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# Structure, Biodiversity, and Historical Biogeography of Nematode Faunas in Holarctic Ruminants: Morphological and Molecular Diagnoses for *Teladorsagia boreoarticus* n. sp. (Nemadota: Ostertagiinae), Dimorphic Cryptic Species in Muskoxen (*Ovibos moschatus*)

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# STRUCTURE, BIODIVERSITY, AND HISTORICAL BIOGEOGRAPHY OF NEMATODE FAUNAS IN HOLARCTIC RUMINANTS: MORPHOLOGICAL AND MOLECULAR DIAGNOSES FOR *TELADORSAGIA BOREOARCTICUS* N. SP. (NEMATODA: OSTERTAGIINAE), A DIMORPHIC CRYPTIC SPECIES IN MUSKOXEN (*OVIBOS MOSCHATUS*)

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ABSTRACT: Discovery of the ostertagiine nematode *Teladorsagia boreoarcticus* n. sp. in muskoxen, *Ovibos moschatus,* from the central Canadian Arctic highlights the paucity of knowledge about the genealogical and numerical diversity of nematode faunas characteristic of artiodactyls at high latitudes across the Holarctic. *Teladorsagia boreoarcticus* is a dimorphic cryptic species distinguished from *Teladorsagia circumcincta*/*Teladorsagia trifurcata* in domestic sheep by a 13% divergence in the ND4 region of mitochondrial DNA, constant differences in the synlophe, and significantly longer esophageal valve, spicules, gubernaculum, and bursa. *Teladorsagia boreoarcticus* represents an archaic component of the North American fauna and may have a Holarctic distribution in muskoxen and caribou. Recognition of *T. boreoarcticus* in muskoxen, in part, corroborates hypotheses for the existence of a cryptic species complex of *Teladorsagia* spp. among Caprinae and Cervidae at high latitudes and indicates the importance of climatological determinants during the late Tertiary and Pleistocene on diversification of the fauna. Also reinforced is the concept of the North American fauna as a mosaic of endemic and introduced species. Discovery of a previously unrecognized species of *Teladorsagia* has additional implications and clearly indicates that (1) our knowledge is incomplete relative to potentially pathogenic nematodes that could be exchanged among domestic and wild caprines; (2) we do not have sufficient knowledge of the fauna to understand the ecological control mechanisms (limitations) on dissemination and host range; and (3) an understanding of historical and geographical influences on the genealogical diversity and distribution of nematode faunas in domestic and wild ruminants is requisite to define the interface between agricultural and natural ecosystems across the Holarctic.

The characteristic nematode fauna in ruminants from the Nearctic is a mosaic that has been assembled over temporal scales that are deep to relatively recent. For example, Holarctic distributions for some endemic and archaic parasite–host assemblages, particularly those associated with wild caprine bovids and cervids, were determined during the late Tertiary and Pleistocene across the Beringian nexus linking the Nearctic and Palearctic (Hoberg and Lichtenfels, 1994; Hoberg et al., 2000). In contrast, the relatively recent introduction and dissemination of parasites with domestic stock coinciding with European contact since the 1500s has had a substantial anthropogenic influence on patterns of parasite distribution in North America and other regions of the world (e.g., Hoberg 1997a; Hoberg and Lichtenfels, 1994; Lichtenfels et al., 1997). As a consequence of this deep history and recent introductions, the possible range of interactions between endemic versus introduced faunas, and the potential for exchange of nematodes among domestic stock and wild hosts is complex.

Ostertagiine nematodes of several genera (e.g., *Teladorsagia* Andreeva and Satubaldin, 1954, *Marshallagia* (Orloff, 1933), *Ostertagia* Ransom, 1907) are components of an archaic and endemic fauna in the Nearctic. Introduction of related ostertagiines could have resulted in (1) displacement of the endemic fauna; (2) hybridization and introgression with an endemic fauna, assuming incomplete species cohesion and barriers to gene flow; or (3) existence of endemic and introduced faunas in allopatry and coexistence of a wild and domestic fauna in zones of contact with the possibility of cross-infection. These issues have not been considered previously with respect to the structure and diversity of the nematode fauna in Nearctic bovids and cervids. It is requisite to define clearly the genealogical and ecological diversity of the nematode faunas in both domestic and sylvatic hosts in order to delineate parasite distribution, faunal history, and potential patterns of interaction for hosts and parasites including responses to global climate change and the emergence of pathogens and disease (Hoberg, 1997a; Hoberg et al., 2000).

Ostertagiine nematodes, particularly those distributed among the bovids of the subfamily Caprinae, provide the basis for examining these concepts. The Ostertagiinae (Skrjabin and Shul'ts, 1937) is a monophyletic group within the Trichostrongylidae (Durette-Desset, 1985; Hoberg and Lichtenfels, 1994). Among the polymorphic ostertagiine nematodes (see Dróżdż, 1995), *Teladorsagia circumcincta* (Stadelman, 1894), including the minor morphotypes, *Teladorsagia trifurcata* (Ransom, 1907) and *Teladorsagia davtiani* Andreeva and Satubaldin, 1954, exhibit a particularly broad host and geographic distribution (e.g., Suarez and Cabaret, 1991) and exceptional morphometric variation (e.g., Becklund and Walker, 1971; Lichtenfels and Pilitt, 1991). *Teladorsagia circumcincta* is a cosmopolitan species in which geographic distribution has been influenced by dissemination throughout the world coincidental with the transport of domestic hosts, particularly sheep (*Ovis aries* L.), since the 1500s (e.g., Hoberg, 1997a; Hoberg et al., 2000). The species also occurs in historically isolated populations of wild caprine bovids and caribou at high latitudes in the Northern Hemisphere. Generally, it is considered a typical abomasal parasite in domestic and wild sheep, other Caprinae, and pronghorn, and occasionally has been reported in cervid hosts across

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the Holarctic (Boev et al., 1963; Govorka et al., 1988; Hoberg et al., 2000).

Based on the observation of broad host range, extensive geographic distribution, and substantial morphological variation, Hoberg et al. (2000) suggested that *T. circumcincta* may represent a complex of cryptic species distributed in wild bovids in the Nearctic and Palearctic. A classical problem of sibling species (see Avise, 1994; Anderson et al., 1998) that collectively occupy a broad host and geographic distribution across the Holarctic is postulated. Lichtenfels and Pilitt (1989) also suggested the occurrence of cryptic species in *Marshallagia* from western North America. An initial test of this hypothesis in the genus *Teladorsagia* is presented herein based on examination of nematodes in historically isolated populations of muskoxen (*Ovibos moschatus* (Zimmermann)) from the central Canadian Arctic.

