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Morphological characterisation of *Paranoplocephala bairdi* (Schad, 1954) (Cestoda: Anoplocephalidae) in heather voles *Phenacomys* spp. and tree voles *Arborimus* spp., and related species in voles and lemmings (Muridae: Arvicolinae)

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Abstract. The taxonomical status of *Paranoplocephala bairdi* (Schad, 1954)-like cestodes (Anoplocephalidae) in heather voles *Phenacomys* spp. and tree voles *Arborimus* spp. (Muridae: Arvicolinae) and their discrimination from five related species of *Paranoplocephala* is assessed using uni- and multivariate morphometrics. The analyses support the independent status and conspecificity of specimens from *Phenacomys* spp. and *Arborimus* spp., and *P. bairdi* is therefore suggested to be a host-specialist species of heather and tree voles with a wide geographical distribution in North America. A redescription is presented for *P. bairdi*.

Heather voles (*Phenacomys* Merriam) and tree voles (*Arborimus* Taylor) represent an assemblage of closely related Nearctic species of arvicoline rodents; see Musser and Carleton (1993), Wilson and Ruff (1999) and Bellinger et al. (2005) for the taxonomy and geographical distribution of heather and tree voles. Heather voles and tree voles occur either in low numbers and/or have a specialised (arboreal) life-style (Verts and Carraway 1998, Wilson and Ruff 1999), which explains the scarcity of parasitological research performed on them. So far, 3–4 species of anoplocephalid cestodes (below) and two species of heligmosomid nematodes (Durette-Desset et al. 1972, Rausch and Rausch 1973) have been reported from *Phenacomys*, but there are no published records of helminths of *Arborimus*, except for the finding of *Andrya* sp. in *A. pomo* (reported as "*Phenacomys longicaudus*" by Voge 1955). Data on helminth parasitism in *Arborimus* spp. would be particularly interesting, since these species are presently listed as endangered or threatened due to the decline and fragmentation of their preferred habitats (old-growth forests; e.g. Verts and Carraway 1998), and obtaining helminth material in future may be uncertain.

Andrya bairdi Schad, 1954 (Anoplocephalidae) was described by Schad (1954) from *Phenacomys ungava* from Quebec, Canada [the host species of *P. bairdi* was erroneously reported as *Microtus chrotorrhinus* (Miller); see Peterson 1962]. *Andrya bairdi* has subsequently been included within the genus *Paranoplocephala* Lühe, 1910, as emended by Rausch (1976), along with other *Andrya*-like cestodes parasitizing arvicoline rodents (voles and lemmings) (e.g. Tenora et al. 1986, Haukisalmi and Henttonen 2000). It has been recently shown by a molecular phylogenetic analysis that *Andrya* and *Paranoplocephala* represent two independent genera, and that all species from arvicoline rodents belong to the latter genus (Wickström et al. 2005).

It should be emphasised that there exist no records of this species after the original description. Haukisalmi and Henttonen (2000) redescribed *P. bairdi* briefly from a single paratype specimen and compared it with *P. fellmani*, a parasite of *Lemmus* spp., but the morphological features that distinguish *P. bairdi* from the other related species have not been defined. Thus, although *P. bairdi* has consistently been recognized as a valid species, the morphological variation, host range and geographical distribution of this species remain poorly known.

We describe here the morphological variation within *P. bairdi*-like cestodes, including the type specimens from *P. ungava*, and compare them with five morphologically related species of *Paranoplocephala* from voles, lemmings and squirrels using uni- and multivariate morphometrics. *Paranoplocephala bairdi* is redescribed according to the material from *Phenacomys* spp. and *Arborimus* spp.

MATERIALS AND METHODS

Cestodes. The *Paranoplocephala* material from *Phenacomys* and *Arborimus* consists of 18 specimens, including the holotype and two paratypes of *P. bairdi* (Table 1). These specimens are compared morphometrically with *P. arctica* (Rausch, 1952) sensu Haukisalmi et al. 2001, *P. fellmani*

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Haukisalmi et Henttonen, 2001, *P. nordenskioeldi* Haukisalmi, Wickström, Hantula et Henttonen, 2001, *P. primordialis* (Douthitt, 1915) and *P. serrata* Haukisalmi et Henttonen, 2000. They resemble *P. bairdi* in having unilateral or infrequently alternating genital pores, small scolex, long and slender neck, long vagina relative to the length of the cirrus sac and basically similar distribution of testes (see Haukisalmi et al. 2002 for main morphological features of *Paranoplocephala* spp. in Holarctic rodents). These five species have either a Nearctic (*P. arctica*, *P. primordialis*) or a wide Holarctic distribution. A sample of each of these species was measured for the present morphometric analysis, and therefore the measurements in Tables 3 and 4 do not exactly correspond to those in the original descriptions or later redescriptions.

Cestodes were fixed in 70% ethanol, 10% formalin or Bouin's fixative, stained usually with Semichon's acetic carmine or Mayer's haemalum and mounted in Canada balsam.

Representative specimens of *P. bairdi* from each host species have been deposited in the United States National Parasite Collection, Beltsville, Maryland (USNPC; Table 1).

Morphometrics. When possible, 19 absolute and 2 relative measurements were recorded from each individual (Tables 3 and 4). Since we have earlier shown that replicate measurements are not necessary for assessing interspecific morphometric differences within *Paranoplocephala* (Haukisalmi and Henttonen 2003, Haukisalmi et al. 2004), organ dimensions were calculated from a single representative mature proglottis from each individual. However, replicate measurements were recorded for the diameter of suckers (usually four measurements per individual) and length of eggs (5–10 measurements per individual). For replicate measurements, the median value was used in the statistical analysis.

The scolex, neck and mature proglottides were drawn on paper with the aid of camera lucida, and various organs were counted and measured from these drawings using a calibrated ruler. Neck length was measured from the posterior margin of suckers to the beginning of visible segmentation. The poral distance of vitellarium (PV) was measured from the midpoint of vitellarium to the poral margin of the proglottis, and the distance between vitellarium and ovary (DO) was measured as the distance between the midpoints of these glands. The distribution of testes was characterized by three absolute variables (TD, PTN and ATN). TD is the transverse width of the testicular field, PTN (number of poral testes) refers to testes situated porally to the midline of the proglottis, and ATN (number of antiporal testes) to those situated antiporally to the ventral osmoregulatory canal. Cirrus sac was measured only if the cirrus was fully invaginated. Maximum length of cirrus sac (CSM) and seminal receptacle (SRM) were recorded from postmature proglottides.

In addition to the absolute measurements, we calculated two relative measurements, which are known as potentially important in the discrimination of anoplocephaline cestodes, i.e. the length/width ratio of mature proglottides and the index of asymmetry, quantifying the asymmetrical position of vitellarium. The latter was calculated as a ratio between the poral distance of vitellarium (measured from the midpoint of vitellarium to the poral margin of the proglottis) and the width of the corresponding proglottis.

