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NEW HOST AND GEOGRAPHIC RECORDS FOR TWO PROTOSTRONGYLIDS IN DALL'S SHEEP

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ABSTRACT: Biodiversity survey and inventory have resulted in new information on the distribution of Protostrongylidae in Dall's sheep (*Ovis dalli dalli*) from the Northwest Territories (NT, Canada) and from Alaska (AK, USA). In 1998, *Parelaphostrongylus odocoilei* adults were found for the first time in the skeletal muscles of Dall's sheep in the Mackenzie Mountains (NT). Adult *P. odocoilei* were associated with petechial and ecchymotic hemorrhages and localized myositis; eggs and larvae in the lungs were associated with diffuse granulomatous pneumonia. Experimental infections of the slugs *Deroceras laeve* and *Deroceras reticulatum* with dorsal-spined first-stage larvae assumed to be *P. odocoilei,* from ground-collected feces from Dall's sheep in the Mackenzie Mountains, yielded third-stage larvae by at least 28 (in *D. laeve*) and 48 (in *D. reticulatum*) days post-infection. Third-stage larvae emerged from *D. laeve* between days 19 and 46 post-infection and emergence occurred both at room temperature and at 10 to 12 C. *Protostrongylus stilesi* were definitively identified from the lungs of Dall's sheep collected in the Mackenzie Mountains, NT in 1998. Specimens collected from sheep in the Mackenzie Mountains, NT in 1971–72, and the Alaska Range, AK in 1972 were also confirmed as *P. stilesi.* Lung pathology associated with adults, eggs, and larvae of *P. stilesi* was similar to that described in bighorn sheep (*Ovis canadensis*). Concurrent infections with *P. odocoilei* and *P. stilesi* in a single host have not been previously reported.

Key words: Mackenzie Mountains, Northwest Territories, parasite, *Parelaphostrongylus odocoilei,* Protostrongylidae, *Protostrongylus stilesi, Ovis dalli,* Subarctic.

INTRODUCTION

Dall's sheep (*Ovis dalli dalli*) are native to mountainous areas of northern British Columbia (BC, Canada), the western Northwest Territories (NT, Canada), and the Yukon Territory (YT, Canada), and Alaska (AK, USA) (Nichols and Bunnell, 1999). Despite their wide geographic distribution and economic importance (Crapo, 2000), little is known about the occurrence or potential impact of parasites in this species of wild sheep. Parasitological investigations of Dall's sheep in Alaska include: A report of the tapeworm *Wyominia tetoni* (Gibbs and Fuller, 1959); an extensive survey of gastrointestinal nematodes (Nielsen and Neiland, 1974); description of three species of *Eimeria* (Clark and Colwell, 1974); histological examination for *Sarcocytis* sp. (Neiland, 1980); and serological surveys for *Psoroptes* sp. (Boyce and Zarnke, 1996) and *Toxoplasma gondii* (Zarnke et al., 2000). An extensive parasitological collection from Dall's sheep in the Mackenzie Mountains (NT) was done by N. Simmons (unpubl. data) for the Canadian Wildlife Service (Fort Smith, Northwest Territories, Canada) in 1971 and 1972.

In addition, at least two species of protostrongylids occur in free-ranging Dall's sheep. First-stage larvae (L1) and gross and histological pulmonary lesions consistent with *Protostrongylus* sp., have been reported in Dall's sheep from AK, YT, and NT (Goble and Murie, 1942; Ericson and Neiland, 1972; Schwantje, 1987). Pulmo-

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nary nematodes isolated from the lungs of Dall's sheep in Alaska by Nielsen and Neiland (1974) and from the Mackenzie Mountains by N. Simmons (unpubl. data) were labeled as *P. stilesi,* but these records were not published. Dorsal-spined first-stage protostrongylid larvae (DS-L1) have also been isolated from the feces of Dall's sheep from the Brooks Range (AK) and were reported as *Muellerius* sp. by Dau (1981). This report has not been substantiated by collection of adult specimens and, therefore, cannot be considered valid.

In bighorn sheep (*Ovis canadensis*), infections with *Protostrongylus* spp. have been associated with a stress-lungworm-pneumonia complex, an important mortality factor in this host in western North America (Forrester, 1971; Bunch et al., 1999). The role of protostrongylids in the health of Dall's sheep populations is unknown; however, die-offs of the magnitude observed for bighorn sheep have not been reported (Bowyer and Leslie, 1992).

The need to more fully assess parasite biodiversity in northern ruminants, as a basis for understanding the potential impacts of specific pathogens under changing climatic conditions in the Subarctic and Arctic, was the foundation for the current study. In 1997, we examined 43 fecal samples from Dall's sheep in the Mackenzie Mountains. The isolation of DS-L1 (77%, mean count = 141 larvae per g [LPG]), along with *Protostrongylus* sp. L1 (74%, mean count = 56 LPG), from these fecal samples prompted further investigations to locate and identify the adult protostrongylids producing these larvae in Dall's sheep.

MATERIALS AND METHODS

Six adult Dall's ewes were collected from the Mackenzie Mountains for post mortem examination: three on 27 October 1998, at 65°01′N, 127°47′W; and three on 7 April 1999, at 65°01′N, 127°50′W. In addition, lungs from four hunter-killed sheep from the Mackenzie Mountains (64°50′N, 127°07′W; 65°00′N, 127°34′W; and 65°04′N, 127°52′W for two sheep) were examined for pulmonary nematodes.

