

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

Faculty Publications from the Harold W. Manter  
Laboratory of Parasitology

Parasitology, Harold W. Manter Laboratory of

---

1-2007

# *Paranoplocephala sciuri* (Cestoda: Anoplocephalidae), a Parasite of the Northern Flying Squirrel (*Glaucomys sabrinus*), with a Discussion of Its Systematic Status

Robert L. Rausch

University of Washington, rausch@uw.edu

Voitto Haukisalmi

Finnish Forest Research Institute, voitto.haukisalmi@metla.fi

Follow this and additional works at: <http://digitalcommons.unl.edu/parasitologyfacpubs>



Part of the [Parasitology Commons](#)

---

Rausch, Robert L. and Haukisalmi, Voitto, "*Paranoplocephala sciuri* (Cestoda: Anoplocephalidae), a Parasite of the Northern Flying Squirrel (*Glaucomys sabrinus*), with a Discussion of Its Systematic Status" (2007). *Faculty Publications from the Harold W. Manter Laboratory of Parasitology*. 343.

<http://digitalcommons.unl.edu/parasitologyfacpubs/343>

This Article is brought to you for free and open access by the Parasitology, Harold W. Manter Laboratory of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications from the Harold W. Manter Laboratory of Parasitology by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

## ***Paranoplocephala sciuri* (Rausch, 1947) (Cestoda: Anoplocephalidae), a Parasite of the Northern Flying Squirrel (*Glaucomys sabrinus*), with a Discussion of Its Systematic Status**

VOITTO HAUKISALMI<sup>1,3</sup> AND ROBERT L. RAUSCH<sup>2</sup>

<sup>1</sup> Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FI-01301 Vantaa, Finland  
(e-mail: voitto.haukisalmi@metla.fi) and

<sup>2</sup> Department of Comparative Medicine, University of Washington School of Medicine, Box 357190, Seattle,  
Washington 98195-7190, U.S.A. (e-mail: rausch@u.washington.edu)

**ABSTRACT:** This study redescribes *Andrya sciuri* Rausch, 1947 (Anoplocephalidae) from the northern flying squirrel, *Glaucomys sabrinus* (Shaw), in North America, to redefine the morphology and generic position of this poorly known cestode. *Andrya sciuri* is shown to belong unambiguously to the genus *Paranoplocephala* Lühe, 1910 sensu Haukisalmi and Wickström (2005). *Paranoplocephala sciuri* is compared with 4 species that resemble it morphologically, and features that can be used in its identification are presented. It is suggested that *P. sciuri* has speciated through a shift from arvicoline rodents (voles and lemmings) to *G. sabrinus*.

**KEY WORDS:** Cestoda, Anoplocephalidae, *Andrya sciuri*, *Paranoplocephala sciuri*, northern flying squirrel, *Glaucomys sabrinus*, Scuriidae, Oregon, U.S.A.

Cestodes are somewhat atypical parasites of arboreal mammals, including flying squirrels (Scuriidae: Pteromyinae). For example, no cestodes are known from the Siberian flying squirrel, *Pteromys volans* (Linnaeus) (see Ryzhikov et al. [1978] and Rausch and Rausch [1982]) and the Nearctic southern flying squirrel, *Glaucomys volans* (Linnaeus) (see Dolan and Carter [1977] and Rausch and Rausch [1982]). However, at least 2 species of anoplocephalid cestodes (i.e., *Andrya sciuri* Rausch, 1947 and *Monoecocestus thomasi* Rausch & Maser, 1977) are obligatory parasites of the northern flying squirrel, *Glaucomys sabrinus* (Shaw), in North America (Rausch and Rausch, 1982; Wells-Gosling and Heaney, 1984). *Catenotaenia* sp. (Catenotaeniidae) (see Rausch and Tiner [1948]) and *Hymenandrya* sp. (Hymenolepididae) (see Rausch and Rausch, [1982]) also have been reported from *G. sabrinus*, but their status remains undefined. The presence of host-specific anoplocephalid cestodes in *G. sabrinus* suggests that it has more terrestrial foraging habits than the related species of flying squirrels. Indeed, the northern flying squirrel relies mainly on hypogeous fungi (truffles) during the warmer months (McKeever, 1960; Maser et al., 1985), which exposes it to soil-dwelling invertebrates, including oribatid mites, which serve as intermediate hosts for anoplocephalid cestodes.

*Bertiella musasabi* Yamaguti, 1942 (syn. *Aprostotandrya petauristae* Sawada & Kugi, 1979; see

Beveridge, 1989) is the only other anoplocephalid cestode known from pteromyine rodents (from *Petaurista* spp. in Japan and Taiwan), and other species of *Bertiella* Stiles & Hassall, 1902 are parasites of arboreal marsupials and dermopterans in Australia and South-East Asia, respectively (Spasskii, 1951; Beveridge, 1989).

