs of primers: (1) LSU5 (forward, 5′ TAGGTCGACCCGCTG AAYTT**Y**AGCA 3′) of Littlewood et al. (2000), except that one "A" was replaced with "Y", and 1200R (reverse, 5′ GCATAGTTCACCATCTTTCGG 3′) of Lockyer et al. (2003) (*c*.1,400 bp), 2) XZ-1 (forward, 5′ ACCCGCTGAA**T**TTAAGCATAT 3′) of Waeschenbach et al. (2007), which differs from the original XZ-1 of van der Auwera et al. (1994) by having one "Y" was replaced with "T", and 1500R (reverse, 5′ GCTATCCTGAGGGAAACTTCG 3′) of Littlewood et al. (2008) (*c*. 1,660 bp), and 3) U178 (forward, 5′ GCACCCGCTGAAYTTAAG 3′) and L1642 (reverse, 5′ CCAGCGCCATCCATTTTCA 3′) (*c*. 1,500 bp), both from Lockyer et al. (2003).

For Nad1, DNA was amplified with primers Cyclo_Nad1F (forward, 5′ GGNTATTSTCARTNT CGTAAGGG 3′) and Cyclo_trnNR (reverse, 5′ TT CYTGAAGTTAACAGCATCA 3′) (*c*. 850 bp) of Littlewood et al. (2008).

Standard 50 μl PCR was performed using hot start, cycling conditions following those of Lockyer et al. (2003), Waeschenbach et al. (2007) and Littlewood et al. (2008) for 28S, and those of Littlewood et al. (2008) for Nad1. Successfully amplified DNA was purified using E.Z.N.A.™ Cycle Pure Kit (OMEGA Bio-Tek). Purified PCR products were direct sequenced using dye terminators and visualized with an ABI 3730xl DNA analyser at Macrogen Inc. (Korea).

Sequences were assembled and edited in Geneious Pro v. 4.8 (Drummond et al., 2009) and aligned with ClustalW (Thompson et al., 1997). Ambiguously aligned sites and gaps were deleted. The best substitution models, selected by the Akaike and Bayesian information criteria implemented in jModelTest (Posada, 2008), were GTR + γ and GTR + I + γ for 28S and Nad1, respectively.

Bayesian phylogenetic analyses (Huelsenbeck et al. 2001) were performed using MrBayes v. 3.1 (Ronquist & Huelsenbeck, 2003). MrBayes was run for 5 million generations, sampled every 1,000 generations, and 500,000 generations were discarded as "burnin". Node support was expressed as posterior probabilities, >95% probabilities being considered significant. Two independent runs performed for both data-sets converged in identical topologies and bootstrap values.

For 28S data, *Raillietina sonini* Spasskaya & Spasskii, 1971 (Davaineidae) (EU665462; Littlewood et al., 2008) and *Dilepis undula* (Schrank, 1788) (Dilepididae) (AF286915; Olson et al., 2001) were used as outgroups, producing a satisfactory level of resolution. For Nad1, two alternative species pairs were tested as outgroups: (1) *Hymenolepis diminuta* (Rudolphi, 1819) (NC_002767; von Nickisch-Rosenegk et al., 2001) and *Arostrilepis* sp. (HM134275; present study) (Hymenolepididae); and (2) *R. sonini* (EU665490) and *D. undula* (EU665482), both from Littlewood et al. (2008).

Cestode material and GenBank accession numbers for 28S and Nad1 sequences are listed in Table 1.

Results

Mosgovoyia pectinata and *M. ctenoides* both included identical sequences, which were discarded from the phylogenetic analyses (Table 1). *M. pectinata* (from England, Finland and East Siberia) and *M. ctenoides* (from Finland and the Canary Islands) showed very limited intraspecific divergence despite the geographical isolation of their host populations.