Preliminary morphometric studies of specimens collected in 1994 suggested that the nematodes regarded as *T. circumcincta*/*T. trifurcata* in *O. moschatus* were distinct at the species level from those in domestic hosts, thus implying that *T. circumcincta* as currently conceived would represent more than a single species. Nematodes were collected in 1996 to address this question specifically by integrating data from comparative morphology and molecular sequences of the ND4 region of mitochondrial (mt)DNA (Blouin et al., 1998). These specimens and analyses constitute the basis for description and diagnosis of a previously unknown species of *Teladorsagia.*

Discovery of a cryptic species of *Teladorsagia* raises questions about the identity of nematodes reported as *T. circumcincta,* along with associated morphotypes, in wild bovids, and occasionally cervids and the actual distribution of *T. circumcincta* sensu stricto in domestic caprines and other ruminants from both the Nearctic and Palearctic. Implied is the possibility that a complex of cryptic species exists in wild ruminant hosts in the Nearctic (e.g., *Ovis dalli* Nelson, *Ovis canadensis* Shaw, *Oreamnos americanus* Blainville, *Antilocapra americana* (Ord), and some cervids) and Eurasia (see Hoberg et al., 2000). Resolution of such a complex will be dependent on integration of morphological and molecular criteria and will have a bearing on understanding the structure and history of the Holarctic fauna.

## MATERIALS AND METHODS

### Taxonomic consistency

In the current paper, *T. circumcincta* sensu stricto and *T. trifurcata* sensu stricto are applied consistently to the major and minor morphotypes limited in distribution to domestic caprine bovids. Specimens in wild bovids and cervids that cannot unambiguously be referred to either of these morphotypes, or to the newly recognized species, are considered as *T. circumcincta*-like or *T. trifurcata*-like for the basis of comparisons and discussion.

### Collections and specimens examined

Specimens were obtained from the abomasa of barren ground muskoxen (*Ovibos moschatus moschatus* (Zimmermann)) collected under scientific permit and from hunter-killed animals during the period 1994–1996 (Fig. 1). In animals necropsied in April 1994 (field numbers COMX 001 and 002 at Cox Lake, near the settlement of Kugluktuk, NWT; ca. 67°54′N, 116°38′W), all nematodes present in abomasal contents and washings were collected and fixed in 10% buffered formalin. In hunter-killed animals taken on 14 November 1994 (field nos. Mx-10, -11, -18, and -26 from north of the Rae River, NWT, ca. 68°04′N, 117°04′W), duplicate 10% aliquots of contents and washings from the abomasum were collected and fixed for later recovery of parasites.

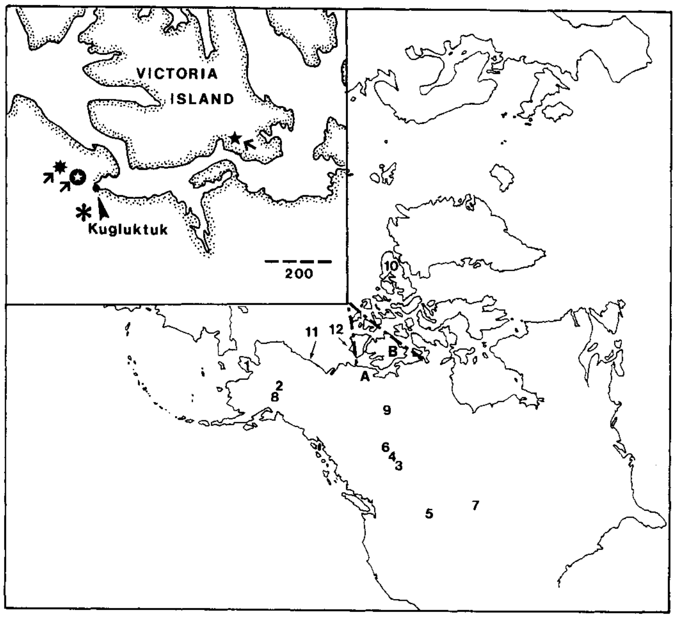


FIGURE 1. General localities of collection for specimens of *Teladorsagia* examined and sequenced during the present study. On main map, sites A and B indicate the approximate localities on the mainland and Victoria Island where specimens of *T. boreoarcticus* n. sp. were collected. Inset map shows specific sites in the central Canadian Arctic (scale = 200 km): (**A**) on the mainland, note position of Kugluktuk, sites at Cox Lake, including the type locality (circle star), adjacent sites on the Rae River (multiple black star), and Hope Lake (asterisk); and (**B**) on Victoria Island, note Ekalluk River (black star). Arrows indicate localities for independent collection of specimens for DNA sequence analysis. Numbering on main map indicates approximate collection localities for specimens previously identified as *T. circumcincta*/*T. trifurcata* in various wild hosts examined in the current study (see Table III): (1) Seward Peninsula, Alaska (in *Rangifer tarandus tarandus,* USNPC, 17477, 26715, 31435); (2) Fairbanks, Alaska (in *Ovibos moschatus wardi,* 41345, 41346); (3) region of Banff and Jasper, Canada (in *Ovis canadensis,* 45175, 46574, 66604, 59747); (4) central Rocky Mountains, Alberta (in *Oreamnos americanus,* 46917, 58736, 58738); (5) Montana (in *O. canadensis,* 56741); (6) British Columbia (in *Rangifer tarandus caribou,* 59295); (7) South Dakota (in *O. americanus,* 66041, 66047, 66048; in *O. canadensis,* 66611); (8) Alaska (in *Ovis dalli,* 75409, 75414); (9) Northwest Territories (in *Rangifer tarandus groenlandicus*); (10) Ellesmere Island, Northwest Territories (in *O. m. wardi,* CMNP 1979-419); (11) Barter Island, Alaska (in *O. m. wardi,* UAM 2572); (12) Banks Island, Alaska.

In 1996, 5 white-faced muskoxen (*Ovibos moschatus wardi* Lyddecker) from the Ekalluk River, Victoria Island, near Wellington Bay and the settlement of Cambridge Bay, NWT (field numbers: C-24, C-36, C-66, C-68, C-76, ca. 69°22′N, 106°12′W), 2 barren ground muskoxen from the mainland (field numbers: A from the Rae River; ca. 68°05′N, 117°15′W; and 26-III-96 from Cox Lake; ca. 67°58′N, 116°45′W) and 2 barren ground caribou, *Rangifer tarandus groenlandicus* (Borowski), from the mainland (field numbers: C-186 and B from Hope Lake; ca. 67°34′N, 115°50–58′W) were examined. Abomasa were immediately frozen in the field at the time of collection at ambient temperatures near −20 C and maintained in a constantly frozen state until processing for the recovery of parasites in the laboratory at the Western College of Veterinary Medicine (WCVM). Abomasa were thawed briefly, and the contents and washings (with saline) of the mucosa were aliquoted (2 × 10% duplicates), sieved (37.5 μm mesh), and fixed in 10% buffered formalin for collection of adult and larval nematodes; material for comparative morphology and subsequent estimates of intensity of infection by nematodes for individual hosts (to be re-

TABLE I. Specimens of *Teladorsagia boreoarcticus* n. sp. examined: including type series in *Ovibos moschatus* and vouchers in *Rangifer tarandus groenlandicus,* along with field collection numbers, museum accession numbers,* and geographic localities in the Northwest Territories.