*Andrya sciuri* was described from *G. sabrinus* in Wisconsin, U.S.A., based on two specimens (Rausch, 1947; Rausch and Tiner, 1948). Later, *A. sciuri* was reported from the same host species in Oregon, U.S.A. (Rausch and Maser, 1977; Rausch and Rausch, 1982) and Saskatchewan, Canada (McGee, 1980), but it has not been found from *G. volans* in Ohio, Michigan, Illinois, Wisconsin (Rausch and Tiner, 1948), Pennsylvania (Patrick, 1991), or Georgia (Pung et al., 2000); thus, it seems to be strictly specific to the northern flying squirrel. The only subsequent piece of morphological information for *A. sciuri* is that of Genov et al. (1996), who illustrated a mature proglottid of the holotype specimen of *A. sciuri*, but they did not provide a redescription. Moreover, the morphology and position of the early uterus, which are crucial for the generic allocation among *Andrya* Railliet, 1893 and *Paranoplocephala* Lühe, 1910 (see Haukisalmi and Wickström [2005]), were not discernible in the holotype of *A. sciuri*.

This study redescribes *A. sciuri* from *G. sabrinus* based on the available museum specimens, including the holotype, and those from the personal collection of one of us (R.L.R.), to redefine the morphology and generic position of *A. sciuri*.

<sup>3</sup> Corresponding author.

**Table 1. Comparison of the type material of *Paranoplocephala sciuri* from Wisconsin, U.S.A., with the material from Oregon, U.S.A. (all from *Glaucomys sabrinus*). Measurements of the Oregon specimens, which are almost or completely nonoverlapping with those of the type specimens, have been indicated in bold.**

Region	Wisconsin ( <i>N</i> * = 2)	Wisconsin ( <i>N</i> = 1)	Oregon ( <i>N</i> = 8)
Source	Rausch, 1947	Present study (holotype)	Present study
Body, length	170		160 (1)†
Body, maximum width	2		<b>3.8–3.9</b> (2)
Mature proglottids, width		0.15	<b>0.22–0.31</b> (14)
Mature proglottids, length/width ratio		0.18–0.27	0.13–0.29 (14)
Scolex, diameter	0.38	0.36	<b>0.50–0.59</b> (4)
Suckers, diameter	0.15	0.17	<b>0.20–0.24</b> (16)
Neck, length	(neck absent)	(neck absent)	<b>0.45–0.60</b> (4)
Neck, minimum width		0.19	<b>0.26–0.38</b> (4)
Testes, total no.	100–110	78–86	86–123 (14)
Poral testes, no.		6	1–8 (10)
Antiporal testes, no.		17–19	0–20 (11)
Longitudinal ventral canals, width	(mean 0.30)	0.026–0.045	0.043–0.10 (20)
Cirrus sac, length	(mean 0.20)	0.18–0.19	<b>0.32–0.50</b> (14)
Ovary, width		0.39–0.62	0.56–0.79 (14)
Vitellarium, width		0.17–0.26	0.21–0.33 (13)
Vitellarium, position (index of asymmetry)		0.46	0.37–0.46 (14)
Vagina, length		0.20	<b>0.34–0.50</b> (6)
Vagina/cirrus sac ratio		ca. 1.0	0.9–1.1 (6)
Seminal receptacle, length	(maximum 0.42)	ca. 0.35	<b>0.50–0.65</b> (6)
Egg, length	0.052–0.056		<b>0.058–0.063</b> (10)

\* *N* is number of specimens studied.

† Number in parentheses is number of measurements.

## MATERIALS AND METHODS

The cestodes examined here have been deposited in the United States National Parasite Collection, Beltsville, Maryland (USNPC), and Harold W. Manter Laboratory of Parasitology, University of Nebraska-Lincoln, Nebraska, U.S.A. (HWML). Eleven mounted specimens identifiable as *A. sciuri* were examined, all from *G. sabrinus*: the holotype specimen (USNPC 45755) from Millston, Jackson County, Wisconsin, U.S.A. (Rausch, 1947), 8 specimens (from 3 host individuals) from Starkey Experimental Forest (45°22'N; 118°51'W), Union County, Oregon, U.S.A. (USNPC 97605–97607; Rausch and Maser, 1977), 1 specimen from Tushar Mountains, Beaver, Utah, U.S.A. (HWML 36319), and 1 specimen from Besnard Lake, Saskatchewan, Canada (USNPC 76100; McGee, 1980). The specimen from Utah, from 1 of the southernmost, isolated populations of *G. sabrinus*, consisted of contracted, poorly stained fragments and was not included in the morphometric analysis or redescription.

