

Anoplocephalid cestodes of wood rats (*Neotoma* spp.) in the western U.S.A.

Voitto Haukisalmi^{1*} and Robert L. Rausch²

¹Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FIN-01301 Vantaa, Finland;

²Department of Comparative Medicine, University of Washington School of Medicine, Box 357190, Seattle, WA 98195-7190, U.S.A.

Abstract

This study reviews the taxonomy of anoplocephaline cestodes of wood rats, *Neotoma cinerea*, *N. fuscipes* and *N. mexicana* (Sigmodontinae) in the western and south-western U.S.A. The anoplocephaline fauna included five species, only one of which, *Andrya neotomae* Voge, 1946, was relatively common and occurred in all three host species. Other species were *Paranoplocephala freemani* Haukisalmi, Henttonen et Hardman, 2006, *P. primordialis* (Douthitt, 1915), both host-generalist species of North American rodents, and two apparently undescribed species of *Paranoplocephala* s. str. *Aprostataandrya octodonensis* Babero et Cattán, 1975 from the indigenous South American rodent *Octodon degus* is regarded as a junior synonym of *A. neotomae*. A redescription is provided for *A. neotomae*.

Key words

Andrya, *Paranoplocephala*, Anoplocephalidae, Cestoda, *Neotoma*, *Octodon*, Sigmodontinae

Introduction

Three species of anoplocephalid cestodes (i.e. *Andrya neotomae* Voge, 1946, *A. primordialis* Douthitt, 1915 and *Monoecestus* sp.) have been reported from wood rats (*Neotoma* Say et Ord, Sigmodontinae) in North America (Voge 1946, 1955; Miller and Schmidt 1982). The taxonomy of anoplocephalid cestodes of wood rats has been studied only by Voge (1946), who described *Andrya neotomae* from *Neotoma fuscipes* (Baird). *A. neotomae* was later reported (without description) from *N. cinerea* Ord by Rausch (1952), Lubinsky (1957) and Miller and Schmidt (1982). In addition, Murphy (1952) briefly described *Andrya* sp. from *N. floridana* Ord, a cestode that clearly is not conspecific either with *A. neotomae* or *A. primordialis*. Thus, the anoplocephaline cestode fauna of wood rats may be more diverse than presently understood, if subjected to detailed taxonomic scrutiny. Other cestodes reported to parasitize wood rats in the adult stage are *Raillietina* sp. (Davaineidae) (see Voge 1955, Miller and Schmidt 1982) and *Catenotaenia neotomae* Babero et Cattán, 1983 (Catenotaeniidae) (see Babero and Cattán 1983, which also includes a list of helminths reported from *Neotoma* spp. prior to 1983).

This study reviews the taxonomy of anoplocephaline cestodes of wood rats based on the available museum specimens

and those from the personal collection of one of the authors (RLR, Table I). *A. neotomae* is redescribed and compared with *Aprostataandrya octodonensis* Babero et Cattán, 1975, a very similar cestode from an indigenous South American rodent. The main morphological features and the host and geographical distribution of the other anoplocephalid cestodes parasitizing wood rats are summarized briefly.

Materials and methods

The material consists of 19 mounted specimens of anoplocephaline cestodes from *N. cinerea*, *N. fuscipes* and *N. mexicana* (Baird) (Table I), and two specimens (holo- and paratype) of *Aprostataandrya octodonensis* from *Octodon degus* (Molina) (USNPC 73439), from the collections of the United States National Parasite Collection, Beltsville, Maryland (USNPC) and the Harold W. Manter Laboratory of Parasitology, University of Nebraska – Lincoln (HWML). Representative specimens (wholemounds) of the present material have been deposited in the USNPC (Table I).

The scolex, neck and 2–3 mature proglottids from each individual were drawn on paper with the aid of a camera lucida, and various organs were counted and measured from these

*Corresponding address: voitto.haukisalmi@metla.fi

Table I. Specimens of *Andrya neotomae* and *Paranoplocephala* spp. from *Neotoma* spp. examined during the present study

Cestode species	Host species	State	County/Locality	Collector	Accession number	n
<i>Andrya neotomae</i>	<i>N. cinerea</i>	Idaho	Benewah Co.	F. Seesee	USNPC 75512	1
		Oregon	Lane Co.	C. Maser	USNPC 97143	1
		Oregon	Lincoln Co.	C. Maser	USNPC 97144	2
	<i>N. fuscipes</i>	California	Monterey Co.	M. Voge	USNPC 97141	1
		Oregon	Coos Co.	C. Maser	USNPC 97142	1
		Oregon	Multnomah Co.	R.L. Rausch	USNPC 97145	2
		Colorado	Larimer	G.D. Schmidt	HWML 35068	1
	<i>N. mexicana</i>	Idaho	Benewah Co.	F. Seesee	USNPC 75512	2
<i>Paranoplocephala</i> sp. I	<i>N. cinerea</i>	Alaska	Juneau	M.L. Johnson	USNPC 97148	2
<i>Paranoplocephala</i> sp. II	<i>N. cinerea</i>	Oregon	Lincoln Co.	C. Maser	USNPC 97146	4
<i>P. freemani</i>	<i>N. fuscipes</i>	California	Monterey Co.	M. Voge	USNPC 97147	1
<i>P. primordialis</i>						

drawings using a ruler. Neck length was measured from the posterior margin of suckers to the beginning of visible segmentation. The pattern of the alternation of genital pores was determined as the mean number of proglottids in each unilateral set for each specimen (low value of index indicates frequent alternation) and as a number of changes per 100 proglottids (high value of index indicates frequent alternation). The width of the ventral longitudinal osmoregulatory canals was recorded at the midpoint of the proglottid (on both sides). The cirrus sac was measured only if the cirrus was fully withdrawn. Maximum length of the cirrus sac was recorded from postmature proglottids. 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 proglottid) and the width of the corresponding proglottid. Egg length is based on five measurements from the terminal proglottids of each fully gravid strobila. All metric data are in millimetres.

