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VERSITA

Taxonomy and genetic divergence of *Paranoplocephala kalelai* (Tenora, Haukisalmi et Henttonen, 1985) (Cestoda, Anoplocephalidae) in the grey-sided vole *Myodes rufocanus* in northern Fennoscandia

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Abstract

Paranoplocephala kalelai (Tenora, Haukisalmi et Henttonen, 1985) is an anoplocephalid cestode that primarily parasitizes the grey-sided vole *Myodes rufocanus* (syn. *Clethrionomys rufocanus*) in northern Fennoscandia. In a preliminary molecular phylogenetic analysis, the cytochrome oxidase I (mtDNA) sequences of *P. kalelai* formed two divergent sublineages originating from two different localities in northern Finland and northern Norway. The present data confirm the existence of two strongly supported clades and show that their geographic distributions are overlapping in northernmost Finland. Relatively deep genetic divergence and coexistence of the two main clades at one of the localities suggest that the material may include two biological species. However, because the specimens representing the two mtDNA clades of *P. kalelai* are not morphometrically sufficiently differentiated and because the mtDNA clade of the specimens from the type locality is unknown, they are not assigned to different species. Comparison with the existing phylogeographic data of *M. rufocanus* suggests that the genetic structure of this host-specific cestode reflects the glacial and post-glacial history of its primary host. A redescription is presented for *P. kalelai*.

Keywords

Cestoda, Anoplocephalidae, *Paranoplocephala kalelai*, Rodentia, *Myodes rufocanus*, cytochrome oxidase I, mtDNA

Introduction

Paranoplocephala kalelai (Tenora, Haukisalmi et Henttonen, 1985) is an anoplocephalid cestode of the grey-sided vole *Myodes rufocanus* (syn. *Clethrionomys rufocanus*), and, less frequently, of the bank vole *Myodes glareolus* (syn. *Clethrionomys glareolus*), in northernmost Fennoscandia (Tenora *et al*. 1985, Haukisalmi *et al*. 1987). The molecular phylogenetic analysis of Haukisalmi *et al*. (2004) and Wickström *et al*. (2005) confirmed the status of *P. kalelai* as an independent species, and showed that *P. kalelai* belongs to *Paranoplocephala* Lühe, 1910 s. str., a monophyletic assemblage including the type species *P. omphalodes* (Hermann, 1783). The main morphological differences between *P. kalelai* and the related, Nearctic *Paranoplocephala macrocephala* (Douthitt, 1915) have been described by Haukisalmi and Henttonen (2003).

Most of the species representing *Paranoplocephala* s. str. parasitize *Microtus* spp. in the Holarctic region (Tenora *et al*. 1999, Haukisalmi *et al*. 2004); *P. kalelai* is the only species within this clade known to be specific to the *Myodes* voles earlier assigned to *Clethrionomys* (for the taxonomy of these vole genera, see Carleton and Musser 2005). The probable sister species of *P. kalelai* is *Paranoplocephala jarrelli* Haukisalmi, Henttonen et Hardman, 2006, a Holarctic parasite of the root/tundra vole *Microtus oeconomus* and other northern *Microtus* species (Haukisalmi *et al*. 2004, 2006). These facts suggest that *P. kalelai* has speciated through a shift from *M. oeconomus* to *M. rufocanus* in northern Europe.

In an earlier molecular phylogenetic analysis (Haukisalmi *et al*. 2004), the four cytochrome oxidase I (COI) sequences (mtDNA) of *P. kalelai* formed two divergent sublineages, which occurred at two different localities in northern Finland and northern Norway. Because of the high genetic distance between the subclades, they may be regarded as independent species providing they exhibit consistent morphological differences. In the present study, extended morphometric and

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molecular data sets are analysed to assess whether two morphologically identifiable groups exist within *P. kalelai* corresponding to the two mtDNA clades. Because many important details (e.g. the structure of the early uterus) were missing in the original description, a redescription is presented for *P. kalelai*.