The ewes collected in October, 1998, were skinned within 3 hr of death, eviscerated, and the right hind legs were removed for an unrelated project. The carcasses were covered with moist cloths and stored at 1 to 5 C until examination (within 48 hr). The skeletal muscles (excluding those of the head) were examined in detail for nematodes. Individual muscles were sliced in 5 mm sections and abnormalities were examined by fine dissection and by compressing thin (2 to 3 mm in width) slices of tissue between two heavy glass plates and examining under a dissecting microscope with direct and transmitted light. The ewes collected in April 1999, were treated similarly except that entire carcasses were available and animals were not skinned until the carcasses were examined.

Lung samples from the caudo-dorsal diaphragmatic lobe and the dorsal middle lobe from each of the six ewes were fixed in 10% formalin. Subsequently, for the ewes collected in October, 1998, lungs were separated and the bronchi of each lung flushed with 360 ml of normal saline. Washings were poured sequentially through 75 and 38 μm sieves (Dual Manufacturing Co., Chicago, Illinois, USA) and material retained on both sieves was examined microscopically. The entire bronchial tree was opened and examined grossly. The caudal halves of the right diaphragmatic lobes, with airways opened, were incubated in a 0.85% saline bath at 35 to 37 C overnight, and the sediment examined the following day. The airways from ewes collected in April 1999, were briefly examined. Lungs from hunter-killed sheep were frozen until the time of examination. When thawed, the airways were flushed with tap water and the wash examined microscopically. Parenchymal lesions and associated bronchi were dissected for adult nematodes.

Intact adult nematodes recovered from muscles and lungs were preserved in steaming 70% ethanol/5% glycerin. Broken specimens were similarly preserved, but at room temperature. Representative specimens were later mounted and cleared in lactophenol, and examined and measured at 400X. Voucher specimens were deposited at the Canadian Museum of Nature Parasitology (CMNP; Ottawa, Ontario, Canada) and the United States National Parasite Collection (USNPC; Beltsville, Maryland, USA). Other adult specimens were examined for comparison, including: (1) *Parelaphostrongylus odocoilei,* neotype and vouchers, USNPC 74634 and 74635 from *Odocoileus hemionus*; (2) *Protostrongylus* sp. collected by K. A. Nieland and C. A. Nielsen from the lungs of a 7-yr-old Dall's ewe from Dry Creek (Alaska Range, AK) on 5

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May 1972 and deposited at the University of Alaska at Fairbanks Museum (UAFM 3580/127 and 128; now USNPC 90718); (3) *Protostrongylus* sp. collected from the lungs of Dall's sheep (71-DS-22 and others) from the Mackenzie Mountains in 1971 by A. Currier, and currently in an unaccessioned orphaned collection at the CMNP; and (4) *Protostrongylus stilesi*, type and voucher specimens, USNPC 29379, 49227, and 75440 in *O. canadensis*.

Rectal feces from all six ewes were examined by beaker Baermann (Forrester and Lankester, 1997). After 18 to 24 hr, three aliquots of the concentrated sediment were examined and the *Protostrongylus* sp. L1 and the DS-L1 were quantified separately. Larvae isolated from the feces of the ewes collected in April, 1999, were placed in a drop of water on a glass slide and heat-fixed over a flame. They were measured at 400× using a drawing tube and then preserved in a solution of 70% ethanol and 5% glycerin.

The slugs *Deroceras laeve* ($n = 13$) and *Deroceras reticulatum* ($n = 13$) were used to investigate development of the DS-L1 and larval emergence, and to produce third-stage larvae (L3) for comparative morphology and measurements. *Deroceras laeve* occurs in habitat used by Dall's sheep in the Mackenzie Mountains (S. Kutz, unpubl. data) and is a suitable intermediate host for the genus *Parelaphostrongylus* (Lankester and Anderson, 1968; Samuel et al., 1985). *Deroceras reticulatum* was used because of the availability of laboratory colonies. Dorsal-spined first-stage larvae for gastropod infection were obtained from a single sample of Dall's sheep feces collected off the snow in the Mackenzie Mountains. Larvae were isolated from the melt water in the collection bag; the ratio of DS-L1 to *Protostrongylus* sp. L1 was 1417:1. Six or seven slugs (each species processed separately) were exposed to approximately 6,000 L1 in a 9 cm Petri dish for 5.5 hr (Hoberg et al., 1995) at room temperature (20 to 22 C). Slugs were then transferred to 4.2 li Rubbermaid® (Wooster, Ohio, USA) containers with autoclaved potting soil and vermiculite as a substrate. Each species was maintained in a separate container at room temperature under natural lighting. Fresh food (washed lettuce, potato, carrots, and chalk) was provided every 3 to 4 days.

On day 19 post-infection (PI), one *D. laeve* was placed in a 5 cm glass Petri dish containing food and water and held at room temperature until day 28 PI. The dish was then examined for emerged L3 (Kutz et al., 2000), and the slug digested in a pepsin and hydrochloric acid solution (Hoberg et al., 1995). On day 33 PI, 12 *D. laeve* were transferred to two 9 cm plastic Petri dishes (6/dish) containing carrots, lettuce, chalk, and water, and housed at 10 to 11 C in the dark. Dishes were examined for emerged L3 on days 36, 40, and 46 PI. On day 46 PI, 11 of the 12 *D. laeve* were digested as described above. Third-stage larvae obtained by digestion were heat-fixed, measured, and preserved as for the L1. The *D. reticulatum* were maintained at room temperature in Rubbermaid® containers throughout the experiment. A single *D. reticulatum* was digested and examined for larvae on day 28 PI, the remaining *D. reticulatum* that survived (7) were digested on day 48 PI.