Results

Andrya neotomae Voge, 1946

Syns: *Paranoplocephala neotomae* (Voge, 1946) (see Tenora *et al.* 1986); *Aprostotandrya octodonensis* Babero et Cattán, 1975 (new synonymy); *Paranoplocephala octodonensis* (Babero et Cattán, 1975) (see Tenora *et al.* 1986)

The redescription is based on 9 specimens from *Neotoma cinerea*, *N. fuscipes* and *N. mexicana* (Table I). The mean and the number of measurements (n) are given in parentheses after the range.

Description (Fig. 1, Table II): Fully developed strobilae 144–174 (160, n = 5) long and relatively wide (4.1–5.3, 4.5, n = 6); maximum width attained in pregravid or gravid proglottids. Number of proglottids up to 240. Scolex 0.45–0.70 (0.59, n = 7) wide. Suckers 0.19–0.30 (0.25, n = 27) in diameter, directed antero-laterally, embedded within scolex or slightly protruding. Neck 0.25–0.50 (0.35, n = 6) long, usually of uniform width (0.30–0.46, 0.35, n = 7), thick relative to

scolex width (53–69%, 59%, n = 7). Proglottids distinctly craspedote. Length/width ratio 0.15–0.28 (0.22, n = 20) in mature proglottids, 0.25–0.48 (0.35, n = 10) in gravid proglottids. Genital pores opening in posterior half of proglottid margin. Genital pores very frequently (and irregularly) alternating, on average with 2.0 proglottids in each unilateral set (range 1–9) or 50.1 changes per 100 proglottids (range 46–54).

Ventral longitudinal osmoregulatory canals 0.04–0.10 (0.056, n = 32) wide at mid-level of proglottid, connected by transverse canals measuring 0.020–0.035. Dorsal longitudinal osmoregulatory canals thin (0.01–0.02), overlapping ventral canals dorsally. Genital ducts passing dorsally across longitudinal osmoregulatory canals and nerve cord.

Testes 57–115 (85.4, n = 19) in number, in 1–3 layers, extending from antiporal to poral ventral osmoregulatory canal, but usually not overlapping either canal. Testes always confluent anterior to ovary. Testes do not usually overlap ovary; distinct transverse gap between antiporal margin of ovary and antiporal testes observed in most proglottids. Diameter of testes 0.05–0.10.

Length of cirrus sac 0.32–0.57 (0.41, n = 17) and width 0.10–0.14 (0.12, n = 17) in mature proglottids; maximum length in postmature proglottids 0.42–0.59 (0.53, n = 5). Cirrus sac usually slightly overlaps ventral longitudinal canal. Thickness of muscle layers of cirrus sac 0.012–0.020 when cirrus withdrawn. Ductus cirri straight, armed with minute spines in its distal part. Internal seminal vesicle elongate, 1/3–2/3 of cirrus sac length when filled with sperm. External seminal vesicle long, often looped, not distinctly separate from vas deferens, covered by thick, intensely stained cell layer.

Vagina 0.27–0.55 (0.37, n = 15) long, usually slightly shorter than cirrus sac (67–100%, 89%, n = 13), tube-like, of uniform width (0.03–0.04), clearly distinct from seminal receptacle, running postero-ventral or posterior to cirrus sac. Vaginal tube very narrow, covered externally by dense layer of small, intensely stained cells, merging with cell layer surrounding genital atrium; no lining observed on internal surface of vagina. Seminal receptacle elongate, 0.44–0.95 long (0.66, n = 18), distinctly sacculated when filled with sperm.