Materials and methods

Four specimens of *P. kalelai* used in the preliminary analysis of Haukisalmi *et al*. (2004) and three additional specimens were sequenced for the mitochondrial cytochrome oxidase I (COI) gene (mtDNA). For the extraction, amplification and sequencing of DNA, see Wickström *et al*. (2003, 2005) and Haukisalmi *et al*. (2004). The GenBank numbers for the COI sequences are given in Table I and Figure 1. Five of the sequenced specimens originated from *M. rufocanus* from Kilpisjärvi (69°03´N, 20°55´E) in north-western Finnish Lapland and two from the same host species from Narvik (68°28′N, 17°26′E) in northern Norway (the two specimens from Narvik were erroneously reported as originating from *Myodes glareolus* in Haukisalmi *et al*. 2004). Sequences of *P. kalelai* (641 bp) were aligned using Clustal X (Thompson *et al*. 1997) with sequences of *P. jarrelli*, *P. omphalodes*, *Andrya rhopalocephala* (Riehm, 1881) and *Neandrya cuniculi* (Blanchard, 1891) (Fig. 1). A neighbour-joining distance phylogram was constructed in PAUP* (version 4.0 b10, Swofford 2002) using Kimura 2-parameter distances. Bootstrap support for the topology was estimated through 10000 replicates.

The cestodes used for morphology were fixed flat (without pressure) in 70% ethanol, stained with Mayer's haemalum, Semichon's acetocarmine or iron-acetocarmine, cleared in eugenol and mounted in Canada balsam. Representative specimens (whole-mounts) of *P. kalelai* have been deposited in the Museum of Southwestern Biology, University of New Mexico, USA (MSB), the Harold W. Manter Laboratory of Parasitology, Nebraska State Museum, USA (HWML), and the Hungarian Natural History Museum, Budapest (HNHM) (Table I).

The material consisted of 33 gravid or pregravid specimens from *M. rufocanus* identifiable as *P. kalelai*, originating from Kilpisjärvi (N = 23), Pallasjärvi (68°03′N, 24°09′E, N = 6) and Inari (68°54´N, 27°05´E, N = 2) in Finnish Lapland, and Narvik (N = 2) in Norway. Twelve additional, poorly stained and/or contracted gravid specimens were used for the measurement of egg length only. The holotype and paratype specimens of *P. kalelai* from *M. rufocanus* from Pallasjärvi, deposited at the Finnish Museum of Natural History (Zoology), Helsinki (nos. 20500 and 20501 + 20502, respectively), were not included in the morphometric analysis.

The morphometric analysis was performed on eight specimens representing the "Narvik" (N = 3) and "Kilpisjärvi" (N = 5) mtDNA clades (below). The analysis included 15 absolute measurements of strobila, scolex, suckers, eggs, and various internal organs. Width of the ovary, vitellarium and ventral longitudinal osmoregulatory canals, number of testes, length of the cirrus sac, and diameter of the seminal receptacle were recorded from 1–4 mature proglottids from each specimen. The maximum dimensions of the cirrus sac, seminal receptacle and ventral longitudinal canals were also re-

Table I. Accession and GenBank numbers for the specimens of *Paranoplocephala kalelai* from *Myodes rufocanus* used in the morphometric analysis and molecular phylogenetic analysis. "Narvik" and "Kilpisjärvi clades" refer to the two mtDNA (COI) clades (see Fig. 1). See Materials and methods for abbreviations of museums used for the deposition of mounted voucher specimens

Clade Locality	Accession numbers for mounted voucher specimens	GenBank numbers for COI sequences
Narvik clade		
Kilpisjärvi, Finland	HNHM 67421	EF583963
Narvik, Norway	–	AY181513
Narvik	MSB Endo 23	AY189959
Kilpisjärvi clade		
Kilpisjärvi	–	EF583961
Kilpisjärvi	MSB Endo 28	EF583962
Kilpisjärvi	MSB Endo 26	AY181511
Kilpisjärvi	MSB Endo 27	AY181512
Clade unknown		
Kilpisjärvi	HWML 16698	–
Kilpisjärvi	HWML 16699	–
Kilpisjärvi	HNHM 67420	–
Kilpisjärvi	MSB Endo 30	–
Pallasjärvi, Finland	MSB Endo 29	–
Pallasjärvi*	MSB Endo 24	–
Inari, Finland	MSB Endo 25	–

