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# Discovery and Description of the "*Davtiani*" Morphotype for *Teladorsagia boreoarcticus* (Trichostrongyloidea: Ostertagiinae) Abomasal Parasites in Muskoxen, *Ovibos moschatus*, and caribou, *Rangifer tarandus*, from the North American Arctic: Implications for Parasite Faunal Diversity

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## DISCOVERY AND DESCRIPTION OF THE “DAVTIANI” MORPHOTYPE FOR *TELADORSAGIA BOREOARCTICUS* (TRICHOSTRONGYLOIDEA: OSTERTAGIINAE) ABOMASAL PARASITES IN MUSKOXEN, *OVIBOS MOSCHATUS*, AND CARIBOU, *RANGIFER TARANDUS*, FROM THE NORTH AMERICAN ARCTIC: IMPLICATIONS FOR PARASITE FAUNAL DIVERSITY

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**ABSTRACT:** Collections to explore helminth diversity among free-ranging ungulates in the North American Arctic revealed the occurrence of a third male, or “davitiani,” morphotype for *Teladorsagia boreoarcticus*. Designated as *T. boreoarcticus* forma (f.) minor B, the males occurred with *T. boreoarcticus* f. major and *T. boreoarcticus* f. minor A in endemic populations of muskoxen (*Ovibos moschatus wardi*) and barrenground caribou (*Rangifer tarandus groenlandicus*) on Victoria Island, Nunavut, Canada, and in muskoxen and Peary caribou (*Rangifer tarandus pearyi*) on Banks Island, Northwest Territories, Canada. These specimens differ from conspecific morphotypes in the structure of the genital cone and Sjöberg’s organ. Relative to *T. boreoarcticus* f. minor A, specimens of *T. boreoarcticus* f. minor B are consistently smaller, and mean dimensions for the bursa and spicules do not overlap. The robust spicules are similar in form, particularly in the relative length of the dorsal and ventral processes, but mean total length is substantially less in specimens of *T. boreoarcticus* f. minor B. Differences that distinguish the minor morphotypes of *T. boreoarcticus* parallel those demonstrated for the *T. trifurcata* and *T. davitiani* morphotypes in association with *T. circumcincta* sensu stricto. New host and geographic records include the 3 morphotypes of *T. boreoarcticus* in muskoxen and Peary caribou from Banks Island and in barrenground caribou from Victoria Island. Recognition of the ubiquitous nature of cryptic species emphasizes the need to effectively develop and use our collections-based resources and museum archives to build a robust understanding of the biosphere. Field inventory should include provisions for integrative approaches that preserve specimens suitable for comparative morphology, multi-faceted molecular investigations, and population genetics.

*Teladorsagia circumcincta* (Stadelman, 1894) and *T. boreoarcticus* Hoberg, Monsen, Kutz and Blouin, 1999 have been shown to represent a potentially diverse complex of cryptic polymorphic species distributed, and probably partitioned, among domestic and free-ranging ungulates across the Holarctic (Hoberg et al., 1999; Leignel et al., 2002; Grillo et al., 2007). In the restricted sense, *T. circumcincta*/*T. trifurcata* (Ransom, 1907)/*T. davitiani* Andreeva and Satubaldin, 1954 (in the taxonomic notation used to designate nominal polymorphic forms representing a single species in Ostertagiinae) is a characteristic polymorphic species of small domestic ruminants, particularly sheep, *Ovis aries* L. (e.g., Drózdź, 1995). Some populations of nematodes restricted to goats, *Capra hircus* L., represent another putative species within *T. circumcincta* that has not yet been fully characterized, further supporting the concept for a diverse assemblage (Gasnier et al., 1997; Leignel et al., 2002). Subsequent to putative origins in Eurasia, *T. circumcincta* has been translocated and disseminated globally coincidental initially with expansion of agriculture and later European exploration after the 1500s (e.g., Hoberg, 1997; Hoberg et al., 2001). Thus, *T. circumcincta* has been widely introduced and is an important element of mosaic nematode faunas (containing both introduced and endemic species) occurring among ungulates (Hoberg et al., 1999, 2001, 2008a; Hoberg, 2010).

Diversity and species limits within the *T. circumcincta* complex have yet to be adequately, or completely, delineated either in domestic or in free-ranging hosts. New geographically extensive surveys in conjunction with integrated approaches linking morphology and molecular systematics are thus required (Gasnier et al., 1997; Hoberg et al., 1999; Leignel et al., 2002; Grillo et al.,

2007). Clear definitions of nematode diversity are increasingly important in the context of ecotones at the borderlands of both managed and wild ecosystems. As part of baselines, they are essential in understanding patterns and history for faunal structure, including the potential exchange of parasites among domestic and free-ranging host species in zones of contact (Hoberg et al., 1999; Cerutti et al., 2010). Furthermore, translocations involving multiple species and subspecies of free ranging hosts (and their parasites) will serve to influence patterns of faunal diversity and the distribution and relationships for parasite populations in newly developed zones of sympatry. Recognition of species limits within the cryptic complex have additional ramifications, because biology, life history, development, population structure, host associations, and responses to environmental change may vary according to the history, evolution, and biogeography for different assemblages of parasites (Suarez and Cabaret, 1991; Hoberg et al., 1999, 2008a; Hoberg, 2010).

*Teladorsagia boreoarcticus* was described as a dimorphic species (with 2 discrete male morphotypes) in ungulates from the continental region of the central Canadian Arctic [muskoxen, *Ovibos moschatus moschatus* (Zimmermann), and barrenground caribou, *Rangifer tarandus groenlandicus* (Borowski)] and low Arctic Islands (*O. m. wardi* Lyddecke) (Hoberg et al., 1999). The original description characterized males of the major morphotype (*T. boreoarcticus* forma [f.] major), including the name bearing holotype, and a minor morphotype (*T. boreoarcticus* f. minor) representing a *T. trifurcata*-like form based on molecular and morphological criteria. Male nematodes corresponding to a *T. davitiani*-like form were not initially recognized. Hoberg et al. (1999) suggested that *T. boreoarcticus* either differed from *T. circumcincta* (with a major and 2 minor male morphotypes) or that the putative third male morphotype should eventually be discovered (Drózdź, 1995). As a basis for comparison, the

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morphology and identity of the respective minor morphotypes for *T. circumcincta* were resolved in studies by Becklund and Walker (1971).

Subsequent to the description of the major and minor morphotypes of *T. boreoarcticus*, specimens of the third putative male (or “*davtiani*” morphotype) were found among collections from Ekalluk River, Victoria Island, Nunavut, Canada, in endemic *O. m. wardi* (field collection C-66). These specimens had been included among the original vouchers (reported as U.S. National Parasite Collection [USNPC] 87902.05) for *T. boreoarcticus* f. minor, and they were not in the paratype series; meristic and structural data from these specimens had not been included in the description of the species (among the 59 paratype specimens of the “*trifurcata*” morph measured and represented in table V in original). Thus, the original description of *T. boreoarcticus* f. minor (or the “*trifurcata*” morph) does not constitute a composite of the 2 discrete minor morphotypes. Furthermore, a subsequent re-examination of the specimens that were sequenced from this host (under USNPC 87902.04; table IV in original), revealed 2 to have been incorrectly identified; these specimens were found to represent the “*davtiani*” morphotype. Specimens representing the “*davtiani*” morphotype were later collected along with the primary major and minor morphotypes of *T. boreoarcticus*, from Banks Island, Northwest Territories (NWT), in an endemic muskox population (*O. m. wardi*). Barrenground caribou on Victoria Island and Peary caribou, *Rangifer tarandus pearyi* Allen, on Banks Island, in sympatry with muskoxen, also were infected with nematodes representing the 3 male morphotypes of *T. boreoarcticus* (data not shown).