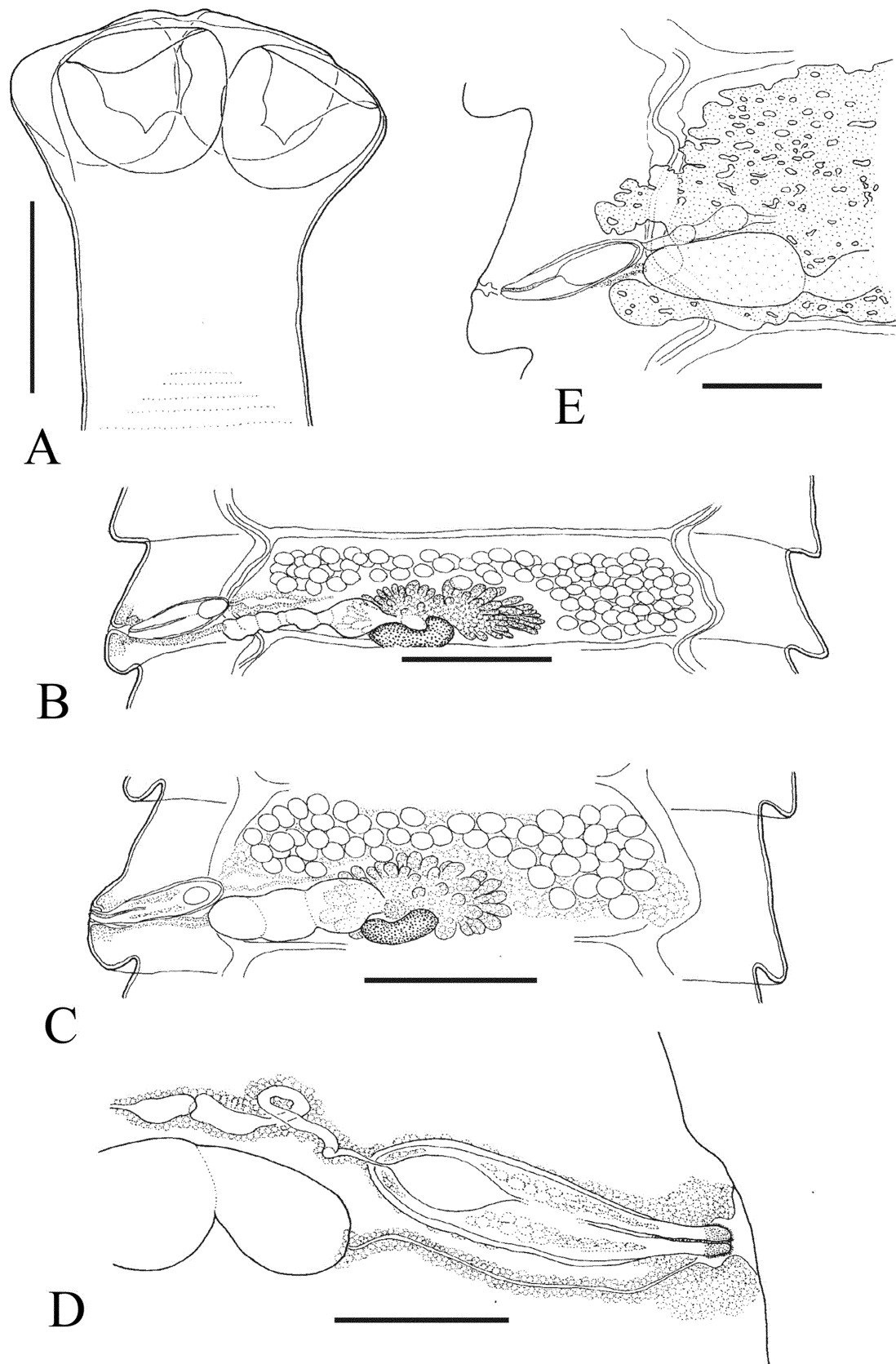


Fig. 1. *Andrya neotomae* from *Neotoma* spp.: **A** – scolex from *N. cinerea*, **B** – mature proglottid from *N. cinerea*, **C** – mature proglottid from *N. fuscipes*, **D** – terminal genital ducts from *N. cinerea*, **E** – uterus in postmature proglottid from *N. cinerea*. Scale bars = 0.30 mm (A); 0.50 mm (B, C); 0.20 mm (D, E)

Vitellarium 0.19–0.38 (0.29, $n = 19$) wide, 0.11–0.25 (0.16, $n = 19$) long, arched, symmetrically or slightly asymmetrically bilobed, positioned slightly porally with respect to midline of proglottid and ovary (index of asymmetry 0.41–0.48, 0.44, $n = 19$), posterior to ovary or partly overlapping posterior margin of ovary. Mehli's gland 0.07–0.10, ovoid or spherical. Ovary 0.44–1.00 (0.65, $n = 18$) wide, 0.15–0.51 (0.31, $n = 17$) long, densely lobulate, positioned medially or slightly porally, separated by wide gap from longitudinal osmoregulatory canals on either side of proglottid.

Uterus initially fine reticulum positioned ventral to testes, not usually overlapping ovary; posterior fringes of uterus usually overlap longitudinal canals dorsally and extend slightly beyond them. Fully developed uterus in pregravid proglottids of variable morphology, usually with irregular marginal diverticula and complex system of internal trabeculae. Testes remain in early pregravid proglottids overlapping developing uterus, terminal genital ducts persist in gravid proglottids; other internal structures disintegrate in fully gravid proglottids. Eggs 0.059–0.070 (0.064, $n = 20$) long, spherical or ovoid, provided with short, poorly developed pyriform apparatus, in which no separate horns could be distinguished.

Remarks

The present redescription of *A. neotomae* generally agrees well with the original description of Voge (1946), differing slightly in the number of testes and length of eggs (both higher in the present material; Table II). It should be mentioned

that Voge's (1946) description was based on cestodes obtained from a single specimen of *N. fuscipes*, and such material may be biased and not representative of the entire species. Contrary to Voge (1946), the cirrus of *A. neotomae* was found to be armed, a condition characterizing all species of *Andrya* Raillet, 1893 and *Paranoplocephala* Lühe, 1910 studied by us.

Voge (1946) did not discuss the differences between *A. neotomae* and *A. rhopalocephala* (Riehm, 1881), since, according to her, the latter species "evidently bears little resemblance to *A. neotomae*". Indeed, *A. rhopalocephala* is a much longer cestode than *A. neotomae*, and its genital pores are unilateral or infrequently alternating, whereas the genital pores of *A. neotomae* alternate very frequently (and irregularly). There are also major differences in the distribution of testes and many additional morphometric features (see Stiles 1896, Rausch 1976, and Haukisalmi and Wickström 2005 for the morphology of *A. rhopalocephala*).

When describing *A. octodonensis*, Babero and Cattán (1975) differentiated the new species from *A. neotomae* primarily by the number of testes (82–109 vs 60–74). However, the present analysis shows that the number of testes overlaps in these two species (96–126 vs 57–107), although *A. octodonensis* has on average more testes than *A. neotomae*. Furthermore, the testis counts are very variable even within the same strobila, and this feature alone can seldom be used for specific diagnosis among anoplocephaline cestodes.