The scolex, neck and 1–2 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 drawings by using a calibrated 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). In addition to the total number of testes, we separately counted the number

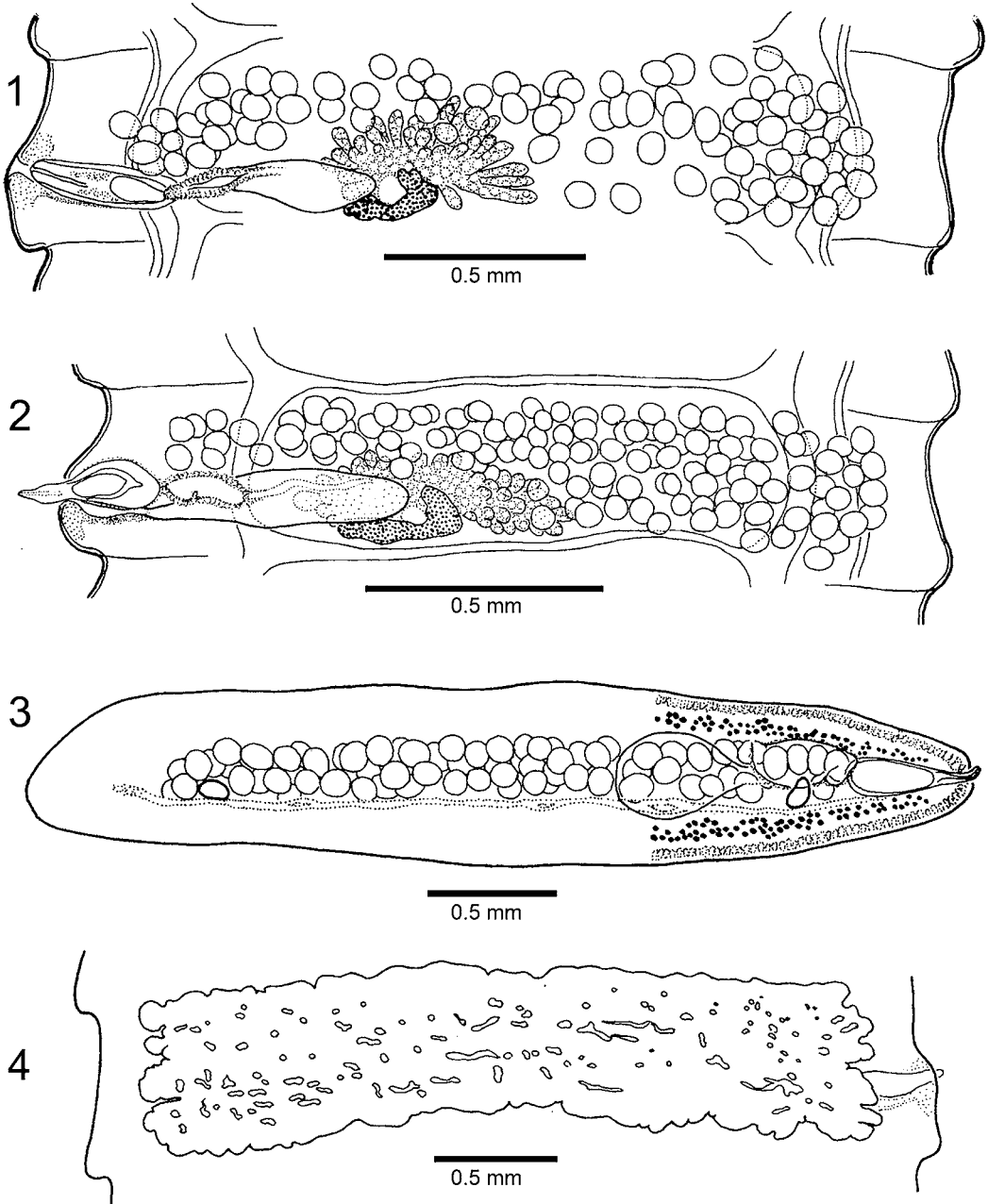
of poral testes (those lateral to the poral ventral osmoregulatory canal) and antiporal testes (those lateral to the antiporal ventral osmoregulatory canal). Cirrus sac was measured only if the cirrus was fully withdrawn; maximum length of the cirrus sac was recorded from postmature proglottids. The asymmetrical position of vitellarium (index of asymmetry) 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. The egg length is based on 5 measurements from terminal proglottids of 2 fully gravid strobilae from Oregon in which eggs had remained intact. Hand-cut transverse sections of mature proglottids were prepared from a single specimen from Oregon. All metric data are in millimeters.

Because all examined specimens were considered to belong to the same species (see Discussion), only combined measurements are given in the description. Table 1 shows measurements separately for the type material and the specimens from Oregon. The mean (if *n* > 4) and number of measurements (*n*) are given in parentheses after the range. See Rausch (1947) and Genov et al. (1996) for illustrations of mature proglottids in the holotype.