The “*davtiani*” morphotype remains unknown in endemic mainland populations of *O. m. moschatus* or in *R. t. groenlandicus* (Hoberg et al., 1999). On the mainland near Aklavik, NWT, however, specimens attributable to the third morphotype were discovered in an introduced and expanding population of *O. m. wardi*. This latter population of muskoxen has a complex history, being derived by sequential translocations from eastern Greenland to Nunivak Island, Alaska (in 1935, via Fairbanks, Alaska), and later (1960s–1970s) from Nunivak Island to Barter Island and the Arctic coastal plain north of the Brooks Range in Alaska (Reynolds, 1998). Subsequent and continuing expansion to the east has resulted in establishment of this population in the Yukon and NWT, Canada, where eventual contact with *O. m. moschatus* is predicted at the Mackenzie River ecotone (Hoberg et al., 2002). Such a history of translocation for hosts, and those associated with introductions of reindeer (*Rangifer tarandus tarandus* (L.)) from varying sources in eastern Siberia and the western Palearctic (e.g., Rausch, 2002), may have driven the development of a high-latitude mosaic fauna at some localities in North America (Hoberg et al., 1999; Hoberg, 2010). The structure and history of assemblage for such mosaics emphasizes the continued need to define species limits within *Teladorsagia* and other pathogenic nematodes among free ranging, semi-domestic, and domestic bovids and cervids.

The discovery of these series of specimens does not alter the original description of *T. boreoarcticus* but now provides the basis for a comprehensive description of the third male morphotype for this species. In the current study, we designate the “*trifurcata*” morphotype as *T. boreoarcticus* f. minor A, and we describe the “*davtiani*” morphotype for *T. boreoarcticus* f. minor B. Formal description of the latter is limited to specimens representing endemic populations from the low Arctic Islands that can unequivocally be referred to *T. boreoarcticus*. These specimens

are compared with those in other free-ranging and domestic ungulates from North America. New information is presented regarding the geographic distribution of *T. boreoarcticus*, and we explore the continuing complexities of ostertagiine taxonomy that emerge from the occurrence of polymorphic species.

## MATERIALS AND METHODS

### Specimens examined

Nematodes representing populations of *T. boreoarcticus* f. minor B in muskoxen and caribou were studied from localities in the central Canadian Arctic (Table I). Additional specimens held in the Canadian Museum of Nature (CMNP 179-419), including 3 *T. boreoarcticus* f. minor B and 3 *T. boreoarcticus* f. minor A in *O. moschatus wardi* from Ellesmere Island, Nunavut, Canada, also were examined (Webster and Rowell, 1980; Hoberg et al., 1999).

Other specimens, designated here as *T. cf. boreoarcticus* f. minor B that could not be unequivocally identified in the absence of minimal DNA sequence data (Hoberg et al., 1999), were examined from *O. m. wardi* (near Aklavik, NWT, Canada, ca. 68°13'0"N, 135°0'0"W, January 2000 by S.J.K. and J. Nagy) and Dall's sheep, *Ovis dalli dalli* (Dry Creek, Alaska Range, Alaska, ca. 53°58'24"N, 119°12'30"W, June 1972 by C. A. Nielsen; Table I). Minor morphotype specimens of *Teladorsagia*, most similar to *T. circumcincta*/*T. davtiani* sensu stricto, were examined from *Oreamnos americana* (Mt. Hammell, Alberta, Canada, 53°58'24"N, 119°12'30"W, September 1961 by G. R. Kerr). Specimens of the minor morphotype, *T. circumcincta*/*T. davtiani* sensu stricto, in domestic sheep from North America and Scotland also were examined for comparative purposes (Table I). Taxonomy for ungulate hosts follows Grubb (2005).

### Microscopy

Nematodes were prepared as temporary whole mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) and examined with interference contrast microscopy. The synlophe was examined in whole mounts with particular attention given to the pattern of ridge systems in the cervical zone and their extent posteriad, consistent with prior studies among the ostertagiines (Lichtenfels et al., 1988; Hoberg et al., 1999, 2010). Patterns for the synlophe in the cervical region are defined according to Lichtenfels et al. (1988); Type 1a lateral is defined as a strongly tapering pattern with multiple pairs of ridges converging and terminating on the single lateral-most ridge in the cervical region; Type B ventral is defined by a single continuous ridge in the ventral field in the cervical zone. Transverse sections were hand cut with a cataract knife and mounted in glycerin jelly for 5 specimens each from Victoria Island and Banks Island. Sections were used to count the number of ridges at the midbody and as a basis for comparison with data for the major and minor morphotypes of *T. boreoarcticus*. The disposition of the papillae and rays of the bursa are described according to Chabaud et al. (1970) and Durette-Desset (1983). The structure of the Sjöberg's organ in the dorsal aspect of the genital cone is described according to Drózdź (1965).

## RESULTS

Field collections to explore helminth diversity among free-ranging ungulates in the North American Arctic revealed the occurrence of a third male, or “*davtiani*,” morphotype for *Teladorsagia boreoarcticus*. These males occurred with *T. boreoarcticus* f. major and *T. boreoarcticus* f. minor A in endemic populations of muskoxen and barrenground caribou on Victoria Island, Nunavut, Canada, and in muskoxen and Peary caribou on Banks Island, NWT. On Victoria Island, *T. boreoarcticus* f. minor B constituted 4 to 15% of the total *Teladorsagia* populations in individual muskoxen and 4 to 41% in individual barrenground caribou during December; overall prevalence was 43% in 28 muskoxen and 25% in 12 caribou. On Banks Island, this morphotype constituted 4 to 100% (November) and 4 to 50%

TABLE I. Specimens examined of the minor morphotypes *Teladorsagia boreoarcticus* forma minor B, *T. cf. boreoarcticus* forma minor B, and *T. circumcincta*/*T. davtiani* sensu stricto with a summary of accession numbers, host species, and general geographic localities for collection.

