DESCRIPTION OF *PARANOPLOCEPHALA YOCCOZI* N. SP. (CESTODA: ANOPLOCEPHALIDAE) FROM THE SNOW VOLE *CHIONOMYS NIVALIS* IN FRANCE, WITH A REVIEW OF ANOPLOCEPHALID CESTODES OF SNOW VOLES IN EUROPE

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Summary:

We describe *Paranoplocephala yoccozi* n. sp. (Cestoda: Anoplocephalidae) from the snow vole *Chionomys nivalis* in Bourg-Saint-Maurice, French Alps, compare it with several related species from rodents, and review the anoplocephalid cestodes of snow voles in Europe. *Paranoplocephala yoccozi* n. sp. is primarily distinguished from the related species by its large scolex of characteristic shape, robust neck region, and the structure of the cirrus sac, vitellarium and vagina. We show that the anoplocephalid cestodes of snow voles in Europe, representing the genera *Anoplocephaloides* and *Paranoplocephala*, include at least seven species. This fauna consists primarily of species that snow voles share with other voles inhabiting the high-mountain areas. Some of the species, including *P. yoccozi* n. sp., appear to have a very localized distribution, which is assumed to be a consequence of the historical fragmentation of snow vole populations.

KEY WORDS : *Paranoplocephala yoccozi* n. sp., Cestoda, Cyclophyllidea, Anoplocephalidae, *Chionomys nivalis*, Arvicolinae, vole.

Résumé : DESCRIPTION DE *PARANOPLOCEPHALA YOCCOZI* N. SP. (CESTODA : ANOPLOCEPHALIDAE) DU CAMPAGNOL DES NEIGES *CHIONOMYS NIVALIS* EN FRANCE, AVEC UNE RÉVISION DES CESTODES ANOPLOCÉPHALIDÉS DES CAMPAGNOLS DES NEIGES EN EUROPE

Nous décrivons Paranoplocephala yoccozi *n. sp. (Cestoda : Anoplocephalidae) du Campagnol des neiges* Chionomys nivalis, *à Bourg-Saint-Maurice, Alpes françaises, le comparons avec d'autres espèces apparentées parasites de rongeurs, et proposons une révision des Cestodes Anoplocéphalidés des campagnols des neiges en Europe.* Paranoplocephala yoccozi *n. sp. se distingue des espèces apparentées d'abord par un large scolex de forme caractéristique, un cou robuste, la structure de la poche du cirre, celle des vitellogènes et celle du vagin. Nous montrons que les Cestodes Anoplocéphalidés des Campagnols des neiges en Europe, représentées par les genres* Anoplocephaloides *et* Paranoplocephala, *comptent au moins sept espèces. Ce groupe contient essentiellement des espèces que les Campagnols des neiges partagent avec d'autres Campagnols vivant en haute montagne. Certaines espèces, entre autres* Paranoplocephala yoccozi *n. sp., semblent avoir une répartition discontinue, résultant probablement de la fragmentation historique des populations de l'hôte.*

MOTS CLÉS : Paranoplocephala yoccozi *n. sp., Cestoda, Cyclophyllidea, Anoplocephalidae,* Chionomys nivalis, *Arvicolinae, Campagnol.*

INTRODUCTION

The snow vole *Chionomys nivalis* (Martins) is an inhabitant of rocky, alpine habitats, with a wide, fragmented distribution on the mountain ranges of southern Europe, Caucasus and parts of western Asia. The snow voles, genus *Chionomys* Miller, have earlier been regarded as a part of *Microtus* Schrank, but their independent generic status has been confirmed by morphological (Nadachowski, 1991; Musser & Carleton, 1993 and references therein) and molecular criteria (Jaarola *et al.*, 2005).

The cestode fauna of *C. nivalis* is dominated by anoplocephalid cestodes representing the genera *Anoplocephaloides* Baer, 1923 and *Paranoplocephala* Lühe, 1910 (e.g. Genov, 1984; Genov & Georgiev, 1988; Feliu *et al.*, 1997); in this respect, it resembles many other arvicoline rodents (voles and lemmings). The *Anoplocephaloides* species parasitizing snow voles in Bulgaria have been subject to detailed taxonomical studies (Genov *et al.*, 1984; Genov & Georgiev, 1988), but the *Paranoplocephala* species of *C. nivalis* have not been scrutinized by comparative morphological methods. Since the taxonomical concepts within *Paranoplocephala* have been reshaped during the recent years, the identity and true diversity of species parasitizing snow voles remain partly unclear.

This study includes a description of *Paranoplocephala yoccozi* n. sp. from the snow vole in French Alps, comparison with several related species from rodents, and review of anoplocephalid cestodes of snow voles in Europe.