*Host *Myodes glareolus*.

corded from each strobila. In addition, 8 relative measurement were calculated: the length/width ratio of mature and gravid proglottids, dimensions of the ovary, vitellarium, cirrus sac and seminal receptacle in relation to the width of the corresponding mature proglottid, and the diameter of suckers and minimum width of the neck in relation to the width of the scolex. Each of these variables was compared between specimens representing the two mtDNA clades (below). Because of the small number of specimens and measurements, no statistical methods were used in this comparison. All measurements are in millimetres.

Results

The seven COI sequences of *P. kalelai* formed two highly supported clades (Fig. 1), corroborating the preliminary results of Haukisalmi *et al*. (2004). However, the present data showed that the "Narvik clade" is not restricted to that particular locality, and that the "Narvik clade" and "Kilpisjärvi clade" co-occur at Kilpisjärvi (Table I). The pairwise Kimura 2-parameter distance between the two clades was 0.037, which is less than the corresponding distances between the other species of *Paranoplocephala* s. str. (0.063–0.116, mean 0.0849, n = 10) (Haukisalmi *et al*. 2004). Both clades included supported subclades.

Among the 23 morphometric variables used, only three were nearly non-overlapping between the two mtDNA clades, i.e. the relative width of the ovary, egg length and maximum length of the seminal receptacle (Table II); the remaining 20 measurements overlapped considerably. The number of significant differences is barely more than the number of significantly different variables expected by chance alone (i.e. 1–2). Moreover, the egg length is based on only two specimens from each clade.

Relatively deep genetic divergence and coexistence of the two main clades at Kilpisjärvi suggest that the material may include two biological species. However, because of the small number of significant quantitative differences and absence of consistent qualitative differences, the specimens representing the two mtDNA clades are not sufficiently differentiated to assign them to different species. Moreover, the mtDNA clade of the holotype specimen of *P. kalelai* from Pallasjärvi, or any other specimens from the type locality, are unknown.