| CMNP no. | USNPC no. | Field no. | Locality | ♂† | ♀† |
|---|---|---|---|---|---|
| Specimens in *O. moschatus*‡ | | | | | |
| *T. boreoarcticus* f. major, males; and females | | | | | |
| 1998-0071 | 87901.01 | C-36 | Ekalluk River, Victoria Is. | 6 | 5 |
| 1998-0073 | 87902.01 | C-66 | Ekalluk River, Victoria Is. | 20 | 25 |
| 1998-0075 | | | | | |
| 1998-0076 | 87904.01 | A | Rae River, mainland | 15 | 25 |
| 1998-0078 | | | | | |
| 1998-0062 | 87905.01 | 26-III-96 | Cox Lake, mainland | 15 | 20 |
| 1998-0063 | | | | | |
| 1998-0064 | | | | | |
| 1998-0066 | | | | | |
| 1998-0067 | 87895.01 | COMX-002 | Cox Lake, mainland | 15 | 15 |
| — | 87896.01 | MX 10 | North of Rae River, mainland | 5 | 10 |
| *T. boreoarcticus* f. minor, males | | | | | |
| 1998-0072 | 87901.02 | C-36 | Ekalluk River, Victoria Is. | 5 | — |
| 1998-0074 | 87902.02 | C-66 | Ekalluk River, Victoria Is. | 20 | — |
| 1998-0077 | 87904.02 | A | Rae River, mainland | 20 | — |
| 1998-0065 | 87905.02 | 26-III-96 | Cox Lake, mainland | 20 | — |
| 1998-0068 | 87895.02 | COMX-02 | Cox Lake, mainland | 10 | — |
| Specimens in *R. t. groenlandicus*: | | | | | |
| *T. boreoarcticus* f. major, males | | | | | |
| — | 87906.01 | C-186 | Hope Lake, mainland | 13 | — |
| *T. boreoarcticus* f. minor, males | | | | | |
| — | 87906.02 | C-186 | Hope Lake, mainland | 3 | — |

* Collection numbers from the Canadian Museum of Nature (CMNP) and the U.S. National Parasite Collection (USNPC).

† Number of specimens examined for each male morphotype and females.

‡ This includes *Ovibos moschatus moschatus* on the mainland and *Ovibos moschatus wardi* on Victoria Island.

ported elsewhere) were derived from these aliquots. Specimens used in comparative morphological studies are documented in Table I.

The remaining contents and washings from those animals collected in 1996 were immediately examined for nematodes to be used for DNA sequence analysis. These specimens were first washed in saline and then either frozen at −70 C or preserved in 50% ethanol and 50 mM EDTA and refrigerated at −20 C prior to processing and extraction of DNA at Oregon State University (OSU) as specified below. Additional specimens in 3 domestic sheep from a farm near Saskatoon, Saskatchewan were collected 26 November 1996, for inclusion in sequence analyses.

### Morphological methods

Nematodes in 6 muskoxen from mainland and island localities were studied in detail and included 76 males of the putative major morpho-

TABLE II. Specimens of *Teladorsagia circumcincta* sensu stricto and the minor morphotype *Teladorsagia trifurcata* sensu stricto examined from domestic sheep and goats including accession numbers and geographic localities.

| USNPC no.* | Species | Host | Locality | ♂† | ♀† |
|---|---|---|---|---|---|
| 49391 | *T. circumcincta* | *Ovis aries* | Oregon | — | 5 |
| 55961 | *T. circumcincta* | *O. aries* | Scotland | 3 | — |
| 59040 | *T. circumcincta* | *O. aries* | Nebraska | 7 | 2 |
| 59293 | *T. circumcincta* | *O. aries* | Canada, B.C. | 6 | 7 |
| 58838 | *T. circumcincta* | *O. aries* | Mississippi | 7 | 10 |
| 70121 | *T. circumcincta* | *Capra hircus* | England | 10 | — |
| 70256 | *T. circumcincta* | *O. aries* | U.S. | 7 | 10 |
| 70257 | *T. circumcincta* | *O. aries* | U.S. | 2 | — |
| 79693 | *T. circumcincta* | *O. aries* | England | 7 | — |
| 88301‡ | *T. circumcincta* | *O. aries* | Iceland | 4 | — |
| 88302‡ | *T. circumcincta* | *O. aries* | Iceland | 4 | — |
| 31426 | *T. trifurcata* | *O. aries* | Vermont | 1 | — |
| 41337 | *T. trifurcata* | *O. aries* | West Virginia | 5 | — |
| 46572 | *T. trifurcata* | *O. aries* | Washington | 4 | — |
| 69762 | *T. trifurcata* | *O. aries* | California | 3 | — |
| 79693 | *T. trifurcata* | *O. aries* | England | 7 | — |

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

† Number of specimens examined.

‡ Data not included in Table VI.

TABLE III. Specimens examined, including those originally identified as *Teladorsagia circumcincta* and *Teladorsagia trifurcata* in wild hosts from North America, with accession numbers and geographic localities.

| USNPC* | Host | Locality† | ♂‡ | ♀‡ |
|---|---|---|---|---|
| *Teladorsagia circumcincta* | | | | |
| 19477 | *Rangifer tarandus tarandus* | Alaska | 6 | 7 |
| 26715 | *R. t. tarandus* | Alaska | 3 | — |
| 41345 | *Ovibos moschatus wardi* | Alaska | 1 | — |
| 41346 | *O. m. wardi* | Alaska | 10 | — |
| 45175 | *Ovis canadensis* | Canada | 2 | — |
| 46574 | *O. canadensis* | Canada | 7 | — |
| 46917 | *Oreamnos americanus* | Canada | 5 | — |
| 56741 | *O. canadensis* | Montana | 2 | — |
| 59295 | *Rangifer tarandus caribou* | Canada | 3 | — |
| 59747 | *O. canadensis* | Canada | 4 | — |
| 66041 | *O. americanus* | South Dakota | — | 8 |
| 66604 | *O. canadensis* | Canada | 8 | — |
| 75409 | *Ovis dalli* | Alaska | 4 | — |
| 79471 | *Rangifer tarandus groenlandicus* | Canada | 1 | — |
| 2572§ | *O. m. wardi* | Alaska | 1 | — |
| Banks—1987‖ | *O. m. wardi* | Canada | 4 | — |
| *Teladorsagia trifurcata*: | | | | |
| 31435 | *R. t. tarandus* | Alaska | 2 | — |
| 41345 | *O. m. wardi* | Alaska | 5 | — |
| 58736 | *O. americanus* | Canada | 1 | — |
| 58738 | *O. americanus* | Canada | 4 | — |
| 66041 | *O. americanus* | South Dakota | 2 | — |
| 66047 | *O. americanus* | South Dakota | 1 | — |
| 66048 | *O. americanus* | South Dakota | 1 | — |
| 66611 | *O. canadensis* | South Dakota | 1 | — |
| 75414 | *O. dalli* | Alaska | 4 | — |
| 1979-419# | *O. m. wardi* | Canada | 6 | — |
| Banks—1987‖ | *O. m. wardi* | Canada | 2 | — |

* Collection numbers from U.S. National Parasite Collection, unless specified otherwise.

† Localities: 19477, 31435, Golovin, Alaska, in introduced reindeer; 26175, Spruce Creek, near Unalakleet, Alaska, in introduced reindeer; 41345, 41346, Fairbanks, Alaska, in muskox during translocation from East Greenland to Nunivak Island; 45175, 46574, 66604, near Banff and Jasper, Alberta, Canada; 46917, Berland River, Alberta; 58736, 58738, Mt. Hamell, Alberta, Canada; 59295, Tweedsmuir, British Columbia, Canada; 59747, Ashnola River, British Columbia, Canada; 66041, 66047, 66048, in introduced host population, Custer County, South Dakota; 66611, in introduced host population; 75409, 75414, Dry Creek, McKinley, Alaska; 79471, in endemic barren ground caribou, Fort Smith, Northwest Territories; CMNP 1979-419, Ellesmere Island, Northwest Territories; UAM 2572, in introduced muskoxen, Barter Island, Alaska; Banks—1987, in endemic muskoxen, Banks Island, Northwest Territories.