### *Paranoplocephala sciuri* (Rausch, 1947) Syn. *Andrya sciuri* Rausch, 1947 (Figs. 1–6; Table 1)

#### Redescription

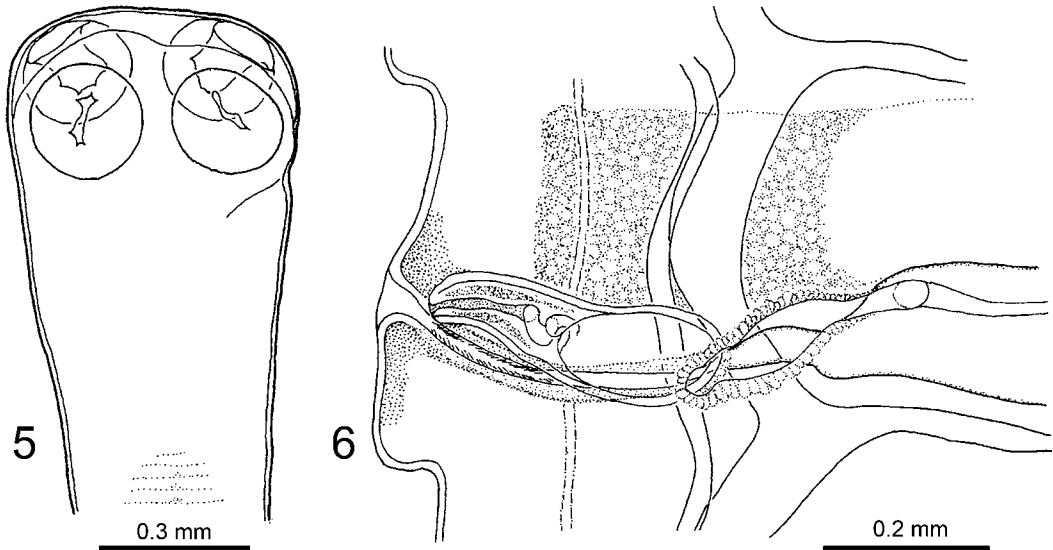
The redescription is based on 11 specimens listed in Materials and Methods.



**Figures 1–4.** *Paranoplocephala sciuri* (Rausch, 1947) from *Glaucomys sabrinus*. **1.** Mature proglottid (Oregon, U.S.A.). **2.** Mature proglottid (Saskatchewan, Canada). **3.** Transverse section of a late mature proglottid (Oregon, U.S.A.). **4.** Fully developed (pregravid) uterus (Oregon, U.S.A.).

Fully gravid strobila ca. 160 long ( $n = 1$ ) and 3.8–3.9 wide ( $n = 2$ ), maximum width attained in pregravid or gravid proglottids. Scolex simple, 0.36–0.59 (0.51;  $n = 5$ ) wide. Suckers relatively small, 0.14–0.24 (0.215;  $n = 19$ ) in maximum diameter,

directed antero-laterally, embedded within scolex. Neck 0.45–0.60 ( $n = 4$ ) long (absent in holotype), slightly tapering posteriorly, minimum width 0.19–0.38 (0.29;  $n = 5$ ). Proglottids craspedote but velum short. Length/width ratio 0.13–0.29 (0.18;  $n = 16$ ) in



Figures 5, 6. *Paranoplocephala sciuri* (Rausch, 1947) from *Glaucomys sabrinus* (Oregon, U.S.A.). 5. Scolex. 6. Terminal genital ducts and a part of the early uterus in a mature proglottid; testes omitted.

mature proglottids, increasing posteriorly. Genital pores opening slightly posterior to middle of proglottid margin. Based on 8 specimens from Oregon, U.S.A., genital pores frequently (and irregularly) alternating, with 1–25 (3.6) proglottids in each unilateral set or 22–37 (27.9) changes per 100 proglottids; only 1 change present in holotype. Longitudinal muscle bundles form irregular aggregations in transverse sections of mature proglottids (distinct layers absent).

Ventral longitudinal osmoregulatory canals 0.03–0.10 (0.063;  $n = 26$ ) wide at mid-level of proglottid, connected by transverse canals measuring 0.025–0.040. Dorsal longitudinal osmoregulatory canals thin (0.008–0.026, 0.019,  $n = 13$ ), positioned lateral to ventral canals. Genital ducts passing dorsally across longitudinal osmoregulatory canals and nerve cord.

Testes numerous (78–123, 102;  $n = 17$ ), widely distributed, confluent, 2–3 layers deep. Testes usually extend across ventral longitudinal canals bilaterally, with 1–8 (3.8;  $n = 13$ ) and 0–20 (9.4;  $n = 14$ ) testes lateral to poral and antiporal ventral longitudinal canals, respectively. Testes always overlapping ventral canals (dorsally), although occasionally not extending across antiporal canal. Few testes usually overlap anterior and antiporal parts of ovary.

Cirrus sac 0.18–0.50 (0.36;  $n = 16$ ) long and 0.06–0.13 (0.105;  $n = 16$ ) wide in mature proglottids; maximum length in postmature proglottids 0.41–0.51 (0.46;  $n = 6$ ). Fully extended cirrus sac usually

slightly overlaps ventral canal or is in contact with it (nonoverlapping in holotype). Ductus cirri slightly convoluted in its proximal part, provided with minute spines in its distal part. Internal seminal vesicle ovoid or slightly elongated. External seminal vesicle large, especially in postmature proglottids, sac-like, covered by thick “glandular” cell layer, distinctly separate from vas deferens.