USNPC*	Identity	Host	Locality	Specimens
87902.04†	<i>T. boreoarcticus</i> f. minor B	<i>Ovibos moschatus wardi</i>	Victoria Is.	1
104766	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Victoria Is.	7
91553	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Victoria Is.	8
91558	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Victoria Is.	12
92072.03	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	24
92075.03	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	17
95981	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	10
96034	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	10
96047	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	9
96122	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	11
96325	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	7
96405	<i>T. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Banks Is.	12
98657	<i>T. boreoarcticus</i> f. minor B	<i>R. tarandus pearyi</i>	Banks Is.	1
98662	<i>T. boreoarcticus</i> f. minor B	<i>R. t. pearyi</i>	Banks Is.	12
91613	<i>T. boreoarcticus</i> f. minor B	<i>R. t. groenlandicus</i>	Victoria Is.	2
91620	<i>T. boreoarcticus</i> f. minor B	<i>R. t. groenlandicus</i>	Victoria Is.	4
91623	<i>T. boreoarcticus</i> f. minor B	<i>R. t. groenlandicus</i>	Victoria Is.	1
98157	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Aklavik, NWT	7
98163	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. m. wardi</i>	Aklavik	9
58736	<i>T. cf. boreoarcticus</i> f. minor B	<i>Oreamnos americanus</i>	Alberta	1
58738	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. americanus</i>	Alberta	5
58741	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. americanus</i>	Alberta	13
58744	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. americanus</i>	Alberta	2
75415	<i>T. cf. boreoarcticus</i> f. minor B	<i>Ovis dalli dalli</i>	Alaska	3
102955	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. d. dalli</i>	Alaska	5
102956	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. d. dalli</i>	Alaska	10
102957	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. d. dalli</i>	Alaska	1
102958	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. d. dalli</i>	Alaska	4
103052	<i>T. cf. boreoarcticus</i> f. minor B	<i>O. d. dalli</i>	Alaska	2
42888	<i>T. circumcincta</i> / <i>davtiani</i>	<i>Ovis aries</i>	Maryland	5
55961	<i>T. circumcincta</i> / <i>davtiani</i>	<i>O. aries</i>	Scotland	8
57130	<i>T. circumcincta</i> / <i>davtiani</i>	<i>O. aries</i>	England	1
57277	<i>T. circumcincta</i> / <i>davtiani</i>	<i>O. aries</i>	Maryland	5
57296	<i>T. circumcincta</i> / <i>davtiani</i>	<i>O. aries</i>	West Virginia	10
57505	<i>T. circumcincta</i> / <i>davtiani</i>	<i>O. aries</i>	Oregon	1
57557	<i>T. circumcincta</i> / <i>davtiani</i>	<i>O. aries</i>	Georgia	2

Is. = Island.

\* Collection numbers from U.S. National Parasite Collection.

† Single male specimen originally identified as *T. boreoarcticus* forma minor A (see Hoberg et al. [1999]). This specimen had been included in the original comparisons of DNA sequences for *T. boreoarcticus*.

Addendum Added in Proof: Specimens of *T. boreoarcticus* f. minor B examined and measured from Victoria Island in *Ovibos moschatus wardi* also included the following: USNPC 91560 (4 specimens); 91563 (6); 91567 (2); 91569 (2); 91580 (11); 91583 (8).

(March–May) of *Teladorsagia* populations in individual muskoxen and 15 to 33% in Peary caribou (February); overall prevalence was 60% in 130 and 83% in 18 muskoxen, respectively, and 66% of 3 Peary caribou.

Morphologically similar nematodes also were found in an introduced mainland population of *O. m. wardi* from the NWT and Yukon Territory, Canada. *Teladorsagia boreoarcticus* f. minor B is described based on specimens in muskoxen and caribou from Nunavut.

## DESCRIPTION

### *Teladorsagia boreoarcticus* f. minor B

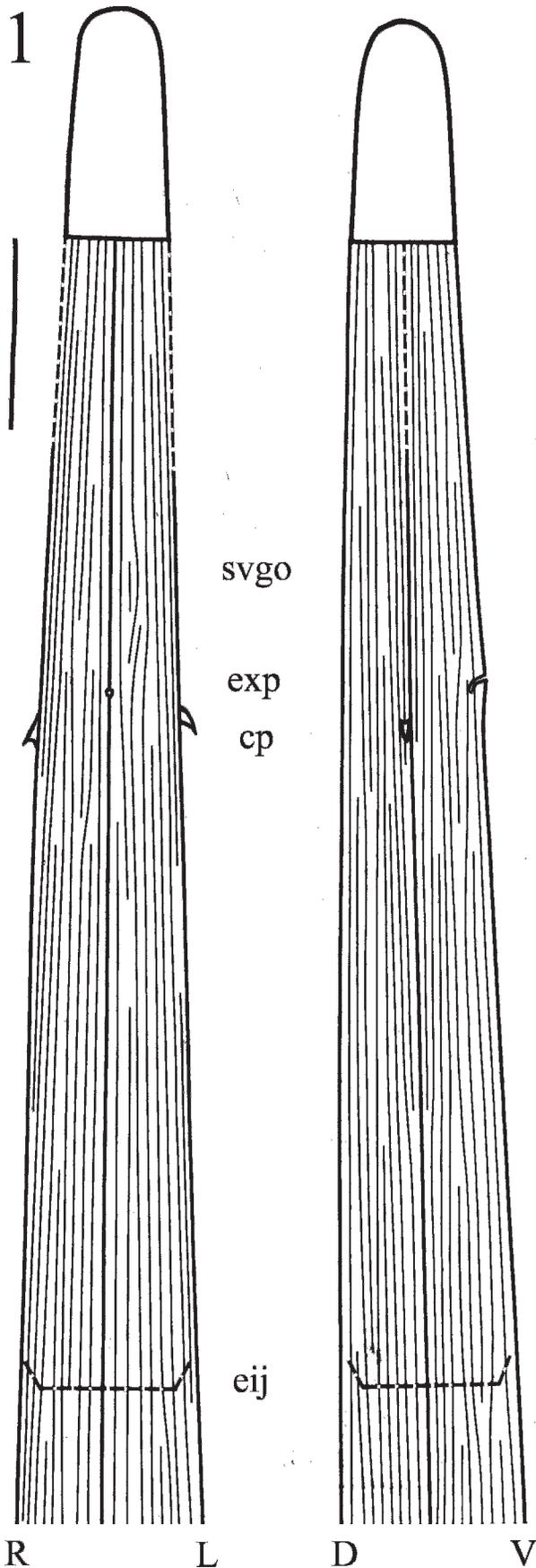
(Figs. 1–6)

*General description:* Trichostrongyloidea, uncoiled, small nematodes. Cuticle with well developed synlophe, lacking gradient, with perpendicular orientation; maximum number of ridges 37–44 attained in first quarter

posterior to esophageal–intestinal junction (EIJ) to level of midbody. Cervical papillae (CP), prominent, triangular, thorn-like, situated posterior to sub-ventral gland orifices (SVG) and excretory pore (EXP) near mid-length of esophagus. Cuticular ornamentation at EXP lacking. Esophagus with prominent valve at EIJ.

*Synlophe:* Synlophe bilaterally symmetrical, with ridges extending from base of cephalic expansion to near caudal extremity. Ridges acutely pointed, with perpendicular orientation and absence of gradient as viewed in transverse section. Anterior to EIJ, cervical pattern, laterally, Type 1b, strongly tapering; ventrally, Type B, parallel. Continuous sub-ventral and sub-lateral ridges present in cervical region. Overall, 1–3 pairs of ridges terminate along lateral-most ridge in cervical region, tapering pattern extends posterior to the EIJ. In specimens from Victoria Island, 34–40 ridges at level of EIJ, 38–44 at first quarter, 37–42 at midbody, 32–43 at third quarter, 6–13 near prebursal papillae (PBP); ridges are retained in lateral and ventral fields, terminate dorsally and ventrally anterior to PBP. In specimens from Banks Island, 32 ridges at EIJ, 30 at first quarter, 25–29 at midbody, 31–32 at third quarter, 10 near PBP.