The present analysis shows that the type material of *A. octodonensis* is actually very similar to *A. neotomae* (cf. Figs 1 and 2; Table II), and the former is therefore considered a jun-

Table II. Main morphometric features of *Andrya neotomae* and *Aprostotandrya octodonensis*

Cestode species	<i>A. neotomae</i>	<i>A. neotomae</i>	<i>A. octodonensis</i>	<i>A. octodonensis</i>
Host species	<i>Neotoma fuscipes</i>	<i>N. fuscipes</i> , <i>N. cinerea</i> , <i>N. mexicana</i>	<i>Octodon degus</i>	<i>Octodon degus</i>
Geographical origin	California (U.S.A.)	Oregon, Idaho, California, Colorado (U.S.A.)	Chile	Chile
Source	Voge (1946)	present study	Babero and Cattán (1975)	present study
Body, length	ca 130	144–174	ca 200	–
Body, maximum width	–	4.1–5.3	(6.2)	2.5–2.6
Scolex, diameter	0.36–0.64	0.45–0.70	0.3–0.4	0.31–0.35
Suckers, diameter	0.20–0.25	0.19–0.30	0.11–0.14	0.12–0.14
Neck, length	0.27–0.53	0.25–0.50	0.28–0.68	0.35–0.40
Neck, minimum width	0.16–0.34	0.30–0.46	0.25–0.33	0.22–0.33
Genital pores, alternation ¹	–	2.0 (1–9)	–	1.9 (1–7)
Testes, total number	60–74	57–115	82–109	92–126
Cirrus sac, length	0.32–0.44	0.32–0.57	0.33–0.42	0.33–0.40
Ovary, width	0.28–0.62	0.44–1.00	–	0.40–0.65
Vitellarium, width	–	0.19–0.38	–	0.15–0.25
Index of asymmetry	–	0.41–0.48	–	0.39–0.47
Seminal receptacle, length	–	0.44–0.95	–	0.53–0.70
Egg, length	0.053	0.059–0.070	0.058	–

¹Mean number of proglottids in each unilateral set (range in parentheses). All metric data are in mm.

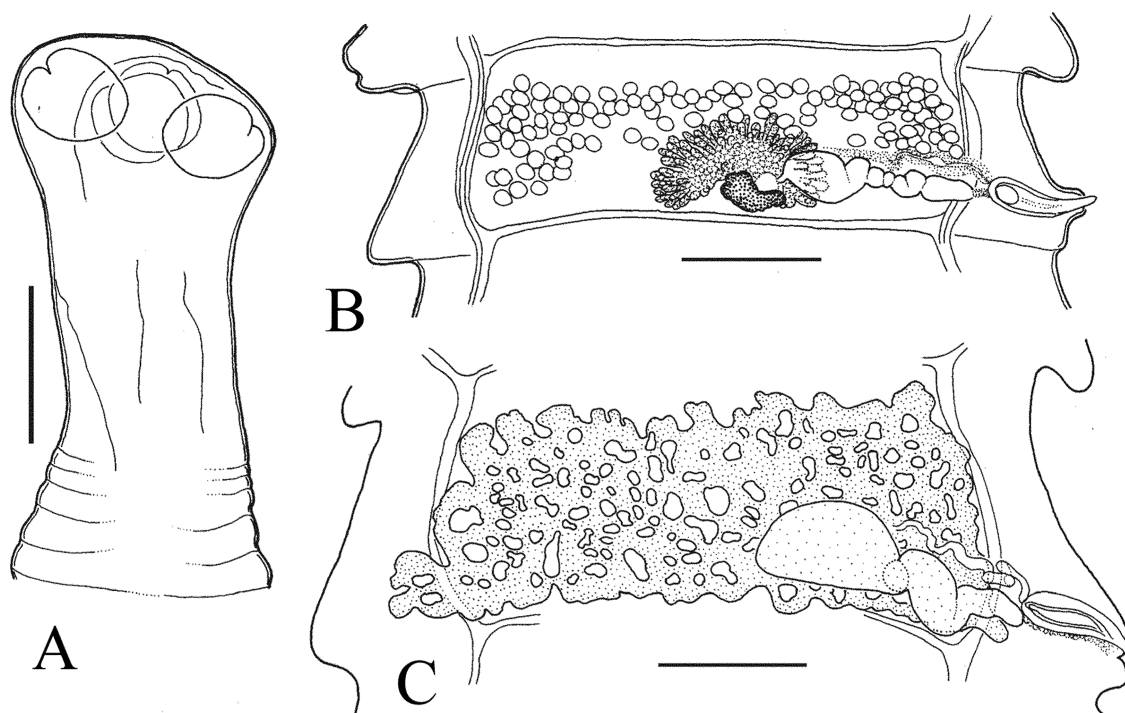


Fig. 2. Type material of *Aprostatandrya octodonensis* from *Octodon degus*, Chile: **A** – scolex, **B** – mature proglottid, **C** – uterus in pregravid proglottid. Scale bars = 0.20 mm (A); 0.50 mm (B, C)

ior synonym of *A. neotomae*. The similarities include the alternation of genital pores (very frequently alternating), distribution of the testes, position of the ovary and vitellarium, structure of the terminal genital ducts, relative position of the ventral and dorsal osmoregulatory canals (overlapping), and most of the quantitative features. The uteri of these two species are also strikingly similar, both having characteristic posterior fringes that extend slightly across longitudinal canals dorsally. The only features that seem to differ slightly between these taxa are the number of testes (above) and the size of the scolex and suckers (larger in *A. neotomae*). The maximum body width for *A. octodonensis* (6.2) reported by Babero and Cattán (1975) may be an error, since the strobilae of the holo- and paratype specimens are only 2.5–2.6 wide.