Meristic data of adult and larval protostrongylids from Dall's sheep were statistically compared to protostrongylids from other host species. Analyses were done using a *t*-test with the level of significance set at $P \leq 0.05$ (Zar, 1984).

RESULTS

Adult nematodes were recovered from the skeletal muscles of two ewes in October and all three ewes in April. These were identified as *P. odocoilei* (Table 1): vouchers include CMNP 2000-0021, 2000-0022 and USNPC 89193 and 89194. Adult protostrongylids were also isolated from the lungs of five of the six ewes and three of the four hunter-killed sheep. These were identified as *P. stilesi* (Table 2). Voucher specimens include CMNP 1998-0048, 1998-0049, 1998-0050 and USNPC 86940 and 90718.

Adult *P. odocoilei* were identified in a total of 59 different lesions in the skeletal muscles of the three ewes collected in April. Lesions were widely distributed throughout the muscles of the forelimbs (22% of the 59 lesions), trunk (39%), and hindlimbs (39%). The majority of the lesions were located in the *biceps femoris* and *infraspinatus* (12% each), the *longissimus dorsi* (10%), the *gracilis* and *pectoralis* (8% each), and the *cutaneous trunci* and *trapezius* (7% each). Only the *longissimus dorsi* and the *biceps femoris* contained nematodes in all three ewes.

Adult *P. odocoilei* that were detected were invariably associated with multifocal petechial, ecchymotic, or linear hemorrhages, both superficial and deep, within the musculature. In these lesions, adult

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TABLE 1. Measurements (in micrometers) of adult male and female *Parelaphostrongylus odocoilei* from Dall's sheep (this study) and from mule deer (Platt and Samuel, and 1978). Values reported in micrometers unless otherwise stated.

		This study	Platt and Samuel (1978)[a]	
	n	mean ± 1 SD (range)	mean (range)	Neotype
Males				
Total length (mm)	8	29 ± 3 (26–36)	23 (18–26)	29
Maximum width	7	138 ± 18 (118–163)	147 (138–156)	147
Esophagus				
Length[b]	8	581 ± 90 (383–660)	653 (565–717)	600
Width	8	88 ± 17 (70–121)	70 (58–85)	79
Cervical papillae[b]	8	97 ± 12 (73–107)	—	—
Excretory pore[b]	8	95 ± 11 (73–106)	75 (56–94)	97
Nerve ring[b]	8	90 ± 6 (84–101)	88 (68–94)	94
Left spicule	11	158 ± 7 (143–165)	149 (132–170)	146
Distance to split	11	115 ± 8 (101–126)	—	—
Right spicule	11	160 ± 8 (146–171)	149 (132–170)	146
Distance to split	10	116 ± 11 (95–134)	—	—
Gubernaculum length (lat)[c]	11	91 ± 5 (84–101)	93 (73–112)	75
Corpus length (lat)[e]	11	87 ± 5 (78–95)	86 ± (65–103)	65
Corpus width (vent)	11	18 ± 3 (14–22)	22 (21–24)	—
Crura length (lat)	12	24 ± 1 (22–25)	24 (21–26)	21
Crura width (vent)	11	10 ± 1 (8–11)	12 (10–14)	12
Crura thickness (lat)	12	8 ± 2 (6–11)	—	—
Bursa				
Width	11	101 ± 5 (95–106)	108 (103–112)	117
Length	10	83 ± 6 (73–90)	89 (80–94)	94
Dorsal ray length	10	22 ± 3 (17–28)	—	—
Females				
Total length (mm)	7	48 ± 3 (43–52)	44 (39–48)	—
Maximum width	7	164 ± 15 (135–179)	163 (141–179)	—
Esophagus				
Length[b]	11	679 ± 105 (532–884)	627 (588–658)	—
Width	11	112 ± 13 (92–135)	70 (65–76)	—
Cervical papillae[b]	10	100 ± 12 (78–115)	—	—
Excretory pore[b]	11	99 ± 11 (78–115)	78 (71–82)	—
Nerve ring[b]	11	99 ± 14 (84–129)	92 (79–106)	—
Vulva to posterior end	11	171 ± 14 (148–196)	178 (161–194)	—
Tail length	11	43 ± 4 (39–50)	48 (44–65)	—
Vagina length	9	1646 ± 413 (574–1917)	—	—

[a] n = 11 and 14 for male and female measurements, respectively.
[b] As measured from cephalic extremity.
[c] Lat–lateral view.
[d] Vent-ventro-dorsal view.

nematodes were found individually or in mixed sex groups of up to four. They were arranged parallel to muscle fibers, perpendicular to and woven among the muscle fibers, or coiled in small nests between the fibers (Fig. 1a, b). Histologically, nematodes were associated with mild eosinophilic and granulomatous myositis and mild hemorrhage (Fig. 1b). Eggs in the perimysium were multicellular with finely granulated, basophilic cytoplasm (Fig. 1c). Some eggs contained developing larvae (Fig. 1d).

