DESCRIPTION OF *PARANOPLOCEPHALA ETHOLENI* N. SP. (CESTODA: ANOPLOCEPHALIDAE) IN THE MEADOW VOLE *MICROTUS PENNSYLVANICUS*, WITH A SYNOPSIS OF *PARANOPLOCEPHALA* S. L. IN HOLARCTIC RODENTS

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Summary:

Paranoplocephala etholeni n. sp., parasitizing the meadow vole *Microtus pennsylvanicus* in Alaska and Wisconsin, USA, is described. *Paranoplocephala etholeni* is morphologically most closely related to the Nearctic *Paranoplocephala ondatrae* (Rausch, 1948). Available data suggest that *P. etholeni* is a host-specific, locally rare species that may have a wide but sporadic geographical distribution in North America. The finding of *P. ondatrae*-like cestodes in *Microtus* spp. suggests that this poorly known species may actually be a parasite of voles rather than muskrat (type host). A tabular synopsis of all the known species of *Paranoplocephala* s. l. in the Holarctic region with their main morphological features is presented.

KEY WORDS: *Paranoplocephala etholeni* n. sp., *Paranoplocephala ondatrae*, Cestoda, Cyclophyllidea, Anoplocephalidae, Anoplocephalinae, *Microtus pennsylvanicus*, Alaska.

Résumé : DESCRIPTION DE *PARANOPLOCEPHALA ETHOLENI* N. SP. (CESTODA: ANOPLOCEPHALIDAE) CHEZ LE CAMPAGNOL DES PRAIRIES *MICROTUS PENNSYLVANICUS*, AVEC UN SYNOPSIS DE *PARANOPLOCEPHALA* S. L. CHEZ LES RONGEURS HOLARCTIQUES

Nous décrivons Paranoplocephala etholeni *n. sp., parasite du Campagnol des Prairies* Microtus pennsylvanicus *en Alaska et Wisconsin.* Paranoplocephala etholeni *est morphologiquement le plus proche de l'espèce néarctique* Paranoplocephala ondatrae *(Rausch, 1948). Les données disponibles suggèrent que* P. etholeni *est une espèce dont l'hôte est spécifique et localement rare, mais néanmoins avec une aire de répartition large et sporadique en Amérique du Nord. La découverte de cestodes du type* P. ondatrae *dans des espèces de campagnols* Microtus *spp. suggèrent que cette espèce peu connue est en fait une espèce parasite des campagnols, plutôt que du rat musqué (décrit comme hôte type). Un synopsis sous forme de tableau de toutes les espèces de* Paranoplocephala *s. l. de la région holarctique avec leurs principales caractéristiques morphologiques est donné.*

MOTS CLÉS : Paranoplocephala etholeni *n. sp.,* Paranoplocephala ondatrae, *Cestoda, Cyclophyllidea, Anoplocephalidae, Anoplocephalinae,* Microtus pennsylvanicus, *Alaska.*

INTRODUCTION

Anoplocephaline cestodes representing the genus *Paranoplocephala* Lühe, 1910 s. l. are ubiquitous parasites of voles and lemmings (Arvicolinae) (e.g. Rausch, 1976; Tenora *et al.*, 1985; Haukisalmi *et al.*, 2001). At least 27 species are known from Holarctic rodents, 10 of which parasitize primarily voles of the genus *Microtus* Schrank (Table I; see also Tenora *et al.*, 1986). Only one of these, *Paranoplocephala omphalodes* (Hermann, 1783), is known to have a Holarctic distribution (Rausch, 1976).

The meadow vole, *Microtus pennsylvanicus* (Ord), has a vast geographical distribution in North America, and it has been subject to several helminthological investigations (e.g. Erickson, 1938; Rausch & Tiner, 1949; Rausch & Schiller, 1949; Rausch, 1952; Kuns & Rausch, 1950; Lubinsky, 1957; Kinsella, 1967; Whitaker & Adalis, 1971). *Paranoplocephala macrocephala* (Douthitt, 1915) and *Paranoplocephala primordialis* (Douthitt, 1915) (both originally assigned to *Andrya*) have frequently been reported as parasites of *M. pennsylvanicus*. However, the concept of *P. macrocephala* has been very broad, and it is probable that other species of *Paranoplocephala* have also been reported under this name (Rausch, 1976). The taxonomy of *P. primordialis* is equally unsettled (Rausch, 1952; Haukisalmi & Henttonen, 2001).

Although the range of the meadow vole covers a considerable part of Alaska, there are no records of *Paranoplocephala* in *M. pennsylvanicus* from that region. Rausch (1952) reported *Paranoplocephala infrequens* (Douthitt, 1915) and *Paranoplocephala borealis* (Douthitt, 1915) as parasites of the meadow vole in Alaska, but these taxa are presently assigned to *Anoplocephaloides* Baer, 1923 as *A. troeschi* (Rausch, 1946) and *A. variabilis* (Douthitt, 1915) respectively (Rausch, 1946, 1952).

Our investigations on anoplocephalid cestodes of Alaska have revealed two species of *Paranoploce-*