Comparisons of absolute and relative measurements between different cestode species were performed using parametric one-way analysis of variance. If this test indicated significant differences ($p<0.05$), Tukey's HSD-test was used to evaluate the pairwise differences between *P. bairdi* and each of the other species (Tables 3 and 4).

Since many of the morphometric variables were found to be strongly correlated with each other, we performed a principal component analysis (PCA) on 13 absolute organ measurements (Table 3). The idea of PCA is to extract a smaller set of new, uncorrelated variables (principal components) from the original, correlated variables. The principal components, which often reflect particular morphometric traits, can then be used in the subsequent statistical comparisons. The external dimensions and egg length (Table 4) were not included in the PCA because of several missing values.

We also performed a discriminant analysis for the six *Paranoplocephala* species using again the 13 absolute organ dimensions (Table 3). However, these results should be interpreted cautiously due to the frequent correlations between morphometric variables. The canonical discriminant functions were calculated using all variables simultaneously. Cross-validation (jack-knifing) was used to evaluate the success of the discriminant functions to correctly classify the specimens under study, i.e. each specimen was classified by the discriminant functions derived from all specimens other than that specimen. No detailed results are shown for the principal component and discriminant analyses.

To improve fit to the normal distribution, arcsin√x-transformation was performed on relative measurements (ratios). Statistical analyses were performed with SPSS for Windows® 10.0.05 (standard version).

RESULTS

Since we could not find consistent morphological differences between the type material of *P. bairdi* (host *P. ungava*) and the specimens from the other *Phenacomys* and *Arborimus* species, they are all classified here as *P. bairdi* (see Discussion).

Univariate comparisons between *Paranoplocephala bairdi* and related species

Each of the species compared here with *P. bairdi* differed significantly for 7–13 morphometric variables (total number of variables 21), *P. primordialis* being particularly distinct from *P. bairdi* in this respect (Tables 3 and 4). Each species also showed 2–5 characters that were nearly or completely non-overlapping with those of *P. bairdi*. Thus, univariate comparisons support the distinctiveness and independent status of *P. bairdi* among the morphologically related species of *Paranoplocephala*. The non-overlapping features in particular provide a reliable means of discriminating *P. bairdi* from the five related species; these are listed below.

Paranoplocephala arctica can be distinguished from *P. bairdi* according to the total number of testes and number of poral testes (lower in *P.b.*), distance between

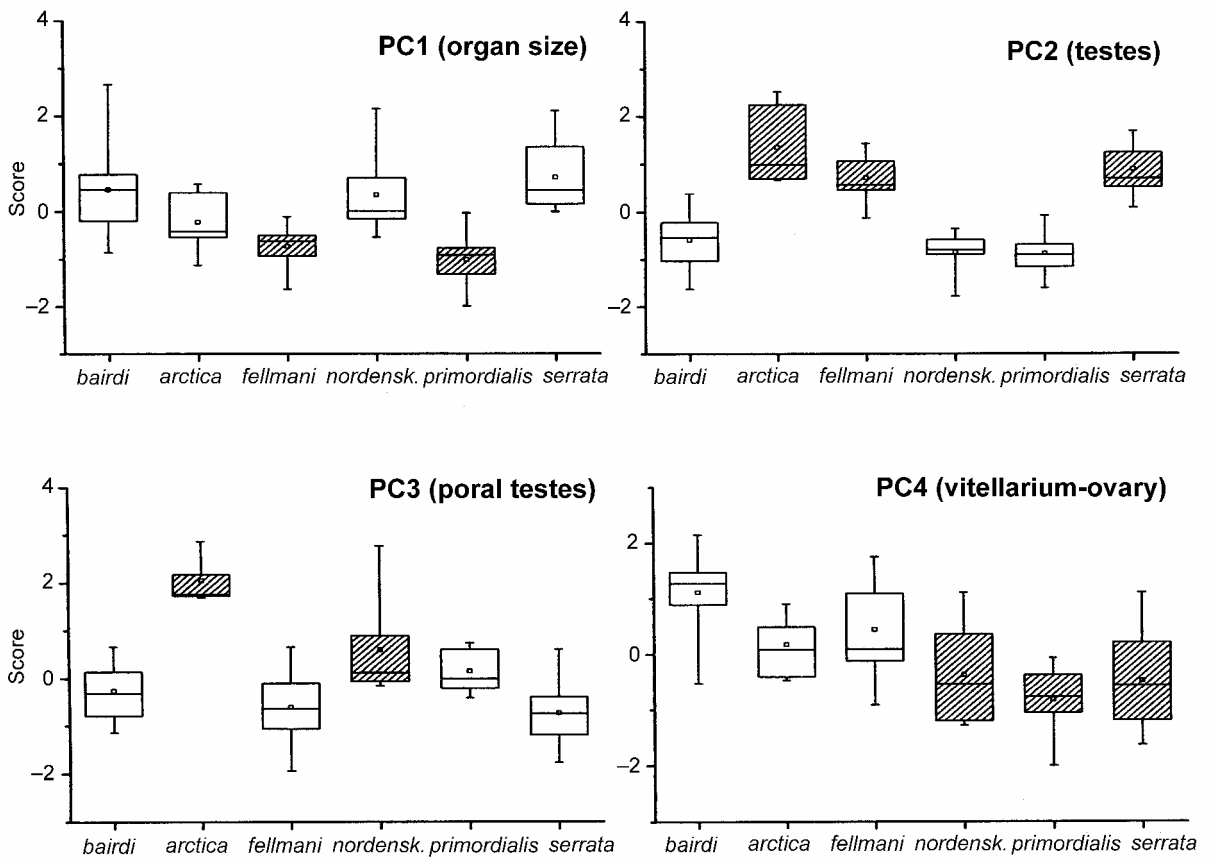

Fig. 1. Comparison of principal component (PC) scores between *Paranoplocephala bairdi* and other species. The graphs show the range (whiskers), lower and upper quartiles (box), median (transverse line within the box) and mean (small square within the box) of scores for each PC. Species differing significantly from *P. bairdi* are indicated by a shaded box. See text (Results) for interpretation of PCs.

the ovary and vitellarium (higher in *P.b.*) and egg length (much lower in *P.b.*). *Paranoplocephala fellmani* differs from *P. bairdi* by the width of the longitudinal ventral canals (higher in *P.b.*), dimensions of the seminal receptacle (higher in *P.b.*) and size of the scolex and suckers (smaller in *P.b.*). *Paranoplocephala nordenskioeldi* differs from *P. bairdi* by its larger scolex, suckers and eggs. *Paranoplocephala primordialis* also has larger scolex and suckers than *P. bairdi*, and it can additionally be distinguished from *P. bairdi* by the distance between the ovary and vitellarium (higher in *P.b.*). *Paranoplocephala serrata* has wider strobila and much larger eggs than *P. bairdi*.