Vagina 0.20–0.50 (0.36;  $n = 7$ ) long, usually as long as cirrus sac, tube-like, increases slightly in width distally (maximum width 0.05–0.07), clearly distinct from seminal receptacle, running ventral to cirrus sac and opening posterior or postero-ventral to male pore. Vaginal tube of fairly uniform width throughout its length, covered externally by dense layer of small, intensely stained cells, merging with cell layer surrounding genital atrium; internal surface of vagina probably lined with delicate hairs. Seminal receptacle initially elongated, 0.35–0.65 (0.55;  $n = 8$ ) long and 0.08–0.27 (0.16;  $n = 8$ ) wide in mature proglottids; when filled with sperm, its proximal part expands, distal part showing as distinct neck; maximum length of seminal receptacle in postmature proglottids 0.57–0.75 ( $n = 4$ ) and maximum width 0.19–0.30 (0.28;  $n = 8$ ). Vitellarium 0.17–0.33 (0.26;  $n = 16$ ) wide and 0.07–0.20 (0.14;  $n = 16$ ) long, asymmetrically bilobed, positioned porally with respect to midline of proglottid and ovary (index of asymmetry 0.37–0.46, 0.42;  $n = 16$ ), overlapping posterior part of ovary. Mehlis’ gland ovoid,

0.06–0.10 in diameter. Ovary 0.39–0.79 (0.62;  $n = 17$ ) wide and 0.13–0.35 (0.26;  $n = 17$ ) long, lobulate, positioned medially or slightly porally, separated by distinct gap from longitudinal osmoregulatory canals on either side of proglottid.

Early uterus seen in mature proglottids as transverse, dorso-ventrally thin, finely reticulated band positioned ventral to testes and longitudinal osmoregulatory canals, markedly extending across ventral canals bilaterally (early uterus indiscernible in holotype). Lateral parts of early uterus slightly wider than middle part, which overlaps slightly anterior margin of ovary. In pregravid proglottids uterus sac-like, covering almost whole medulla; irregular, indistinct lateral sacculations and internal trabeculae present. Eggs round or slightly ovoid, 0.058–0.063 (0.061;  $n = 10$ ) in maximum diameter (no fully developed eggs in holotype). Pyriform apparatus present; no separate horns discernible.

### Taxonomic summary

*Type host*: Northern flying squirrel, *Glaucomys sabrinus* (Shaw).

*Type locality*: Millston, Jackson County, Wisconsin, U.S.A.

*Type specimen*: Holotype (USNPC 45755).

*Voucher specimens*: See Materials and Methods.

### Remarks

The taxonomic relationships of *A. sciuri* with some of the subsequently described species are obscure. We therefore compared *A. sciuri*, based on the present redescription, with 4 species that resemble *A. sciuri* in having widely distributed testes that overlap or extend across longitudinal ventral canals bilaterally, finely/completely reticulated early uterus, and irregularly alternating genital pores (Table 2). *Andrya sciuri* seems to be well differentiated from *Paranoplocephala freemani* Haukisalmi, Henttonen & Hardman, 2006. However, *Paranoplocephala alternata* Haukisalmi, Wickström, Hantula & Henttonen, 2001, *Paranoplocephala aquatica* Genov, Vasileva & Georgiev, 1996 (*Paranoplocephala genovi* Gubányi, Tenora & Murai, 1998 is considered here a junior synonym of *P. aquatica*), and *Paranoplocephala ondatrae* (Rausch, 1948) are fairly similar to *A. sciuri*, but they can be differentiated from it by three or more of the following characters: the position and size of the cirrus sac, shape of the seminal receptacle, position of the vitellarium, and egg length. Because the 4 related species are parasites

of arvicoline rodents (voles and lemmings), *A. sciuri* is unlikely to be confused with any of them in practice. Moreover, *P. aquatica* has a western Eurasian distribution and *P. alternata* and its hosts (collared lemmings, *Dicrostonyx* spp.) inhabit the Subarctic and Arctic regions only (Table 2). The Nearctic *P. freemani* and *P. ondatrae* might occur sympatrically with *A. sciuri*, but cross-infections do not seem probable.

### DISCUSSION

The holotype specimen was found to conform well with the original description of *A. sciuri* (Table 1; Rausch, 1947; also see Genov et al., 1996). However, the material from Oregon, U.S.A. (and also from Saskatchewan, Canada) showed some quantitative differences compared with the type material from Wisconsin, U.S.A. (Table 1). In the type material, the genital pores tend to be unilateral (Rausch, 1947; 1 change in the holotype), whereas in the other specimens examined the genital pores alternate frequently (on average, 28 changes per 100 proglottids). In addition, the maximum body width; diameter of the scolex and suckers; width of the neck; and length of the cirrus sac, vagina, and seminal receptacle are smaller in the holotype than in the other specimens. Eggs are also slightly smaller in the type material (Table 1).