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MATERIALS AND METHODS

France: 36 individuals of *C. nivalis* captured by N.G. Yoccoz from Beaupré (45° 40' N, 6° 50' E) and Les Chapieux (45° 43' N, 6° 44' E), Bourg-Saint-Maurice municipality, French Alps, during 2000-2002 were checked for intestinal helminths. Eleven (30.5 %) of the snow voles were infected with *P. yoccozi* n. sp., with 1-4 specimens in each infected host. The cestodes collected during the first year were fixed unrelaxed *in situ*, and these specimens were not included in the morphometric analysis. The material from 2001-2002, used for the description of *P. yoccozi* n. sp., consists of nine cestode specimens relaxed in water and fixed flat (without pressure) in 70 % ethanol. Seven gravid specimens were used for morphometrics. Six individuals of *Microtus arvalis* (Pallas) and three individuals of *Clethrionomys glareolus* (Schreber) were also examined from the same high-mountain locality but none of these carried *P. yoccozi* n. sp.

Italy: 13 individuals of *C. nivalis* captured during May 2000 from Trento (46° 04' N, 11° 08' E), Italian Alps, were examined for helminths by us. This material, which did not include *P. yoccozi* n. sp., was used for a review of anoplocephalid cestodes of snow voles in Europe (Table II).

Cestodes were stained with Mayer's hemalum, Semichon's acetic carmine or iron aceto-carmine, cleared in eugenol and mounted in Canada balsam.

For the description, the scolex, neck and 2-3 mature proglottides from each individual were drawn on paper with the aid of camera lucida, and various organs were counted and measured from these drawings using a calibrated ruler. Cirrus sac was measured only if the cirrus was fully invaginated. The maximum dimensions of the cirrus sac and seminal receptacle were recorded from postmature proglottides. Number of poral testes refers to testes situated porally to the midline of the proglottis, and the number of antiporal testes to those situated antiporally to the ventral osmoregulatory canal. The index of asymmetry, quantifying the asymmetrical position of vitellarium, 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. Egg dimensions are based on measurements from terminal proglottides of each fully gravid strobila. All metric data are in mm if not otherwise stated.

The type specimens (whole-mounts) of *P. yoccozi* n. sp. have been deposited in the United States National Parasite Collection (USNPC) in Beltsville, Maryland, and the Hungarian Natural History Museum (HNHM), Budapest. We have also deposited voucher specimens of *Anoplocephaloides dentata* (Galli-Valerio, 1905) (coll. no. 95383) and *Anoplocephaloides* cf. *variabilis* (Douthitt, 1915) (coll. no. 95382) from *C. nivalis* (France) in the USNPC. During the present study, we examined a paratype specimen of *Paranoplocephala janickii* Tenora, Murai & Vaucher, 1985 from the HNHM (coll. no. 5885).

Host nomenclature follows Musser & Carleton (1993).

RESULTS

Family Anoplocephalidae Cholodkovsky, 1902.
Subfamily Anoplocephalinae Blanchard, 1891.

PARANOPLOCEPHALA YOCCOZI N. SP.

Host: *Chionomys nivalis* (Rodentia, Muridae, Arvicolinae).

Site: duodenum, exceptionally jejunum or ileum.

Holotype: USNPC, coll. no. 95380, collected from Beaupré, Bourg-Saint-Maurice, France, by N. Yoccoz on 25 July 2001. The holotype specimen was accompanied with three other specimens of *P. yoccozi* n. sp., but only one of them (the holotype) was fully gravid.

Paratypes: *i)* USNPC, coll. no. 95381, collected from Les Chapieux, Bourg-Saint-Maurice, France, by N. Yoccoz on 20 July 2002; *ii)* HNHM, coll. no. 69913, other data as in the former paratype.

Etymology: the name of the new species refers to Nigel G. Yoccoz, the collector of the type material of *P. yoccozi* n. sp. and a specialist of Arctic and alpine rodents.

DESCRIPTION (Fig. 1, Table I)

Gravid strobila 53-107 long (mean 69), relatively wide, maximum width attained in pregravid or gravid proglottides. All proglottides much wider than long; length/width ratio constant in immature, mature and postmature proglottides (mean 0.22-0.26), slightly higher in gravid proglottides (mean 0.38). Scolex wide (0.67-0.85, mean 0.76) but relatively short, apical region flattened, with irregular protuberances formed by large intensely staining cells. Suckers large (0.27-0.34, mean 0.30), spherical, directed laterally or antero-laterally, surrounded posteriorly and laterally with prominent collar. Neck short (0.42-0.59) and thick (0.44-0.67), minimum width 62-79 % of scolex width. Scolex often separated from neck by distinct groove.