*Male:* Small nematodes with prominent copulatory bursa. Total length (n = 105) 7,765–11,360 (9,329 ± 736); maximum width attained at



pre-bursal papillae. Cephalic vesicle (n = 32) 88–123 (106 ± 9) long. Esophagus (n = 104) 605–850 (716 ± 48) long; 6.8–9.1% of total body length. Esophageg valve (n = 101) 68–108 (88 ± 8) long, 30–75 (48 ± 8) in maximum width. SVGO (n = 101) 232–328 (274 ± 21), nerve ring (n = 10) 282–325 (303 ± 12), EXP (n = 105) 295–412 (357 ± 21), CP (n = 104) 312–440 (386 ± 24) from cephalic extremity. Copulatory bursa symmetrical, strongly bilobed with prominent dorsal lobe; lateral bursal rays disposed in 2-2-1 pattern; length of bursa from pre-bursal papillae, (n = 105) 242–400 (314 ± 41). Pattern and orientation of supporting rays as in *T. boreoarcticus* f. major and *T. boreoarcticus* f. minor A. Genital cone prominent, complex, with well developed, cuticularized telamon surrounding cloaca. Papillae “0” disposed on ventral aspect of genital cone, enveloped by prominent bilobed ventral membrane anterior to cloacal aperture. Rays “7” terminate in paired papilliform protuberances extending through concavity on postero-ventral margin of robust Sjöberg’s organ; in ventro-dorsal view, Sjöberg’s organ broader than long, rectangular. Dorsal ray (n = 68) 68–125 (92 ± 13) long; primary bifurcation 48–63% (55 ± 3) from anterior; dorsal lobe disposed ventrally to externo-dorsal or Rays 8. Spicules alate, broad, robust, trifurcate, straight in lateral view, equal in length; right spicule (n = 107) 171–255 (215 ± 20) with trifurcation 59–66% (62 ± 1.4) from anterior; left spicule (n = 106) 172–258 (219 ± 21) with trifurcation at 60–65% (62 ± 1.3). Main shaft of each spicule terminates in massive hyaline foot. Dorsal, ventral processes near equal in length, extending from one third to slightly less than 50% of length of spicule tip from trifurcation. Ventral process narrow, acutely pointed. Dorsal process, broad, triangular at base, with narrow acute point. Gubernaculum (n = 85) 66–108 (87 ± 10) in length, narrow, irregular in dorso-ventral view, with sinuous distal tip in lateral view.

*Female:* Previously characterized in original description of *T. boreoarcticus* by Hoberg et al. (1999).

**Taxonomic summary**

*Host:* Muskoxen, *Ovibos moschatus wardi* Lydecker. Also in *Rangifer tarandus pearyi* Allen and *R. tarandus groenlandicus* (Borowski).

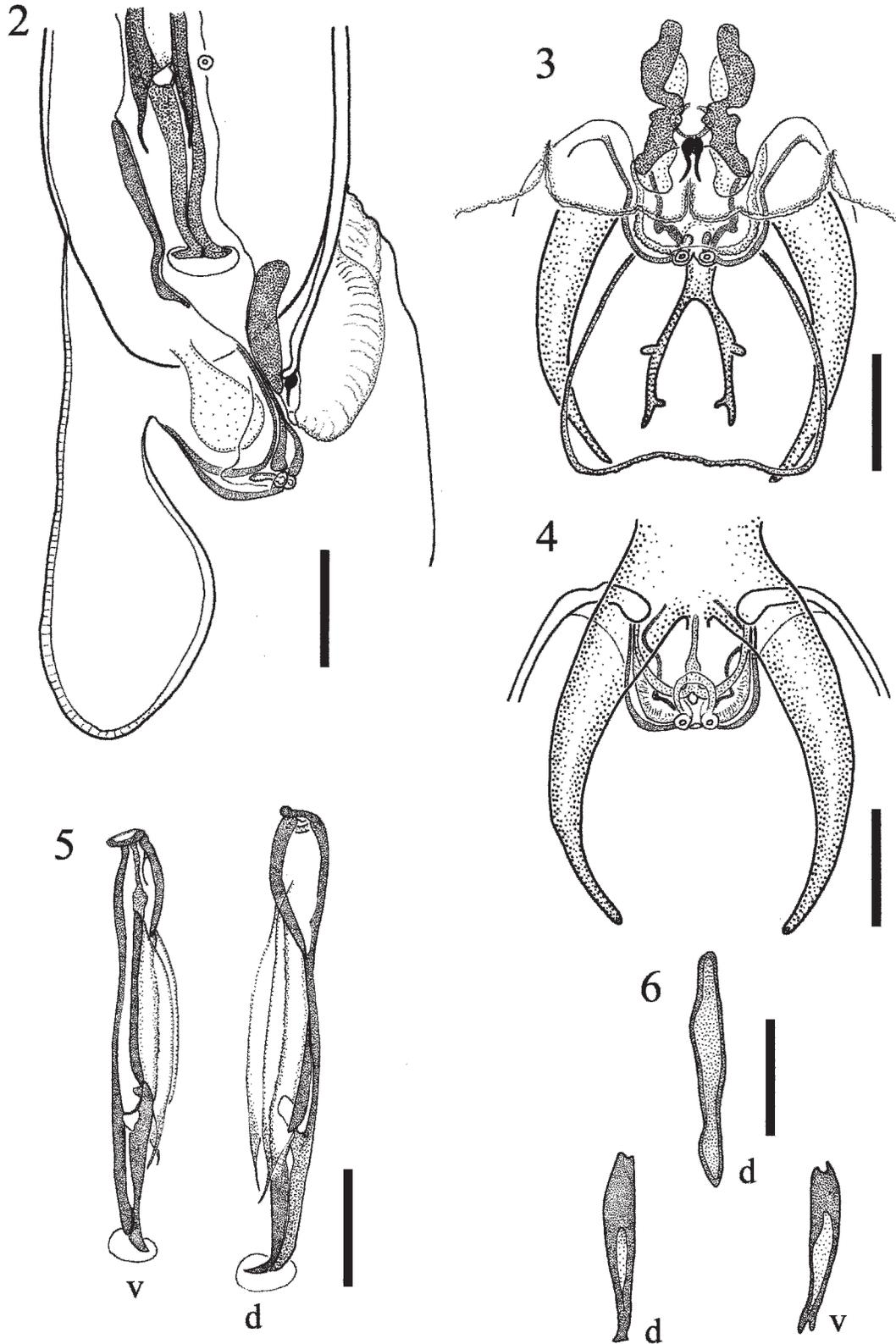
*Locality:* In muskoxen at Ekalluk River, adjacent to Wellington Bay and the hamlet of Iqaluktuutiaq (formerly Cambridge Bay), Victoria Island, Nunavut, Canada, ca. 69°22’N, 106°12’W on 18 March 1996 and December 1998 by S.J.K. Other localities: In muskoxen near Sachs Harbor, Banks Island, Nunavut, Canada, ca. 71°59’08”N, 125°14’53”W, during November 1999 by J. Nagy and B. Elkin. In barreground caribou at Victoria Island during December 1998 by S.J.K. and in Peary caribou at Banks Island during February 2003 by S.J.K. and J. Nagy.