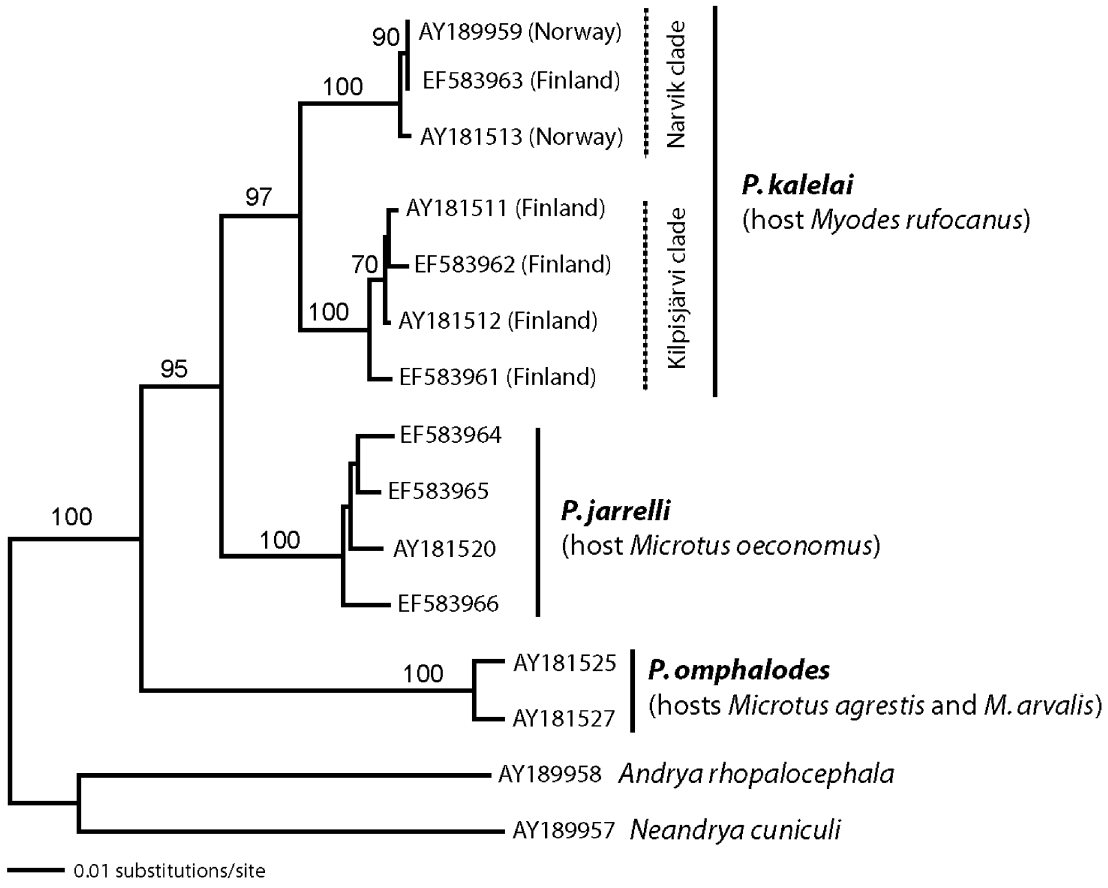

Fig. 1. A neighbour-joining reconstruction of partial cytochrome oxidase I (mtDNA) sequences of *Paranoplocephala kalelai*, *P. jarrelli* and *P. omphalodes*. *Andrya rhopalocephala* and *Neandrya cuniculi* from lagomorphs were used as an outgroup. The labels show the GenBank number and locality. Values at nodes show the percentage from 10000 bootstrap replicates

***Paranoplocephala kalelai* (Tenora, Haukisalmi et Henttonen, 1985)** (Figs 2 and 3)
Syn.: *Andrya kalelai* Tenora, Haukisalmi et Henttonen, 1985

The redescription is based on 30 specimens from *Myodes rufocanus* from Finnish Lapland. The mean and number of measurements (n) are given in parentheses after the range, and the deviating maximum values of the original description (Tenora *et al*. 1985) are shown in brackets.

Description: Fully developed strobila 95–167 [191] (130, n = 17) long and relatively thin; maximum width 0.98–2.06 [2.3] (1.55, n = 20), attained in pregravid or gravid proglottids. Number of proglottids 300–350 (n = 5). Scolex 0.60–0.97 [1.16] (0.73, n = 22) wide, with protruding, crateriform suckers usually directed anteriorly; width of suckers 0.28–0.36 [0.40] (0.325, n = 22) or 37–54% (45%, n = 22) of scolex width. Neck 0.3–0.7 (0.51, n = 18) long and usually very narrow: 0.13–0.31 (0.19, n = 23) or 17–43% (26%, n = 22) of scolex width. Proglottids craspedote, but velum very short or absent in well-relaxed specimens. Length/width ratio 0.20 –0.65 (0.36, n = 36) in mature proglottids, increasing markedly in gravid proglottids (0.43–1.02, 0.63, n = 21). Genital