Proglottides craspedote with well-developed velum. Genital pores strictly unilateral, either dextral (5/7) or sinistral (2/7), opening slightly posterior to middle of proglottis margin in mature proglottides.

Ventral longitudinal osmoregulatory canals relatively thin (0.038-0.079, mean 0.056), strongly arched, of uniform width and shape. Transverse commissures of ventral canals ca. 0.02-0.04. Dorsal longitudinal osmoregulatory canals thin (0.008-0.013), lateral to ventral canals. Genital ducts pass dorsally to longitudinal osmoregulatory canals.

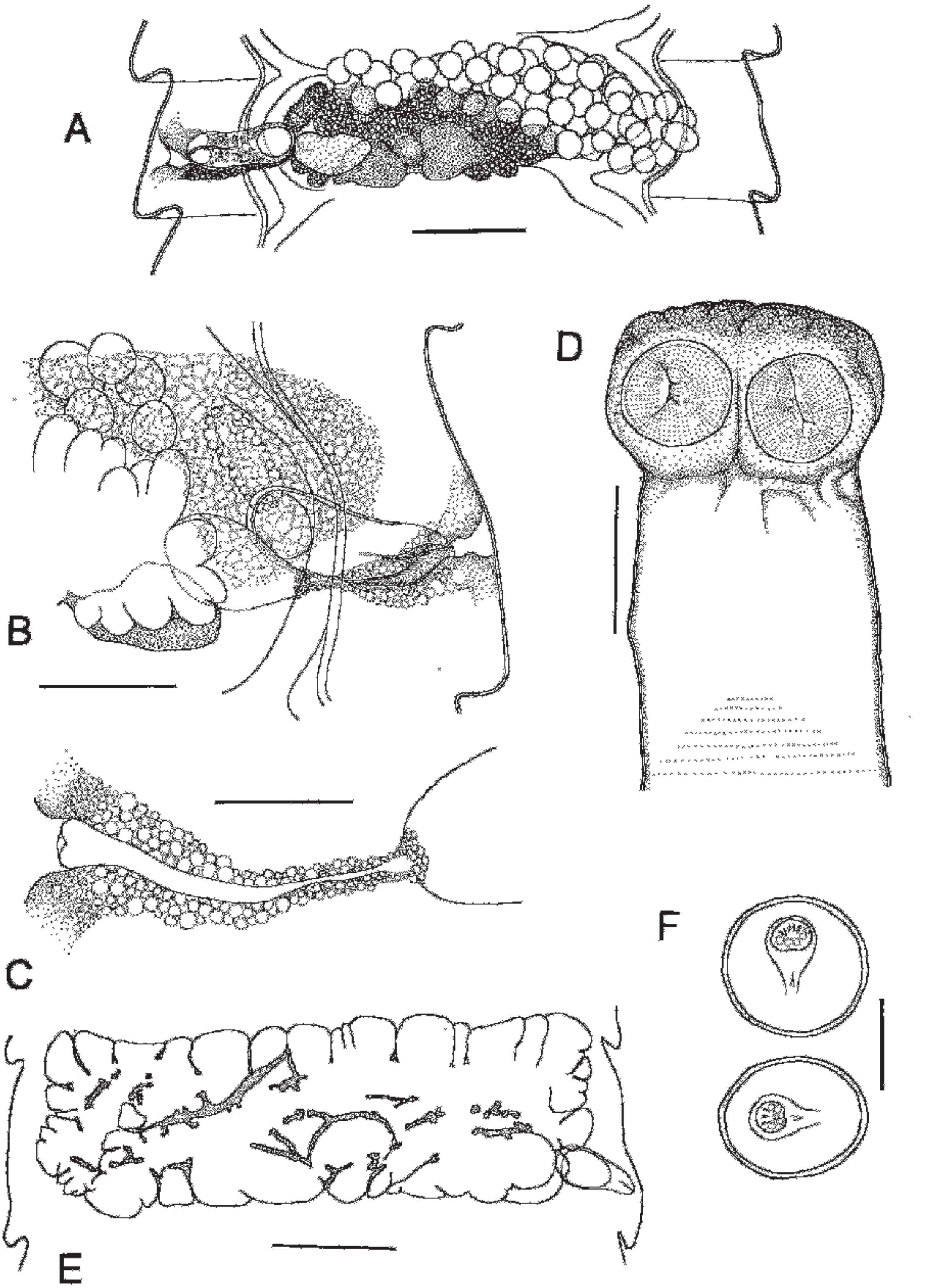

Fig. 1. – *Paranoplocephala yoccozi* n. sp. A, mature proglottis (scale-bar: 0.30 mm). B, terminal genital ducts and early uterus (scale-bar: 0.20 mm). C, vagina (scale-bar: 0.10 mm). D, scolex and neck (scale-bar: 0.40 mm). E, pregravid proglottis with fully developed uterus (scale-bar: 0.50 mm). F, eggs (scale-bar: 0.030 mm).