Multivariate morphometrics

The PCA extracted four principal components (PCs) with Eigenvalues exceeding 1, each of them representing a statistically independent morphometric trait. PC1, accounting for 42% of the total variance, reflects the general size of various organs, including the width of the testicular field and poral distance of vitellarium. PC2 (18%) combines two related features, the total number of testes and the number of antiporal testes. PC3 (11%) and PC4 (8%) are primarily measures of two individual traits, the number of poral testes and the distance between vitellarium and ovary, respectively.

According to PC1, *P. bairdi* has significantly larger organs (and other correlated features) than *P. primordialis* and *P. fellmani* (Fig. 1). Additionally, PC2 separates *P. bairdi* from *P. fellmani*, *P. serrata* and *P. arctica*, and PC3 from *P. nordenskioeldi* and *P. arctica*, indicating that there are significant differences in the number and distribution of testes between *P. bairdi* and the other species. Finally, PC4 further supports the observation that *P. bairdi* differs from most of the other species by its higher distance between vitellarium of ovary (cf. Table 3).

The overall classification success of the discriminant analysis, i.e. the proportion of all specimens assigned to the correct species, was 85.1%. The classification success for different species varied from 60% (*P. nordenskioeldi*) to 100% (*P. arctica* and *P. fellmani*). Three of the 14 specimens of *P. bairdi* were misclassified as *P. nordenskioeldi* and *P. serrata*, giving a classification success of 78.6% for *P. bairdi*. Thus, the classification phase of the discriminant analysis shows relatively

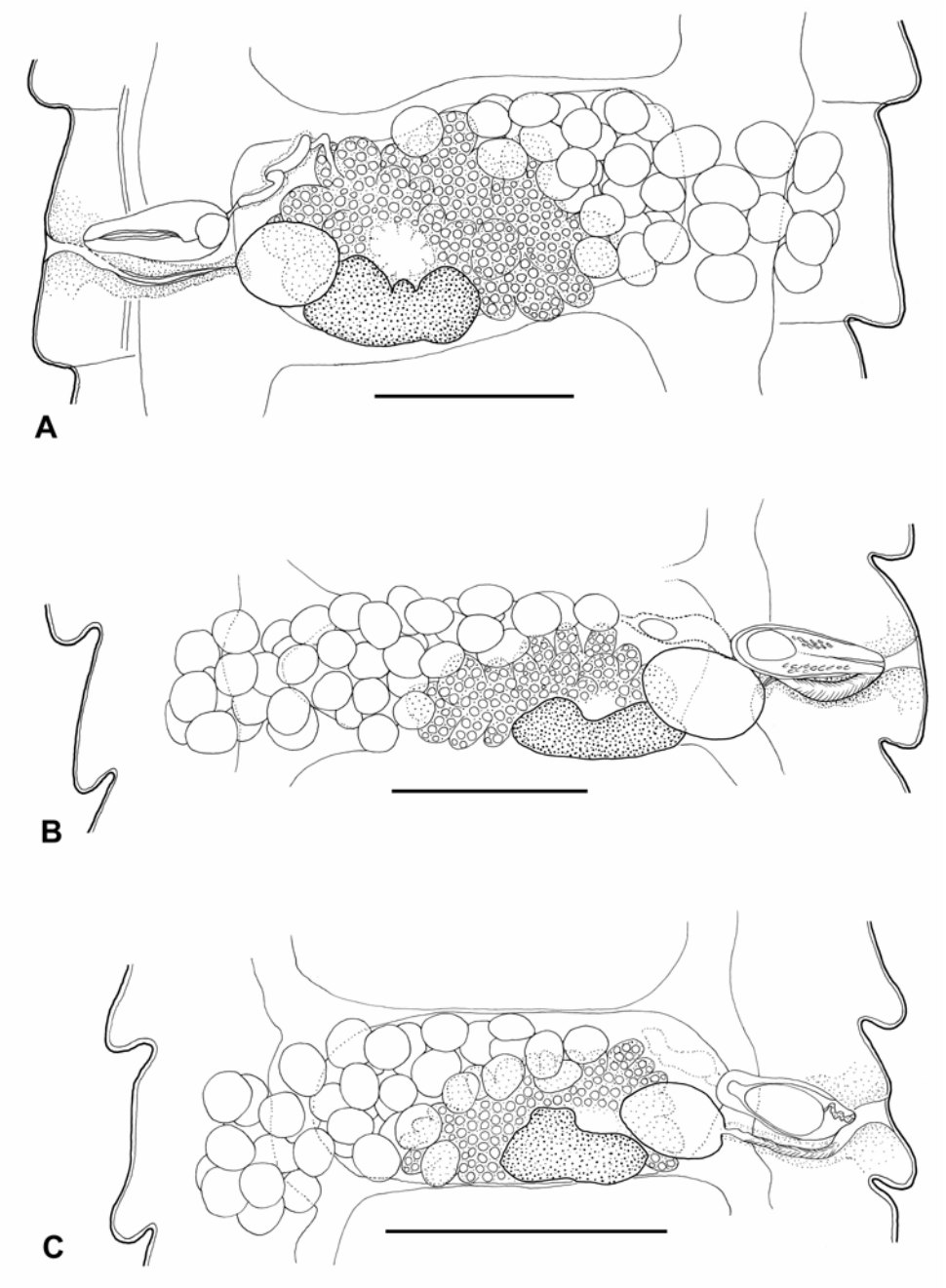

Fig. 2 A–C. Mature proglottides of *Paranoplocephala bairdi* from *Phenacomys ungava* (**A** – holotype), *P. intermedius* (**B**) and *Arborimus albipes* (**C**). Scale bars = 0.30 mm.

successful separation among the six species with partial morphometric overlap and occasional misclassifications between *P. bairdi*, *P. nordenskioeldi* and *P. serrata*.

Paranoplocephala bairdi (Schad, 1954)

Syn. *Andrya bairdi* Schad, 1954

The following redescription is based on 18 specimens from *Phenacomys* spp. and *Arborimus* spp. (Table 1). All measurements are in mm.