The 28S data showed that *M. pectinata* and *M. ctenoides* are among the basal species in the

Table 1 Cestode species, their background information and GenBank accession numbers for 28S rRNA and Nad1 sequences. New sequences in bold. Letters (A–C) in the last columns indicate identical sequences

Cestode species	Host species	Country	Region, locality	28S	Nad1
Anoplocephala perfoliata	*Equus caballus*	Australia	Victoria, Werribee	AY569769	**HM134260**
Anoplocephala magna	*Equus* (zebra)	Australia	Victoria, Werribee	AY586610	
Anoplocephaloides dentata	*Chionomys nivalis*	Italy	Trentino, Monte Bondone	EU664384	
A. dentata	*Microtus guentheri*	Turkey	Gundalan		**HM134272**
Anoplocephaloides kontrimavichusi	*Synaptomys borealis*	USA	Alaska, YUCH[1]	AY569732	
A. kontrimavichusi	*S. borealis*	USA	Alaska, GAAR[2]		**HM134274**
Andrya rhopalocephala	*Lepus europaeus*	Hungary	Hódmezővásárhely	AY569724	**HM134265**
Ctenotenia marmotae	*Marmota marmota*	France		**HM138529**	**HM134271**
Diandrya composita	*Marmota caligata*	USA	Alaska, YUCH[1]	AY569741	
Equinia mamillana	*Equus caballus*	Germany		AY569770	**HM134268**
Mosgovoyia ctenoides	*Oryctolagus cuniculus*	Finland	Helsinki	**HM045016**	**HM134262**
M. ctenoides	*O. cuniculus*	Spain	Canary Islands, La Palma	**HM045015 (A)**	**C**
M. ctenoides	*O. cuniculus*	Spain	Canary Islands, El Hierro	**A**	**HM134263** (**C**)
Mosgovoyia pectinata	*Lepus timidus*	Finland	Asikkala	**HM045013**	**HM134259**
M. pectinata	*L. timidus*	Russia	Magadanskaya Oblast, Omolon R.	**HM045012** (**B**)	**HM134261**
M. pectinata	*L. timidus*	Russia	Republic of Sakha, Elgi River	**B**	
M. pectinata	*Oryctolagus cuniculus*	England	North Yorkshire	AY569771	
Microcephaloides krebsi	*Dicrostonyx groenlandicus*	Russia	Wrangel Island	AY569754	
Microcephaloides sp. A	*Microtus agrestis*	Finland	Pallasjärvi	AY569737	
Microcephaloides sp. A	*Microtus oeconomus*	Finland	Pallasjärvi		**HM134258**
Microcephaloides sp. B	*Microtus guentheri*	Turkey	Ödemis		**HM134273**
Neandrya cuniculi	*Oryctolagus cuniculus*	Spain	Canary Islands, Tenerife	AY569723	
Paranoplocephala etholeni	*Microtus pennsylvanicus*	USA	Alaska, Fairbanks	AY569774	**HM134264**
Paranoplocephala jarrelli	*Microtus oeconomus*	USA	Alaska, WRST[3]	AY586609	
P. jarrelli	*M. oeconomus*	USA	Alaska, GAAR[2]		**HM134269**
Paranoplocephala macrocephala	*Microtus pennsylvanicus*	USA	Alaska, YUCH[1]	AY586608	
P. macrocephala	*Microtus xanthognathus*	USA	Alaska, GAAR[2]		**HM134270**
Schizorchis caballeroi	*Ochotona collaris*	USA	Alaska, YUCH[1]	AY569775, **HM045014**	**HM134266**, **HM134267**

[1] Yukon Charley Rivers National Preserve; [2] Gates of the Arctic National Park and Preserve; [3] Wrangell-St. Elias National Park and Preserve

present assemblage of anoplocephaline cestodes (Fig. 1). However, the two *Mosgovoyia* species were clearly non-monophyletic and the sister species of *M. pectinata* was *Schizorchis caballeroi*. For *Ctenotaenia marmotae*, only a forward sequence (950 bp) was available (HM138529). In a separate