Host species	*P. yoccozi* n. sp. *Chionomys nivalis*	*P. fellmani* *Lemmus* spp.	*P. gubanovi* *Myopus schisticolor*	*P. janickii* *Microtus arvalis*	*P. gracilis* *Microtus, Chionomys, Arvicola, Clethrionomys*	*P. montana* *M. arvalis, C. nivalis*
Distribution	French Alps	Holarctic	Eastern Siberia	Central Europe	Europe	Caucasus
Source	1	2	3	4	4	5
Body, length	53-107	65-107	**29-31**	40-100	60-120, 178[8]	65
Body, maximum width	2.0-3.6	1.28-2.05	**1.40-1.55**	1.6-2.5	1.5-2.5, 2.9[8]	3
Scolex, diameter	0.67-0.85	**0.40-0.53**	**0.40-0.50**	**0.32-0.45**	**0.37-0.60**	**0.37**
Suckers, diameter	0.27-0.34	**0.17-0.24**	**0.15-0.18**	**0.17-0.22**	**0.18-0.24**	**0.08-0.12**
Neck, length	0.4-0.6	0.3-0.9	–	0.5-0.7	**0.8**	**0.8-1.0**
Neck, minimum width	0.44-0.67	**0.15-0.27**	**0.19-0.25**	**0.23**[7]	**0.17-0.39**[8]	**0.25-0.32**
Mature proglottides, l/w ratio	0.20-0.37	**0.38-0.58**	**0.34-0.57**[6]	0.17-0.25	0.17-0.50	–
Testes, total number	47-67	33-59	**40-48**	50-60, 42[7]	40-55	**20-25**
Antiporal testes, number	0-8	1-14	none/few	none/few	none/few	several
Extent of poral testes	poral lobe/margin of vitellarium	antiporal/poral margin of vitellarium	**antiporal margin/ mid-vitellarium**[6]	**overlapping ventral canal**	**overlapping/across ventral canal**	**mid-vitellarium**[9]
Cirrus sac, length	0.23-0.38	0.16-0.36	0.26-0.30	**0.17-0.25**	**0.18-0.20**	**0.13**
Cirrus sac, position	across ventral canal	across ventral canal	across ventral canal	**overlapping v.c.**	variable[8]	**overlapping v.c.**[9]
Ovary, width	0.46-0.82	**0.22-0.43**	0.45-0.52	**0.37-0.49**	0.30-0.65	**up to 0.43**
Vitellarium, width	0.27-0.44	**0.10-0.22**	**0.16-0.25**	**0.18-0.28**	0.16-0.30	**0.18**
Index of asymmetry	0.42-0.48	0.32-0.51	0.38-0.45[6]	0.40-0.44[7]	0.41-0.51[8]	0.42[9]
Vagina, length	0.19-0.35	0.14-0.22	**0.11-0.13**	**0.09-0.16**	0.20-0.30	–
Vagina/cirrus sac ratio	0.6-1.0	0.6-1.1	0.6-0.7[6]	0.5-0.7, 0.8[7]	0.7-1.0[8]	**ca. 0.5**[9]
Seminal receptacle, length	0.16-0.46	0.05-0.23	**0.12-0.16**	0.20-0.36	0.22-0.50	0.22
Seminal receptacle, shape	pyriform/elongate	**spherical/ovoid**	**spherical/ovoid**	pyriform	**spherical/ovoid**	pyriform
Early uterus, structure	fine reticulum	**sparse reticulum**	**sparse reticulum?**	fine reticulum[7]	fine reticulum[8]	"reticulum"
Egg, length	0.042-0.050	0.040-0.047	**0.035-0.040**	**0.036-0.042**	0.037-0.048	0.046-0.050

Sources: 1, present study. 2, Haukisalmi & Henttonen, 2001. 3, Gulyaev & Krivopalov, 2003. 4, Tenora *et al.*, 1985. 5, Kirshenblat, 1941.

Comments.: [6] An estimate based on the figures of Gulyaev & Krivopalov (2003). [7] Additional, deviating observations based on a paratype specimen (HNHM 5885). [8] Additional or deviating observations based on Finnish material. [9] An estimate based on the figure of Kirshenblat (1941).

Table I. – The main morphological features of *Paranoplocephala yoccozi* n. sp. compared with related *Paranoplocephala* species. Characters that are completely or nearly non-overlapping with those of *P. yoccozi* n. sp. are shown in bold. All metric data are in mm.