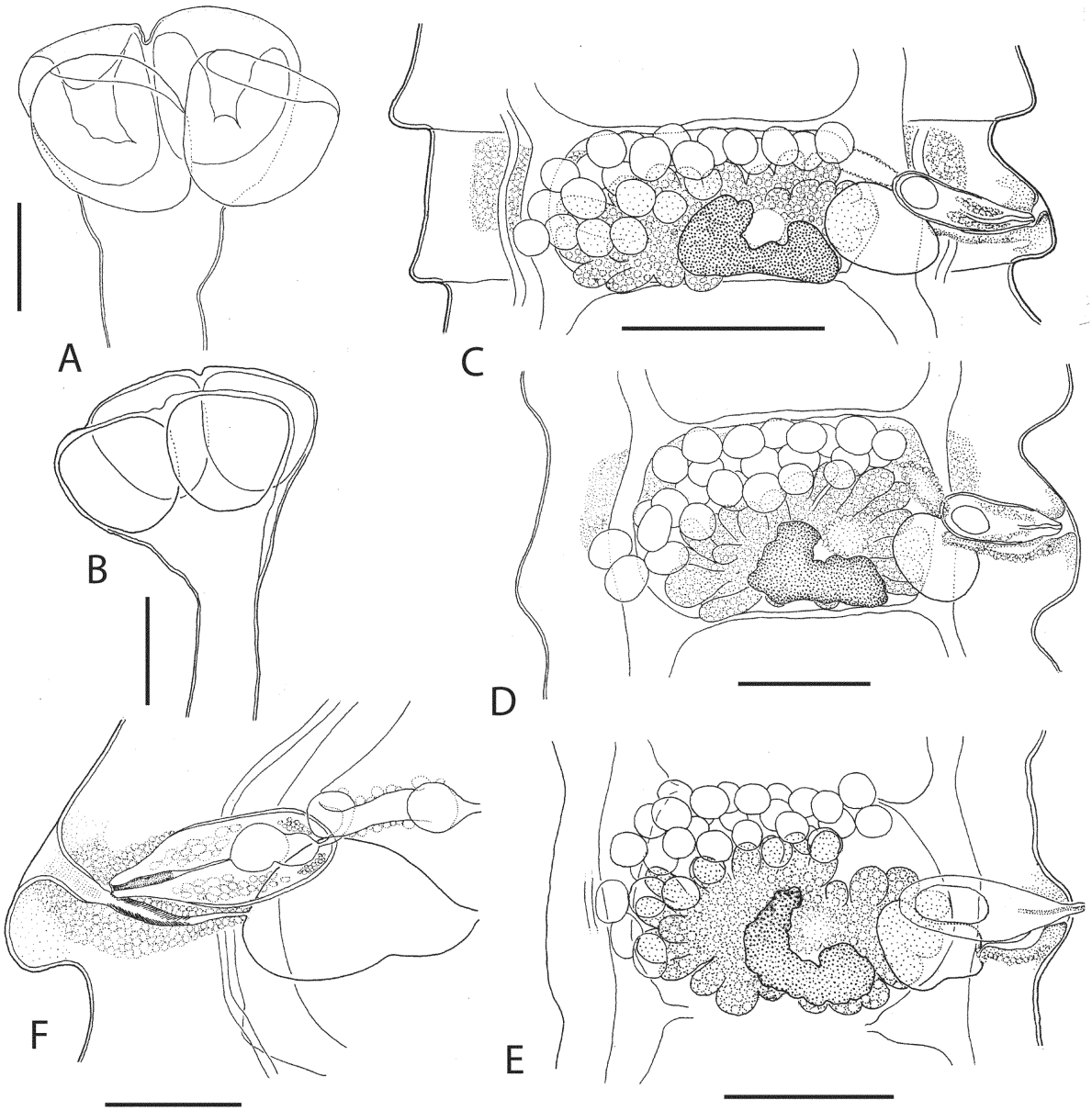

Fig. 2. Scolex and mature proglottids of *Paranoplocephala kalelai* from *Myodes rufocanus*: **A** – scolex, Kilpisjärvi, Finland ("Kilpisjärvi clade"). **B** – scolex, Kilpisjärvi ("Narvik clade"). **C** – mature proglottid, Pallasjärvi, Finland (mtDNA-clade unknown). **D** – mature proglottid, Kilpisjärvi ("Kilpisjärvi clade"). **E** – mature proglottid, Narvik, Norway ("Narvik clade"). **F** – terminal genital ducts, Kilpisjärvi (mtDNA-clade unknown). Scale bars = 0.20 mm (A, D, E), 0.30 mm (B, C), 0.10 mm (F)