*Specimens:* USNPC 87902.04, 2 males from Victoria Island in *O. m. wardi* (tails as vouchers for molecular sequencing, originally reported in Hoberg et al., 1999). USNPC 91558, and 91553 from Victoria Island in *O. m. wardi*. USNPC 104766 (originally voucher specimens under USNPC 87902.05) from Victoria Island in *O. m. wardi* as reported in Hoberg et al. (1999). USNPC 92072.03, 92075.03, 95981, 96304, 96047, 96122, 96325, and 96405 from Banks Island in *O. m. wardi*. USNPC 98657 and 98662 from Banks Island in *R. t. pearyi*. USNPC 91613, 91620, and 91623 from Victoria Island in *R. t. groenlandicus*.

**Remarks**

Nematodes in *O. m. wardi*, *R. t. pearyi*, and *R. t. groenlandicus* from Victoria Island and Banks Island are referred to *T. boreoarcticus* based on the structure of the synlophe and general configuration of the copulatory bursa including the lateral rays (2-2-1 pattern), dorsal ray or papillae 9/10,

FIGURE 1. *Teladorsagia boreoarcticus* forma minor B showing pattern for the synlophe in lateral and ventral fields in the cervical zone anterior to the base of the esophagus, based on USNPC 96405; bar = 100 µm. Note strongly tapering Type 1b system laterally and parallel Type B ventral system ventrally. Cervical papillae (CP) adjacent to lateralmost ridge and excretory pore (EXP) on ventralmost ridge; orifices of the sub-ventral esophageal glands (SVGO) are situated anterior to the EXP and CP; orientation is indicated by L = lateral, D = dorsal, and V = ventral.



FIGURES 2–6. *Teladorsagia boreoarcticus* forma minor B showing structure of genital cone and spicules for voucher specimens in muskoxen from Victoria Island and Banks Island. All bars = 50  $\mu$ m. (2) Genital cone and dorsal lobe (USNPC 104766  $\sigma$ 4), right lateral view, with medial view of left spicule tip and lateral view of gubernaculum. Note prominent membrane on antero-ventral aspect of genital cone. (3) Genital cone, ventral view (USNPC 104766  $\sigma$ 1), showing position of Sjöberg's organ relative to dorsal lobe and externo-dorsal Rays-8. (4) Genital cone, dorsal view (USNPC 104766  $\sigma$ 1). (5) Spicules, right, in dorsal (d) (USNPC 96122  $\sigma$ 3) and ventral (v) (USNPC 96122  $\sigma$ 1) views. (6) Gubernaculum in dorsal (d) and ventral (v) view from 3 specimens (left to right, USNPC 96122  $\sigma$ 1, 104766  $\sigma$ 1, 96122  $\sigma$ 3).

TABLE II. Morphometric comparisons for specimens of *Teladorsagia boreoarcticus* forma minor B in muskoxen (*Ovibos moschatus wardi*) and Peary caribou (*Rangifer tarandus pearyi*) from the central Canadian Arctic.

Character	<i>O. m. wardi</i> , Banks Island	<i>O. m. wardi</i> , Victoria Island	<i>R. t. pearyi</i> , Banks Island	<i>R. t. groenlandicus</i> , Victoria Island
No. examined	100	60	13	7
Body length	(98)* 7,765–10,950 (9,159 ± 645)	(58) 7,975–11,625 (9,501 ± 1,013)	(13) 8,500–10,325 (9,483 ± 529)	(7) 9,385–10,550 (10,071 ± 482)
Cephalic capsule	(31) 88–123 (106 ± 9)	(7) 80–125 (97 ± 17)	(5) 82–105 (98 ± 9)	(5) 98–125 (110 ± 11)
Esophagus length	(97) 605–815 (710 ± 44)	(58) 585–850 (723 ± 60)	(13) 620–770 (710 ± 43)	(7) 710–830 (773 ± 41)
Esophagus % of body length	(96) 6.8–9 (7.8 ± 0.5)	(58) 6.6–9.1 (7.7 ± 0.5)	(13) 6.5–8.8 (7.5 ± 0.6)	(7) 7.3–8 (7.7 ± 0.3)
Esophageal–intestinal valve length	(94) 68–105 (87 ± 7)	(55) 70–108 (89 ± 8)	(9) 68–92 (83 ± 8)	(7) 80–100 (94 ± 7)
Esophageal–intestinal valve width	(94) 30–66 (47 ± 6)	(54) 28–75 (49 ± 10)	(9) 45–58 (51 ± 4)	(7) 50–75 (59 ± 9)
Subventral esophageal gland orifices†	(94) 232–328 (273 ± 20)	(56) 228–322 (278 ± 26)	(13) 252–310 (277 ± 18)	(7) 280–302 (293 ± 10)
Nerve ring‡	(7) 282–316 (298 ± 10)	(27) 254–350 (311 ± 25)	(2) 300–305	(2) 305–312
Excretory pore‡	(98) 295–412 (357 ± 21)	(58) 298–406 (354 ± 27)	(13) 325–362 (346 ± 12)	(7) 346–395 (367 ± 16)
Cervical papillae‡	(97) 312–440 (386 ± 24)	(58) 320–442 (383 ± 31)	(13) 352–392 (373 ± 12)	(7) 370–420 (393 ± 16)
Spicule length, left	(99) 172–258 (218 ± 20)	(60) 180–270 (223 ± 26)	(13) 192–238 (215 ± 13)	(7) 208–265 (232 ± 18)
Spicule, left, % trifurcation‡	(99) 60–65 (62 ± 1.3)	(60) 59–66 (62 ± 1.3)	(13) 61–65 (62 ± 1.3)	(7) 59–64 (61 ± 1.7)
Spicule length, right	(100) 171–255 (214 ± 20)	(60) 178–268 (220 ± 25)	(13) 190–232 (210 ± 12)	(7) 212–258 (227 ± 18)
Spicule, right, % trifurcation‡	(100) 59–66 (62 ± 1.5)	(60) 59–66 (62 ± 1.4)	(13) 61–64 (62 ± 0.9)	(7) 60–63 (62 ± 1)
Dorsal ray	(67) 68–125 (91 ± 13)	(34) 70–150 (95 ± 19)	(5) 84–105 (91 ± 9)	(3) 100–115 (105 ± 9)
Dorsal ray, % bifurcation§	(66) 48–63 (55 ± 3)	(33) 48–66 (56 ± 4)	(5) 45–56 (53 ± 4)	(3) 54–60 (57 ± 3)
Gubernaculum	(84) 66–108 (87 ± 10)	(48) 75–115 (90 ± 10)	(11) 72–95 (81 ± 6)	(3) 75–100 (89 ± 13)
Bursa length	(98) 242–400 (310 ± 38)	(60) 238–415 (323 ± 50)	(13) 285–360 (316 ± 22)	(7) 300–375 (335 ± 29)

\* Sample size (n) for specimens examined and measurements of individual structural characters.

† Measured from anterior extremity.

‡ Percentage from anterior to trifurcation of spicule tip.

§ Percentage from anterior to bifurcation of dorsal ray.

|| Bursa length determined from prebursal papillae.

and well developed dorsal lobe (Hoberg et al., 1999). Meristic data from these populations and other structural characters addressed below serve to distinguish *T. boreoarcticus* f. minor B from *T. boreoarcticus* f. major and *T. boreoarcticus* f. minor A (Tables II, III; Hoberg et al., 1999).