Number of testes 47-67 (mean 57), distributed anteriorly and antiporally to ovary in 2-3 dorsoventral layers, few (0-8) testes usually extending dorsally beyond antiporal ventral canal. Several (4-14) testes always found porally to midline of proglottis, forming narrow band reaching level of poral lobe or poral margin of vitellarium or slightly beyond, not being in contact with poral ventral canal. Testes overlap slightly margins of ovary. Diameter of testes 0.08-0.11. Cirrus sac 0.23-0.38 (mean 0.30) in length, 0.08-0.15 (mean 0.11) in width, usually extending markedly across ventral longitudinal canal, maximum size (0.34-0.38) attained in postmature proglottides. When cirrus fully withdrawn, distal end of cirrus sac usually blunt, distended, often as wide as proximal part; distal part formed internally by few large, oblong vesicles. Muscle layers of proximal cirrus sac thin, less than 0.01 when muscles not contracted. Cirrus sac covered by loose cell layer. Ductus cirri armed densely with minute spines in its distal part. Internal seminal vesicle initially rounded, may elongate considerably when filled with sperm, covering up to 4/5 of cirrus-sac length. External seminal vesicle prominent, 0.14-0.25 long and 0.05-0.09 wide, usually straight, covered with thick cell layer.

Ovary large (width 0.46-0.82, mean 0.65), coarsely lobed, positioned slightly porally, covering 2/4-3/4 of space between longitudinal osmoregulatory canals. Vitellarium large (width 0.27-0.44, mean 0.37), usually distinctly bilobed, lobes connected by narrow isthmus; positioned slightly porally with respect to mid-line of proglottis and ovary, overlapping posterior edge of ovary. Mehlis' gland spherical or subspherical, situated between lobes of vitellarium, 0.08-0.11 in diameter. Vagina 0.19-0.35 (mean 0.25) long, usually somewhat shorter than cirrus sac (85 % on average), slightly curved, running postero-ventrally or posteriorly to cirrus sac and opening postero-ventrally or ventrally to male pore. Internally, vagina formed by distinct, thin-walled tube tapering proximally. In holotype, distal vaginal tube forms distinct funnel within genital atrium (seen poorly in other specimens). Internal surface of distal part of vagina, excluding funnel, lined with delicate hair-like microtrichi pointing distally. Vaginal tube possibly forms short dilatation before entering seminal receptacle. Vaginal tube and poral end of seminal receptacle covered by layer of large, rounded cells; layer around vagina widens distally and merges with cell layer surrounding genital atrium. Seminal receptacle 0.16-0.39 in length (mean 0.22), 0.10-0.27 (mean 0.13) in maximum width, (asymmetrically) elongate or pyriform, clearly separate from vagina; attains maximum size (0.27-0.46) in postmature proglottides. Uterus appears in early mature proglottides as fine reticulum ventral to other organs and anterior to ovary, its lateral parts extending more posteriorly than middle part and across ventral longitudinal osmoregulatory canals. Lateral margins of early uterus not distinct. Uterus in pregravid proglottides covering most of medulla with irregular anterior, posterior and lateral sacculations and varying internal trabeculae, which tend to form transverse concentration in middle of proglottis. Sacculations and trabeculae disintegrate partly in fully gravid proglottides. Cirrus sac, vagina and accessory organs persist in pregravid proglottides, only cirrus sac present in fully gravid proglottides. Eggs 0.042-0.050 (mean 0.046) long, 0.033-0.042 (mean 0.037) wide, spherical in surface view, ovoid in side view. Pyriform apparatus present.

DISCUSSION

COMPARISON WITH OTHER SPECIES

Paranoplocephala yoccozi n. sp. is compared here with six related species of *Paranoplocephala* characterized by unilateral (or, as exception, infrequently alternating) genital pores and testes situated antiporally and anteriorly (but not anteroporally) to ovary; these are *P. fellmani* Haukisalmi & Henttonen, 2001, *P. gracilis* Tenora & Murai, 1980, *P. gubanovi* Gulyaev & Krivopalov, 2003, *P. janickii*, *P. montana* (Kirshenblat, 1941) and *P. nevoi* Fair, Schmidt & Wertheim, 1990. However, the comparison excludes *P. longivaginata* Chechulin & Gulyaev, 1998, *P. nordenskioeldi* Haukisalmi, Wickström, Hantula & Henttonen, 2001 and *P. serrata* Haukisalmi & Henttonen, 2000, species that also share the two key features with the new species, but which are markedly different from *P. yoccozi* n. sp. with respect to body dimensions and structure of the scolex, neck and genital ducts. Also, we do not compare *P. yoccozi* n. sp. with the Nearctic *P. arctica* (Rausch, 1952) *sensu* Haukisalmi & Henttonen, 2001 and *P. primordialis* (Douthitt, 1915), since most of the testes are situated anterior to ovary in the latter two species. For the main morphological features of *Paranoplocephala* spp. in Holarctic rodents, see Haukisalmi *et al.* (2002).