Paranoplocephala sciuri (Rausch, 1947) from the northern flying squirrel *Glaucomys sabrinus* (Shaw) is also morphologically related to *A. neotomae*, but the former species differs fundamentally from *A. neotomae* in the extent and relative position of the uterus (extending ventrally across the longitudinal canals in *P. sciuri*; Rausch 1947, V. Haukisalmi and R.L. Rausch, unpubl. observations).

***Paranoplocephala freemani* Haukisalmi, Henttonen et Hardman, 2006**

Paranoplocephala freemani is reported for the first time from *N. cinerea*. It was described recently from *Microtus xanthognathus* (Leach) and *Ondatra zibethicus* (L.) from Alaska (Hau-

kisalmi *et al.* 2006). Morphologically it is characterized by numerous, widely distributed testes, several of which extend across the antiporal ventral longitudinal canal, a relatively short cirrus sac and a seminal receptacle of typical shape (Fig. 3A–C). *P. freemani* is most closely related to two European species from semiaquatic voles, i.e. *P. aquatica* Genov, Vasileva et Georgiev, 1996 and *P. genovi* Gubányi, Tenora et Murai, 1998 (see Haukisalmi *et al.* 2006). The present finding confirms that *P. freemani* is not restricted to higher latitudes, and that it may also (sporadically) parasitize non-arvicoline rodents. Overall, the host and geographical distribution of *P. freemani* is quite unpredictable, and because of its rarity it may remain undetected in smaller data sets of rodents. *P. freemani* has not been found outside North America.

***Paranoplocephala primordialis* (Douthitt, 1915)**

Re-examination of Vogé's (1955) material of *P. primordialis* from *N. fuscipes* confirmed its identity. *P. primordialis* is a host-generalist parasite of arvicoline rodents and sciurids in North America (Rausch and Schiller 1949, Haukisalmi and Henttonen 2000, Haukisalmi *et al.* 2005). It has unilateral or infrequently alternating genital pores and a small number of relatively large testes distributed anteriorly and antiporally to the ovary (Fig. 3D, E). Most of the verified findings of *P. primordialis* originate from *Microtus* Schrank and *Clethrionomys* Tilesius voles from high latitudes, particularly from Alaska (Haukisalmi *et al.* 2005).