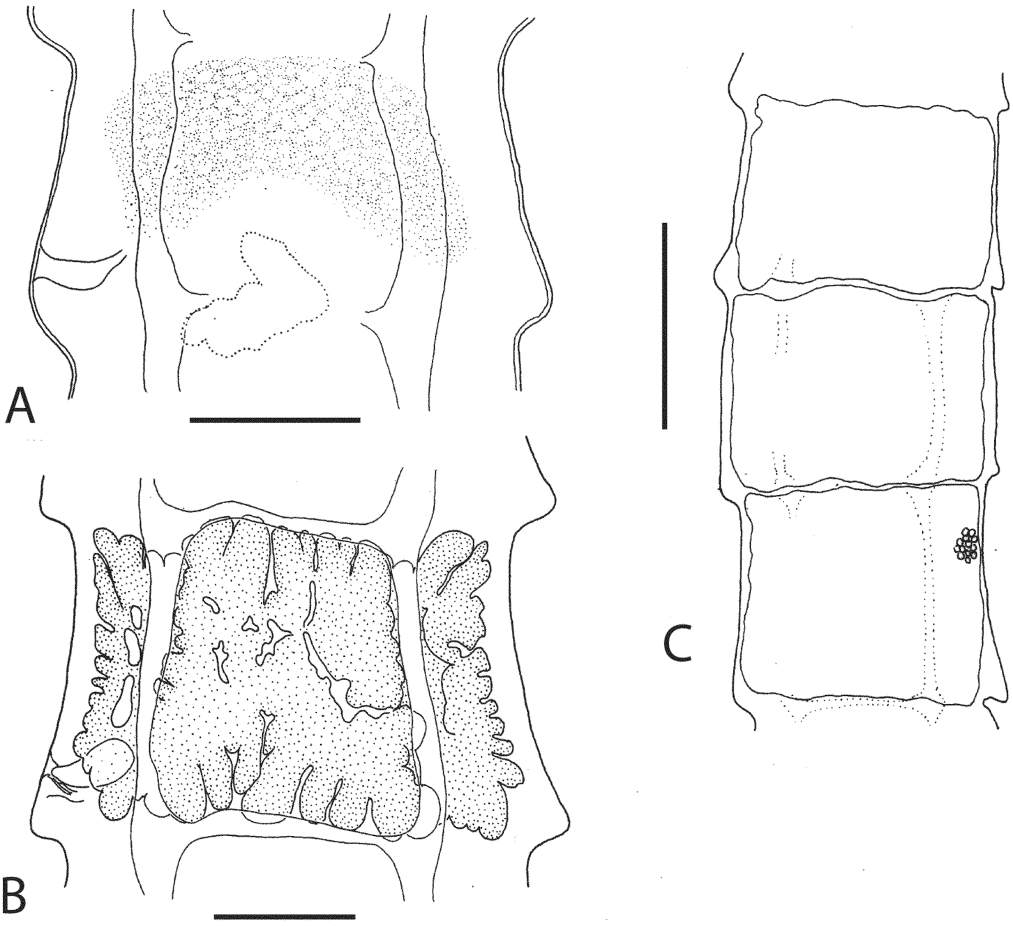

Fig. 3. Uterine development in *Paranoplocephala kalelai* from *Myodes rufocanus* from Kilpisjärvi, Finland: **A** – early uterus in a mature proglottid ("Kilpisjärvi clade"). **B** – fully developed uterus in a pregravid proglottid (mtDNA-clade unknown). **C** – fully gravid terminal proglottids (mtDNA-clade unknown). Scale bars = 0.20 mm (A), 0.30 mm (B, C)

pores opening in posterior half of proglottid margin. Genital pores irregularly alternating, exceptionally unilateral or with single change per strobila; in specimens with multiple changes on average 13.3 proglottids in each unilateral set or 8.5 changes per 100 proglottids.

Ventral longitudinal osmoregulatory canals 0.015–0.085 (0.048, n = 40) wide in mature proglottids, maximum width (0.05–0.11, 0.08, n = 22) attained usually in pregravid or gravid proglottids. Ventral longitudinal canals connected by transverse canals measuring 0.014–0.030. Dorsal longitudinal osmoregulatory canals 0.011–0.020 wide, lateral to ventral canals. Genital ducts passing dorsally across longitudinal osmoregulatory canals and nerve cord.