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Cestode species	Host genus	Distribution	SC	NE	UT	VA	TE 1	TE 2	CI	AL
P. alternata Haukisalmi, Wickström, Hantula & Henttonen, 2001	*Dicrostonyx*	Holarctic	**S**	L	**C**	L	AAA	C	L	**F**
P. apodemi (Iwaki, Tenora, Abe, Oku & Kamiya, 1994)*	*Apodemus*	Palearctic	**S**	**S**	P	L	**AA**	**N**	L	U
P. aquatica Genov, Vasileva & Georgiev, 1996	*Arvicola, Ondatra*	Palearctic	**S**	L	**C**	L	AAA	C	L	**F**
P. arctica (Rausch, 1952); see also Haukisalmi *et al.*, 2001	*Dicrostonyx*	Nearctic	**S**	L	**C**	L	**AA**	C	L	U
P. bairdi (Schad, 1954); see also Haukisalmi & Henttonen, 2000	*Phenacomys*	Nearctic	**S**	L	P	L	A	C	L	U
P. blanchardi (Moniez, 1891) sensu Tenora *et al.* 1985*	*Microtus*	Palearctic	**S**	**S**	**C**	**S**	A	C	L	U
***P. etholeni* n. sp.**	***Microtus***	**Nearctic**	**S**	**S**	**C**	**S**	**AA**	**N**	**S**	**F**
P. fellmani Haukisalmi & Henttonen, 2001	*Lemmus*	Holarctic	**S**	L	S	L	**AA**	C	L	U
P. feodorovi (Gulyaev & Chechulin, 1996)	*Arvicola, Microtus*	Palearctic	**S**	**S**	P	L	A	**N**	L	**F**
P. genovi Gubányi, Tenora & Murai, 1998*	*Ondatra*	Palearctic	**S**	L	?	L	AAA	C	**S**	U
P. gracilis Tenora & Murai, 1980*	*Microtus, Clethrionomys*	Palearctic	**S**	L	P	L	AAA	C	L	U
P. janickii Tenora, Murai & Vaucher, 1985*	*Microtus*	Palearctic	**S**	L	P	**S**	**AA**	C	L	U
P. kalelai (Tenora, Haukisalmi & Henttonen, 1985)*	*Clethrionomys*	Palearctic	**S**	L	P	L	**AA**	**N**	L	**F**
P. kirbyi Voge, 1948	*Microtus*	Nearctic	L	L	P	L	A	C	L	**F**
P. krebsi Haukisalmi, Wickström, Hantula & Henttonen, 2001	*Dicrostonyx*	Nearctic	**S**	**S**	P	L	A	C	L	U
P. longivaginata Chechulin & Gulyaev, 1998*	*Clethrionomys*	Palearctic	**S**	L	**C**	L	AAA	**N**	L	**F**
P. macrocephala (Douthitt, 1915)*; see also Genov *et al.*, 1996	*Microtus, Geomys*	Nearctic	L	L	P	L	**AA**	**N**	L	**F**
P. maseri Tenora, Gubányi & Murai, 1999*	*Lemmiscus*	Nearctic	L	L	P	L	A	**N**	L	U
P. microti (Hansen, 1947)*	*Microtus*	Nearctic	L	L	P	L	A	C	L	**F**
P. montana (Kirschenblat, 1941)	*Microtus, Chionomys*	Palearctic	**S**	L	?	L	**AA**	C	L	U
P. neotomae (Voge, 1946)	*Neotoma*	Nearctic	**S**	L	?	L	AAA	**N**	L	**F**
P. nevoi Fair, Schmidt & Wertheim, 1990	*Spalax*	Palearctic	**S**	L	?	?	AAA	C	**S**	U
P. nordenskioeldi Haukisalmi, Wickström, Hantula & Henttonen, 2001	*Dicrostonyx*	Holarctic	**S**	L	P	L	**AA**	C	L	U
P. omphalodes (Hermann, 1783)*; see Tenora & Murai, 1980	*Microtus*	Holarctic	L	L	P	L	A	C	L	**F**
P. ondatrae (Rausch, 1948); see also Genov *et al.*, 1996	*Ondatra*	Nearctic	**S**	L	**C**	**S**	AAA	C	**S**	**F**
P. primordialis (Douthitt, 1915); see also Haukisalmi & Henttonen, 2001	*Microtus, Tamiasciurus*	Nearctic	**S**	L	S	L	**AA**	C	L	U
P. rauschi (Fair, Schmidt & Wertheim, 1990)	*Microtus*	Palearctic	L	L	?	L	A	**N**	L	**F**
P. sciuri (Rausch, 1947); see also Genov *et al.*, 1996	*Glaucomys*	Nearctic	**S**	L	?	L	AAA	C	**S**	U
P. serrata Haukisalmi & Henttonen, 2000	*Dicrostonyx*	Holarctic	**S**	L	P	L	A/**AA**	C	L	U

* The existing (re)descriptions have been supplemented with personal observations, concerning mostly the development of uterus, on type specimens or other available material.

Notes: *P. bialowiezensis* (Soltys, 1949), *P. campestris* (Cholodkovsky, 1912) and *P. communis* (Douthitt, 1915) are treated as *species inquirendae*, *P. translucida* (Douthitt, 1915) as a synonym of *P. macrocephala*, and *P. caucasica* (Kirschenblat, 1938) as a synonym of *P. omphalodes*. According to our unpublished observations, *P. mascomai* Murai, Tenora & Rocamora, 1980 (host *Microtus cabrerae*) should be assigned to the genus *Anoplocephaloides* because of its tube-like early uterus (see also Genov & Georgiev, 1988).

Table I. – *Paranoplocephala* spp. in Holartic rodents, with data on host genera, geographical distribution and main morphological features of cestodes. SC, morphology of scolex and suckers: S, scolex small, suckers embedded in scolex; L, scolex large, suckers protruding, bowl-shaped. NE, dimensions of neck: L, long and thin (relative to scolex); S, short and wide (relative to scolex). UT, structure of early uterus: C, completely reticulated (e.g. *P. alternata*: Haukisalmi *et al.*, 2001a); P, partly reticulated (e.g. *P. omphalodes*: Rausch, 1976); S, sparsely reticulated (e.g. *P. fellmani*: Haukisalmi *et al.*, 2001b). VA, length of vagina relative to the length of the cirrus sac: L, long (≥ 60 %); S, short (< 60 %). TE 1, overall distribution of testes: A, antiporally to ovary; AA, antiporally and anteriorly to ovary; AAA, antiporally, anteriorly and antero-porally to ovary. TE 2, antiporal distribution of testes: C, crossing antiporal ventral osmoregulatory canal; N, not crossing antiporal ventral canal. CI, length and position of cirrus sac: L, long, overlapping or crossing poral ventral osmoregulatory canal; S, short, not overlapping poral ventral osmoregulatory canal. AL, alternation of genital pores: F, frequently (and irregularly) alternating; U, unilateral or infrequently alternating. Character states corresponding to those in *P. etholeni* n. sp. have been indicated in bold.

phala as parasites of *M. pennsylvanicus*: the common and wide-spread *Paranoplocephala macrocephala* (see Haukisalmi & Henttonen, 2003) and a rare taxon of *Paranoplocephala* that was found to be morphologically distinct from its congeners; it is here described as *P. etholeni* n. sp. We also present a tabular synopsis of all the known species of *Paranoplocephala* s. l. in the Holarctic region with their main morphological features (Table I). These data can be used as an aid in the differential diagnosis among species of *Paranoplocephala* s. l. and in the construction of phylogenetic hypotheses for this genus.