Morphotypes of *T. boreoarcticus* are consistently distinguished from those attributed to *T. circumcincta* sensu stricto based on the numbers of ridges at the midbody of adult male and female worms, and other more subtle characters of the spicules and genital cone in males and the vulva in females (Hoberg et al., 1999). Specimens of *T. boreoarcticus* f. minor B are structurally distinct from conspecifics *T. boreoarcticus* f. major and *T. boreoarcticus* f. minor A and are consistently larger and distinct relative to those nematodes attributed to *T. circumcincta*/*T. davtiani* sensu stricto (Tables II, III).

New sequence data from the mitochondrial ND4 gene were not generated for the current study because attempts to extract and amplify DNA from suitable specimens from Victoria and Banks Island were not successful. Re-determination of the identity for 2 specimens sequenced during the original study (USNPC 87902.04), however, indicates that the 3 morphotypes of *T. boreoarcticus*, based minimally on nematodes from Victoria Island and the adjacent mainland, represent a single species (Hoberg et al., 1999).

The synlophe in *T. boreoarcticus* is consistent among the 3 male morphotypes and females with respect to the strongly tapering cervical pattern (Type 1 A) and numbers of ridges at the midbody (Fig. 1; Hoberg et al., 1999). Males of *T. boreoarcticus* f. minor B or the “*davtiani*” morphotype from Victoria Island were characterized by 37–42 ridges at the midbody. This is similar to the range of 39–46 midbody ridges (maximum of 47 in the anterior fourth of the body) based on specimens of the major and minor A morphotypes in the original description of *T. boreoarcticus* (Hoberg et al., 1999). In addition, this is consistent with the 42–44 ridges (maximum 45) observed in the major (USNPC 96403) and minor A or “*trifurcata*” (USNPC 95937, 96403) morphotypes attributed to *T. boreoarcticus* from Banks Island during the current study.

In contrast, ridge counts for some specimens of *T. boreoarcticus* f. minor B in muskoxen from Banks Island (e.g., within lots USNPC 92075.03 and 96405) were substantially less (32 ridges at EIJ, 30 at first quarter, 25–29 at midbody, 31–32 at third quarter) and were most similar to values

established for *T. circumcincta* sensu stricto in previous studies (Hoberg et al., 1999). Prior evaluations of the synlophe among ostertagiines have not demonstrated substantial variation in ridge counts among conspecifics (either between males and females or among polymorphic males), and definable limits seem to characterize respective species across many genera (Hoberg et al., 1999, 2009b, 2010). Thus, ridge counts demonstrated for some specimens of *T. boreoarcticus* f. minor B on Banks Island may represent a departure from prior observations about variation among congeners and conspecifics in the Ostertagiinae. These specimens, however, do not differ meristically or in other structural details from populations examined on Victoria Island in both muskoxen and barren-ground caribou (Tables II, III).

Population genetic evaluations of the nematodes from Banks Island and other localities have yet to be conducted and may serve to reveal more information about the identity of parasites. Current evidence suggests that the population of *T. boreoarcticus* on Banks Island, including the 3 morphotypes that have been studied, represents a single species (consistent with parasites in endemic hosts on Victoria Island and the mainland). In addition, the 2 minor morphotypes, represented by very small nematodes in muskoxen from Ellesmere Island (CMNP 1979-419), now seem referable to *T. boreoarcticus* (Webster and Rowell, 1980; Hoberg et al., 1999), although at the lower end of the range for measurements for most characters. In the absence of molecular based comparisons, however, the possibility of unrecognized cryptic diversity cannot be immediately discounted.

Aside from the synlophe, specimens of *T. boreoarcticus* f. minor B from Victoria and Banks Island are morphologically consistent. These specimens differ from conspecific morphotypes in the structure of the genital cone and Sjöberg’s organ (Hoberg et al., 1999). Relative to *T. boreoarcticus* f. minor A, specimens of *T. boreoarcticus* f. minor B are consistently smaller, and mean dimensions for the bursa and spicules do not overlap (Table II) (Hoberg et al., 1999). The robust spicules are similar in form, particularly in the relative length of the dorsal and ventral processes, but mean total length is substantially less in specimens of *T. boreoarcticus* f. minor B. Generally the differences that distinguish the minor morphotypes of *T. boreoarcticus* parallel those demonstrated for the *T. trifurcata* and *T. davtiani* morphotypes in association with *T.*

TABLE III. Morphometric comparisons for male specimens of representing *Teladorsagia*. Included are (1) *Teladorsagia* cf. *boreoarcticus* forma minor B in free-ranging ungulates from North America (specimens in *Ovibos moschatus wardi* and *Ovis dalli dalli*), (2) specimens similar to the minor morphotype *T. circumcincta*/*T. davtiani* sensu stricto (in *Oreamnos americana*), and (3) the minor morphotype *T. circumcincta*/*T. davtiani* sensu stricto in domestic sheep from North America and Europe.

Character	<i>O. m. wardi</i> Aklavik, NWT	<i>O. d. dalli</i> Dry Creek, Alaska	<i>O. americanus</i> Alberta, Canada	<i>O. aries</i> North America/Scotland
No. examined†	16	25	21	33
Body length	(16)* 10,200–11,490 (10,800 ± 372)	(21) 8,150–13,075 (11,039 ± 1,407)	(18) 5,825–10,200 (7,844 ± 980)	5,640–9,400 (8,170 ± 894)
Cephalic capsule	—	(2) 100–118	(5) 75–108 (87 ± 17)	(1) 84
Esophagus length	(16) 745–885 (806 ± 42)	(23) 700–840 (761 ± 37)	(20) 550–670 (606 ± 37)	(20) 535–608 (563 ± 21)
Esophagus % of body length	(16) 6.6–8.2 (7.5 ± 0.4)	(21) 6–8.8 (7 ± 0.8)	(17) 6.2–9.2 (7.6 ± 0.7)	(14) 6.1–10.5 (7 ± 1.1)
Esophageal–intestinal valve length	(16) 82–110 (96 ± 8)	(23) 85–120 (95 ± 8)	(19) 65–92 (77 ± 7)	(22) 48–70 (62 ± 6)
Esophageal–intestinal valve width	(16) 50–65 (58 ± 4)	(23) 40–60 (51 ± 6)	(19) 45–58 (50 ± 3)	(22) 28–50 (40 ± 5)
Subventral esophageal gland orifices†	(15) 284–335 (309 ± 14)	(23) 275–345 (307 ± 17)	(19) 205–264 (232 ± 15)	(22) 180–242 (217 ± 17)
Nerve ring†	—	(1) 315	(17) 238–300 (263 ± 20)	(5) 238–288 (263 ± 20)
Excretory pore†	(16) 370–425 (394 ± 18)	(23) 340–432 (393 ± 25)	(20) 250–360 (305 ± 28)	(20) 278–362 (325 ± 20)
Cervical papillae†	(16) 398–468 (428 ± 21)	(23) 368–468 (429 ± 26)	(21) 278–405 (332 ± 30)	(25) 305–402 (354 ± 23)
Spicule length, left	(16) 218–252 (238 ± 9)	(25) 248–320 (278 ± 19)	(18) 178–225 (202 ± 14)	(29) 158–222 (195 ± 13)
Spicule, left, % trifurcation‡	(16) 57–63 (60 ± 1.5)	(25) 59–66 (61 ± 1.7)	(18) 60–65 (62 ± 1)	(26) 58–65 (61 ± 1.4)
Spicule length, right	(16) 215–250 (234 ± 10)	(25) 248–315 (274 ± 19)	(18) 178–222 (199 ± 14)	(29) 156–225 (193 ± 14)
Spicule, right, % trifurcation‡	(16) 57–66 (61 ± 2.0)	(25) 58–66 (61 ± 1.7)	(18) 61–64 (62 ± 1)	(26) 58–64 (61 ± 1.6)
Dorsal ray	(11) 92–118 (106 ± 8)	(16) 115–140 (126 ± 6)	(3) 75–94 (86 ± 10)	(13) 55–84 (72 ± 9)
Dorsal ray, % bifurcation§	(11) 49–60 (55 ± 4)	(16) 48–63 (53 ± 4)	(3) 53–59 (55 ± 3)	(13) 50–63 (55 ± 4)
Gubernaculum	(12) 85–100 (92 ± 4)	(16) 95–122 (108 ± 9)	(12) 65–88 (77 ± 7)	(12) 75–92 (82 ± 5)
Bursa length	(16) 325–395 (361 ± 19)	(24) 300–415 (376 ± 28)	(16) 225–295 (267 ± 20)	(26) 168–285 (249 ± 24)