Description (Figs. 2–4, Tables 2–4). Fully developed strobila long (up to 243), relatively thin. Maximum width attained in pregravid proglottides. Scolex small, globular, not distinctly set off from neck. Suckers relatively small, ovoid, directed laterally. Neck 0.47–0.75 long, of uniform width; minimum width 0.11–0.29. Proglottides craspedote but velum usually short. Length/width ratio of mature proglottides variable (0.15–0.48, mean 0.26), remains comparable in postmature proglot-

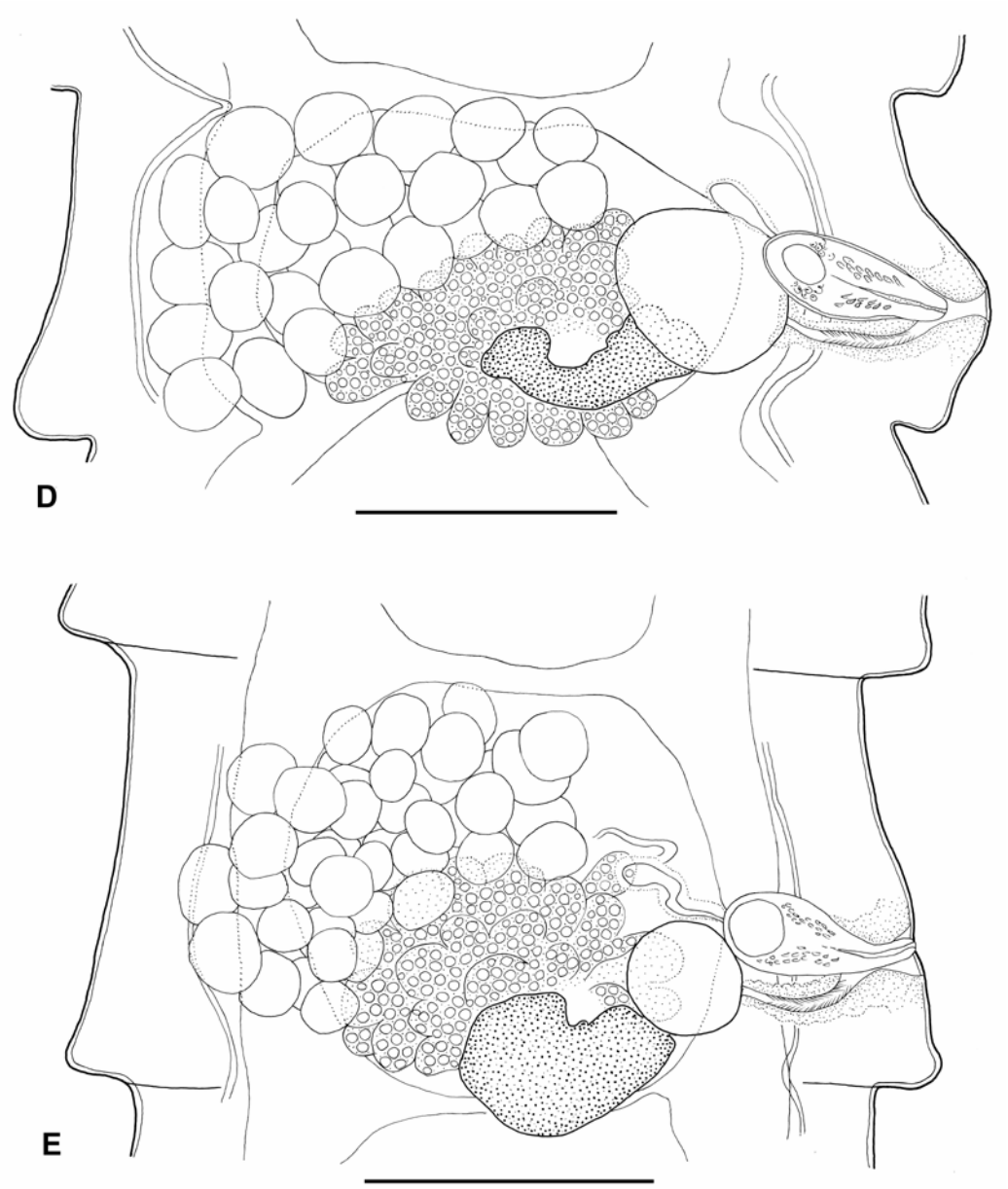

Fig. 2 D, E. Mature proglottides of *Paranoplocephala bairdi* from *Arborimus longicaudus* (**D**) and *A. pomo* (**E**). Scale bars = 0.30 mm.

tides (0.19–0.35, mean 0.26), increasing in pregravid (0.24–0.67, mean 0.46) and gravid proglottides (0.59–1.01, mean 0.84). Genital pores either unilateral or infrequently (and irregularly) alternating. In mature proglottides genital pores opening in middle of proglottis margin or slightly posteriad.

Ventral longitudinal osmoregulatory canals wide, particularly in type material. Ventral canals connected by relatively wide transverse canals. Dorsal longitudinal osmoregulatory canals 0.007–0.030 in type material, 0.005–0.008 in other specimens, situated lateral to ventral canals. Genital ducts pass dorsally to longitudinal osmoregulatory canals.

Testes 28–51 (mean 41.1) in number, situated antiporally and anteriorly to ovary in 2–3 dorso-ventral layers. Several testes usually laterally to antiporal ventral canal; testes cross this canal dorsally (occasionally 1–3 testes found ventral to canal). Position of poral testes from level of antiporal border of vitellarium to mid-vitellarium, few testes usually porally to midline of proglottis. Testes overlap slightly margins of ovary, being never in contact with vitellarium. Diameter of testes 0.06–0.08. Cirrus-sac elongate or pyriform, ca. 20% of mature proglottis width; maximum size attained in postmature proglottides. Cirrus-sac wall with thin muscle layers. Proximal cirrus-sac overlaps regularly