The comparison of *P. yoccozi* n. sp. with the related species shows that each of them differs from the new species by several taxonomically important features (Table I). Particularly, *P. yoccozi* n. sp. is distinguished by its large scolex of characteristic shape, large suckers and robust neck region. In addition, the structure of the cirrus sac (blunt, distended distal end), vitellarium (two distinct lodes connected by narrow isthmus) and perhaps also vagina (with distal funnel) are unique among all *Paranoplocephala* species examined by us. Although the latter features are subject to variation, in combination with other characteristics they provide additional means of separating *P. yoccozi* n. sp. from the related species. In the following pairwise comparisons we focus on other qualitative and quantitative differences.

The two species from lemmings, *P. fellmani* and *P. gubanovi*, are morphologically closely related to each other (*cf.* Haukisalmi & Henttonen, 2001; Gulyaev & Krivopalov, 2003; Table I). They both differ from *P. yoccozi* n. sp. by their high length/width ratio of mature proglottides and distinctly spherical seminal receptacle (elongated or pyriform in *P. yoccozi* n. sp.). Also, the early uterus of *P. fellmani*, and possibly also that of *P. gubanovi* (*cf.* Gulyaev & Krivopalov, 2003), is "sparsely reticulated", whereas the early uterus of *P. yoccozi* n. sp. is finely reticulated, corresponding to the prevailing type within *Paranoplocephala*. The extent of poral testes and egg size additionally distinguish *P. gubanovi* from the new species.

Paranoplocephala montana was described by Kirshenblat (1941) from *M. arvalis* and *C. nivalis* (one case) from Caucasus (Armenia and Georgia). *Paranoplocephala montana* has never been found in Europe, but it has frequently been reported as a parasite of voles and mice in various parts of the former Soviet Union (Ryzhikov *et al.*, 1978). However, due to the lack of descriptions, the presence of *P. montana* in other regions and host species can not be verified. Kirshenblat (1941) emphasized the different distribution of testes in the early mature and fully mature proglottides of *P. montana*, which has later been accepted as the main differentiating feature of this species (Tenora *et al.*, 1986b). However, the early mature proglottis that Kirshenblat (1941) illustrated was distinctly elongated, and it can be suspected that the concentration of testes in the central field was due to the overextended state of the anterior strobila. This phenomenon is also seen in other *Paranoplocephala* species, and it is clearly of no taxonomical value. Since the description of Kirshenblat (1941) includes little information on morphological variation or anatomical details, *P. montana* can not be reliably differentiated from any of the related species. However, *P. montana* evidently differs from *P. yoccozi* n. sp. by the number and position of testes and relatively shorter vagina (Table I). Kirshenblat (1941) did not designate a type specimen for *P. montana*.

Paranoplocephala gracilis is a host-generalist species of voles in Europe (Tenora & Murai, 1980; Tenora *et al.*, 1985) which has frequently been found also from the snow vole (Table II). It is easily distinguished from *P. yoccozi* n. sp. by the different extent of poral testes, centrally positioned ovary that often covers the whole space between ventral longitudinal canals, prominent, spherical or ovoid seminal receptacle and long vagina with thick external cell layer throughout its length (Fig. 2A, Table I).

Paranoplocephala janickii, known only from *M. arvalis* in Hungary and France (Tenora *et al.*, 1985; Gubányi *et al.*, 1992), is perhaps most closely related to *P. yoccozi* n. sp. among the species considered here (Fig. 2B, Table I). However, in addition to the major differences concerning the scolex and neck, *P. janickii* is distinguished from *P. yoccozi* n. sp. by its shorter vagina, shorter and more muscular cirrus sac, different extent of poral testes and smaller eggs. In the paratype specimen of *P. janickii* examined by us, the testes distribution was highly variable both porally and antiporally but it is not known whether this is a true species characteristic (testes distribution is fairly constant in *P. yoccozi* n. sp.).