Dorsal-spined first-stage larvae, presumably *P. odocoilei*, were isolated from the lung washes of all six ewes collected in October or April. Grossly, these lungs were abnormally large, heavy, and rubbery. Numerous dark red, 1 to 2 mm circular foci, often with pale centers, were on the pleu-

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TABLE 2. Adult male posteriors of *Prostostrongylus stilesi* from Dall's sheep in the Mackenzie Mountains (NT) and the Alaska Range (AK) and as described by Dikmans (1931); values reported in micrometers.

	n	Mackenzie Mt. mean ± 1 SD (range)	*n*	Alaska Range mean ± 1 SD (range)	Dikmans, 1931[a] mean (range)
Left spicule	6	299 ± 8 (288–312)	3	(273–312)	(300–340)
Right spicule	6	296 ± 11 (276–307)	3	(278–304)	(300–340)
Gubernaculum	6	175 ± 17 (161–203)	3	(159–174)	—[b]
Body	6	99 ± 16 (78–125)	3	(73–91)	58[c]
Legs	6	77 ± 5 (70–83)	3	(73–86)	96
Sickle plate	3	18	2	(21–23)	NA
Ventral plate	3	(78–81)	1	62	NA

[a] Sample size not provided.
[b] No measurement given.
[c] Includes only the heavily cuticularized distal portion of body.

ral surface of all lung lobes and extended 1 to 2 mm into the parenchyma. Histologically, DS-L1 and eggs indistinguishable from those in the muscles were present throughout the parenchyma of all lobes. They were generally found individually, were often associated with hemorrhage, and were surrounded by small clusters of macrophages, occasional multi-nucleated giant cells, lymphocytes, plasma cells, and eosinophils (Figs. 2a, b).

In addition, five of six of these ewes and three of the four hunter-killed sheep had firm, pale, coalescing lesions, 5–70 mm in diameter, located primarily, but not exclusively, along the caudo-dorsal border of the diaphragmatic lobes. These lesions were invariably associated with adults, eggs, and larvae of *P. stilesi.* On cut section, lesions extended 5 to 30 mm into the parenchyma and had a gritty texture. Histologically, there were large, locally extensive aggregations of lymphocytes, macrophages, plasma cells, and few eosinophils surrounding accumulations of eggs, larvae, and adult nematodes (Fig. 3a, b). Eggs were often found in clusters and contained large eosinophilic granules. Adult nematodes and L1 seen in section (Fig. 3b) were consistent with other descriptions of *P. stilesi* (Spraker et al. 1984). Other histological findings in the lungs included focal areas of fibrosis, scattered lymphocytic nodules, bronchiolar hyperplasia, and mild fibrino-hemorrhagic exudate.

Dorsal-spined larvae were isolated from the feces of all six ewes, with lower mean larval counts in October (501 ± 358 LPG) than in April (3423 ± 2231 LPG). *Protostrongylus* sp. L1 were present in the feces of only one of three ewes in October (128 LPG) and all three in April (1389 ± 1224 LPG).

The tails of the DS-L1 were characterized by two distinct forms. In lateral view both had a triangular dorsal spine typical of the Elaphostrongylinae, but the terminal region of the tail differed between the two forms (Fig. 4a, b). The first form had a slightly kinked tail with two cuticular folds and a terminal spike located symmetrically at the tip of the caudal extremity (Fig. 4a). The second form had a straight, digitiform tail lacking cuticular folds, and a rounded caudal extremity with a subterminal spike located asymmetrically on its ventral aspect (Fig. 4b). There was no significant difference in the meristic data for these morphologically divergent forms (*t*-test, df = 19, $P < 0.05$), so in subsequent comparisons the data were combined (Table 3). The DS-L1 from Dall's sheep were consistent in length with the description of *P. odocoilei* by Hobmaier and Hobmaier (1934) (*t*-test, df = 20, $P = 0.77$), but, although not signifi-