‡ Number of specimens examined.

§ University of Alaska Museum.

‖ Based on data from Ott (1998) for 4 males identified as *T. circumcincta* and 2 as *T. trifurcata*; specimens not seen, but morphometric data and morphology are consistent with *T. boreoarcticus*.

\# Canadian Museum of Nature, Parasite Collection.

type, 75 males of the minor morphotype, and 100 females. Nematodes in caribou from the mainland included 13 major and 3 minor morphotype males (Table I; Fig. 1). Morphotype is consistent with the concepts outlined in Dróżdż (1995).

Nematodes were prepared as temporary whole mounts cleared in phenol–alcohol and examined with interference contrast microscopy at the Biosystematics and National Parasite Collection Unit (BNPCU). Characters studied have been previously outlined in detail (e.g., Hoberg et al., 1993a). The synlophe (see Lichtenfels et al., 1988) was studied in whole mounts and in transverse sections; hand-cut sections were prepared from 8 females (4 Victoria Island; 2 Rae River, 2 Cox Lake), and 11 males (7 major morphotype: 3 Victoria Island, 2 Rae River, 2 Cox Lake; 4 minor morphotype: 2 Victoria Island, 1 Rae River, 1 Cox Lake). Bursal ray patterns and numbering of the bursal papillae are consistent with Chabaud et al. (1970) and Durette-Desset and Chabaud (1981). Spicules were dissected from 2 males of each morphotype. The structure and description of the ovejectors are consistent with Lichtenfels et al. (1993). Measurements are in micrometers unless indicated otherwise. In the description and Tables V–IX, the sample size (n=) is followed by the range and mean ± 1 SD in parentheses. Statistical comparisons of morphometric data for some characters (length of esophageal valve, spicules, gubernaculum, and copulatory bursa) were performed with the *F*-test examining the null hypothesis that mean values did not vary significantly between the putative new species and *T. circumcincta*/*T. trifurcata* sensu stricto.

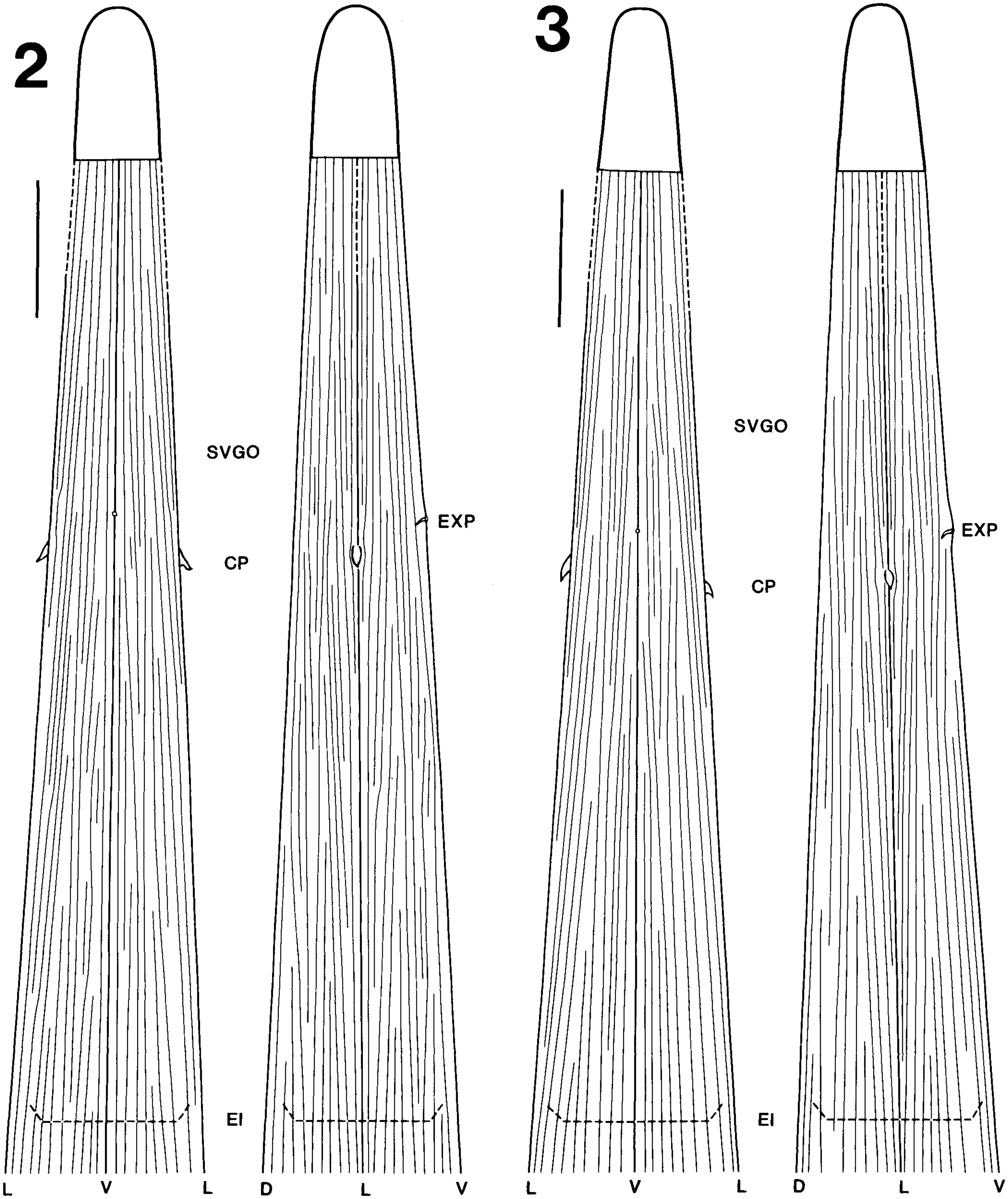
TABLE IV. Specimens of male paratypes of *Teladorsagia boreoarcticus* n. sp. in *Ovibos moschatus* used for analysis of ND4 sequences of mtDNA.

| USNPC no.* | Field no. | Morphotype | Locality | ♂† |
|---|---|---|---|---|
| 87902.04 | C-66 | Major | Victoria Island | 3 |
| 87902.04 | C-66 | Minor | Victoria Island | 2 |
| 87904.05 | A | Major | Rae River, mainland | 3 |
| 87905.05 | 26-III-96 | Major | Cox Lake, mainland | 3 |

* Collection numbers for tails of male specimens deposited in the U.S. National Parasite Collection.