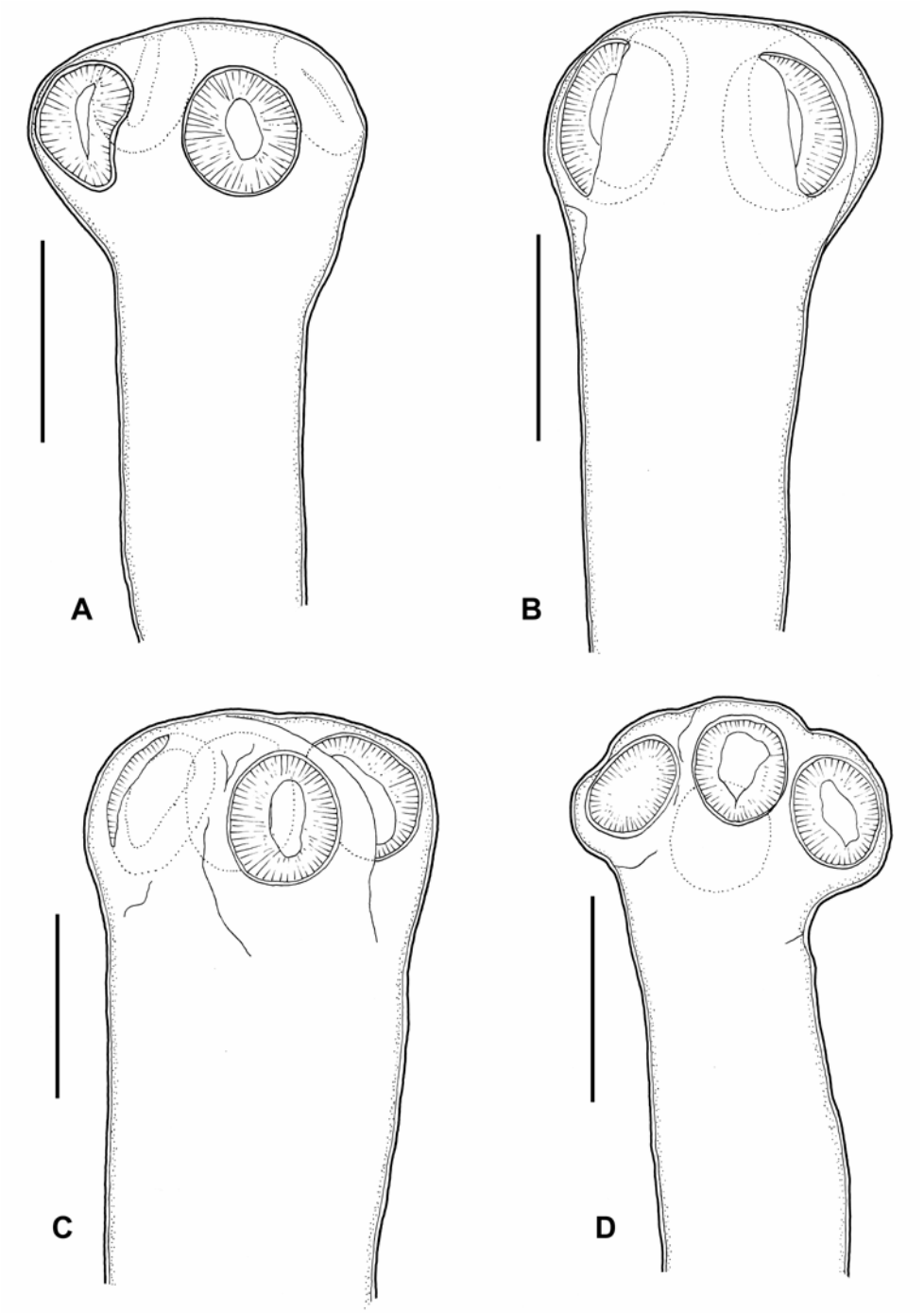

Fig. 3. Scolex and neck of *Paranoplocephala bairdi* from *Phenacomys ungava* (**A** – holotype), *P. intermedius* (**B**), *Arborimus longicaudus* (**C**) and *A. pomo* (**D**). Scale bars = 0.20 mm.

poral ventral canal and sometimes extends beyond it. Ductus cirri densely armed with short spines. Internal seminal vesicle 0.035–0.110 in mature proglottides, increasing slightly in size in postmature proglottides. External seminal vesicle relatively long and thin, irregularly looped, covered with loose cell layer.

Vagina 0.15–0.23 (mean 0.19) long, on average 86% of cirrus-sac length, maximum width 0.035–0.060 (mean 0.048). Vagina slightly curved, running posteriorly to cirrus-sac and opening ventrally or posteroventrally to male pore. Internally vagina formed by distinct tube tapering proximally. Internal surface of vagina

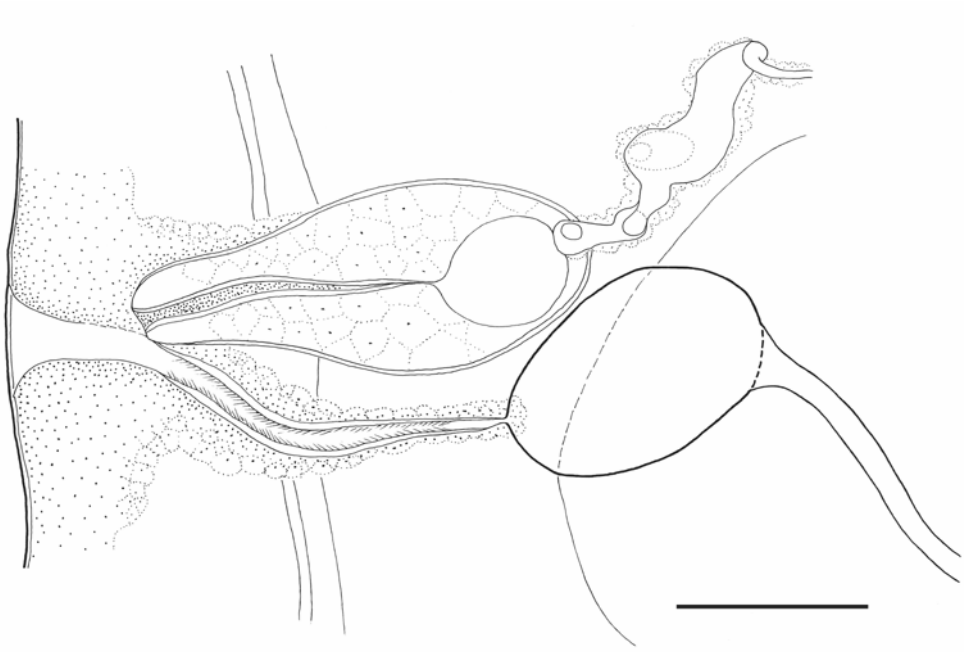

Fig. 4. Terminal genital ducts of *Paranoplocephala bairdi* from *Phenacomys ungava* (holotype). Scale bar = 0.10 mm.

lined with fine bristles pointing distally. Vagina covered externally by thick cell layer that increases distally in width, merging with cell layer surrounding genital atrium. Seminal receptacle ovoid or circular, distinctly set off from vagina, usually partly overlapping ventral osmoregulatory canal; increases markedly in size in postmature proglottides, retaining its ovoid/circular shape. Ovary sparsely lobed, situated centrally or slightly porally, covering ca. 2/3 of space between longitudinal ventral canals. Vitellarium asymmetrically bilobed or irregularly shaped, positioned porally with respect to ovary. Uterus appears ventrally in anterior proglottis as thin cell layer of reticulate appearance. Lateral parts of early uterus extend more posteriorly than central part and across ventral longitudinal canals bilaterally. In some specimens, central part of early uterus appears to be formed by transverse, anastomosing tubules. Margins of early uterus undefined. With further development central part expands posteriorly to form irregular compartments that rapidly fill with eggs; at this stage lateral parts of uterus consist of irregular, reticulated diverticula. Fully developed uterus in pregravid proglottides occupies most of medulla, with irregular anterior, posterior and lateral sacculations and complex system of internal trabeculae. Testes remain in postmature and early pregravid proglottides, overlapping developing uterus; cirrus sac, vagina and accessory organs persist in pregravid or early gravid proglottides. Eggs round in surface view, ovoid in side view. Eggs provided with pyriform apparatus, length 0.030–0.033 (details not seen).