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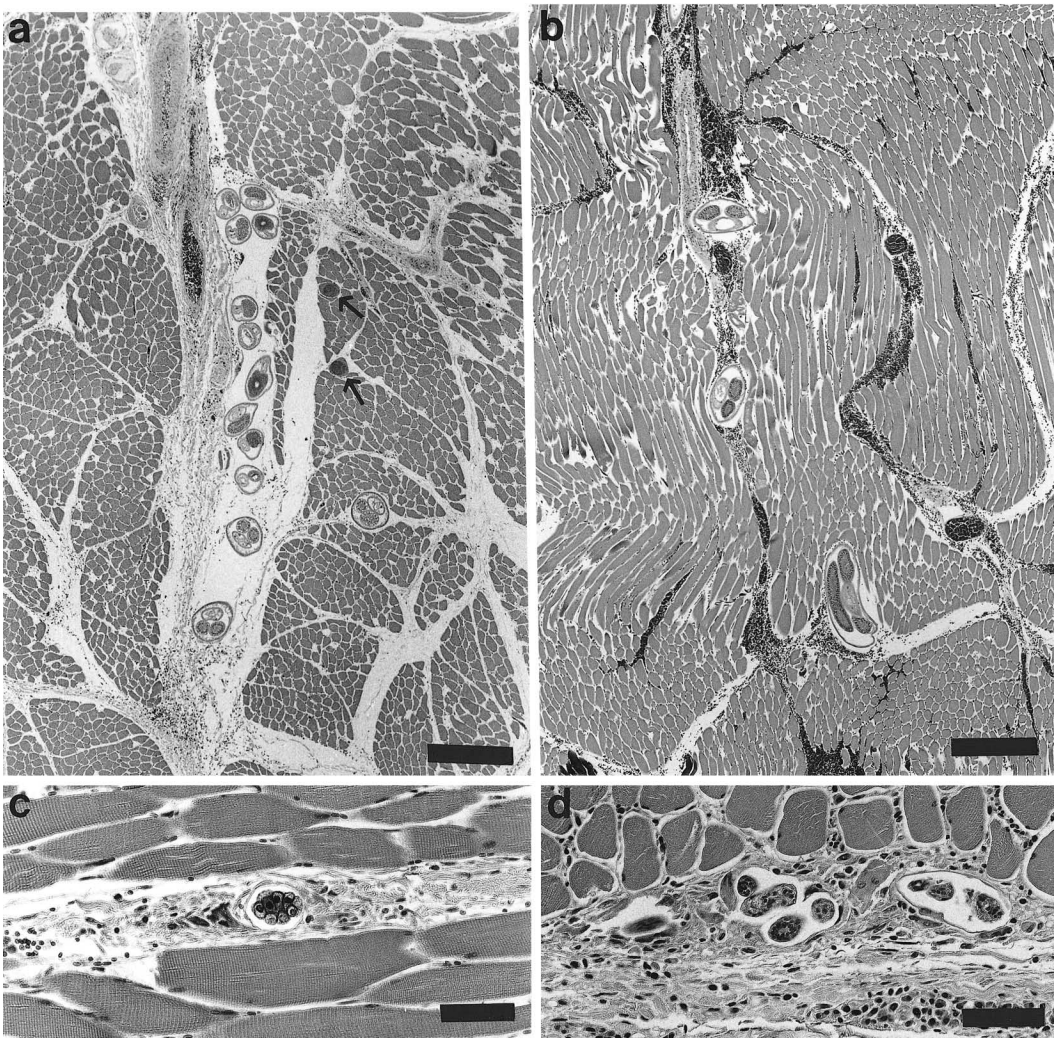


FIGURE 1. *Parelaphostrongylus odocoilei* in the skeletal muscles of Dall's sheep. (a) Adult nematodes within the perimysium. (*Sarcocystis* sp. are also present in myocytes - thin arrows). Bar = 300 μm. (b) Adult nematodes associated with hemorrhage within the musculature. Bar = 300 μm. (c) Single egg in perimysium. Bar = 60 μm. (d) Eggs containing developing first-stage larvae in the perimysium. Bar = 60 μm.

cantly, tended to be longer than those described by Platt (1978) (*t*-test, df = 20, *P* = 0.08). *Protostrongylus stilesi* L1 were morphologically and morphometrically similar to those described by Pillmore (1956) (Table 3).

Development of *P. odocoilei* from L1 to L3 was more rapid, and intensity of infection was greater, in *D. laeve* than in *D. reticulatum.* At day 28 PI, 101 L3 were recovered by digestion from the single *D. laeve,* but only three second-stage larvae (L2) were recovered from the single *D. reticulatum.* On day 46 PI, a total of 978 L3 were recovered from 11 *D. laeve* (median of 66 L3/slug, range of 31-249 L3/slug); one *D. laeve* was not examined. In contrast, on day 48 PI, totals of only 13 L3, 10 L2, and six L1 were recovered from seven surviving *D. reticulatum.* Eleven L3 were recovered from the Petri dish housing the single *D. laeve* between days 19 and 28 PI, and 55 L3 were found in the Petri dishes housing the 12 *D. laeve* from

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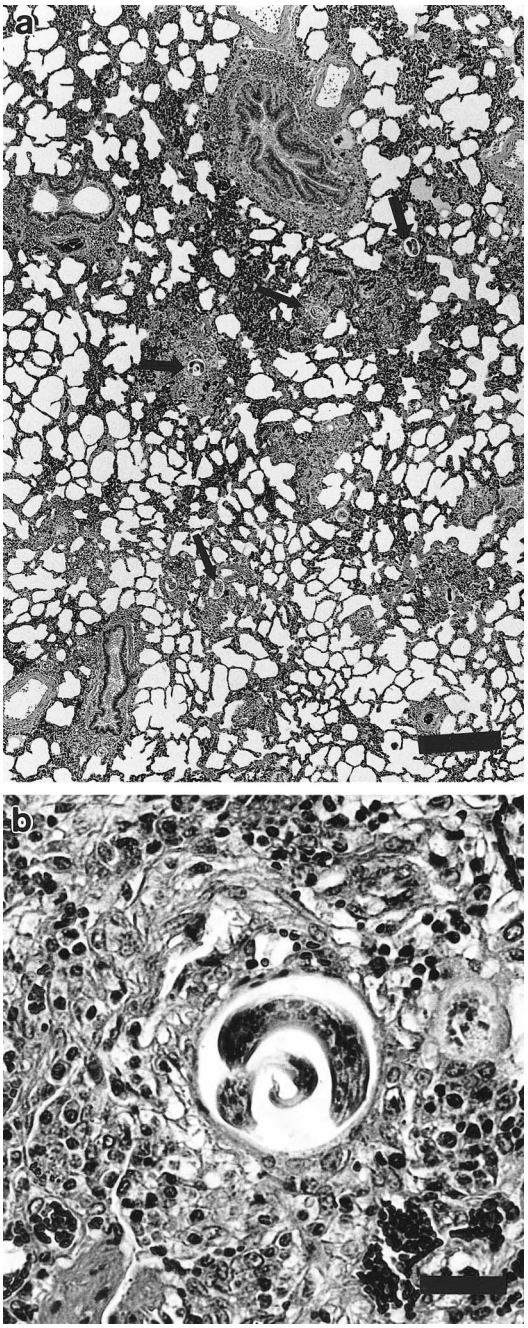