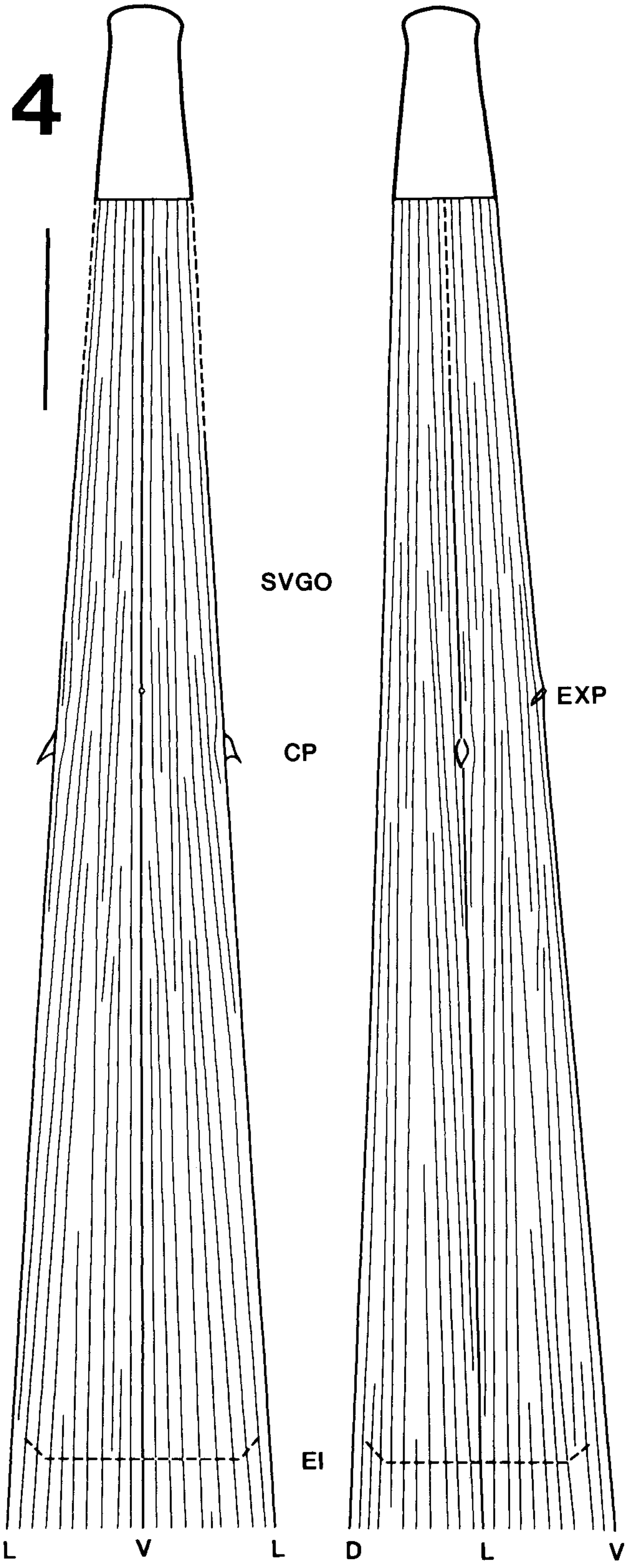
† Number of specimens sequenced.

The type series and voucher specimens were deposited in the parasite collection of the Canadian Museum of Nature (CMNP), Ottawa, Ontario, Canada, and in the U.S. National Parasite Collection (USNPC), Agricultural Research Service, USDA, Beltsville, Maryland.



FIGURES 2–4. Synlophe in the cervical zone in specimens of *Teladorsagia boreoarcticus* n. sp., showing variation in lateral and ventral patterns (scale bar = 100 μm). **2.** *Teladorsagia boreoarcticus* f. major, male. **3.** *Teladorsagia boreoarcticus* f. minor, male. **4.** Female.

**4**



FIGURES 2–4. Continued.

Specimens of *T. circumcincta*/*T. trifurcata* for comparative morphological studies were obtained from the USNPC, CMNP, and University of Alaska Museum, Fairbanks (UAM). Material included nematodes in domestic sheep and goats, *T. circumcincta*/*T. trifurcata* sensu stricto (Table II) and specimens representing *Teladorsagia* sp. in wild bovids, caribou (*Rangifer tarandus caribou* (Gmelin) or woodland caribou, and *R. t. groenlandicus*), and semidomesticated reindeer (*Rangifer tarandus tarandus* (Linnaeus)) from Alaska and northern Canada (Table III; Fig. 1); specimens in *Rangifer tarandus granti* Allen, Alaskan barren ground caribou and *Rangifer tarandus pearyi* (Allen), Peary caribou were not available. Photomicrographs and morphometric data for specimens of *Teladorsagia* in *O. m. wardi* from Banks Island were evaluated (Ott, 1998). Additionally, specimens of "*T. circumcincta*" in barren ground muskoxen collected by Gibbs and Tener (1958) from Thelon Sanctuary, NWT, and those of "*T. trifurcata*" in reindeer collected by Choquette et al. (1957) from Aklavik, NWT could not be located. Nematodes identified by Ott (1998) as *T. circumcincta*/*T. trifurcata* in *O. m. wardi* from Banks Island, NWT, and specimens collected by Korsholm and Olesen (1993) in muskoxen and Caribou from West Greenland were not available for study. Specimens in pronghorn were not studied at this time.

### Statistical methods

Data for major and minor morphotype males and females of the putative new species were compared to those from *T. circumcincta*/*T. trifurcata* sensu stricto and analyzed using the linear mixed model procedures (SAS, version 6.12). For esophageal valves, data were evaluated for both male morphotypes and females; for spicules, gubernaculum, and bursa, the male morphotypes were treated separately. Therefore, species was the only fixed effect, whereas within species and the variations among nematodes within host (residual variance) were defined as random. In addition to tests of differences between means, features of the mixed procedure were used to determine if there were significant differences in variances between species for all measured variables and between genders for valve measurements. For all tests, an $\alpha = 0.05$ was used to denote significant differences.

### Molecular methods

Specimens of the putative undescribed species of *Teladorsagia* used in analysis of mtDNA represented male nematodes collected from muskoxen at 2 mainland localities and Victoria Island, NWT (Table IV; Fig. 1); specimens of 2 male morphotypes were analyzed. At the time of processing at OSU, the caudal extremity was cut from each worm, and identity of these specimens was determined at the BNPCU by examination of structural characters of the bursa and spicules. Additionally, the identity of specimens of *T. circumcincta* sensu stricto collected from domestic sheep (USNPC 88299, 88300) was confirmed in the same manner. All material used for DNA analysis had been frozen at −70 C; specimens preserved in 50% ethanol/50 mM EDTA were not used in the study.

We sequenced 390 bp at the 3′ end of the mitochondrial ND4 gene from 11 nematodes in muskoxen and 3 in domestic sheep. Individual nematodes were crushed with a pestle in 50 μl of extraction buffer (100 mM NaCl, 50 mM Tris, pH 7.5, 50 mM EDTA, pH 8, 1 mg/ml proteinase K, 1% sodium dodecyl sulfate), and incubated for 4 hr at 55 C, and then at 95 C for 5 min. Five microliters of the supernatant from each specimen was used to amplify the ND4 region in a 25-μl polymerase chain reaction (PCR) reaction (3 mM MgCl, 0.8 μM primers, Promega Taq and buffer) using a Perkin-Elmer 9600 thermocycler (94 C denature for 3 min, then 35 cycles of 94 C for 30 sec, 40 C for 30 sec, 72 C for 30 sec; then a 7-min extension to 72 C). The PCR product was then purified using an Ultrafree-MC 30,000 NMWL spin column (Millipore, Bedford, MA), and sequenced on an ABI 377 automated sequencer using the PCR primers as sequencing primers. Primers used were: forward (mb43): 5′ ATA ACT ATA AGA AGT AAA GTG GC 3′; reverse (mb44): 5′ TTA AAA GAA CAA TCT CAG TCA AA 3′.