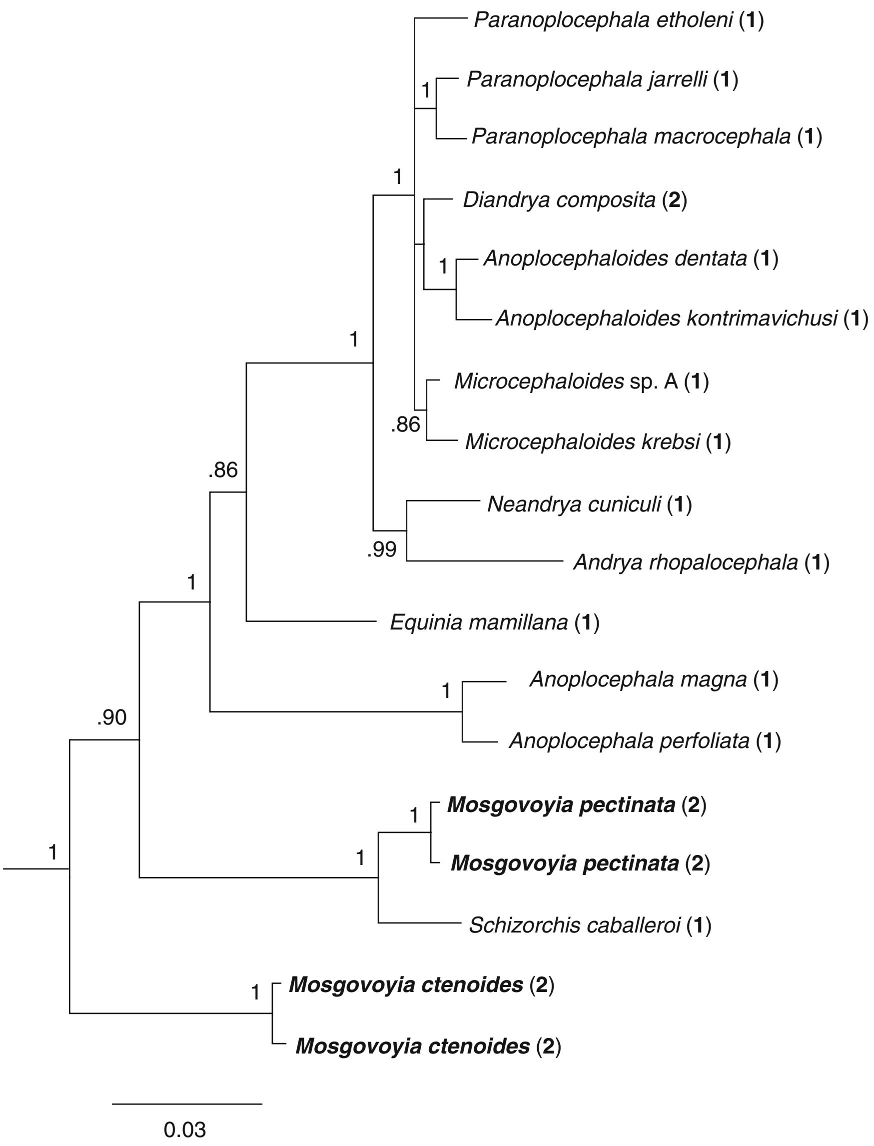

Fig. 1 Bayesian inference tree of phylogenetic relationships of *Mosgovoyia* spp. and other anoplocephaline cestodes of mammals based on sequences of partial 28S ribosomal RNA. *Raillietina sonini* and *Dilepis undula* were used as outgroups. Posterior probabilities (when ≥80%) indicated at nodes. Number of genitalia per proglottid (one or two) in parentheses after the species names

28S analysis (800 bp alignment), it grouped strongly (100%) with *Andrya rhopalocephala* (Riehm, 1881) (results not shown), thus having a more derived phylogenetic position than the two *Mosgovoyia* species.

The overall resolution of the Nad1 tree was limited, irrespective of the outgroups used (Fig. 2). The two trees (based on different outgroups) differed in the position of *Anoplocephala perfoliata* (Goeze, 1782), which was the basal species in the supported crown clade when two hymenolepidids were used as outgroups data (Fig. 2), but appeared to be associated with *M. pectinata* and *S. caballeroi* when a davaineid and dilepidid cestode were used as an outgroup (with 93% support, not shown). However, both Nad1 analyses supported unambiguously the sister species status of *M. pectinata* and *S. caballeroi*, and the independence and non-monophyly of the two *Mosgovoyia* species. In addition, *C. marmotae* grouped strongly with *Andrya rhopalocephala*, as