Testes 24–38 (29.6, n = 37) in number, forming compact group extending from antiporal to poral ventral osmoregulatory canal, often overlapping former canal dorsally, but not extending across it. Testes overlap ovary, often in contact with antiporal lobe of vitellarium. Diameter of testes 0.050–0.075.

Cirrus sac 0.15–0.23 (0.19, n = 40) long and 0.050–0.095 (0.070, n = 39) wide in mature proglottids, elongate, shallow constriction sometimes present at its proximal third. Length of cirrus sac increases marginally in postmature proglottids; maximum length 0.18–0.25 (0.21, n = 23). Muscle layers of cirrus sac poorly developed. Cirrus sac overlaps ventral longitudinal canal or extends across it; rarely non-overlapping with ventral canal. Ductus cirri short, usually straight, with minute spines in its distal part. Internal seminal vesicle initially spherical or ovoid, elongate when filled with sperm, filling up to 2/3 of cirrus sac length. External seminal vesicle fairly long, usually looped, covered by loose, poorly stained cell layer.

Vagina 0.11–0.16 (0.14, n = 12) long or 57–89% (77%, n = 12) of cirrus sac length, running posteriorly or postero-ventrally to cirrus sac. Walls of vagina formed by dense layer of large cells; this cell layer thickens distally, merging with cell layer surrounding genital atrium. Distal vaginal tube lined internally by delicate microtriches (seen best in sections); vaginal tube widening distally. Seminal receptacle 0.10–0.19 (0.14, n = 24) long and 0.07–0.13 (0.10, n = 24) wide in mature proglottids; asymmetrically elongate, pyriform or ovoid when filled with sperm. Maximum length of seminal receptacle (0.18–0.28, 0.23, n = 24) attained in postmature proglottids. Vitellarium asymmetrically bilobed, 0.14–0.25 (0.19, n = 40)

Table II. The morphometric variables that were completely or nearly non-overlapping between the two mtDNA clades of *Paranoplocephala kalelai*. The twenty other absolute and relative measurements (see Materials and methods) were widely overlapping between the clades

	Narvik clade (N = 3)		Kilpisjärvi clade (N = 5)	
	n	range (mean)	n	range (mean)
Ovary, relative width	5	0.54–0.62 (0.59)	11	0.44–0.55 (0.49)
Egg, length	18	0.040–0.045 (0.042)	12	0.035–0.040 (0.036)
Seminal receptacle, max. length	2	0.20–0.25	3	0.18–0.20

N – number of specimens examined, n – number of measurements.

wide and 0.08–0.19 (0.12, n = 37) long, positioned usually slightly porally with respect to mid-line of ovary and proglottid (index of asymmetry 0.38–0.51, 0.44, n = 40). Ovary large (width 0.26–0.51, 0.37, n = 38; length 0.15–0.27, 0.21, n = 34), coarsely lobed, positioned medially, usually covering whole space between ventral longitudinal canals, often slightly overlapping them.

Uterus appears in early mature proglottids as transverse, finely reticulated band positioned anteriorly and ventrally to other organs and extending across longitudinal osmoregulatory canals bilaterally. Lateral ends of early uterus extend more posteriorly than central part; early uterus does not markedly overlap ovary. Fully developed uterus covering most of medulla, with few anterior, posterior and lateral sacculations; internal structures simple. Eggs 0.030–0.045 (0.038, n = 214) long and 0.025–0.036 (0.028, n = 47) wide, spherical or slightly ovoid in surface view, usually slightly citriform in side view. Pyriform apparatus present.

Discussion

Paranoplocephala kalelai is the most common tapeworm of *M. rufocanus* in northern Fennoscandia, its overall prevalence ranging between 21–27%. However, the prevalence may reach 90% in adult, overwintered males (Haukisalmi *et al*. 1987). *Paranoplocephala kalelai*, or morphologically corresponding cestodes, have not been reported outside northern Fennoscandia, including the extensive study Yushkov (1995) from north-western Russia. The endemicity of *P. kalelai* suggests that the shift from *M. oeconomus* and subsequent divergence in *M. rufocanus* have taken place in north-western Eurasia. The Holarctic *P. jarrelli*, the probable precursor of *P. kalelai*, presently has an overlapping distribution with the latter species in northern Fennoscandia.