The 11 sequences from the Arctic were aligned with 40 ND4 sequences from *T. circumcincta* sensu stricto in domestic sheep across the United States by Blouin et al. (1995); also included were 3 new specimens in domestic sheep from Saskatchewan for a total of 43 sequences. Trees were constructed for the entire data set of 54 sequences using UPGMA and neighbor joining with Jukes–Cantor distances (in

PHYLIP; Felsenstein, 1993). Parsimony analysis was conducted on first and second codon position sites in a data set consisting of sequences from 11 arctic specimens plus 10 specimens of *T. circumcincta* (Branch and Bound, in PAUP 3.1; Swofford, 1993) and with parsimony analysis of amino acid sequences (PAUP 3.1; Swofford, 1993). Sequences have been deposited in Genbank: AF14451 to AF144561.

Nucleotide diversity ($\pi$; Nei, 1987) and its standard error in each data set was estimated using the DnaSP software (Rozas and Rozas, 1997). Victoria Island is an insular locality and the site of collection at Ekalluk River near the settlement of Cambridge Bay is approximately 550 km (straight-line distance) from the region of Cox Lake/Rae River on the mainland. Thus, there may be restricted gene flow between putative populations of parasites (and hosts). We also estimated the proportion of sequence divergence distributed between Cox Lake/Rae River and Ekalluk River (Nst; Lynch and Crease, 1990) using DnaSP.

## RESULTS

Ostertagiine nematodes were found in the abomasa of 13 muskoxen (complete data available for 11 animals) and 2 caribou collected in the region of Kugluktuk and Ekalluk River, Victoria Island, NWT between 1994 and 1996 (Fig. 1); specific details of multispecies infections are to be reported elsewhere. In muskoxen, specimens of a dimorphic species of *Teladorsagia* occurred with a prevalence of 100% (n = 13) and range in intensity from 35 to 7,215 (n = 11; $\bar{x}$ = 1,676 ± 2,068), including 2 male morphotypes and associated females. The minor morphotype occurred in 11 of 12 muskoxen and represented from 7 to 67% ($\bar{x}$ = 26%) of the total population of male *Teladorsagia* in individual hosts; in 2 hosts from Victoria Island (C-66 and C-76) the minor morphotype exceeded 50% of the population. Both barren ground caribou were infected with *Teladorsagia* sp.; intensity ranged from 15 to 155. It was determined that specimens in muskoxen, based on morphometric and molecular criteria, represented an undescribed species; specimens in caribou were morphometrically consistent with these nematodes but were not available for sequence analysis. Descriptions of the 2 male morphotypes and females are presented based on material in *O. moschatus*.

## MORPHOLOGICAL DESCRIPTION

### *Teladorsagia boreoarcticus* n. sp.

(Figs. 2–36)

*General description:* Trichostrongylidae, Ostertagiinae, uncoiled, reddish-brown in life; 2 male morphotypes, 1 female morphotype. Cephalic expansion present. Cuticle with prominent synlophe throughout length. Cervical papillae triangular, prominent, near level of excretory pore; orifices of subventral esophageal glands (SVGO) anterior to cervical papillae, excretory pore. Exophagus tripartite, attains maximum width at base; prominent valve at esophageal–intestinal junction (EIJ).

*Synlophe:* Bilaterally symmetrical synlophe largely identical in 2 male morphotypes and females. In cervical zone, 20–22 ridges extend to base of cephalic expansion; approximately 34–36 ridges at level of cervical papillae dependent on origin/termination of individual ridges. Laterally, synlophe tapers (the Type I pattern of Lichtenfels et al. [1988]); 1–3.5 pairs of ridges terminate on lateralmost ridge anterior to EIJ. Tapering pattern extends posteriorly 1500–3700 from cephalic extremity or approximately 10–44% of body length from anterior; termination of pattern may be asymmetric on left, right lateral fields; synlophe entirely parallel following termination of tapering pattern. Ventrally in cervical zone, single ventralmost ridge extends from base of cephalic expansion, other continuous and discontinuous ridges disposed laterally (the Type B ventral pattern of Lichtenfels et al. [1988]). Cervical synlophe partitioned by continuous ventral, dorsal, subdorsal, and subventral ridges.

In males (n = 11 specimens), numbers of ridges usually increase posteriad until beginning of last quarter of body anterior to bursa: 38–43 (40 ± 1.8) at EIJ; 38–47 (44 + 3.2) at ¼; 39–46 (43 ± 2.1) at midbody; 25–44 (35 ± 5.7) at ¾; 10–18 (14 ± 3.0) anterior to spicule capitulum. Ridges begin to terminate in ventral and dorsal fields near ¾ total length from anterior; ridges are retained laterally, becoming diminished in height and mass, extending to near level of prebursal papillae. Termination of synlophe ventrally at 2,062–3,087, dorsally at 2,100–3,075 anterior to prebursal papillae (major morphotype); ventrally at 2,525–3,200, dorsally at 2,150–2,700 (minor); arcuate gaps in the synlophe extend anterior to prebursal papillae.

In females, numbers of ridges (n = 8) increase posteriad: 38–44 (40 ± 2.2) at EIJ; 40–45 (42 ± 2.5) at ¼; 37–46 (41 ± 3.4) at midbody; 40–55 (48 ± 4.8) at ¾; (n = 2) 38–40 at vulva; 40–53 (46 ± 5.1) anterior to anus. Interval between ridges increases in dorsal, ventral fields near vulva and anterior to anus; laterally ridges remain close; synlophe is continuous posterior to anus, extending to near apex of tail.

*Teladorsagia boreoarcticus* forma (f.) major, male: Small nematodes with prominent copulatory bursa. Total length (n = 53) 8,275–12,240 (10,649 ± 851.6); maximum width attained at level of prebursal papillae. Cephalic vesicle (n = 42) 88–152 (111 ± 11.4) in length. Esophagus (n = 52) 700–915 (813 ± 40.7) long; 6.8–9.5% of total body length. Esophageal valve (n = 53) 80–112 (101 ± 6.71) long, 40–88 (66 ± 8.03) in maximum width. SVGO (n = 51) 288–342 (312 ± 13.26), nerve ring (n = 46) 234–365 (325 ± 24.7), excretory pore (n = 53) 258–435 (378 ± 31.1), cervical papillae (n = 53) 292–480 (410 ± 32.9) from anterior.

Copulatory bursa symmetrical, strongly bilobed, with prominent dorsal lobe; bursal rays disposed in 2-2-1 pattern (consistent with Durette-Desset [1983]); (n = 43) 405–510 (464 ± 32.23) long (as measured from the prebursal papillae). 0 papillae paired; prebursal papillae prominent. Rays 2, 3 near equal length, convergent at tips, extending to margin of bursal membrane. Rays 4, 5, parallel, diverging at tips, nearly attaining bursal margin; approximately equal in length. Ray 6, isolated, thin, elongate, extending to bursal margin. Rays 7 divergent, contained in weakly bilobed accessory bursal membrane on dorsal aspect of genital cone; dorsal ray (rays 9/10) contained in dorsal lobe, disposed dorsally to accessory bursal membrane, extending ventrally to externodorsal (ray 8); (n = 37) 122–170 (145 ± 11.3) in length; bifurcates at 49–65% (58 ± 3.28) of length from anterior.