FIGURE 2. Histological section from the dorsal region of the middle lung lobe of a Dall's sheep showing lesions probably caused by *Parelaphostrongylus odocoilei*. (a) Small, multifocal clusters of inflammatory cells surrounding single eggs (thin arrows) and developing larvae (thick arrow) throughout the lung parenchyma. Bar = 300 μm. (b) An egg containing a developing, dorsal-spined larva. Bar = 40 μm.

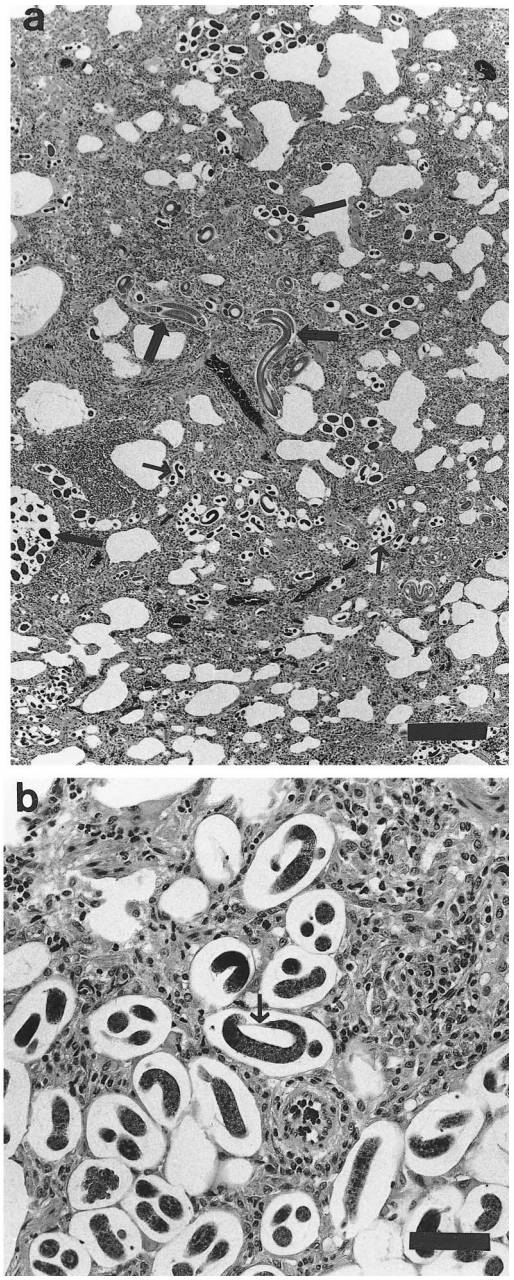


FIGURE 3. Histological section from the caudodorsal region of the diaphragmatic lung lobe of a Dall's sheep showing lesions consistent with *Protostrongylus stilesi*. (a) Large aggregations of inflammatory cells surrounding adults (thick arrows), eggs (medium arrows) and developing first-stage larvae (thin arrow) of *P. stilesi*. Bar = 300 μm; (b) Eggs with developing larvae. The straight tail of *P. stilesi* is visible (arrow). Bar = 60 μm.

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FIGURE 4. Tails of dorsal-spined larvae recovered from the feces of Dall's sheep in the Mackenzie Mountains (Northwest Territories, Canada); (Top) Typical elaphostrongyline-type morphology with dorsal spine (thin arrow); (Bottom) A ventral, sub-terminal spike is visible (thick arrow). Bar = 10 micrometers (μm).

days 33 to 46 PI. *Deroceras reticulatum* were not examined for larval emergence.

The L3 digested from *D. laeve* at day 28 PI were significantly longer than those of *P. odocoilei* originally described by Hobmaier and Hobmaier (1934) (*t*-test, df = 23, $P < 0.01$), but not longer than those redescribed by Platt (1978) (*t*-test, df = 23, $P > 0.05$) (Table 3). Many, but not all L3, had a subterminal dorsal protrusion at the posterior extremity similar to that described by Platt (1978) and Ballantyne and Samuel (1984).

DISCUSSION

Dall's sheep and other Caprini have not previously been recognized as hosts for *P. odocoilei,* nor has this elaphostrongyline been found at subarctic latitudes. The records documented in this study represent a substantial extension of the known range for this parasite and indicate that the report of *Muellerius* in Dall's sheep in the Brooks Range (Dau, 1981), based only on recovery of first-stage larvae, should be reconsidered. Based on the findings of the present study it may be more likely that these DS-L1 were *P. odocoilei.* Other protostrongylids with DS-L1 that are found at northern latitudes in North America include *Parelaphostrongylus andersoni, Umingmakstrongylus pallikuukensis,* and species of *Varestrongylus* (Boev, 1975; Lankester and Hauta, 1989; Hoberg et al., 1995). None of these species, however, have been documented in Caprini from North America.