Paranoplocephala kalelai is the only host-specific helminth of *M. rufocanus* in the western part of its range (Haukisalmi *et al*. 1987). In Central and eastern Siberia, *M. rufocanus* is parasitized by another host-specialist cestode, *Paranoplocephala buryatiensis* Haukisalmi, Hardman, Hardman, Laakkonen, Niemimaa et Henttonen, 2007 (see Haukisalmi *et al*. 2007), and in Hokkaido (Japan) by *Anoplocephaloides dentatoides* Sato, Kamiya, Tenora et Kamiya, 1993, also a host-specific, endemic anoplocephalid cestode of the grey-sided vole (Sato *et al*. 1993). Interestingly, the three known host-specific anoplocephalid cestodes of *M. rufocanus* have non-overlapping distributions.

The pronounced genetic structure of *P. kalelai* suggests that its glacial and postglacial history differs from those of the other northern European *Paranoplocephala* and *Anoplocephaloides* species of voles (Wickström 2004, L.M. Hardman *et al*., unpubl.). The presence of two divergent clades within *P. kalelai* may due to isolation of *M. rufocanus* at least in two glacial refugia, and subsequent recolonization and spatial overlap of the diverged populations. Some rodents have recolonized Fennoscandia via two main routes, i.e. through a periodical isthmus in present-day Denmark and southern Sweden (western route), and from the south-east through present-day Finland (Jaarola *et al*. 1999), but there are no hypotheses or data on the post-glacial colonization of *M. rufocanus* into northern Fennoscandia. The oldest fossils of *M. rufocanus* are from Middle Pleistocene from Japan and the Baikal area, which led Chaline and Graf (1988) to propose that *M. rufocanus* probably diverged in the Far East ca. 0.7 Mya. To our knowledge, no fossils of *M. rufocanus* have been found in western Eurasia.

There exists a single spatially extensive molecular phylogenetic data set of *M. rufocanus*, i.e. the cytochrome *b* (mtDNA) sequence data of Cook *et al*. (2004), consisting of 13 specimens of *M. rufocanus* from its western- and eastern-most populations. These data do not give unambiguous support for the monophyly of *M. rufocanus*; in fact, the grey-sided vole may be paraphyletic with respect to *Myodes regulus* (syn. *Eothenomys regulus*) and *Myodes smithii* (syn. *Phaulomys smithii*) from Korea and Japan, respectively. However, there are two strongly supported monophyletic groups within *M. rufocanus*, i.e. a Japanese clade and another, widely distributed clade, spanning from Finnish Lapland and Kola Peninsula (Russian Federation) in the west to Magadan (Russian Federation) in the east. Within the latter clade, there is a strongly supported western subclade at Kilpisjärvi and on the Kola Peninsula. These data also show that two separate sublineages of *M. rufocanus* co-occur at Kilpisjärvi.

Thus, the two main lineages of *P. kalelai* may have diverged as a response to a corresponding split in its primary host. No divergence time estimates are available for *M. rufo-*

canus, but the deepness of the cestode divergence suggests that it probably predates the latest glacial cycle and may have occurred repeatedly. In the absence of fossils and comprehensive phylogeographic data for the western populations of the grey-sided vole, the possible glacial refugia of *M. rufocanus* and *P. kalelai* cannot, however, be identified.

Although the existing data on the phylogeography of *P. kalelai* and *M. rufocanus* are scanty, they suggest that the genetic structure of this host-specific cestode reflects the glacial and post-glacial history of its host. However, the patterns of host-anoplocephaline cestode coevolution may actually be complex and include shifts of parasites to alien host lineages and other deviations from the assumption of parasite-host cophylogeny (Haukisalmi *et al*. 2004, Hu *et al*. 2005, Wickström *et al*. 2005).

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