The different pattern of genital pore alternation and multiple metric differences seem to suggest that 2 species are involved. However, most of the observed quantitative differences reflect the fact that the type specimens were smaller (i.e. thinner) than the other specimens, and because body size variation of anoplocephalid cestodes may be very pronounced even within the same study locality, absolute body size and correlated features have relatively low taxonomic value. In addition, the pattern of genital pore alternation may vary markedly in different parts of a cestode's geographical distribution (Haukisalmi and Henttonen, 2000). Thus, the deviating features of the type material probably reflect local variation or chance effects due to the small number of available specimens, or both. The conspecificity of *A. sciuri*-like cestodes is supported by the similar morphology of the scolex and genital ducts, distribution of testes, and similarity of their relative measurements, i.e., vagina/cirrus sac ratio and asymmetry index (Table 1; Figs. 1, 2). However, the present data have revealed pronounced variation in the number of poral (1–8) and antiporal (0–20) testes within the same locality (Oregon, U.S.A.). According to Rausch (1947), the



**Table 2.** Comparison of main morphologic features in 5 *Paranoplocephala* species with widely distributed testes (overlapping or extending across longitudinal ventral canals bilaterally), completely/finely reticulated early uterus, and irregularly alternating genital pores. Mean in parentheses after the range (if number of measurements >4). The values for *Paranoplocephala alternata*, *Paranoplocephala freemani*, *Paranoplocephala ondatrae*, and *Paranoplocephala aquatica* are shown in bold when completely or nearly nonoverlapping with those for *Paranoplocephala sciuri*. All measurements in millimeters, except the egg length (in micrometers).

Cestode species	<i>P. sciuri</i>	<i>P. alternata</i>	<i>P. aquatica</i>	<i>P. freemani</i>	<i>P. ondatrae</i>
Host species	<i>Glacomys sabrinus</i>	<i>Dicrostonyx</i> spp.	<i>Arvicola terrestris</i> , <i>Ondatra</i>	<i>Microtus xanthognathus</i> , <i>Ondatra</i> , <i>Neotoma</i>	<i>Ondatra</i>
Distribution	Nearctic	Nearctic	Western Palearctic	Nearctic	Nearctic
Source	Rausch, 1947; present study	Haukisalmi et al., 2001	Genov et al., 1996	Haukisalmi, Henntonen et al., 2006; Haukisalmi and Rausch, 2006	Rausch, 1948; Genov et al., 1996
Body, length	160–170	74–147 (102)	178	<b>200–250</b>	122–155
Body, maximum width	2.0–3.9	1.7–3.0 (2.4)	1.9–2.7 (2.3)	<b>5.0–5.5</b>	2.6–3.0
Mature proglottids, length/width ratio	0.13–0.29 (0.18)	0.14–0.75 (0.37)	0.23–0.32	0.09–0.17 (0.13)	0.20–0.37
Scolex, diameter	0.36–0.59 (0.51)	0.24–0.50 (0.31)	0.41–0.62 (0.475)	<b>0.65–0.69</b>	<b>0.67–0.68</b>
Suckers, diameter	0.14–0.24 (0.22)	0.14–0.23 (0.16)	0.15–0.24 (0.19)	<b>0.25–0.29 (0.27)</b>	0.24–0.25
Testes, total no.	78–123 (102)	45–101 (74)	76–110 (92)	<b>45–88 (69)</b>	75–95
Poral testes, no.	1–8 (3.8)	0–10 (4.8)	0–3*	<b>0–1 (0.2)</b>	0 or few
Antiporal testes, no.	0–20 (9.4)	2–29 (16.3)	10–12*	3–18 (11.0)	0 or few
Cirrus sac, maximum length†	0.41–0.51 (0.46)	0.42–0.62 (0.48)	<b>0.20‡</b>	<b>0.30–0.39</b>	
Cirrus sac, position	Overlapping poral v.l.o.c.§	<b>Across poral v.l.o.c.§</b>	Overlapping/across	<b>Nonoverlapping</b>	<b>Nonoverlapping</b>
Vagina/cirrus sac ratio	0.9–1.1 (1.0)	0.65–1.00 (0.79)	0.53–0.79 (0.65)	<b>0.6–0.8 (0.72)</b>	<b>0.20–0.26</b>
Seminal receptacle, shape	Ampulliform	<b>Ovoid/irregular</b>	<b>Elongate/pyriform</b>	Ampulliform	Ampulliform
Vitellarium, position (index of asymmetry)	0.37–0.46 (0.42)	<b>0.43–0.64 (0.51)</b>	<b>0.30–0.38 (0.33)</b>	0.34–0.42 (0.39)	<b>0.46–0.50</b>
Egg, length	58–63 (61.0)	40–61 (49.1)	<b>38–41 (39)</b>	<b>40–45 (41.0)</b>	<b>33–40</b>

\* Based on the figures of Genov et al. (1996).

† In postmature proglottids.

‡ Maximum value in mature proglottids.

§ Ventral longitudinal osmoregulatory canal.

|| With distinct distal neck.

cirrus of *A. sciuri* is unarmed (poorly seen in the holotype), but it was found to be armed in all other specimens examined here.