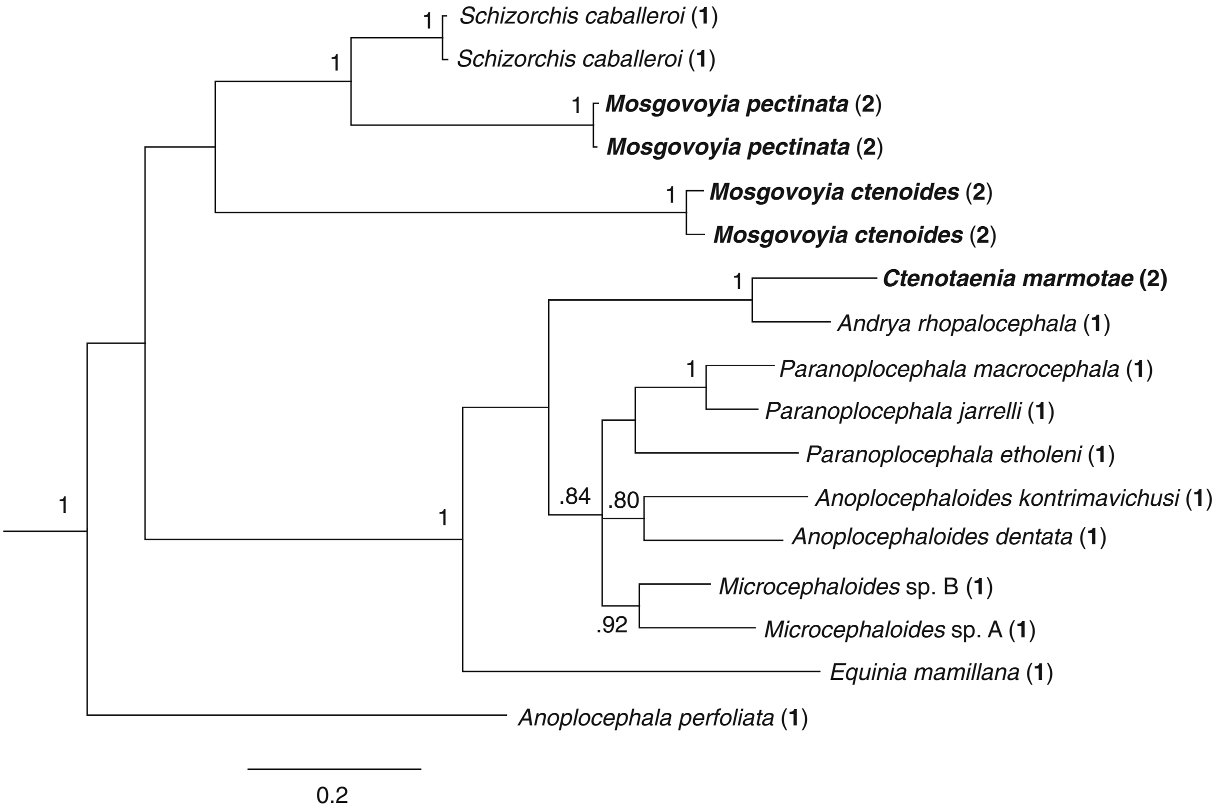

Fig. 2 Bayesian inference tree of phylogenetic relationships of *Mosgovoyia* spp. and other anoplocephaline cestodes of mammals based on sequences of partial mitochondrial Nad1 gene. *Hymenolepis diminuta* and *Arostrilepis* sp. were used as outgroups. Labels as in Fig. 1

with the 28S data. The present Nad1 data also confirmed the monophyly of the crown assemblage of *Equinia mamillana* (Mehlis in Gurlt, 1831) and more derived species, although there was less supported structure within this clade compared with phylogenies based on 28S (Fig. 1; see also Wickström et al., 2005).

Discussion

Despite the limited overall resolution of Nad1 data, both data-sets agreed in that *Mosgovoyia pectinata* and *Schizorchis caballeroi* are sister species, which are phylogenetically independent from *M. ctenoides*. The strong sister-group relationship between *M. pectinata* and *S. caballeroi* is also supported by the ITS1 rRNA sequence data of Wickström et al. (2005). Thus, the present phylogenies show unambiguously that *Mosgovoyia* [*sensu* Beveridge (1978)] is a non-monophyletic assemblage. This strongly supports the validity of *Neoctenotaenia*, erected for *Cittotaenia ctenoides* by Tenora (1976), but later synonymised with *Mosgovoyia* by Beveridge (1978).