MATERIALS AND METHODS

The main material of *P. etholeni* n. sp. was obtained from *M. pennsylvanicus* collected between the 2-4th August 2000 from Bonanza Creek Flat, 25 km southwest of Fairbanks, Alaska, USA (64° 42' N, 148° 16' W). The voles were dissected and examined for helminths immediately after trapping. Twelve of the 144 meadow voles examined for helminths were infected with *P. etholeni* (prevalence 8.3 %, intensity 1-16). Of the 35 worms recovered, 21 gravid specimens (1-4 from each infected host) were stained and mounted for study.

Four additional specimens of *P. etholeni* were found among 14 cestodes collected by one of us (RLR) from *M. pennsylvanicus* from Ohio, Michigan and Wisconsin, USA, between 1944-1948 (see Rausch & Schiller, 1949). The specimens of *P. etholeni* were all collected in 1948 from Madison, Wisconsin. Two of these specimens (one gravid and one pregravid) were examined morphometrically. This material also included a single specimen from Madison, Wisconsin (personal collection of R.L. Rausch no. 581) that closely resembles *Paranoplocephala ondatrae* (Rausch, 1948) from muskrat. Because *P. ondatrae* is known from a single specimen only and because it resembles *P. etholeni*, we illustrate the main morphological features of this specimen. The other nine specimens from the Great Lakes Region represented *P. macrocephala* s. l. (Haukisalmi & Henttonen, 2003).

We also describe briefly another specimen of *Paranoplocephala* that is apparently related to *P. ondatrae*. The host, montane vole *Microtus montanus* (Peale), was collected by John D. Boone on the eastern slope of the Sierra Nevada mountains, Nevada, USA (38° 13.8' N, 119° 23.0' W), on 9th August 1995. The specimen has been deposited in the United States National Parasite Collection as *Paranoplocephala* sp. (coll. no. 91877). Because only two specimens resembling *P. ondatrae* were available, we do not present morphometric data for them.

The cestodes from Alaska and Nevada were washed and relaxed in tap water for several hours, fixed in 70 % alcohol, stained with Mayer's haemalum or Semichon's acetic carmine, cleared in eugenol and mounted in Canada balsam. Hand-cut transverse sections of mature proglottides were also examined. The cestodes from the Great Lakes Region were fixed in formalin-alcohol-acetic acid solution and stained with Semichon's acetic carmine (Rausch & Schciller, 1949).

The morphometric analysis follows that of Haukisalmi & Henttonen (2000, 2001). The length of the neck was measured from the posterior margin of suckers to the beginning of visible segmentation. Various reproductive organs were measured and counted from 1-5 mature proglottis from each individual. The first mature proglottis was defined as the one in which the internal seminal vesicle was first seen clearly differentiated and the last mature proglottis as the one in which the vitellarium was last compact. The width of the ventral longitudinal osmoregulatory canals were measured at the mid-level of the mature proglottides. The cirrus sac was measured only if the cirrus was inverted. Testes were counted by drawing them on paper with the aid of camera lucida. "The index of asymmetry" of female organs was quantified as the distance from the midpoint of the vitellarium to the poral margin of the proglottis relative to the corresponding width of proglottis at the level of the vitellarium. Egg dimensions are usually based on five measurements from each fully gravid strobila. The alternation of the genital pores was quantified as the number of changes per 100 proglottides and average length of unilateral series in each strobila.

All measurements are in millimeters unless otherwise stated.

The type and voucher specimens of cestodes have been deposited in the United States National Parasite Collection in Beltsville, Maryland, USA. Samples of the type host (*M. pennsylvanicus*) from Alaska have been deposited in the University of Alaska Museum at Fairbanks, Alaska, USA.

RESULTS

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

PARANOPLOCEPHALA ETHOLENI N. SP.

Host: *Microtus pennsylvanicus* (Rodentia, Muridae, Arvicolinae).

Site: small intestine (jejunum/ileum).

Localities: Bonanza Creek Flat, Alaska, USA (type locality) and Madison, Wisconsin, USA.

Holotype: United States National Parasite Collection, Beltsville, Maryland, USA, coll. no. 91874, host *Microtus* *pennsylvanicus*, collected from Bonanza Creek Flat in Alaska, USA, by H. Henttonen, J. Laakkonen and J. Niemimaa, on 4th August 2000.

Paratypes: coll. nos. 91875 and 91876, other data same as in the holotype.

Etymology: The name of the new species refers to Arvid Adolf Etholén, a Finn who served as a chief manager of Alaska during 1840-1845. Etholén was a keen collector of ethnographic artifacts of Aleutians and other native inhabitants of western Alaska. His renowned collections are deposited in the Finnish National Museum.

DESCRIPTION (Figs. 1-3, Table II)

Strobila ca. 100 in length, relatively wide and robust. Maximum width attained in pregravid or gravid proglottides. Scolex not clearly distinct from neck. Suckers small, spherical, directed laterally or antero-laterally, embedded in scolex. Neck short and thick, minimum width ca. 60 % (32-89 %) of scolex width, attained at 0.20-0.47 (mean 0.38) from posterior margin of suckers. Longitudinal muscle bundles form two separate layers in mature proglottides.

Proglottides craspedote. Length/width ratio of proglottides fairly constant in immature, mature and postmature proglottides (mean 0.19-0.20), but markedly higher in gravid proglottides (mean 0.40). Genital pores opening in middle of proglottis margin or slightly posteriad. Genital pores frequently and irregularly alternating with 6.5-13.5 (mean 9.8) changes per 100 proglottides. Average length of unilateral series 7.4-15.5 (overall range 1-46) proglottides.