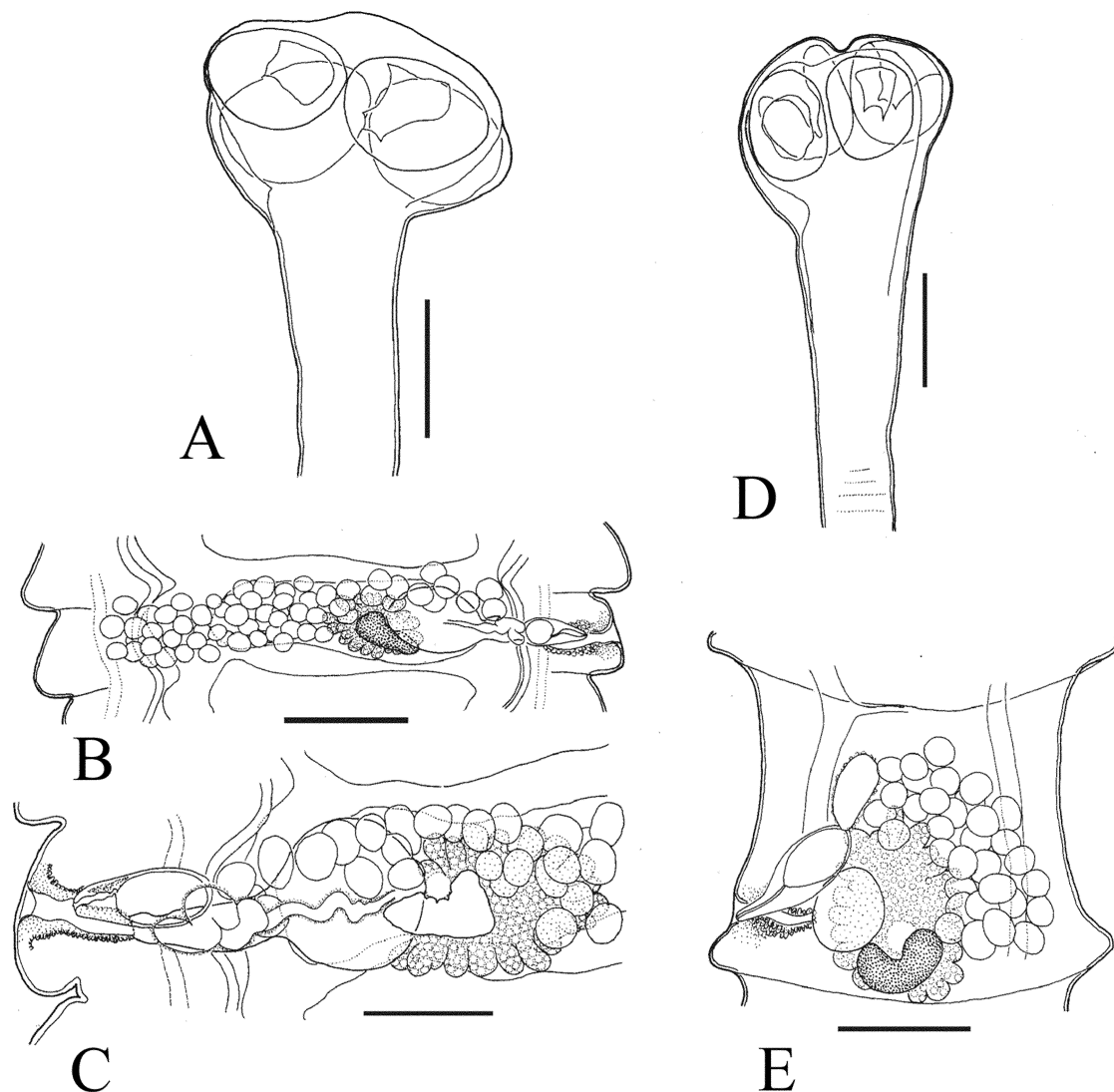


Fig. 3. *Paranoplocephala freemani* from *Neotoma cinerea* (A–C) and *Paranoplocephala primordialis* from *Neotoma fuscipes* (D, E): **A** – scolex, **B** – mature proglottid, **C** – terminal genital ducts, **D** – scolex, **E** – mature proglottid. Scale bars = 0.30 mm (A, C, D, E); 0.50 mm (B)

Paranoplocephala sp. I

Paranoplocephala sp. I belongs to *Paranoplocephala* s. str., as defined by Haukisalmi and Henttonen (2003), according to the morphology of the scolex, suckers, terminal genital ducts and early uterus. The monophyly of *Paranoplocephala* s. str. with respect to other *Paranoplocephala* species in rodents has been confirmed by Haukisalmi *et al.* (2004) and Wickström *et al.* (2005). *Paranoplocephala* sp. I differs from all species within *Paranoplocephala* s. str. by the extent of the poral and/or antiporal testes and egg length (0.06–0.65 in *Paranoplocephala* sp. I, usually less than 0.045 in the other species) (see Tenora *et al.* 1999, Haukisalmi and Henttonen 2003, Haukisalmi *et al.* 2004) (Fig. 4A, C; Table III). *Paranoplocephala* sp. I is perhaps most closely related to *Paranoplocephala maseri* Tenora, Gubányi et Murai, 1999 from the North

American sagebrush vole *Lemmys curtatus* (Cope), but, in addition to the features mentioned above, it differs from *Paranoplocephala* sp. I by the alternation of the genital pores (unilateral in *P. maseri*) and length of the cirrus sac (0.11–0.14 in *P. maseri*) (Tenora *et al.* 1999). The available information thus suggests that *Paranoplocephala* sp. I represents an undescribed species.

It should be mentioned that the specimens identified as *Paranoplocephala neotomae* by Miller et Schmidt (1982) (USNPC 75512) include both *A. neotomae* and *Paranoplocephala* sp. I (Table I).

Paranoplocephala sp. II

Paranoplocephala sp. II, which also belongs to *Paranoplocephala* s. str., is a robust cestode with an exceptionally wide

Table III. Selected morphological features of *Paranoplocephala* sp. I and II from *Neotoma cinerea*

Cestode species	<i>Paranoplocephala</i> sp. I	<i>Paranoplocephala</i> sp. II
Geographical origin	Idaho, U.S.A.	Alaska, U.S.A.
Accession number	USNPC 75512	USNPC 97148
Body, length	108–210	249
Body, maximum width	3.3–3.7	7.4
Scolex, diameter	0.7–0.8	1.4–1.7
Suckers, diameter	0.31–0.35	0.52–0.60
Genital pores, alternation	frequently alternating	infrequently alternating
Testes, total number	60–70	60–70
Cirrus sac, length	0.20–0.26	0.30–0.40
Index of asymmetry	0.40	0.28–0.31
Egg, length	0.060–0.065	0.055–0.057

All metric data are in mm.

strobila and scolex; in this respect it differs from all species within *Paranoplocephala* s. str., including *Paranoplocephala* sp. I above (Fig. 4B, D; Table III). Within *Paranoplocephala* s. str., *Paranoplocephala* sp. II most closely resembles *P. batzlii* Haukisalml, Henttonen et Hardman, 2006, a parasite of the

singing vole *Microtus miurus* Osgood in Alaska, which also is a relatively large-bodied species with irregularly alternating genital pores and with a testis distribution approaching that of *Paranoplocephala* sp. II (Haukisalml *et al.* 2006). However, *Paranoplocephala* sp. II can be distinguished from *P. batzlii*