The proposed generic distinction of *M. pectinata* and *N. ctenoides* is supported by pronounced morphological differences between them (Fig. 3). The (tubular) early uterus of *M. pectinata* does not overlap the ventral longitudinal canal, whereas the early uterus of *N. ctenoides* extends significantly across this canal. In addition, the cirrus-sac of *M. pectinata* is long and slender, usually extending across the ventral longitudinal canal, and opening anterior to the middle of the proglottid margin, thus differing from the short, oval cirrus-sac of *N. ctenoides* that opens posterior to the middle of the proglottid margin. These features have been shown to be important in the generic classification of *Anoplocephaloides* [*sensu* Rausch (1976)] (see Haukisalmi 2009). *M. pectinata* and *N. ctenoides*

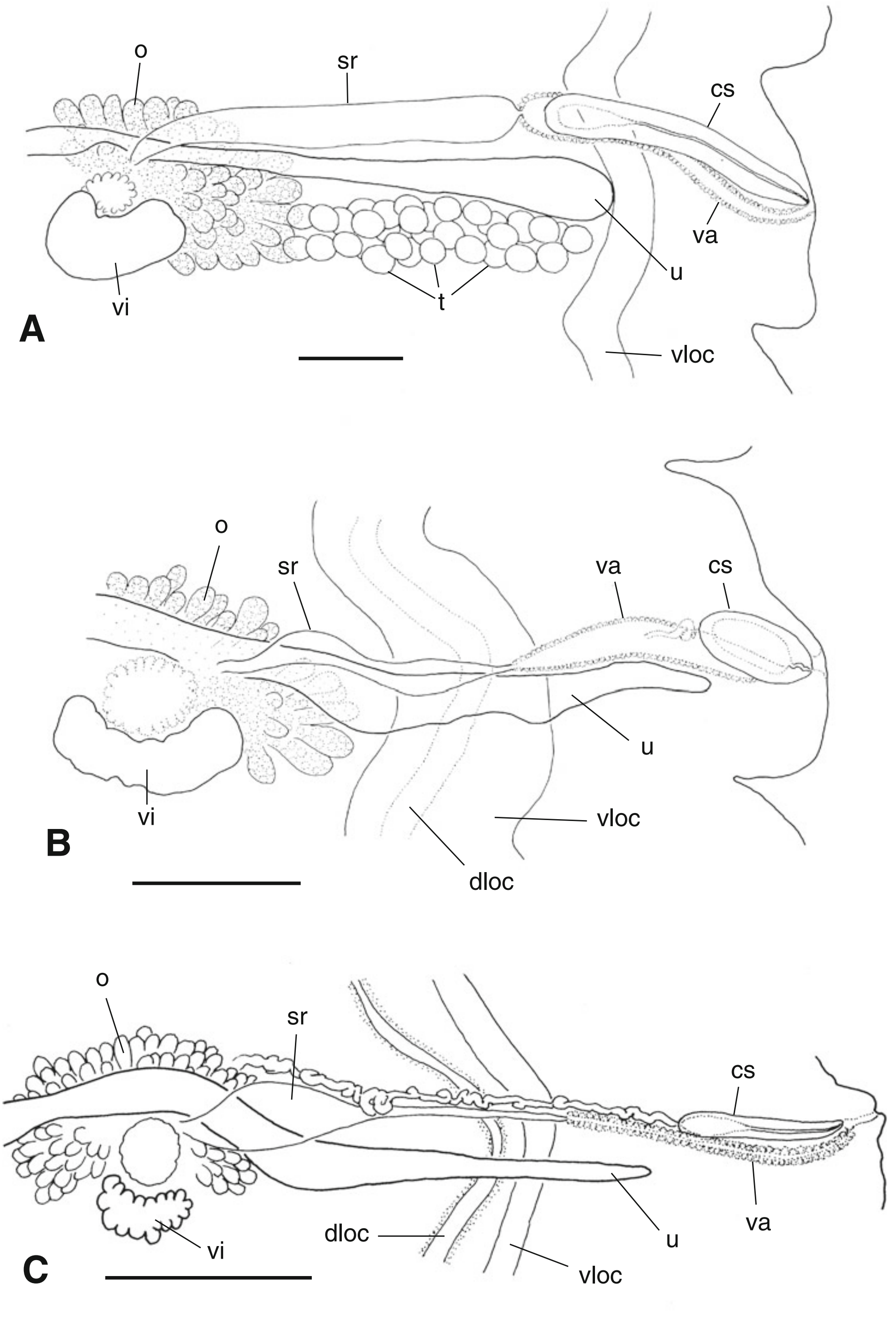

Fig. 3 Poral part of mature proglottids in *Mosgovoyia pectinata* (A), *Neoctenotaenia ctenoides* (B) and *N. variabilis* (C). C redrawn from Beveridge (1978). *Abbreviations*: o, ovary; vi, vitellarium; sr, seminal receptacle; va, vagina; u, uterus; t, testes; cs, cirrus-sac; vloc, ventral longitudinal osmoregulatory canal; dloc, dorsal longitudinal osmoregulatory canal. *Scale-bars*: 0.30 mm

also differ with respect to the poral extent of testes (always occurring poral to the female glands in the former species, but not usually in the latter), but the role of this feature in the generic level classification of anoplocephaline cestodes is undefined. In addition, *M. pectinata* should have numerous accessory osmoregulatory canals connecting transverse canals of adjacent proglottids (Spasskii, 1951; Beveridge, 1978), but these structures could not be seen in our specimens from Finland and England. Accessory canals are absent in *N. ctenoides* (see Beveridge, 1978).

Although the morphological distinction of *M. pectinata* and *N. ctenoides* is straightforward, *M. variabilis*, a species also assigned to *Mosgovoyia* by Beveridge (1978), appears to be morphologically intermediate between them (Fig. 3). The early uterus of *M. variabilis* extends across the ventral canal and the cirrus-sac is short (not reaching the ventral canal), and there are no testes poral to the female