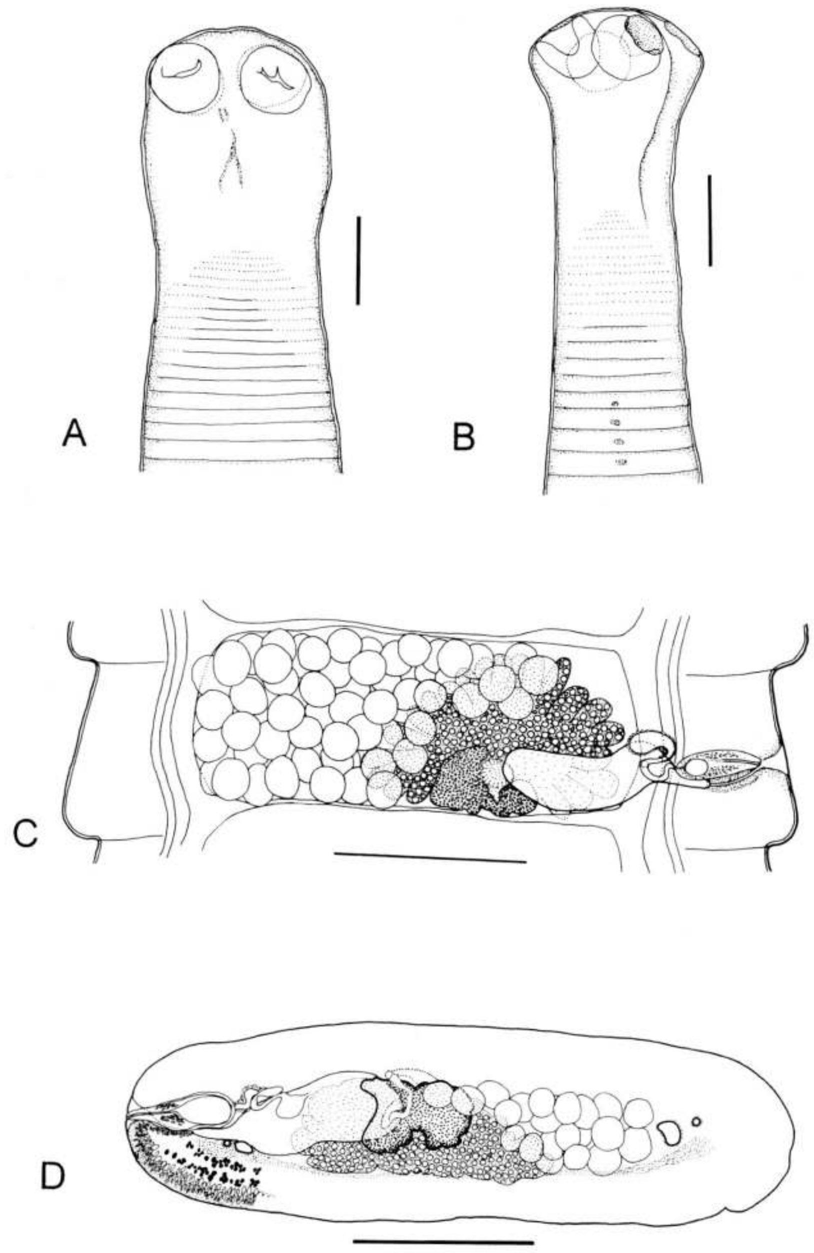

Fig. 1. – *Paranoplocephala etholeni* n. sp. in *Microtus pennsylvanicus* from Alaska, USA. A, B, scolex and neck (scale bar: 0.30 mm). C, mature proglottis (scale bar: 0.50 mm). D, transverse section of mature proglottis (scale bar: 0.50 mm).

Ventral longitudinal osmoregulatory canals thin, 0.02-0.10 (mean 0.06) at middle of proglottis; longitudinal canals connected by thin transverse canals. Dorsal longitudinal osmoregulatory canals 0.013-0.032 (mean 0.019) in width, lateral to ventral canals. Genital ducts passing dorsally across longitudinal osmoregulatory canals.

Testes numerous, situated mostly in antiporal part of proglottis. Few testes may overlap antiporal ventral osmoregulatory canals, but usually no testes extend antiporally across this canal. Position of most poral testes varies from level of mid-vitellarium to poral margin of vitellarium. Testes may overlap ovary slightly, but do not usually reach margin of vitellarium. Testes in 2-4 dorso-ventral layers in antiporal part of proglottis; 1-2 layer(s) of testes overlap(s) ovary. Diameter of testes 0.07-0.10.

Cirrus sac pyriform, relatively short, 10-17 % (mean 13 %) of mature proglottis width. Cirrus sac does not usually overlap poral ventral osmoregulatory canals. Absolute length of cirrus sac increases slightly in postmature proglottides. Muscle layers of cirrus sac poorly developed. Distal part of ductus cirri armed with short spines, proximal part usually uncoiled. Length of