\* Sample size (n) for specimens examined and measurements of individual structural characters.

† Measured from anterior extremity.

‡ Percentage from anterior to trifurcation of spicule tip.

§ Percentage from anterior to bifurcation of dorsal ray.

|| Bursa length determined from prebursal papillae.

*circumcincta* sensu stricto (e.g., Becklund and Walker, 1971). In specimens of *T. boreoarcticus* f. minor B, the “7” papillae are narrowly spaced distally and protrude from the postero-ventral margin of the Sjöberg’s organ.

Specimens in *O. m. wardi* from the mainland near Aklavik, NWT, were excluded in the current description as their origin is uncertain. These specimens are morphologically similar to those from both Banks Island and Victoria Island (Tables II, III), but they were from introduced hosts with an independent history. Muskoxen at Aklavik were translocated onto the Arctic Coastal Plain from East Greenland (via Fairbanks and then Nunivak Island, Alaska; Reynolds, 1998). Although *Teladorsagia* is known in Greenland muskoxen, the specific identity of these nematodes remains undetermined, because specimens necessary for morphological and molecular characterization have not been available. Furthermore, domestic sheep and caribou (or reindeer) may be involved in transmission of these parasites across the geographic range in Greenland (Rose et al., 1984; Korsholm and Olesen, 1993), suggesting the potential for a history of natural expansion in the Quaternary and secondary translocation, and introductions with both domestic and free-ranging ungulates that may extend to Viking occupation.

Considering the “*davtiani*” morphotype, meristic data for specimens from Aklavik and those from the core endemic range for *T. boreoarcticus* overlap extensively (Tables II, III); data for other morphotypes in introduced muskoxen from Alaska and Canada exhibit a similar range in variation comparable with *T. boreoarcticus* (Hoberg et al., 1999). Species limits within the complex remain to be completely characterized based on an integrative approach for comparative morphology and molecular sequencing (Hoberg et al., 1999).

Other specimens designated here as *T. cf. boreoarcticus* f. minor B in Dall’s sheep are consistently large (Table III), revealing a trend identified for both major and “*trifurcata*” morphotypes in the original studies of *Teladorsagia* spp. in northern ungulates (Hoberg et al., 1999). For example, mean values for spicule length among the morphotypes of *Teladorsagia* sp. in Dall’s sheep substantially exceed those representing *T. boreoarcticus*. Specific identity of *Teladorsagia* sp. in *O. dalli* remains to be

explored based on molecular data, although it has been suggested that nematodes in these wild sheep represent another undescribed cryptic species (Hoberg et al., 1999).

Alternatively, specimens in *O. americana* seem similar to *T. circumcincta*/*T. davtiani* (Table III) and both the major and the minor B morphotypes, and they are consistently smaller, based on all characters considered in the current study, relative to nematodes in other free-ranging hosts (Hoberg et al., 1999). In contrast, meristic data for the minor A morphotype in mountain goats in the original study are consistent with of *T. boreoarcticus* (Hoberg et al., 1999). This observation points to the difficulty in separating these species in the absence of molecular data.

Although Becklund (1962) and Becklund and Walker (1971) examined numerous specimens attributed at that time to *T. davtiani* in domestic sheep and free-ranging ungulates (78 specimens in 7 host species), they did not specify the origins of particular lots of worms relative to hosts or geographic site of collection. The range for spicule length was reported as 156–238 µm (mean = 196). Conclusions from these studies suggested that *T. davtiani* (and other morphotypes later recognized) was among those species with extensive host and geographic distribution and a considerable level of morphological variation. Hoberg et al. (1999) and Leignel et al. (2002) have demonstrated that *Teladorsagia* is a species complex. Thus, the apparent geographically widespread distribution, broad host associations, and substantial morphological variation are consistent with the occurrence of multiple cryptic species, for which a clear definition for species limits and the extent of diversity have remained elusive.

## DISCUSSION

### Defining species limits

Specimens of *T. boreoarcticus* and its morphotypes are distinguished structurally from those attributed to *T. circumcincta* sensu stricto based on the numbers of ridges at the midbody and other more subtle characters of adult males and females, although

limits for the former species remain incompletely defined. Limited data from mitochondrial DNA (mtDNA) sequences further establishes reciprocal monophyly for these species (Hoberg et al., 1999). In the decade since the description of *T. boreoarcticus*, however, the status of nematode populations among an array of free-ranging bovids (wild sheep and mountain goats), pronghorn, and cervids, e.g., woodland caribou (*Rangifer tarandus caribou* [Gmelin]) and barren-ground caribou, in North America has remained unresolved; this observation further applies to global populations of *Teladorsagia* in both domestic and free-ranging ungulates (e.g., Leignel et al., 2002; Grillo et al., 2007). Current evidence is consistent with a putative assemblage of cryptic species (e.g., Pérez-Ponce de Leon and Nadler, 2010). Exploration of this hypothesis has been hindered by the logistic difficulty in acquiring the necessary specimens that will support comprehensive phylogeographic comparisons to reveal genetic structure, patterns of diversity and host–geographic associations across the broader range occupied by this assemblage.

### Nomenclatural challenges and polymorphism

There is no consistent nomenclature that is currently applied to polymorphic ostertagiines. Polymorphism among males of certain genera of the Ostertagiinae has been recognized and documented since the 1970s (Daskalov, 1974; Drózdź, 1974, 1995). Among the nominal taxa now recognized in the subfamily, polymorphism is characteristic in males among 5 of 15 genera (Hoberg and Abrams, 2008; Hoberg et al., 2009a). Before recognition of this phenomenon, there had been a considerable proliferation of both generic and species names to account for the broad morphological diversity observed among the ostertagiines. Historically, the occurrence of polymorphism complicated the generic level taxonomy for the subfamily, because the major and minor morphotypes characteristic of some species had been partitioned among multiple genera (Andreeva, 1956; Gibbons and Khalil, 1982); or respective morphotypes were listed as valid species (Durette-Desset, 1989).