The status of the genera *Andrya* and *Paranoplocephala* has remained confusing, because there do not seem to exist any straightforward features to distinguish between them (e.g., Rausch, 1976; Tenora et al., 1986; Beveridge, 1994; Genov et al., 1996). Therefore, the species from lagomorphs and rodents have conveniently been assigned to *Andrya* and *Paranoplocephala*, respectively, and *A. sciuri* became thus *Paranoplocephala sciuri* in the classifications of Tenora et al. (1986) and Genov et al. (1996).

A recent molecular phylogenetic study (Wickström et al., 2005) has confirmed that *Andrya* and *Para-*

*noplocephala* are independent genera, although the monophyly of *Paranoplocephala* is still uncertain. Based on the combination of molecular and morphological evidence, Haukisalmi and Wickström (2005) have proposed a modified classification scheme for *Andrya/Paranoplocephala*-like cestodes, which is based on the extent and dorsoventral position of the uterus with respect to the testes and longitudinal osmoregulatory canals. According to this scheme, *Paranoplocephala* is characterized by a reticulated early uterus that is positioned ventrally to testes and extends ventrally across the osmoregulatory canals. The early uterus of *Andrya* also is reticulated and is positioned ventral to the testes, but it does not extend laterally across the osmoregulatory canals; however,

the lateral fringes of the uterus occasionally overlap the ventral canals dorsally. The genus *Andrya* presently includes only 2 species, the type species *A. rhopalocephala* (Riehm, 1881) from western Eurasian leporids and *A. neotomae* Voge, 1946 from North American *Neotoma* spp., including its putative junior synonym *Aprostotandrya octodonensis* (Barbero & Cattán, 1975) from an indigenous South American rodent (see Haukisalmi and Rausch [2006] for discussion of the taxonomic status of *A. neotomae* and *A. octodonensis*). Although *A. neotomae* resembles *A. sciuri*, they can be easily differentiated by the position and extent of the uterus (and other features; Haukisalmi and Rausch, 2006). In the genus *Neandrya* Haukisalmi & Wickström, 2005, which was erected for *Andrya cuniculi* (Blanchard, 1891) from European leporids, the uterus lies among testes in the dorsoventral plane and extends markedly across longitudinal osmoregulatory canals dorsally (Haukisalmi and Wickström, 2005). This classification places *A. sciuri* unambiguously within *Paranoplocephala*.

Although molecular data for *P. sciuri* are not available, its morphological similarity to the species mentioned above strongly suggests that it shares a phylogenetic history with some of the *Paranoplocephala* species. *Paranoplocephala* spp. belong to the “arvicoline clade” of cestodes together with *Anoplocephaloides* spp. from arvicoline rodents (Wickström et al., 2005). Surprisingly, *Diandrya composita* Darrah, 1930 from Nearctic marmots (*Marmota* spp., Sciuridae) also belongs to this clade, suggesting that *D. composita* has diverged through a shift from voles or lemmings to marmots. A corresponding history of host colonization also seems probable for *P. sciuri*. If the divergence of *P. sciuri* has taken place in the Nearctic, its possible precursors include *P. freemani* and *P. ondatrae*.

Besides *P. sciuri*, 2 other *Paranoplocephala* species have been found sporadically from squirrels, i.e., *P. primordialis* (Douthitt, 1915) from *Tamiasciurus hudsonicus* (Erxleben) in the Nearctic (Douthitt, 1915; McGee, 1980) and *P. longivaginata* Chechulin & Gulyaev, 1998 from *Sciurus vulgaris* Linnaeus in the Palearctic (Chechulin and Gulyaev, 1998; Haukisalmi, Hardman et al., 2006). Both species are primarily parasites of voles (*Clethrionomys* Tilesius and *Microtus* Schrank, respectively). Similar flexibility in host selection may have predisposed the precursor of *P. sciuri* to colonize the northern flying squirrel. However, molecular data are ultimately needed to determine the closest relatives and phylogenetic history of *P. sciuri*.

## ACKNOWLEDGMENTS

We thank Eric P. Hoberg, Patricia Pilitt (USNPC) and Scott L. Gardner (Harold W. Manter Laboratory of Parasitology, University of Nebraska–Lincoln), who kindly helped in the examination and deposition of museum specimens.