Paranoplocephala nevoi Fair, Schmidt & Wertheim, 1990 was described from the mole-rat *Nannospalax ehrenbergi* (Nehring) (Spalacidae) from Syria (Fair *et al.*, 1990). The description is brief and somewhat contradictory but it shows that *P. nevoi* is a short-bodied (40-50) tapeworm which has slightly smaller scolex (0.42-0.69) and suckers (0.14-0.23) and thinner neck (ca. 0.3) than *P. yoccozi* n. sp. but also fewer testes (26-44) and distinctly shorter (0.12-0.16) and wider cirrus-sac, which does reach even the dorsal osmoregulatory canal. Female genital ducts were not described or illustrated. Since the early uterus was des-

Mountain range **Country** **Source**	Alps France 1	Alps Italy 1	Alps Austria 2, 3	Pyrenees Spain 4, 5	Pirin Mts Bulgaria 6, 7, 8	Carpathians Romania 9, 10	Carpathians Slovakia 10, 11
Anoplocephaloides dentata	+	+	+	+	+		+
A. rauschi					+		
A. tenoramuraiae					+		
A. cf. *variabilis*	+	+					
Paranoplocephala gracilis				+	+	+	+
P. omphalodes				+	+	+	+
P. yoccozi n. sp.	+						

Sources: 1, present study. 2, Prokopic & Mahnert, 1970. 3, Tenora *et al.*, 1971. 4, Mas-Coma *et al.*, 1978. 5, Feliu *et al.*, 1997. 6, Genov, 1984. 7, Genov *et al.*, 1984. 8, Genov & Georgiev, 1988. 9, Mészáros & Murai, 1979. 10, Tenora & Murai, 1980. 11, Tenora, 1967.

Table II. – Records of anoplocephalid cestodes from *Chionomys nivalis* in Europe.

cribed as an "aggregation of cells", the generic position of *P. nevoi* needs to be confirmed.

Finally, the independent status of *P. yoccozi* n. sp. (as "*Paranoplocephala* sp.") among 19 species of *Paranoplocephala* from voles and lemmings was confirmed by Wickström *et al.* (2005) based on sequencing of partial COI (mtDNA) gene (GenBank acc. no. AY568188).

ANOPLOCEPHALID CESTODES OF SNOW VOLES

The anoplocephalid cestodes of snow voles in Europe include at least seven species of known taxonomical status (Table II). Clearly the most common and predictable species is *Anoplocephaloides dentata* (Galli-Valerio, 1905), which was present in all four mountain ranges and in all but one of the seven regions. *Anoplocephaloides dentata* is a characteristic species of *Microtus* and *Chionomys* throughout the Palearctic, and it has been suggested that *A. dentata* may include multiple species but the existing morphological data have failed to show this (Rausch, 1976; Genov & Georgiev, 1988), with the exception of *A. dentatoides* Sato, Kamiya, Tenora & Kamiya, 1993 parasitizing *Clethrionomys rufocanus* on the Island of Hokkaido, Japan (Sato *et al.*, 1993). However, the recent molecular phylogenetic analysis of Wickström *et al.* (2005) suggests that there are three cryptic *A. dentata*-like species in Europe, the true *A. dentata* occurring in snow voles and associated *M. arvalis* on the mountains of southern and Central Europe. Thus, all *A. dentata*-like cestodes from the snow vole probably represent a single species. The other three *Anoplocephaloides* species of snow voles are much more sporadic, and two of them (*A. rauschi* and *A. tenoramuraiae*) may be restricted to the mountains of Bulgaria. The two latter species also parasitize the sympatric *Microtus subterraneus* (de Selys-Longchamps) (Genov & Georgiev, 1988). *Anoplocephaloides* cf. *variabilis* from snow voles is evidently conspecific with the related cestode from *Microtus* voles in northern Europe (Tenora *et al.*, 1986a; Haukisalmi *et al.*, 1994; Wickström *et al.*, 2005).

The host and geographical range of *P. yoccozi* n. sp. are still unknown, but since it has not been encountered in other host species in the type locality or in other snow vole populations, it may be a localized, host-specific species of the snow vole. The two other *Paranoplocephala* species of snow voles (*P. omphalodes* and *P. gracilis*) are host-generalists that they share with other voles inhabiting the high-mountain regions. However, it has been recently confirmed that there are two *P. omphalodes*-like species in Europe, one being