glands; these features associate it with *Neoctenotaenia* (*ctenoides*). Also, both *N. ctenoides* and *M. variabilis* have a cellular lining of the dorsal longitudinal osmoregulatory canals, which is lacking in *M. pectinata* (see Beveridge, 1994). On the other hand, the cirrus-sac of *M. variabilis* is very slender, resembling that in *M. pectinata* (and *Schizorchis*), and its genital ducts open on the middle of the proglottid margin or more anteriorly, as in *M. pectinata*. However, the overall evidence suggests that *M. variabilis* is more closely related to *Neoctenotaenia* than to *Mosgovoyia*, supporting the view of Tenora (1976). This assignment should, however, be tested by a phylogenetic analysis of anoplocephaline cestodes including *N. variabilis*.

The phylogenetic affinity between *Mosgovoyia* (*pectinata*) and *Schizorchis* (*caballeroi*) implies that their divergence has been accompanied by a change in the number of genitalia per proglottid (two and one, respectively). It has been suggested that the anoplocephaline cestodes with a double set of genitalia have arisen from related cestodes with a single set of genitalia (Baer, 1955; Beveridge, 1994). The basal relationships of mammalian anoplocephalines are partly unresolved, but in the present 28S assemblage *N. ctenoides* and *M. pectinata* (both with a double set of genitalia) belong to the basal lineages. This implies that *Schizorchis,* with a single set of genitalia, would have arisen from a *Mosgovoyia*-like ancestor with a double set of genitalia, opposite to the general assumption.

The morphologically related *Ctenotaenia marmotae* clearly represents a more derived lineage, being positioned as the sister species of *Andrya rhopalocephala*. Our mitochondrial cytochrome oxidase I (COI) sequence data of anoplocephaline cestodes available from GenBank confirm the position of *C. marmotae* (AY568187) as the sister species of *A. rhopalocephala* (AY189958), which in turn are sister to *Neandrya cuniculi* (Blanchard, 1891) (AY189957) (results not shown). The latter configuration supports the independence of *Neandrya* Haukisalmi & Wickström, 2005 with respect to *Andrya* Railliet, 1893 and other anoplocephaline cestodes (see Haukisalmi & Wickström, 2005).