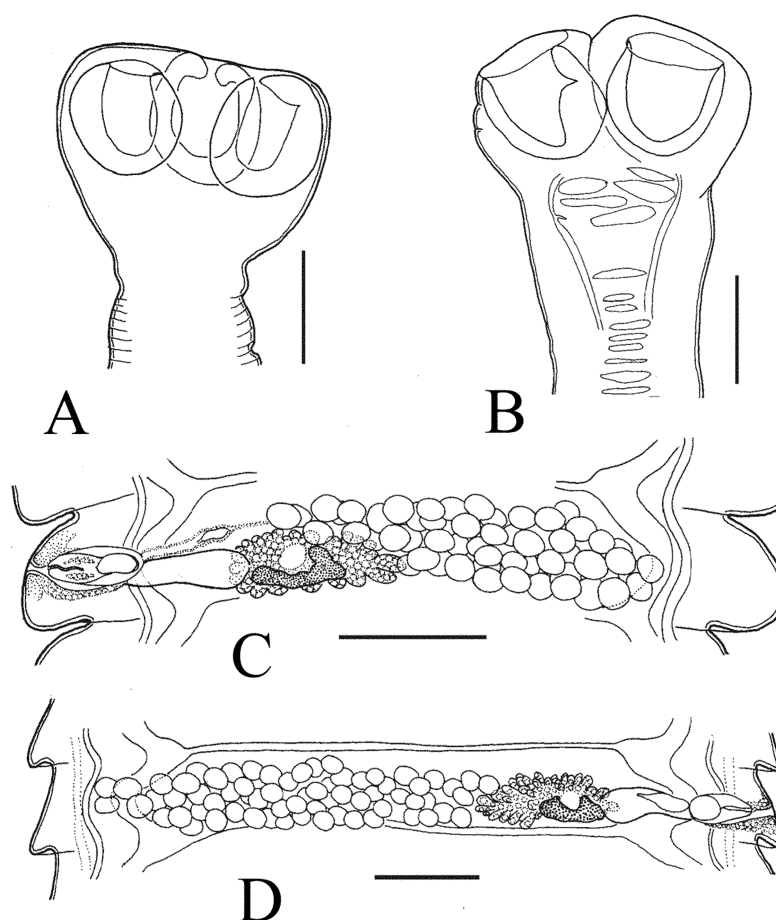


Fig. 4. *Paranoplocephala* sp. I (A, C) and *Paranoplocephala* sp. II (B, D) from *Neotoma cinerea*: **A** – scolex, **B** – scolex, **C** – mature proglottid, **D** – mature proglottid. Scale bars = 0.30 mm (A, C); 0.50 mm (B, D)

by the width of the transverse osmoregulatory canals (thinner in *Paranoplocephala* sp. II), position of the female glands (more poral in *Paranoplocephala* sp. II) and egg length (higher in *Paranoplocephala* sp. II). Since *Paranoplocephala* sp. II does not fully conform to any known *Paranoplocephala* species, it probably represents another undescribed species.

The cestode ("*Andrya* sp.") found by Murphy (1952) in *N. floridana* probably also belongs to *Paranoplocephala* s. str., although its taxonomic status remains unclear as no voucher specimens were deposited.

Discussion

Contrary to previous reports, the anoplocephalid cestode fauna of wood rats was found to be diverse, consisting of at least five species, two of which appear to be previously unknown. The present material was, however, too limited for a description of new species. The taxonomic status and host distribution of *Paranoplocephala* sp. I and II requires further study based on additional material. Moreover, the taxonomy of the Nearctic species of *Paranoplocephala* s. str. outside Alaska is poorly understood and needs to be revised using a combination of molecular and morphological methods (see Haukialmi and Henttonen 2003, Haukialmi *et al.* 2006). Only one of the species, *A. neotomae*, appears to be relatively widespread and regularly found in wood rats. However, *A. neotomae* has not been reported from *N. floridana* in the south-eastern U.S.A. (Murphy 1952, Boren *et al.* 1993). With the possible exception of *A. neotomae* (below), all species recognized in this study are probably strictly Nearctic and two of them have been found only in wood rats.

The allocation of *A. neotomae* to *Andrya sensu* Haukialmi *et al.* Wickström (2005) is based on the morphology and position of the uterus, which is initially reticulate, positioned ventral to testes and largely confined between the longitudinal canals, with its postero-lateral fringes regularly overlapping the canals dorsally. The other recognized species of *Andrya* is *A. rhopalocephala* (type species) from the western Eurasian leporids. According to the scheme proposed by Haukialmi and Wickström (2005), the species in which the reticulated uterus extends ventrally across the longitudinal canals are assigned to *Paranoplocephala* (mostly from arvicoline rodents), and those in which the uterus is situated between the testes in dorso-ventral planes and extending dorsally across the longitudinal canals are assigned to *Neandrya* Haukialmi *et al.* Wickström, 2005, the latter based on a single species, *N. cuniculi* (Blanchard, 1891) (syn. *Andrya cuniculi*) from European leporids. The genus *Aprostotandrya* Kirshenblat, 1938, to which *A. octodonensis* was originally assigned, is unequivocally a junior synonym of *Paranoplocephala* (see Haukialmi and Henttonen 2003, Haukialmi *et al.* 2004).

The known host and geographical distribution of the two species of *Andrya* recognized here (*A. rhopalocephala* and *A. neotomae*, the latter including *A. octodonensis*) raises obvious questions of the origins and evolutionary affinities of

these taxa. Since the three host groups (leporids, neotomines, octodontids) represent distant phylogenetic lineages, it is not possible to suggest a plausible explanation for the current distribution of *Andrya* spp., other than that they may represent relicts of an ancient lineage, with much broader host and geographical distributions, coupled with colonization of distant host lineages. A corresponding explanation was used to account for the disjunct distribution of the anoplocephaline genus *Leporidotaenia* Genov, Murai, Georgiev *et al.* Harris, 1990 in hares and rabbits of the western Eurasia and Central America (Genov *et al.* 1990).