The problem was addressed by Drózdź (1995) and Hoberg et al. (1999) but not resolved. Among nominal species and those recognized over the past century, taxonomic construction had been proposed where the major morphotype is listed first, followed by 1, or rarely 2, minor morphotypes, e.g., *T. circumcincta*/*T. trifurcata*/*T. davtiani*. Such a construction clearly represents the relationships between, or among, the major and minor morphotypes, but it does not address the problems that emerge from issues of taxonomic priority when species names are necessarily reduced to synonymy (Hoberg et al., 1999). For *T. circumcincta*, this species name has priority and would remain the name-bearing type for the genus. In other cases, however, it would be 1, or another, of the minor morphotypes, because of date of publication that would assume priority (Hoberg et al., 2001), a situation that would not preserve taxonomy, promote stability, or provide a clear distinction of the relationships among the major (generally most commonly occurring) and minor (generally rare) morphotypes (Hoberg et al., 1999).

Consequences of this confused taxonomy are manifested in how records are reported, with morphotypes still being regarded as discrete species. For example, even within single papers, taxonomic use has not been consistent with respect to the application of various names to either morphotypes or putative

cryptic species within *T. circumcincta* (Leignel et al., 2002). This problem is a generality across the 5 genera where polymorphism has been recognized, and it is not simply limited to *Teladorsagia* spp. Furthermore, some reports of survey and inventory for nematode faunas in free-ranging ungulates failed to recognize the phenomenon, leading to erroneous and potentially implausible records for host and parasite associations (discussed in Santín-Durán et al., 2004).

### Clarifying some records

A recent report of *T. circumcincta* sensu stricto in the Dolphin-Union (DU) caribou herd from the central Canadian Arctic is a misidentification (Hughes et al., 2009). In that paper, the host and geographic distributions of *T. boreoarcticus* were incorrectly characterized, with the implication by these authors that this ostertagiine had originally only been identified on and was limited to Victoria Island. To the contrary, it had already been documented as a widely distributed abomasal parasite (in reference to morphological and molecular criteria) at a minimum in mainland populations of *O. m. moschatus* and *R. t. groenlandicus* (Hoberg et al., 1999, 2001) and is now definitively known to occur in the DU herd based on the present study. Furthermore, Hughes et al. (2009) provided no basis other than assertion that the parasites in question were consistent with *T. circumcincta*/*T. trifurcata* sensu stricto. That the population of *Teladorsagia* sp. found in the DU herd was dimorphic is consistent, however, with the original observations for *T. boreoarcticus* f. major/*T. boreoarcticus* f. minor A on the mainland, and subsequent surveys that have failed to demonstrate a third male morphotype except in the Arctic islands (Hoberg et al., 1999; E.P.H. and S.J.K., unpubl. obs.). Definitive confirmation of identity for the DU specimens can be based on our current observations of *T. boreoarcticus* in this herd and the understanding that these animals move freely across Coronation Gulf and the Dolphin and Union Strait from Victoria Island to the mainland (Gunn et al., 1997). Direct comparisons, however, may not be possible because no morphological criteria were presented (Hughes et al., 2009), nor were specimens from their study retained as vouchers in a museum repository (see Hoberg, Pillitt, and Galbreath, 2009).

Some outcomes of incorrect identification are apparent: (1) erroneous interpretations about evolutionary history and host associations (Brooks and Hoberg, 2006) and (2) conflation of life-history information that is misleading in the context of multiple species and highly variable environmental settings (Irvine et al., 2000). Although the extent across the Holarctic of this assemblage in free-ranging hosts remains unresolved, current evidence suggests that *T. circumcincta* sensu stricto, *T. boreoarcticus*, and a putative array of cryptic species have been on divergent evolutionary trajectories for a considerable period (Hoberg et al., 1999; Leignel et al., 2002). Implications for faunal assemblage and mosaic structure in the context of natural expansion events and anthropogenic translocations are apparent and directly relate to how species are distributed in space and time, and how parasites may respond to perturbation, including climate change (Hoberg et al., 2008a; Hoberg, 2010). Furthermore, life-history patterns for ostertagiines in Arctic environments seem to be in contrast to the standard wisdom obtained for related species in domestic hosts and under intense management (Irvine et al., 2000; Hoberg et al.,

2008b). For example, and pertinent here, are observations that indicate species of ostertagiines in free-ranging ungulates in the Arctic have considerably longer life spans, different environmental tolerances, and developmental thresholds relative to those such as *T. circumcincta* circulating in domestic sheep (Hoberg et al., 1999). Consequently, species diversity and correct identification have implications for understanding and predicting the range of potential responses to rapidly accelerating climate change in northern environments (Kutz et al., 2004, 2009; Hoberg et al., 2008b; Davidson et al., 2011).

The geographic and host range for *T. boreoarcticus* can be further clarified. Specimens reported in Peary caribou on Banks Island and barren-ground caribou on Victoria Island represent new records for *T. boreoarcticus* and its 3 morphotypes. Specimens of *T. boreoarcticus* f. minor B have not been demonstrated on the mainland of the Canadian Arctic except in introduced and expanding populations of *O. m. wardi* at Aklavik, NWT (E.P.H. and S.J.K., unpubl. obs.). At mainland sites and in endemic host populations of caribou and muskoxen, *T. boreoarcticus* continues to be represented by 2 male morphotypes and previously *T. boreoarcticus* f. major/*T. boreoarcticus* f. minor A was reported definitively in *O. m. moschatus*, and *R. t. groenlandicus* (Hoberg et al., 1999).

In contrast, nematodes referred to *T. cf. boreoarcticus*, including the major and 2 minor morphotypes, are known in *R. t. caribou* and *O. dalli* at subarctic to Arctic latitudes (Hoberg et al., 1999; E.P.H. and S.J.K., unpubl. obs.). In addition, *T. cf. boreoarcticus* has been reported in introduced populations of *O. m. wardi* and *R. t. tarandus* from Alaska and the central Canadian Arctic (Hoberg et al., 1999). Specimens in *O. americanus* at subarctic to boreal latitudes, however, seem morphologically divergent from *T. boreoarcticus* and superficially are most similar to *T. circumcincta* and its morphotypes. Conspecificity across this assemblage remains to be determined based on new comparisons of sequences from mtDNA (Hoberg et al., 1999). Our understanding of distribution may reflect the limitations for current sampling of host populations, the rare occurrence of the parasite at low prevalence and intensity, or other factors that may serve to determine the geographic range of the 3 male morphotypes.

Elsewhere, we have discussed the challenges posed by a paucity of voucher and other representative specimens held in museum collections (Hoberg, Piliitt, and Galbreath, 2009). Archival collections represent the self-correcting records of diversity and are the essential baselines and foundation for understanding patterns of distribution and structure for faunal assemblages. Resolution of the complex history for *Teladorsagia* (and a wide array of parasites in either vertebrate or invertebrate hosts) can emerge from continued field-based collections tied to the development of archival resources for specimens and informatics. Furthermore, such a field inventory should include provisions for integrative approaches that preserve specimens suitable for both comparative morphology and multi-faceted molecular investigations and population genetics. We have always argued for the maximum use of any host specimens that are collected, a situation heightened by environmental perturbation and the increasing difficulty of conducting inventories of common, threatened, or endangered species (Brooks and Hoberg, 2000). Concurrently, recognition of the ubiquitous nature of cryptic species among nematodes and other helminths emphasizes the need to effectively develop and use our collections-based resources to build a robust

understanding of the biosphere (Pérez-Ponce de Leon and Nadler, 2010).

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