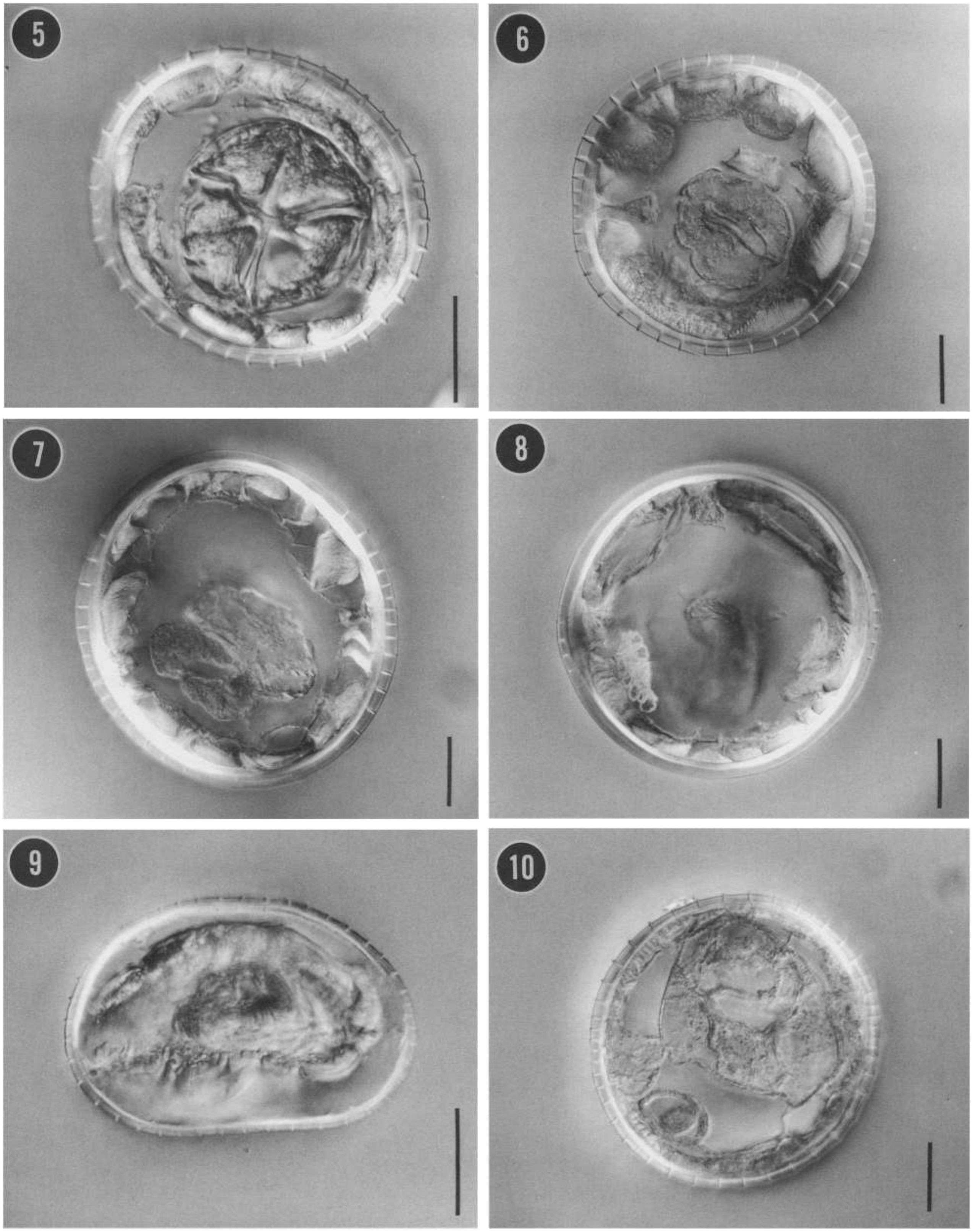
Spicules alate, narrow, elongate, trifurcate, strongly curved, concave in lateral view; equal in length, (n = 52) 350–460 (409 ± 26.0), with trifurcation 70–78% (73 ± 2.12) from anterior in right spicule; (n = 52) 350–460 (409 ± 26.3), with trifurcation 70–78% (74 ± 1.99) in left spicule. Main shaft of spicule terminates in hyaline foot. Dorsal and ventral processes unequal. Ventral process, narrow, pointed, extending to near tip of main shaft. Dorsal process, broad, pointed, extending $\leq$50% of length of ventral process. Gubernaculum with broad, tapering head, narrow, filiform in posterior; (n = 38) 110–142 (123 ± 8.99) long.

Genital cone complex, with prominent bilobed membrane disposed ventrally to apex, enveloping 0 papillae. Accessory bursal membrane broad, bilobed, concave along posterior margin; situated ventrally to dorsal lobe, dorsal to cloaca.