However, it is possible that the similar uterine morphology has developed convergently within *Andrya* spp., and that *A. rhopalocephala* is actually not closely related to *A. neotomae*. Even then it would be hard to reconstruct the evolutionary history of *A. neotomae* in *Neotoma* and *Octodon* Bennett, the genera representing different suborders of rodents, Sciurognathi and Hystricognathi, respectively, and having presently non-overlapping ranges. Since there are hardly any morphological differences between *A. neotomae* and *A. octodonensis*, it seems unlikely that the current host distribution of *A. neotomae* would reflect an ancient appearance in the precursor of the all extant rodents and subsequent "coaccommodation" in *Neotoma* and *Octodon*. An alternative, perhaps more plausible explanation is that the genera *Neotoma* and *Octodon*, or their precursors, have historically had overlapping geographical ranges, providing an opportunity for a host shift from either direction. For example, it may be hypothesized that *A. neotomae* or its precursor had been present in the sigmodontine rodents colonizing South America, although the genus *Neotoma* itself has not managed to colonize this continent. However, this hypothesis assumes that *A. neotomae* would occur in other sigmodontine rodents either in North, Central or South America, for which there is as yet no evidence. In addition, we are not aware of other close faunistic affinities between helminths of indigenous, unrelated South and North American mammals, which could be used to explain the disjunct distribution of *A. neotomae*. The presence of *A. neotomae* in a South American hystricognath rodent is so unexpected that the possibility of a technical error should not be dismissed. Further material, preferably accompanied with molecular phylogenetic data (cf., Wickström *et al.* 2005), are needed for resolving the uncertainty concerning the taxonomic position of *A. octodonensis* vs *A. neotomae*.

Acknowledgements. We would like to thank Patricia Pilitt, Eric P. Hoberg (USNPC) and Scott L. Gardner (HWML) for the loan and deposition of museum specimens.

References

- Babero B.B., Cattán P.E. 1975. Helmintofauna de Chile: III. Parásitos del roedor degú, *Octodon degus* Molina, 1782, con la descripción de tres nuevas especies. *Boletín Chileno de Parasitología*, 30, 68–76.

- Babero B.B., Cattán P.E. 1983. *Catenotaenia neotomae* sp. n. (Cestoda: Dilepididae) parásito de *Neotoma lepida* (Rodentia: Cricetidae) en Nevada, U.S.A. *Boletín Chileno de Parasitología*, 38, 12–16.
- Boren J.C., Lochmiller R.L., Boggs J.F., Leslie D.M., Jr. 1993. Gastrointestinal helminths of eastern woodrat populations in central Oklahoma. *Southwestern Naturalist*, 38, 146–149.
- Genov T., Murai E., Georgiev B.B., Harris E.A. 1990. The erection of *Leporidotaenia* n. g. (Cestoda: Anoplocephalidae) for *Anoplocephaloides* spp. parasitizing Leporidae (Lagomorpha). *Systematic Parasitology*, 16, 107–126.
- 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. *Systematic Parasitology*, 45, 219–231.
- Haukisalmi V., Henttonen H. 2003. What is *Paranoplocephala macrocephala* (Douthitt, 1915) (Cestoda: Anoplocephalidae)? *Systematic Parasitology*, 54, 53–69.
- Haukisalmi V., Henttonen H., Hardman L.M. 2006. Taxonomy and diversity of *Paranoplocephala* spp. (Cestoda: Anoplocephalidae) in voles and lemmings of Beringia, with a description of three new species. *Biological Journal of the Linnean Society*, in press.
- Haukisalmi V., Rausch R.L., Henttonen H. 2005. 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). *Folia Parasitologica*, 52, 311–321.
- Haukisalmi V., Wickström L.M. 2005. Morphological characterisation of *Andrya* Railliet, 1893, *Neandrya* n. g. and *Paranoplocephala* Lühe, 1910 (Cestoda: Anoplocephalidae) in rodents and lagomorphs. *Systematic Parasitology*, 62, 209–219.
- 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). *Zoologica Scripta*, 33, 277–290.
- Lubinsky G. 1957. List of helminths from Alberta rodents. *Canadian Journal of Zoology*, 35, 623–627.
- Miller G.E., Schmidt G.D. 1982. Helminths of bushy-tailed wood rats, *Neotoma cinerea* subsp. from Colorado, Idaho, and Wyoming. *Proceedings of the Helminthological Society of Washington*, 49, 109–117.
- Murphy M.F. 1952. Ecology and helminths of the Osage wood rat, *Neotoma floridana osagensis*, including the description of *Longistriata neotoma* n. sp. (Trichostrongylidae). *American Midland Naturalist*, 48, 204–218.
- Rausch R. 1947. *Andrya sciuri* n. sp., a cestode from the northern flying squirrel. *Journal of Parasitology*, 33, 316–318.
- Rausch R.L. 1952. Studies on the helminth fauna of Alaska. XI. Helminth parasites of microtine rodents – taxonomic considerations. *Journal of Parasitology*, 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. *Annales de Parasitologie Humaine et Comparée*, 51, 513–562.
- Rausch R., 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). *Journal of Parasitology*, 35, 306–314.
- Stiles C.W. 1896. A revision of the adult tapeworms of hares and rabbits. *Proceedings of the United States National Museum*, 19, 145–235.
- Tenora F., Gubányi A., Murai É. 1999. *Paranoplocephala maseri* n. sp. (Cestoda, Anoplocephalidae), a parasite of sagebrush voles *Lemmus curtatus* (Rodentia) in the USA. *Systematic Parasitology*, 42, 153–158.
- Tenora F., Murai É., Vaucher C. 1986. On *Andrya* Railliet, 1893 and *Paranoplocephala* Lühe, 1910 (Cestoda, Monieziinae). *Parasitologica Hungarica*, 19, 43–75.
- Wickström L.M., Haukisalmi V., Varis S., Hantula J., Henttonen H. 2005. Molecular phylogeny and systematics of anoplocephaline cestodes in rodents and lagomorphs. *Systematic Parasitology*, 62, 83–99.
- Voge M. 1946. A new anoplocephalid cestode, *Andrya neotomae*, from the wood rat *Neotoma fuscipes*. *Journal of Parasitology*, 32, 36–39.
- Voge M. 1955. A list of cestode parasites from California mammals. *American Midland Naturalist*, 54, 413–417.