Adult *P. odocoilei* dwell in the skeletal musculature primarily of deer from western North America. This species has been reported in black-tailed deer (*Odocoileus hemionus columbianus*) from the central Coast mountain range of California (Hobmaier and Hobmaier, 1934), and Vancouver Island, BC (Pybus et al., 1984); in Californian mule deer (*O. hemionus californicus*) from the western Sierra Nevada mountains (Brunetti, 1969); and in mule deer (*O. hemionus hemionus*) from Jasper National Park, Alberta (AB) (Platt and Samuel, 1978a) and the Okanagan Valley (BC; Lankester, 2000). *Parelaphostrongylus odocoilei* has also been confirmed in woodland caribou (*Rangifer tarandus caribou*) from west-central AB (Gray and Samuel, 1986) and mountain goats (*Oreamnus americanus*) from AB, central BC, and Washington (Pybus et al., 1984). Dimensions of DS-L1 from bighorn sheep in AB and BC, Canada (Pybus and Shave, 1984) and Washington, USA (W. A. Foreyt, pers. comm.), suggest that *P. odocoilei* may have a broader host and geographic range than originally believed, but this remains to be confirmed by locating and identifying adult nematodes.

Structurally distinct forms of DS-L1, such as those of *P. odocoilei* in the present study, have not been described for any other elaphostrongyline. Consistency in

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TABLE 3. Measurements of *Parelaphostrongylus odocoilei* first (L1) and third-stage larvae (L3) from Dall's sheep, black-tailed deer, and mule deer, and of *Protostrongylus stilesi* L1 from Dall's sheep and bighorn sheep; mean ± standard deviation (range) in micrometers.

	P. odocoilei L1			*P. odocoilei* L3			*P. stilesi* L1	
	Dall's Po	Po[a]	Po[b]	Dall's Po	Po[a]	Po[b]	Dall's Ps	Ps[c]
Number examined	21	—	25	24	—	25	20	15
Total length	387 ± 30	378	330	813 ± 42	624	734	364 ± 10	—
	(334–428)	—	(286–361)	(740–922)	—	(562–855)	(342–382)	(245–328)
Width at base of esophagus	18 ± 2	17	20	42 ± 4	47	37	17 ± 1	—
	(15–20)	—	(18–23)	(36–49)	—	(32–43)	(15–20)	(16–19)
Nerve ring[d]	104 ± 9	—	85	114 ± 7	—	101	87 ± 4	—[e]
	(89–117)	—	(62–106)	(97–130)	—	(89–118)	(78–93)	—
Excretory pore[d]	105 ± 8	98	84	132 ± 11	100	104	93 ± 4	—
	(92–117)	—	(68–98)	(119–162)	—	(93–125)	(87–99)	(72–104)
Esophagus[d]	181 ± 14	166	159	266 ± 14	218	216	150 ± 6	—
	(160–206)	—	(134–179)	(235–293)	—	(212–322)	(136–160)	(110–155)
% Total length	47 ± 2	44	48	33 ± 2	35	29	41 ± 1	—
	(44–50)	—	—	(30–33)	—	—	(39–43)	—
Genital primordium[d]	256 ± 20	—	212	495 ± 37	386	456	220 ± 8	—
	(219–285)	—	(178–237)	(435–596)	—	(358–558)	(206–234)	(166–225)
% Total length	66 ± 2	—	64	61 ± 3	—	62	61 ± 1	—
	(64 − 73)	—	—	(50–68)	—	—	(57–62)	—
Anus[d]	348 ± 28	—	—	765 ± 40	—	—	305 ± 9	—
	(300–390)	—	—	(697–869)	—	—	(287–322)	—
Tail length	39 ± 4	40	36	48 ± 4	40	34	59 ± 3	—
	(33–46)	—	(30–42)	(43–55)	—	(29–43)	(55–64)	(45–65)
Caudal tail spike	—	—	—	—	—	—	29 ± 2	(18–31)
							(26–32)	

[a] From black-tailed deer (Hobmaier and Hobmaier, 1934).
[b] From mule deer (Platt, 1978).
[c] From bighorn sheep (Pillmore, 1956).
[d] As measured from the cephalic extremity.
[e] Described as "immediately before excretory pore."

meristic data for these morphotypes suggests that they may represent a single species where structurally divergent tails represent typical variation. Preliminary analyses of the ITS-2 sequences for adults and the two larval morphotypes do not refute this conclusion based on meristic data (B. Rosenthal, M. Wong, E. P. Hoberg, unpubl. data). Consequently, although further study is required, the distinct caudal morphology of *P. odocoilei* may be attributed to polymorphism. These findings, combined with the wide range of measurements reported for L1 and L3 of *P. odocoilei* (Hobmaier and Hobmaier, 1934; Platt, 1978; Gray and Samuel, 1986) and variability in the description of the adult parasites (Hobmaier and Hobmaier, 1934; Platt and Samuel, 1978a; Carreno and Lankester, 1993), accentuate the need for molecular methods for identifying larval and adult protostrongylids as well as for comparing populations across their range (Gajadhar et al., 2000).

Emergence of L3 of *P. odocoilei* from gastropod intermediate hosts has not previously been reported. Although this phenomenon has been described for a number of other protostrongylids (Boev, 1975; Kralka and Samuel, 1984; Kutz et al., 2000), this is the first report for a member of the Elaphostrongylinae. The significance of L3 emergence for the epidemiology of *P. odocoilei* and other elaphostrongylines should be investigated.