DISCUSSION

Although the number of *Paranoplocephala* specimens from the *Phenacomys/Arborimus* complex was too low for a proper statistical comparison (Table 2), there were some obvious metric differences between cestodes from different host species. Specifically, the specimens from *P. ungava* had wider ventral osmoregulatory canals, the specimens from *P. intermedius* had larger eggs and the specimens from *A. pomo* had more frequently alternating genital pores than the specimens from the other host species (Table 2). There were also clear differences in the length/width ratio of proglottides (Fig. 2). Of these variables, the pattern of genital pore alternation has been traditionally given a high taxonomic weight within *Paranoplocephala*. However, the relatively frequent alternation in the specimens from *A. pomo* (9–13 changes per strobila) was approached by the specimens from *P. intermedius*, among which alternation varied from unilateral to 8 changes per strobila within the same locality (Deschutes County, Oregon).

We assume that the differences mentioned above reflect intraspecific variation rather than existence of multiple species. First, most of the taxonomically important features, such as the size and structure of the scolex, number and distribution of testes, position of female glands, and dimensions and morphology of genital ducts, showed little variation among the cestode samples. Second, none of the samples was consistently different from the other samples, and the observed differences fall within the range of intraspecific variation

Table 1. Specimens of *Paranoplocephala bairdi* from *Phenacomys* and *Arborimus* species used in the present analysis.

Host species	Region	Locality	Collector	Field code	Accession number	n	Scolex	Eggs
P. ungava	Quebec	Seven Islands	G.A. Schad	–	USNPC 48758 (holotype)	1	–	+
P. ungava	Quebec	Fort McKenzie	G.A. Schad	–	USNPC 48759 (paratype)	1	+	–
P. ungava	Quebec	Fort McKenzie	G.A. Schad	–	PPC[1] (paratype)	1	–	+
P. intermedius	Oregon	Deschutes Co.	C. Maser	37190	USNPC 95384	4	+	–
P. intermedius	Oregon	Deschutes Co.	C. Maser	37191	–	2	–	+
P. intermedius	Wyoming	Moran Co.	R.L. Rausch	2	–	1	–	+
P. intermedius	Montana	Glacier Park	V. Walters	11189	–	1	+	+
A. longicaudus	Oregon	Coos Co.	C. Maser	39600	–	1	+	–
A. longicaudus	Oregon	Tillamook Co.	M.L. Johnson	–	USNPC 95385	2	+	+
A. longicaudus	Oregon	Tillamook Co.	M.L. Johnson	5169	–	1	–	+
A. pomo	California	Sonoma Co.	M. Voge	793	USNPC 95386	2	+	+
A. albipes	Oregon	Lane Co.	C. Maser	40334	USNPC 95387	1	–	+

[1] Lawrence R. Penner Parasitology Collection, University of Connecticut, Storrs, USA; no accession number specified.

Table 2. Range of absolute measurements of *Paranoplocephala bairdi* in different species of *Phenacomys* and *Arborimus*. Maximum body width in mm, other measurements in µm.

	P. ungava		*P. intermedius*		*A. longicaudus*		*A. pomo*		*A. albipes*	
	n	range	n	range	n	range	n	range	n	range
Body, maximum width	2	1.90–2.00	6	1.27–2.05	3	1.27–1.81	1	1.25	1	1.30
Scolex, width	1	330	2	325–335	2	275–385	1	315	–	–
Suckers, diameter	1	130	2	155–160	2	138–150	1	108	–	–
Neck, length	1	470	1	750	2	500–750	1	600	–	–
Neck, minimum width	1	150	1	160	2	105–290	1	170	–	–
Ventral canals, width	3	118–152	6	40–122	3	40–85	2	60–82	1	45
Cirrus sac, length	3	215–255	6	140–313	3	170–220	2	195–200	1	150
Testes, number	3	42–51	6	28–45	3	33–47	2	44	1	41
Seminal receptacle, length	3	125–200	6	130–310	3	120–210	2	123–185	1	120
Vitellarium, width	3	200–270	6	175–300	3	106–250	2	190–220	1	155
Ovary, width	3	385–502	6	305–632	3	206–400	2	335–352	1	302
Egg, length	2	41.7–43.1	2	47.0–57.1	2	37.0–41.0	1	39.8	1	44.3
Genital pores, alternation[1]	3	0–1	6	0–8	3	0	2	9–13	1	1

[1]Number of changes per strobila.

Table 3. Mean and range (in parentheses) of absolute and relative organ measurements of *Paranoplocephala* spp. Values marked with an asterisk differ significantly ($p<0.05$), and values in bold italics are nearly or completely non–overlapping with those of *P. bairdi*. All measurements in μm.

	P. bairdi n = 14	*P. arctica* n = 6	*P. fellmani* n = 10	*P. nordenskioeldi* n = 10	*P. primordialis* n = 13	*P. serrata* n = 16
Ventral canals, width (VC)	89.6 (40–152)	43.2 (35–62)*	***31.2 (20–45)****	57.7 (35–90)*	49.9 (20–100)*	62.8 (35–120)
Cirrus sac, length (CS)	222 (150–313)	228 (150–340)	247 (173–320)	241 (210–285)	192 (130–250)	287 (230–390)*
Cirrus sac, max. length (CSM)	283 (230–350)	283 (250–340)	325 (300–360)	264 (220–310)	230 (190–290)*	372 (280–440)*
Testes, distribution (TE)	521 (400–779)	445 (360–534)	384 (290–554)*	531 (388–832)	391 (266–530)*	483 (337–690)
Testes, number (TN)	41.1 (28–51)	***60.5 (49–80)****	48.3 (33–58)	37.7 (28–52)	27.3 (19–39)*	44.1 (31–52)
Antiporal testes, no. (ATN)	6.2 (1–10)	12.2 (8–16)*	7.3 (1–12)	2.6 (0–6)	1.4 (0–4)*	12.3 (5–21)*
Poral testes, no. (PTN)	2.1 (0–5)	***12.3 (10–17)****	3.8 (0–8)	5.1 (2–11)*	6.4 (3–10)*	1.0 (0–5)
Seminal receptacle, length (SR)	173 (120–310)	191 (155–260)	***87 (60–105)****	206 (135–285)	130 (85–180)	201 (100–323)
Seminal receptacle, max. length (SRM)	371 (255–550)	438 (350–570)	***158 (120–200)****	330 (250–550)	199 (130–290)*	481 (320–680)*
Vitellarium, width (VI)	220 (106–300)	201 (150–220)	173 (125–240)	242 (180–390)	180 (120–255)	194 (150–296)
Poral distance of vitellarium (PV)	464 (350–688)	352 (265–470)	342 (270–417)	471 (378–690)	371 (278–460)	476 (360–610)
Ovary, width (OV)	404 (206–632)	312 (255–386)	307 (196–420)	431 (295–640)	321 (145–430)	416 (350–635)
Distance between ovary and vitellarium (DO)	75.9 (50–125)	***17.7 (10–28)****	47.0 (0–103)	43.4 (10–95)*	***10.7 (–25–35)****	32.8 (0–77)*
Mature proglottides, length/width ratio	0.26 (0.15–0.48)	0.57 (0.42–0.69)*	0.50 (0.38–0.68)*	0.23 (0.15–0.42)	0.37 (0.21–0.52)*	0.23 (0.14–0.37)
Vitellarium, index of asymmetry	0.41 (0.39–0.48)	0.48 (0.45–0.52)*	0.43 (0.37–0.50)	0.47 (0.38–0.54)*	0.49 (0.43–0.55)*	0.43 (0.37–0.50)