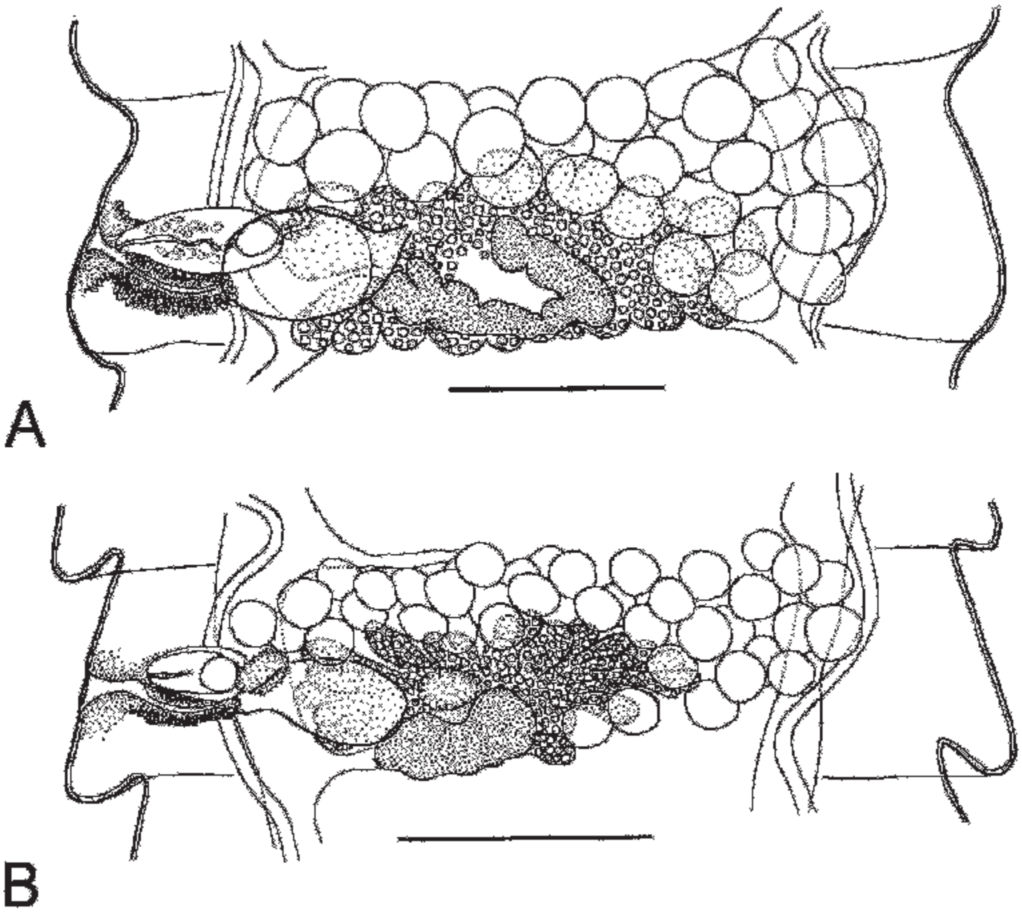

Fig. 2. – A, *Paranoplocephala gracilis*, mature proglottis (host *Microtus agrestis*, Finland) (scale-bar: 0.30 mm). B, *Paranoplocephala janickii*, mature proglottis (host *Microtus arvalis*, Hungary, paratype HNHM 5885). (scale-bar: 0.30 mm).

specific to *M. oeconomus* (primarily a northern European species) and another, the true *P. omphalodes*, occurring in *M. agrestis* and *M. arvalis* but also in *C. glareolus* (Haukisalmi *et al.*, 2004). Thus, the species in snow voles is probably the true *P. omphalodes* but this needs to be verified by molecular or morphometric analyses. *Paranoplocephala gracilis* is a morphologically distinctive species that occurs in *Microtus*, *Chionomys*, *Clethrionomys* Tilesius, *Arvicola* Lacepede and *Lemmus* Link throughout Europe (e.g. Tenora & Murai, 1980; Haukisalmi *et al.*, 1994; Haukisalmi & Henttonen, 2001; Feliu *et al.*, 1997). The conspecificity of *P. gracilis* from various vole species has been confirmed by molecular criteria (Wickström, 2004).

It should be noticed that *Paranoplocephala macrocephala* (Douthitt, 1915) was earlier reported as a parasite of *C. nivalis* (Prokopic & Mahnert, 1970; Ryzhikov *et al.*, 1978; Tenora, 1967; Tenora *et al.*, 1971) but it has later been proven that *P. macrocephala* is a Neartic species (or species complex) of *Microtus* voles and pocket gophers (Geomyidae) (Haukisalmi & Henttonen, 2003; Haukisalmi *et al.*, 2004). The reports of *P. macrocephala* from Europe probably concerned *P. omphalodes* and *P. gracilis*.

To summarize, the anoplocephalid cestode fauna of snow vole seems to consist primarily of species that it shares with other voles inhabiting the high-mountain areas; the same pattern has been observed in nematodes (e.g. Feliu *et al.*, 1997). Some of the anoplocephalid species are only known from areas inhabited by snow voles (true *A. dentata, A. rauschi*, *A. tenoramuraiae*, *P. yoccozi* n. sp. and perhaps *P. montana*) whereas others are wide-spread host-generalist species that snow voles occasionally acquire from other voles (true *P. omphalodes* and *P. gracilis*). Since some of the species appear to have a very sporadic distribution, the historical fragmentation of snow vole populations may have either promoted speciation in some of the cestode lineages or induced local extinctions in originally wide-spread species, or both (*cf.* Nadachowski, 1991). We predict that snow voles will be found to host additional unknown anoplocephalid cestodes characterized by restricted or sporadic geographical distribution.

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