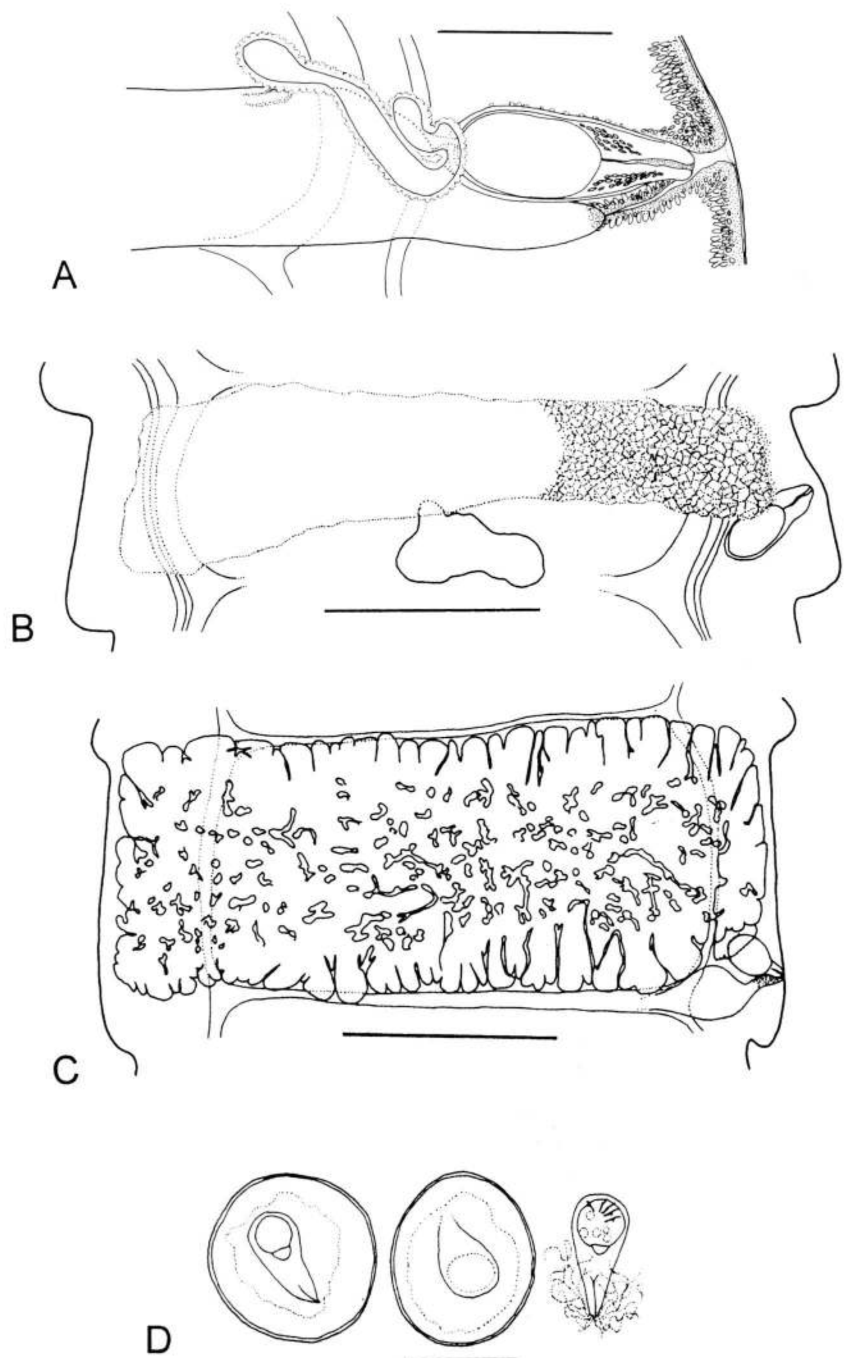

Fig. 2. – *Paranoplocephala etholeni* n. sp. in *Microtus pennsylvanicus* from Alaska, USA. A, terminal genital ducts (scale bar: 0.20 mm). B, early-stage uterus in mature proglottis (scale bar: 0.50 mm). C, fully developed uterus in pregravid proglottis (scale bar: 1.0 mm). D, egg in surface and side view, and pyriform apparatus (scale bar: 0.030 mm).

internal seminal vesicle ca. half of cirrus sac length in mature proglottides. External seminal vesicle irregularly looped, lying anterior or partly dorsal to seminal receptacle. Surface of external seminal vesicle covered with layer of large cells.

Vagina tube-like organ of uniform width, lying ventrally or postero-ventrally to cirrus sac. Length of vagina ca. half of cirrus sac length (41-73 %, mean 56 %). Walls of vagina formed by dense layer of intensely stained cells. No lining observed on internal surface of vagina. Seminal receptacle long, asymmetrically ampulliform, distal part forming distinct neck. Proximal part of seminal receptacle usually bent posteriorly. Vagina, cirrus sac and accessory organs persist in gravid proglottides.

Vitellarium and ovary poral, vitellarium and Mehlis' gland lying middle of and dorsally to ovary. Width of

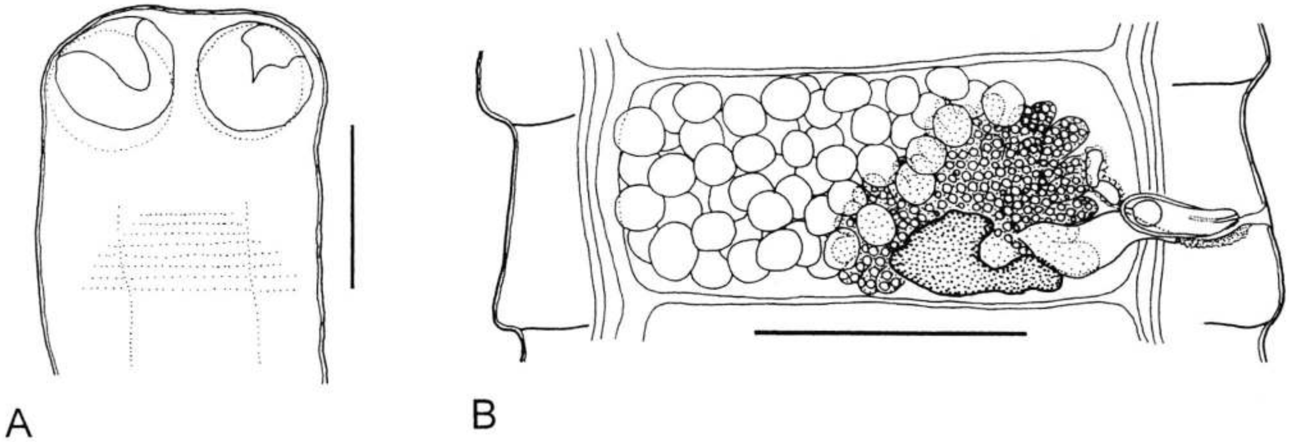

Fig. 3. – *Paranoplocephala etholeni* n. sp. in *Microtus pennsylvanicus* from Wisconsin, USA. A, scolex and neck (scale bar: 0.30 mm). B, mature proglottis (scale bar: 0.50 mm).