The phylogenetic association of *C. marmotae* and *A. rhopalocephala* is unexpected, because *C. marmotae* appears to be morphologically similar to *Anoplocephaloides* [*sensu* Rausch (1976)] and has been suggested to have arisen by genital duplication from the latter (Beveridge, 1994). Moreover, *C. marmotae* has a double set of genitalia and a tubular early uterus, whereas *A. rhopalocephala* and *N. cuniculi* have a single set of genitalia and a reticulated early uterus. In addition to the colonisation of a novel host lineage, the divergence of *C. marmotae* and *A. rhopalocephala* was thus accompanied by two major morphological changes. Because all species (except *Diandrya composita* Darrah, 1930) in the crown clade of anoplocephaline cestodes have a single set of genitalia (Figs. 1, 2; Wickström et al., 2005), *C. marmotae* has probably diverged from a *A. rhopalocephala*-like ancestor. This divergence differs from all the other supposed doublings of the genitalia in anoplocephaline cestodes in that the diverging parasites do not represent the same host group (lagomorphs vs. rodents) (see Beveridge, 1994). However, the present analysis still lacks many of the mammalian anoplocephaline genera, and their inclusion could lead to different interpretations about evolutionary changes in the number of sets of genitalia.

Despite major morphological differences between *A. rhopalocephala, N. cuniculi* and *C. marmotae*, they are similar in their extensive distribution of testes longitudinally (anterior and posterior to the early uterus in *C. marmotae*). In this respect they differ from *Mosgovoyia* spp., *Schizorchis* spp. and *N. ctenoides*, in which testes are confined to the posterior part of the proglottid (posterior to the uterus). In fact, in the present assemblage the extensive longitudinal distribution of testes provides a synapomorphy for the crown-clade consisting of *Anoplocephala* spp. and the more derived taxa.

The present findings indicate the need for modified diagnoses of both *Mosgovoyia* and *Neoctenotaenia*.

Mosgovoyia Spasskii, 1951

Strobila of intermediate size. Scolex small. Proglottids craspedote, much wider than long. Two pairs of longitudinal osmoregulatory canals present; ventral canals connected by transverse anastomoses; accessory canals connecting transverse canals of adjacent proglottids may be present. Genitalia paired. Genital ducts cross longitudinal osmoregulatory canals dorsally. Cirrus-sac long and elongate, may extend significantly across ventral longitudinal canal. Internal seminal vesicle present; external seminal vesicle absent. Testes as single band or two (partly) separate, transverse bands posterior to early uterus and female glands, extending porally to latter but not reaching longitudinal osmoregulatory canals. Vagina long, overlapping or extending across ventral longitudinal canal, covered by distinct cell layer. Vagina ventral to cirrus-sac, opening posterior or postero-ventral to it. Elongate seminal receptacle present. Early uterus single or double, transverse, tubular, terminating posterior to genital ducts, not overlapping longitudinal osmoregulatory canals. Fully-developed uterus sac-like, with or without anterior and posterior sacculations. Eggs with pyriform apparatus. In lagomorphs (Leporidae). Type-species: *M. pectinata* (Goeze, 1782) Spasskii, 1951 (for synonyms, see Beveridge, 1978).

Neoctenotaenia Tenora, 1976

Strobila large. Scolex small. Proglottids craspedote, much wider than long. Two pairs of longitudinal osmoregulatory canals present; ventral canals connected by transverse anastomoses; accessory canals absent. Genitalia paired. Genital ducts cross longitudinal osmoregulatory canals dorsally. Cirrus-sac short, not reaching ventral longitudinal canal. Internal seminal vesicle present; external seminal vesicle absent. Testes as single band or two separate, transverse bands posterior to early uterus; few testes may extend porally to female glands. Vagina long, may overlap ventral longitudinal canal, covered by distinct cell layer. Vagina posterior, ventral or postero-ventral to cirrus-sac. Elongate seminal receptacle present. Early uterus single or double, transverse, tubular, extending significantly across longitudinal osmoregulatory canals dorsally, terminating posterior to genital ducts. Fully-developed uterus sac-like, with or without anterior and posterior sacculations. Eggs with pyriform apparatus. In lagomorphs (Leporidae). Type-species: *N. ctenoides* (Railliet, 1890) Tenora, 1976 (for synonyms, see Beveridge, 1978). Other species: *N. variabilis* (Stiles, 1895) Tenora, 1976 (for synonyms, see Beveridge, 1978).

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