## LITERATURE CITED

- Beveridge, I.** 1989. Species of *Bertiella* (Cestoda: Anoplocephalidae) in dermopterans and squirrels from South-East Asia. *Systematic Parasitology* 14:1–15.
- Beveridge, I.** 1994. Family Anoplocephalidae Choldkovsky, 1902. Pages 315–366 in L. F. Khalil, A. Jones and R. A. Bray, eds. *Keys to the Cestode Parasites of Vertebrates*. CAB International, Wallingford, Oxfordshire, U.K.
- Chechulin, A. I., and V. D. Gulyaev.** 1998. *Paranoplocephala longivaginata* sp. n. (Cyclophyllidea: Anoplocephalidae)—novaya cestoda ot gryzunov Vostochnoi Sibiri. *Parazitologiya* 32:352–356.
- Dolan, P. G., and D. C. Carter.** 1977. *Glaucomys volans*. Mammalian Species No. 78.
- Douthitt, H.** 1915. Studies on the cestode family Anoplocephalidae. *Illinois Biological Monographs* 1:1–96.
- Genov, T., G. P. Vasileva, and B. B. Georgiev.** 1996. *Paranoplocephala aquatica* n. sp. (Cestoda, Anoplocephalidae) from *Arvicola terrestris* and *Ondatra zibethica* (Rodentia), with redescrptions and comments on related species. *Systematic Parasitology* 34:135–152.
- Haukisalmi, V., L. M. Hardman, M. Hardman, J. Laakkonen, J. Niemimaa, and H. Henttonen.** 2007. Morphological and molecular characterisation of *Paranoplocephala buryatiensis* n. sp. and *P. longivaginata* Chechulin & Gulyaev, 1998 (Cestoda: Anoplocephalidae) in voles of the genus *Clethrionomys*. *Systematic Parasitology* 66:55–71.
- Haukisalmi, V., and H. Henttonen.** 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., H. Henttonen, and L. M. Hardman.** 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* 89:277–299.
- Haukisalmi, V., and R. L. Rausch.** 2006. Anoplocephalid cestodes of wood rats (*Neotoma* spp.) in the western U.S.A. *Acta Parasitologica* 51:91–99.
- Haukisalmi, V., and L. M. Wickström.** 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., L. M. Wickström, J. Hantula, and H. Henttonen.** 2001. Taxonomy, genetic differentiation and Holarctic biogeography of *Paranoplocephala* spp. (Cestoda: Anoplocephalidae) in collared lemmings



- (*Dicrostonyx*; Arvicolinae). Biological Journal of the Linnean Society 74:171–196.
- Maser, Z., C. Maser, and J. M. Trappe.** 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63:1084–1088.
- McGee, S. G.** 1980. Helminth parasites of squirrels (Sciuridae) in Saskatchewan. Canadian Journal of Zoology 58:2040–2050.
- McKeever, S.** 1960. Food of the northern flying squirrel in northeastern California. Journal of Mammalogy 41: 270–271.
- Patrick, M. J.** 1991. Distribution of enteric helminths in *Glaucomys volans* L. (Sciuridae): a test for competition. Ecology 72:755–758.
- Pung, O. J., L. A. Durden, M. J. Patrick, T. Conyers, and L. R. Mitchell.** 2000. Ectoparasites and gastrointestinal helminths of southern flying squirrels in southeast Georgia. Journal of Parasitology 86:1051–1055.
- Rausch, R.** 1947. *Andrya sciuri* n. sp., a cestode from the northern flying squirrel. Journal of Parasitology 33: 316–318.
- Rausch, R.** 1948. Notes on cestodes of the genus *Andrya* Railliet, 1883, with the description of *A. ondatrae* n. sp. (Cestoda: Anoplocephalidae). Transactions of the American Microscopical Society 67:187–191.
- 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. L., and C. Maser.** 1977. *Monoecocestus thomasi* sp. n. (Cestoda: Anoplocephalidae) from the northern flying squirrel, *Glaucomys sabrinus* (Shaw), in Oregon. Journal of Parasitology 63:793–799.
- Rausch, R., and J. D. Tiner.** 1948. Studies on the parasitic helminths of the North Central States. I. Helminths of Sciuridae. American Midland Naturalist 39: 728–747.
- Rausch, V. R., and R. L. Rausch.** 1982. The karyotype of the Eurasian flying squirrel, *Pteromys volans* (L.), with a consideration of karyotypic and other distinctions in *Glaucomys* spp. (Rodentia: Sciuridae). Proceedings of the Biological Society of Washington 95: 58–66.
- Ryzhikov, K. M., E. V. Gvozdev, M. M. Tokobaev, L. S. Shaldybin, G. V. Macaberidze, I. V. Merkusheva, E. V. Nadtochii, I. G. Hohlova, and L. D. Sharpilo** 1978. Opredelitel' Gelmintov Gryzunov Fauny SSSR. Cestody i Trematody. Nauka, Moskva. 231 pp.
- Spasskii, A. A.** 1951. Anoplocephalate Tapeworms of Domestic and Wild Animals. 233–262 in K. I. Skrijabin, ed. Essentials of Cestodology, volume 1. The Academy of Sciences of the USSR, Moscow. Translated from Russian for the U.S. National Science Foundation and Department of Agriculture by the Israel Program for Scientific Translations, 1961. Office of Technical Services, U.S. Department of Commerce, Washington.
- Tenora, F., E. Murai, and C. Vaucher.** 1986. On *Andrya* Railliet, 1893 and *Paranoplocephala* Lühe, 1910 (Cestoda, Monieziinae). Parasitologica Hungarica 19: 43–75.
- Wells-Gosling, N., and L. R. Heaney.** 1984. *Glaucomys sabrinus*. Mammalian Species No. 229.
- Wickström, L. M., V. Haukisalmi, S. Varis, J. Hantula, and H. Henttonen.** 2005. Molecular phylogeny and systematics of anoplocephaline cestodes in rodents and lagomorphs. Systematic Parasitology 62:83–99.