Table 4. Mean and range of external dimensions and egg length of *Paranoplocephala* spp. Values marked with an asterisk differ significantly ($p<0.05$), and values in bold italics are nearly or completely non-overlapping with those of *P. bairdi*. Maximum body width in mm, other measurements in μm.

	P. bairdi			*P. arctica*			*P. fellmani*			*P. nordenskioeldi*			*P. primordialis*			*P. serrata*		
	n	mean	range	n	mean	range	n	mean	range	n	mean	range	n	mean	range	n	mean	range
Body, max. width	12	1.56	1.25–2.05	6	1.90	1.28–2.85	7	1.49	1.27–1.71	10	1.92	1.40–2.87	10	1.36	0.75–2.05	***14***	***2.65***	***2.05–3.35****
Scolex, width	6	328	275–385	5	288	215–335	***10***	***455***	***400–530****	***6***	***443***	***370–610****	***10***	***490***	***430–560****	15	355	260–430
Suckers, diameter	6	140	108–160	5	142	105–165	***10***	***197***	***170–235****	***6***	***208***	***175–250****	***10***	***189***	***153–225****	15	167	130–200
Neck, length	5	614	470–750	–	–	–	5	448	170–850	3	357	270–450	7	593	300–1,000	13	549	140–1,100
Neck, min. width	5	175	105–290	4	104	80–125	6	196	130–270	4	116	90–150	9	219	125–300	14	146	70–270
Egg, length	7	41.9	37–47	***6***	***66.8***	***64–69****	7	43.9	39–46	***9***	***50.7***	***47–55****	11	48.9	41–66*	***14***	***60.4***	***55–69****

normally seen within *Paranoplocephala* spp. In addition, the multivariate analyses suggest that the specimens from *Phenacomys* and *Arborimus* represent a relatively uniform group of cestodes that is morphometrically distinct from the other, related species of *Paranoplocephala*. *Paranoplocephala bairdi*, *P. nordenskioeldi* and *P. serrata* resemble each other in many respects, including the uterine development. The structure of the early uterus in these three species fully corresponds to that of *P. omphalodes*, the type species of *Paranoplocephala* (cf. Rausch 1976, Genov et al. 1996), but the uterine development of *P. arctica* (Haukisalmi et al. 2001), *P. fellmani* (Haukisalmi and Henttonen 2001) and, possibly, *P. primordialis* (Douthitt 1915) represents other subtypes recognized within *Paranoplocephala*. However, none of the species considered here, including *P. bairdi*, belongs to *Paranoplocephala* sensu stricto, as defined by Haukisalmi and Henttonen (2003), mainly because of differences in the morphology of the scolex, suckers and genital ducts.

Despite the apparent similarity between *P. bairdi*, *P. nordenskioeldi* and *P. serrata*, they remained largely separate in the discriminant analysis and showed several statistically significant differences, including diagnostic, non-overlapping features. Egg length seems to be the most clear-cut individual feature separating these three species. In addition to the quantitative differences considered in this analysis, *P. nordenskioeldi* and *P. serrata* differ from *P. bairdi* with respect to the structure of the scolex and genital ducts (Haukisalmi and Henttonen 2000, Haukisalmi et al. 2001). The classification success of *P. bairdi* in the discriminant analysis was not perfect (78.6%), but it still exceeded *P. nordenskioeldi* (60%) in this respect; the independent status of the latter species has been confirmed by molecular methods (Haukisalmi et al. 2001). In a methodologically comparable morphometric analysis of *P. omphalodes*-like species, the classification success varied between 80–90%, also suggesting that occasional misclassifications do occur even among biologically valid anoplocephaline species defined by molecular methods (Haukisalmi et al. 2004).

Paranoplocephala bairdi also resembles *Paranoplocephala montana* (Kirshenblat, 1941), described from *Microtus arvalis* (Pallas) and *Chionomys nivalis* (Martins) from Caucasus (Georgia and Armenia), but they can be reliably separated by the length of the strobila (much longer in *P.b.*), shape of the seminal receptacle (elongate or pyriform in *P.m.*), width of the ventral longitudinal canals (wider in *P.b.*) and other quantitative features. Kirshenblat (1941) did not designate a type specimen for *P. montana*, and new material is needed to define more precisely the morphology and intraspecific variation of this poorly known species.

Thus, the combined evidence from uni- and multivariate morphometrics and qualitative comparisons suggest that all available specimens of *Paranoplocephala* from *Phenacomys* and *Arborimus* represent a single species, i.e. *P. bairdi*. Since there are no reports or descriptions of *P. bairdi*-like cestodes from other species of voles and lemmings, we consider *P. bairdi* a host-specialist species of heather voles and tree voles with a wide geographical distribution in North America. *Paranoplocephala bairdi* is so far the only cestode species in *Phenacomys* and *Arborimus* whose identity has been confirmed by comparative morphological analysis (below).

Other *Paranoplocephala* species reported from *Phenacomys* are *P. communis* (Douthitt, 1915) (see Lubinsky 1957) and *P. primordialis* (see Rausch and Schiller 1949, Rausch 1952, Kinsella 1967). Lubinsky (1957) also mentioned *P. variabilis* (Douthitt, 1915) as a parasite of *Phenacomys*, but this species is presently assigned to *Anoplocephaloides* Baer, 1923 (see Rausch 1976).

Paranoplocephala communis is usually considered a synonym of *P. primordialis* (see Baer 1927, Rausch and Schiller 1949, Spasskii 1951) or *species inquirenda* (Tenora et al. 1986), although Tenora (1996) described specimens from North American *Clethrionomys* spp. under the former name. The original description of *P. communis* is based on contracted, sectioned fragments and its taxonomical status remains obscure. The presence of *P. primordialis* in *Phenacomys* can not be verified due to the lack of descriptions, and it is possible that some of the existing reports actually concerned *P. bairdi*.