	P. etholeni n. sp. Alaska (n = 13) Host: *Microtus pennsylvanicus*			**P. etholeni n. sp.** Wisconsin (n = 2) Host: *M. pennsylvanicus*			**P. ondatrae** (Rausch, 1948) Source: Genov *et al.*, 1996 (n = 1) Host: *Ondatra zibethicus*		
Characters	Range	Mean	N	Range	Mean	N	Range	Mean	N
Body length	71-124	100.7	12	91	–	1	122	–	1
Number of proglottides	151-196	179.0	12	–	–	–	369	–	1
Maximum width	2.83-4.95	3.81	13	4.08	–	1	2.58	–	1
Scolex, diameter	0.50-0.69	0.597	11	0.53-0.72	0.625	2	0.665	–	1
Suckers, diameter	0.21-0.25	0.222	41	0.21-0.27	0.238	8	0.237-0.250	0.246	4
Neck, length	0.20-0.55	0.351	10	0.40	–	1	0.70	–	1
Neck, width	0.38-0.67	0.508	11	0.48-0.53	0.505	2	0.24	–	1
Testes, total number	53-79	66.9	28	62-84	74.0	5	80-95	86	15
Cirrus sac, length	0.17-0.32	0.256	32	0.22-0.36	0.298	5	0.210-0.228	0.221	12
Cirrus sac, width	0.07-0.13	0.096	32	0.07-0.15	0.095	5	0.113-0.125	0.117	12
Cirrus sac, maximum length[a]	0.29-0.40	0.335	13	0.31-0.36	0.335	5	–	–	–
Ovary, width	0.50-1.06	0.751	32	0.50-0.80	0.696	5	–	–	–
Ovary, length	0.29-0.46	0.364	32	0.33-0.52	0.408	5	–	–	–
Vitellarium, width	0.21-0.52	0.344	32	0.32-0.39	0.347	5	–	–	–
Vitellarium, length	0.12-0.19	0.151	32	0.14-0.1	0.156	5	–	–	–
Index of asymmetry	0.36-0.049	0.424	31	0.39-0.43	0.407	5	0.46-0.50	0.48	12
Vagina, length	0.11-0.18	0.143	32	0.13-0.18	0.153	5	0.045-0.058	0.051	12
Vagina, maximum width	0.032-0.060	0.046	32	0.030-0.040	0.038	5	0.040-0.049	0.043	12
Vagina/cirrus sac ratio	0.41-0.73	0.565	32	0.48-0.59	0.519	5	0.20-0.26	0.23	12
Seminal receptacle, length	0.30-1.10	0.540	32	0.31-0.42	0.365	2	0.626-0.693	0.669	10
Seminal receptacle, width	0.11-0.24	0.157	32	0.10-0.12	0.108	2	0.112-0.215	0.143	10
Seminal receptacle, max. length[a]	0.57-1.25	0.870	13	0.55	–	1	–	–	–
Egg, length	34-46	41.3	55	38-42	39.7	8	34-38	36	15
Egg, width	30-38	35.4	13	35-39	38.6	8	–	–	–

[a] Postmature proglottides.

Table II. – Main morphometric features of *Paranoplocephala etholeni* n. sp. and *P. ondatrae* (Rausch, 1948). All measurements are in millimeters except for the egg dimensions which are in micrometers. n, number of specimens. N, number of measurements.

ovary ca. 1/3 of mature proglottis width. Vitellarium may overlap slightly seminal receptacle.

Uterus appears in premature proglottides as dense, dorso-ventrally thin reticulum formed by fine threads, lying ventral to other organs and extending across longitudinal osmoregulatory canals bilaterally. Antiporal part of early uterus usually extends more posteriad than poral part. Lateral margins of reticulum not distinct. In late mature proglottides, lumen rapidly appears and marginal sacculations and internal trabeculae are formed within uterus, first in lateral parts of uterus. At this stage, vitellarium and ovary disappear simultaneously, but testes remain, overlapping developing uterus in early postmature proglottides. Fully developed uterus (pregravid proglottides) with anterior, posterior and lateral sacculations, and complex system of anastomosing internal trabeculae, but no fenestrations. All internal structures of uterus usually disappear in fully gravid proglottides.

Eggs spherical in surface view, ovoid in side view. Length of pyriform apparatus 0.025-0.030, width 0.013-0.015. Horn of pyriform apparatus may be partially divided; tip of horn(s) armed with bunch of fine hairs. Length of oncospheral hooks ca. 0.005.

DISCUSSION

INTRASPECIFIC VARIATION

Morphological and morphometric data show convincingly that the specimens of *P. etholeni* from Alaska and Wisconsin are conspecific; they agree well in most qualitative and quantitative features (Figs 1-3, Table II). We could find only a single consistent difference between these populations, i.e. the cirrus sac of the specimens from Wisconsin seems to be slightly longer, and therefore overlaps the poral ventral osmoregulatory canals more than the cirrus sac of the specimens from the type locality. However, considering the high overall similarity and small sample size for Wisconsin population, this deviation can not be given significant taxonomic weight.

DIFFERENTIAL DIAGNOSIS

Table I shows eight morphological features for *P. etholeni* and other species of *Paranoplocephala* s. l. in Holarctic rodents. These characters were selected because they were available for most of the species, because they usually show limited intraspecific variation, and because they have traditionally been used in species-level taxonomy of anoplocephaline cestodes of rodents. *Paranoplocephala* spp. occurring south of the Holarctic Region (Africa and South America) were excluded; these species are *P. dasymidis* (Hunkeler, 1972), *P. gundii* (Joyeux, 1923), and *P. octodensis* (Babero & Cattan, 1975).