Protostrongylus stilesi occurs in bighorn sheep and mountain goats from western North America, as well as in introduced European mouflon (*Ovis musimon*) (Boev, 1975; Samuel et al., 1977; Uhazy et al., 1973). There have been unconfirmed reports, based on L1 and pulmonary pathology, of *Protostrongylus* sp. in Dall's sheep across their range (Goble and Murie, 1942; Simmons et al., 1984; Schwantje, 1987; R. L. Rausch and E. P. Hoberg, unpubl. obser. USNPC 88303); however, the present study is the first to confirm the presence of *P. stilesi* in Dall's sheep by examination of adult specimens. These findings, along with the adult specimens of *P. stilesi* that we have recently discovered in museum collections in Canada (CMNP unaccessioned collection) and Alaska (UAFM 3580/127 and 128, now USNPC 90718), as well as widespread geographical fecal surveys (E. Jenkins and A. Veitch, unpubl. data), suggest that *P. stilesi* is a common and widespread parasite in Dall's sheep.

Protostrongylus rushi, an airway dwelling protostrongylid common in bighorn sheep and mountain goats, was not found in the Dall's sheep examined in the present study. This parasite, however, has been collected from at least one Dall's sheep in the YT (CMNP 1988-0522). Continued survey and inventory is necessary to define the potential geographic distribution of *P. rushi* in Dall's sheep.

The pathological patterns of *P. stilesi* and *P. odocoilei* in Dall's sheep are consistent with those in bighorn sheep (Spraker et al., 1984) and mule deer (Platt and Samuel, 1978b; Pybus and Samuel, 1984a, b), respectively. In the present study, the two parasites induced distinct patterns of pulmonary pathology. Lesions scattered throughout the parenchyma of all lobes, similar to those reported in mule deer experimentally infected with *P. odocoilei* (Pybus and Samuel, 1984a), were likely a result of haematogenously delivered eggs and developing larvae of *P. odocoilei.* The severe verminous lesions associated with adult parasites, eggs, and L1 in the diaphragmatic lobes were consistent with those reported for *P. stilesi* in bighorn sheep. *Protostrongylus stilesi* has been implicated in the stress-lungworm-pneumonia complex of bighorn sheep (Spraker et al., 1984), and *P. odocoilei* is known experimentally to cause fatal pneumonia in mule deer fawns (Pybus and Samuel, 1984a). Our finding of concurrent infections with these species in an individual host is unusual and the possible synergistic effects of this dual infection are being investigated.

The host and geographic distributions of

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P. odocoilei and *P. stilesi* require better definition. Both parasites may be widespread in Dall's sheep across their range. The presence of *P. odocoilei* in this host, while absent or rare in bighorn sheep, is enigmatic. It is unlikely that significant contact between Dall's sheep and mule deer (the 'typical' host) has occurred in Recent time (Kuyt, 1966; Scotter, 1974). Other sympatric ruminants include woodland caribou, mountain goats, moose, and muskoxen. Woodland caribou in Alberta are natural hosts of *P. odocoilei* (Gray and Samuel, 1986). In the Mackenzie Mountains, NT, woodland caribou have a low prevalence (9.5%) and low mean larval count (0.1 LPG) of an as yet unidentified DS-L1 (R. Popko, A. Veitch, B. Wagner, unpubl. data). Mountain goats are natural hosts of *P. odocoilei* (Pybus et al., 1984) and *P. stilesi* (Samuel et al., 1977), but are uncommon in the northern Mackenzie Mountains (A. Veitch, unpubl. obs.). Moose, which are present throughout the Mackenzie River Valley and surrounding mountain ranges (Veitch et al., 1996; Veitch et al., 2000), can be experimentally infected with *P. odocoilei* (Platt and Samuel, 1978b), but natural infections are not known. There are no records of either *P. odocoilei* or *P. stilesi* from muskoxen in North America, however, dorsal-spined first-stage larvae and *Protostrongylus* sp. L1 have recently been found in the feces of muskoxen in the northern Yukon and Richardson Mountains, NT (S. Kutz, B. Wagner, J. Nagy, B. Elkin, and M. Branigan, unpubl. obs.). The potential role of caribou, mountain goats, moose, and muskoxen in the introduction or maintenance of these protostrongylids in Dall's sheep remains undetermined.

Currently, numbers of Dall's sheep in the Mackenzie Mountains, NT, appear to be relatively stable (Veitch and Simmons, 1999). The apparent absence of the major mortality events that occur in bighorn sheep populations may in part reflect the isolation of this northern habitat. There is low to moderate hunting pressure (Veitch et al., 2000), no contact with domestic animals, no communities or roads, and no loss of range due to human encroachment (Veitch and Simmons, 1999). This environment, however, is being exposed to increasing anthropogenic and climatologically driven change and it is critical, therefore, to recognize the presence and understand the effects of these potentially pathogenic parasites in Dall's sheep. Clearly, further characterization of the parasite fauna of Dall's sheep and other northern ruminants is needed. Baseline data are essential for identifying parasite biodiversity, describing geographic and host range, monitoring population health, and finally, for measuring the effects of environmental change on patterns of parasite distribution, transmission, and emergence of parasite associated disease (Hoberg, 1997; Brooks and Hoberg, 2000).

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