Finally, the present analysis emphasises the need to apply a wide range of morphometric characters and multivariate statistical analyses to discriminate species within the large and morphologically relatively uniform genus *Paranoplocephala* (see also Haukisalmi et al. 2004).

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REFERENCES

BAER J.G. 1927: Monographie des cestodes de la famille des Anoplocephalidae. Bull. Biol. Fr. Belg. (Suppl.) 10: 1–241.

BELLINGER M.R., HAIG S.M., FORSMAN E.D., MULLINS T.D. 2005: Taxonomic relationships among *Phenacomys* voles as inferred by cytochrome *b*. J. Mammal. 86: 201–210.

DOUTHITT H. 1915: Studies on the cestode family Anoplocephalidae. Ill. Biol. Monogr. 1: 1–96.

DURETTE-DESSET M.-C., KINSELLA J.M., FORRESTER D.J. 1972: Arguments en faveur de la double origine des Nématodes néarctiques du genre *Heligmosomoides* Hall, 1916. Ann. Parasitol. Hum. Comp. 47: 365–382.

GENOV T., VASILEVA G.P., GEORGIEV B.B. 1996: *Paranoplocephala aquatica* n. sp. (Cestoda, Anoplocephalidae) from *Arvicola terrestris* and *Ondatra zibethica* (Rodentia), with redescriptions and comments on related species. Syst. Parasitol. 34: 135–152.

HAUKISALMI V., HENTTONEN H. 2000: Description and morphometric variability of *Paranoplocephala serrata* n. sp. (Cestoda: Anoplocephalidae) in collared lemmings (*Dicrostonyx* spp., Arvicolinae) from Arctic Siberia and North America. Syst. Parasitol. 45: 219–231.

HAUKISALMI V., HENTTONEN H. 2001: Biogeography of helminth parasitism in *Lemmus* Link (Arvicolinae), with the description of *Paranoplocephala fellmani* n. sp. (Cestoda: Anoplocephalidae) from the Norwegian lemming *L. lemmus* (Linnaeus). Syst. Parasitol. 49: 7–22.

HAUKISALMI V., HENTTONEN H. 2003: What is *Paranoplocephala macrocephala* (Douthitt, 1915) (Cestoda: Anoplocephalidae)? Syst. Parasitol. 54: 53–69.

HAUKISALMI V., HENTTONEN H., NIEMIMAA J., RAUSCH R.L. 2002: Description of *Paranoplocephala etholeni* n. sp. (Cestoda: Anoplocephalidae) in the meadow vole *Microtus pennsylvanicus*, with a synopsis of *Paranoplocephala* s.l. in Holarctic rodents. Parasite 9: 305–314.

HAUKISALMI V., WICKSTRÖM L.M., HANTULA J., HENTTONEN H. 2001: Taxonomy, genetic differentiation and Holarctic biogeography of *Paranoplocephala* spp. (Cestoda: Anoplocephalidae) in collared lemmings (*Dicrostonyx*; Arvicolinae). Biol. J. Linn. Soc. 74: 171–196.

HAUKISALMI V., WICKSTRÖM L.M., HENTTONEN H., HANTULA J., GUBÁNYI A. 2004: Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Cestoda, Anoplocephalidae) in *Microtus* voles (Arvicolinae). Zool. Scr. 33: 277–290.

HOBERG E.P., KUTZ S.J., GALBREATH K.E., COOK J.A. 2003: Arctic biodiversity: from discovery to faunal baselines – revealing the history of a dynamic ecosystem. J. Parasitol. 89 (Suppl.): S84–S95.

KINSELLA J.M. 1967: Helminths of Microtinae in western Montana. Can. J. Zool. 45: 269–274.

KIRSHENBLAT Y.D. 1941: A new tepeworm from Transcaucasian voles. Soobsch. Akad. Nauk GrSSR 2: 273–276. (In Russian.)

LUBINSKY G. 1957: List of helminths from Alberta rodents. Can. J. Zool. 35: 623–627.

MUSSER G.G., CARLETON M.D. 1993: Family Muridae. In: D.E. Wilson and D.M. Reeder (Eds.), Mammal Species of the World. Smithsonian Institution Press, in association with the American Society of Mammalogists, Washington and London, pp. 501–755.

PETERSON R.L. 1962: Notes on the distribution of *Microtus chrotorrhinus*. J. Mammal. 43: 420.

RAUSCH R.L. 1952: Studies on the helminth fauna of Alaska. XI. Helminth parasites of microtine rodents – taxonomic considerations. J. Parasitol. 38: 415–444.

RAUSCH R.L. 1976: The genera *Paranoplocephala* Lühe, 1910 and *Anoplocephaloides* Baer, 1923 (Cestoda: Anoplocephalidae), with particular reference to species in rodents. Ann. Parasitol. Hum. Comp. 51: 513–562.

RAUSCH R.L., RAUSCH V.R. 1973: *Heligmosomoides johnsoni* sp. nov. (Nematoda: Heligmosomatidae) from the heather vole, *Phenacomys intermedius* Merriam. Can. J. Zool. 51: 1243–1247.

RAUSCH R.L., SCHILLER E.L. 1949: A critical study of North American cestodes of the genus *Andrya* with special reference to *A. macrocephala* Douthitt, 1915 (Cestoda: Anoplocephalidae). J. Parasitol. 35: 306–314.

SCHAD G.A. 1954: Helminth parasites of mice in northeastern Quebec and the coast of Labrador. Can. J. Zool. 32: 215–224.

SPASSKII A.A. 1951: [Anoplocephalate tapeworms of domestic and wild animals.] The Academy of Sciences of the USSR, Moscow, 783 pp.

TENORA F. 1996: *Andrya communis* Douthitt, 1915 (Anoplocephalidae), a parasite of *Clethrionomys* spp. (Arvicolidae) in the Nearctic region. Helminthologia 33: 37–41.

TENORA F., MURAI É., VAUCHER C. 1986: On *Andrya* Railliet, 1893 and *Paranoplocephala* Lühe, 1910 (Cestoda, Monieziinae). Parasitol. Hung. 19: 43–75.

VERTS B.J., CARRAWAY L.N. 1998: Land Mammals of Oregon. University of California Press, Berkeley and Los Angeles, 668 pp.

WICKSTRÖM L.M., HAUKISALMI V., VARIS S., HANTULA J., HENTTONEN H. 2005: Molecular phylogeny and systematics of anoplocephaline cestodes in rodents and lagomorphs. Syst. Parasitol. (in press).

WILSON D.E., RUFF S. (Eds.) 1999: The Smithsonian Book of North American Mammals. Smithsonian Institution Press, in association with the American Society of Mammalogists, Washington and London, 750 pp.

VOGE M. 1955: A list of cestode parasites from California mammals. Am. Midl. Nat. 54: 413–417.

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