According to Table I, *P. etholeni* is morphologically distinct from all other species of *Paranoplocephala*. There is only one species, *P. ondatrae*, that shares five features and five species, *Paranoplocephala apodemi* (Iwaki, Tenora, Abe, Oku & Kamiya, 1994), *Paranoplocephala blanchardi* (Moniez, 1891), *Paranoplocephala feodorovi* (Gulyaev & Chechulin, 1996), *Paranoplocephala kalelai* (Tenora, Haukisalmi & Henttonen, 1985) and *P. longivaginata* Chechulin & Gulyaev, 1998, that share four features with *P. etholeni* (Table I). The other species of *Paranoplocephala* parasitizing *Microtus* spp. in North America, *Paranoplocephala microti* (Hansen, 1947), *Paranoplocephala kirbyi* Voge, 1948, *P. macrocephala*, *P. omphalodes* and *P. primordialis*, are morphologically unrelated to *P. etholeni*, sharing only 1-2 features with it.

The most similar species, *P. ondatrae*, was described by Rausch (1948) based on a single specimen from muskrat *Ondatra zibethicus* (Linnaeus) from Ohio, USA. Rausch & Schiller (1949) later synonymized *P. ondatrae* with *P. macrocephala*, a common parasite of *Geomys* Rafinesque and *Microtus* in North America, but the redescriptions of Genov *et al.* (1996) show that these two species are separate. Following the original description, *P. ondatrae* has not been reported from North America, but Tenora & Murai (1980) described it from muskrat from Hungary and the former Czechoslovakia. However, these specimens were later identified as *Paranoplocephala aquatica* Genov, Vasileva & Georgiev, 1996 (Genov *et al.*, 1996) and finally described as *Paranoplocephala genovi* Gubányi, Tenora & Murai, 1998 (Gubányi *et al.*, 1998). The detailed redescription of the holotype of *P. ondatrae* by Genov *et al.* (1996) shows that its early-stage uterus is similar to that of *P. etholeni* (dense reticulum covering most of the medulla). The structure of the (early) uterus has been a key characteristic in the classification of anoplocephaline cestodes (Beveridge, 1994), and the similarity of this complex structure in *P. etholeni* and *P. ondatrae* suggests a close (phylogenetic) relationship. Other morphological similarities between *P. etholeni* and *P. ondatrae* include the structure and dimensions of the scolex, cirrus sac and vagina (*cf.* Fig. 4), and the pattern of the alternation of the genital pores. Of these, the shortness of the cirrus sac and vagina are of special significance, because these features are rare among *Paranoplocephala* spp. (Table I). However, the vagina of *P. ondatrae* is actually shorter (relative to the length of the cirrus sac) than that of *P. etholeni* (Table II), although both species were classified as having a short vagina. *Paranoplocephala etholeni* differs from *P. ondatrae* also in the morphology of the neck and by number and distribution of testes. *P. etholeni* has a short, wide neck (relative to the size of the scolex), an uncommon characteristic among *Paranoplocephala* spp., whereas *P. ondatrae* has a typical "paranoplocephaloid" neck (long and slender). Although neck dimensions can be markedly affected by the degree of relaxation, the differences between the two neck types in *Paranoplocephala* are so distinct and consistent that they must represent true interspecific variation. In *P. ondatrae*, there is a large number of testes anterior to ovary and the poral testes reach the poral ventral osmoregulatory canal and may overlap it (*cf.* Fig. 4), whereas in *P. etholeni* there are only a few testes anterior to ovary and they do not extend further poral than the poral margin of vitellarium.

Additionally, the shape of the seminal receptacle is unique in *P. etholeni*, separating it from all other species of *Paranoplocephala*.

Paranoplocephala cf. *ondatrae* from voles

The specimen of *P. cf. ondatrae* from *M. pennsylvanicus* from Wisconsin (Fig. 4A, C) is morphologically very closely related to *P. ondatrae* from muskrat. For

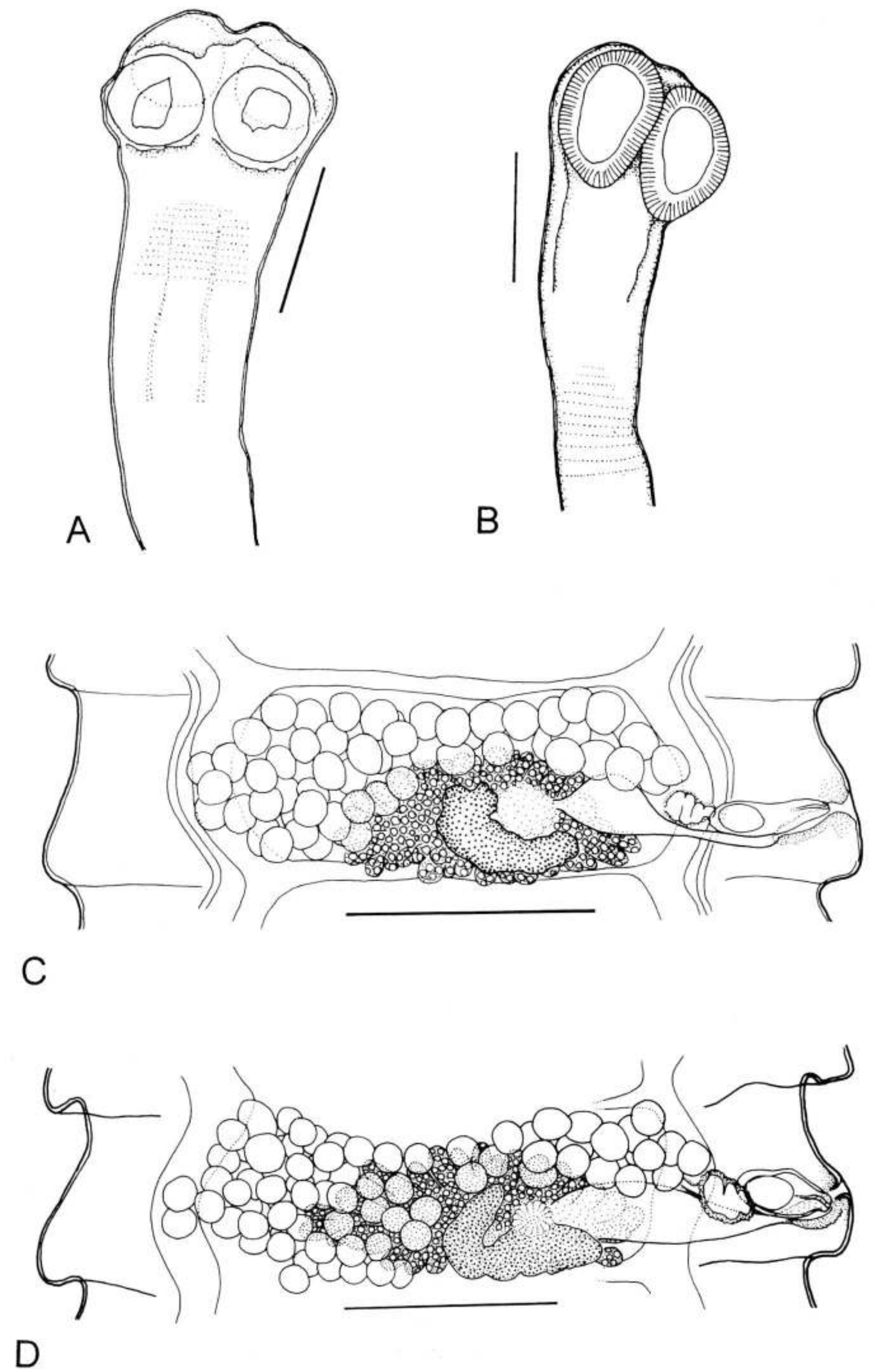

Fig. 4. – *Paranoplocephala* cf. *ondatrae* in *Microtus pennsylvanicus* from Wisconsin, USA (A, C) and in *Microtus montanus* from Nevada, USA (B, D). A, B, scolex and neck (scale bar: 0.30 mm). C, D, mature proglottides (scale bar: 0.50 mm).

example, both taxa have a similar, completely reticulate early uterus, small scolex, long and slender neck, similar overall distribution of testes (from antiporal to poral ventral osmoregulatory canals and identical genital ducts (very short and thick vagina, short cirrus sac, long seminal receptacle with narrow distal "neck" and expanded, ovoid proximal part). The slight difference in the distribution of testes (a larger proportion of testes lies anterior to ovary in *P. ondatrae* than in *P. cf. ondatrae*), possibly reflecting host-induced variation, seems to be the only qualitative feature separating these taxa. These specimens also originate from the same geographical region (Ohio and Wisconsin, respectively).

The specimen from *M. montanus* from Nevada (Fig. 4B, D) resembles both *P. ondatrae* from muskrat and *P.* cf. *ondatrae* from meadow vole, but differs from them by the relative size of suckers (larger in the specimen from *M. montanus*) and distribution testes with respect to ovary (testes overlapping ovary more in the specimen from *M. montanus*).

The similarity of these three taxa, and especially those from muskrat and meadow vole, suggests that they are either conspecific or closely related (sister) taxa. It is therefore possible that *Microtus*-voles are the natural definitive hosts for *P. ondatrae*, instead of muskrat, which would explain the extreme rarity of *P. ondatrae* in the type host (*cf.* Rausch, 1948). However, because there are no data for morphological and morphometric variation within these taxa, definitive conclusions about their conspecificity would be premature. Further taxonomic research on the *P. ondatrae*-complex based on more representative samples is clearly warranted.

HOST AND GEOGRAPHICAL DISTRIBUTION OF *PARANOPLOCEPHALA ETHOLENI*

The existing data suggest that *P. etholeni* is a specific parasite of *M. pennsylvanicus*, at least in Alaska. We have previously examined large samples of *Microtus miurus* Osgood and *M. oeconomus* (Pallas) from the northern Alaska (Haukisalmi *et al.*, 1995), and *Dicrostonyx* spp. (Haukisalmi *et al.*, 2001) and *Lemmus* spp. (Haukisalmi & Henttonen, 2001) from Arctic Siberia and North America without finding any cestodes resembling the new species. *Paranoplocephala etholeni* was also absent in the 48 *Clethrionomys rutilus* (Pallas), five *M. oeconomus* and 12 *Synaptomys borealis* (Richardson) originating from the type locality of the new species (southwest of Fairbanks; Haukisalmi & Henttonen, unpubl.). In addition, we have not found *P. etholeni* among anoplocephalid cestodes of voles collected in connection of the Beringian Coevolution Project (BCP), organized by the University of Alaska Museum, Fairbanks (project leaders: Joseph Cook, Eric P. Hoberg and Sam R. Telford). The Alaskan voles examined for helminths by the BCP include ca. 200 *M. pennsylvanicus*, collected from various sites in the Yukon-Charley Rivers National Preserve, and large samples of *Microtus xanthognathus* (Leach), *M. miurus*, *M. oeconomus* and *C. rutilus* from diverse localities in Alaska.

The finding of *P. etholeni* in *M. pennsylvanicus* from Wisconsin suggests that this species may actually have a wide distribution in North America. Although *P. etholeni* was evidently not found in other host species examined by Rausch & Schiller (1949), it remains to be shown whether it is strictly specific to the meadow vole in the more southern regions where *Microtus*-assemblages differ from those in Alaska. Other published records of *Paranoplocephala* spp. from North American *Microtus* (for a review, see Timm, 1985) can not be compared with *P. etholeni*, because no descriptions were presented.

Because several independent species of *Paranoplocephala* have evidently been (mis)identified as *P. macrocephala*, we examined the available samples in the US National Parasite Collection from *Microtus* spp., labelled as "*Paranoplocephala macrocephala*" (USNPC 84515) or "*Andrya macrocephala*" (USNPC 44447, 44655), but none of these represented *P. etholeni*.

To summarize the available pieces of information, *P. etholeni* is a host-specific, locally rare species that may have a wide but sporadic geographical distribution in North America.

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