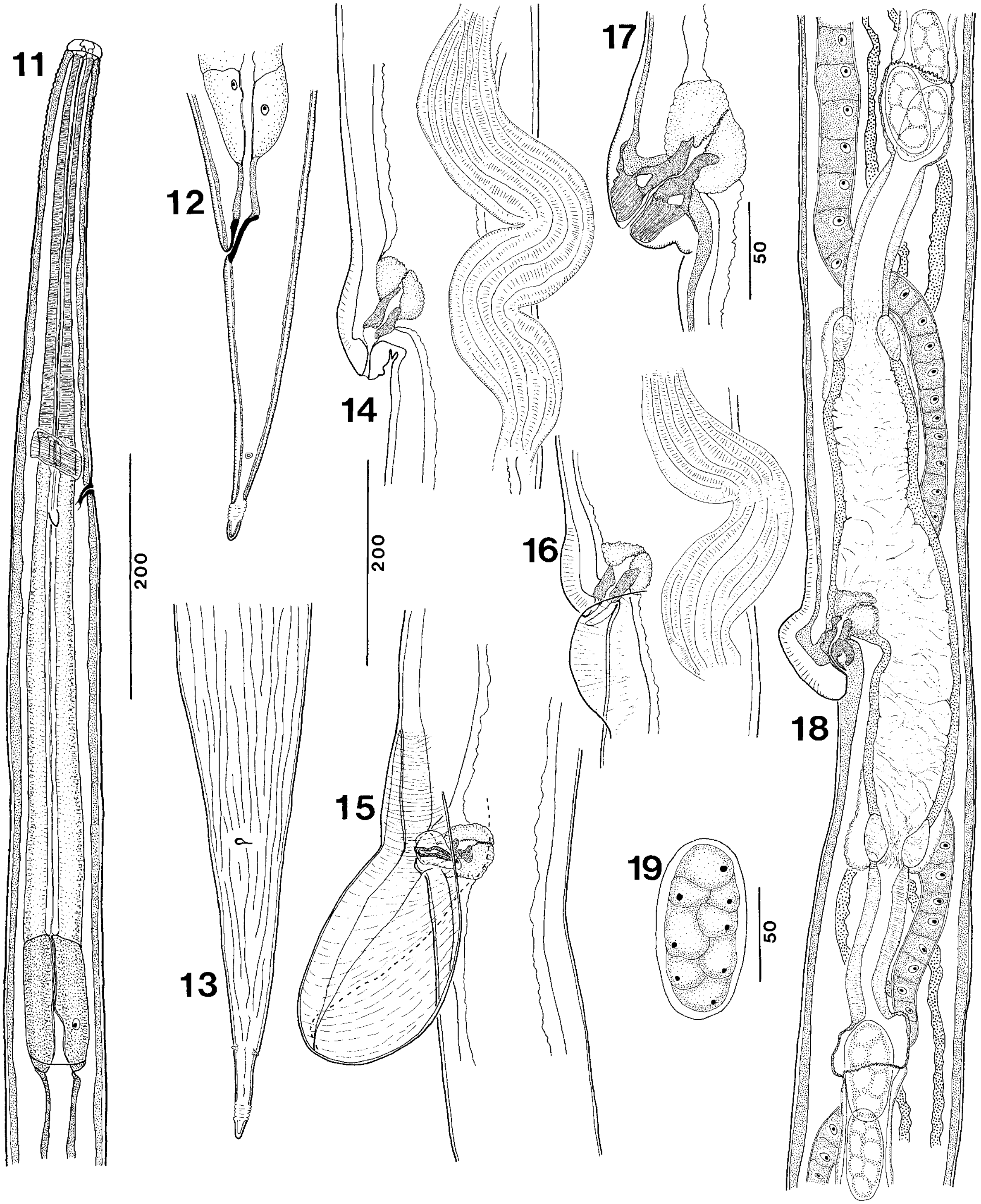
*Teladorsagia boreoarcticus* f. minor, male: Small nematodes with prominent copulatory bursa. Total length (n = 59) 8,425–12,950 (11,228 ± 971.5); maximum width attained at level of prebursal papillae. Cephalic vesicle (n = 51) 94–142 (112 ± 12.0). Esophagus (n = 59) 675–900 (814 ± 43.3) long; 6.0–9.1% of total body length. Esophageal valve (n = 59) 80–126 (100 ± 8.28) long, 42–80 (65 ± 8.02) in maximum width. SVGO (n = 58) 250–348 (310 ± 16.82), nerve ring (n = 55) 255–362 (332 ± 20.91), excretory pore (n = 59) 305–440 (391 ± 31.0), cervical papillae (n = 59) 332–490 (426 ± 35.0) from anterior.

Copulatory bursa symmetrical, strongly bilobed, with prominent dorsal lobe; bursal rays disposed in 2-2-1 pattern (consistent with Durette-Desset [1983]); (n = 59) 300–485 (410 ± 35.28) long (as measured from the prebursal papillae). Rays generally as in major morphotype. Rays 7 divergent, contained in cuticularized Sjoberg's organ. Dorsal ray (n = 49) 78–150 (122 ± 13.2) in length; bifurcates at 42–60% (51 ± 3.16) of length from anterior.

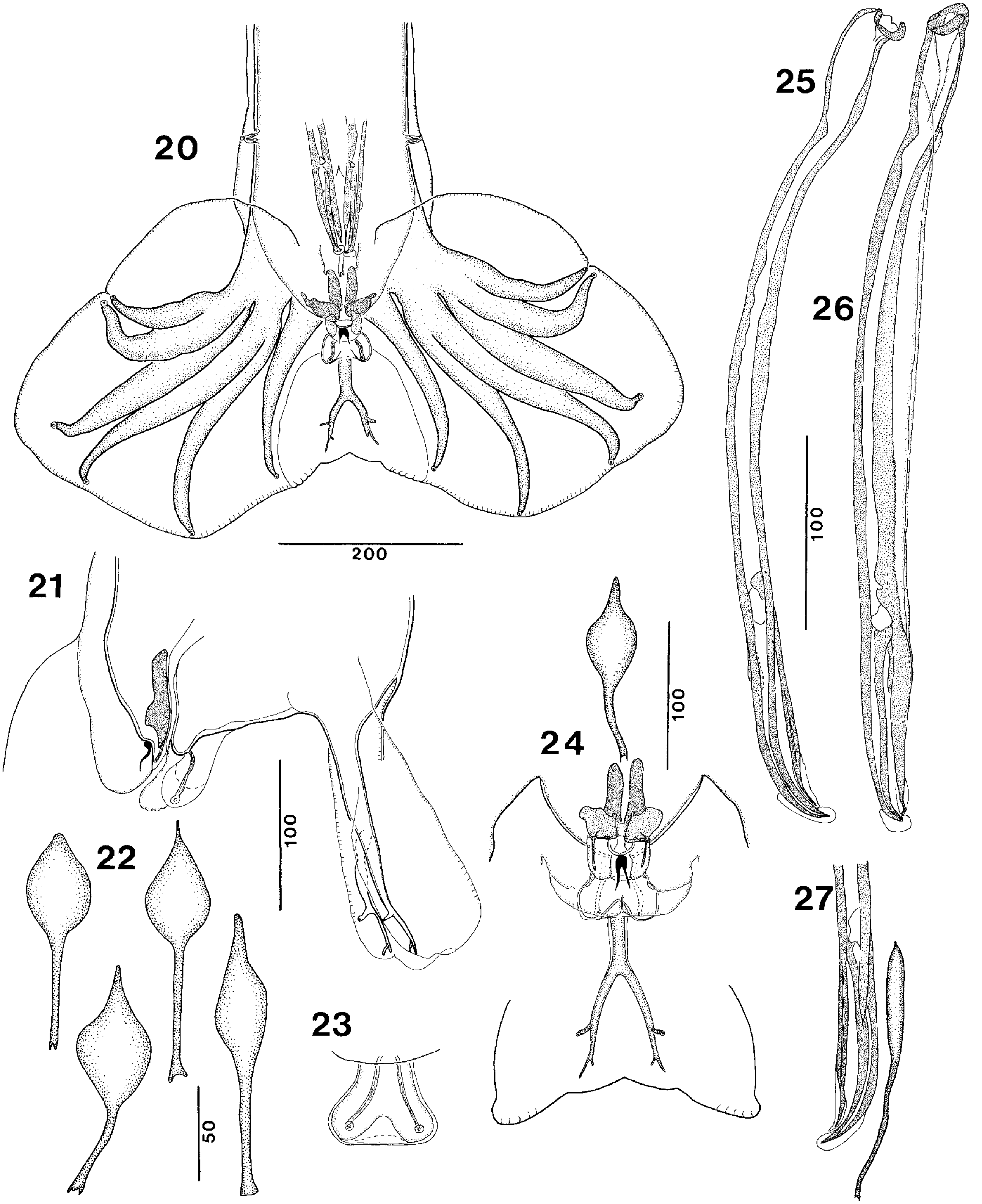
Spicules, alate, broad, robust, trifurcate, straight in lateral view; equal in length (n = 58) 225–312 (282 ± 18.3), with trifurcation 60–66% (63 ± 1.2) from anterior in right spicule; (n = 59) 228–318 (287 ± 18.8), with trifurcation 60–65% (62 ± 1.4) in left spicule. Main shaft



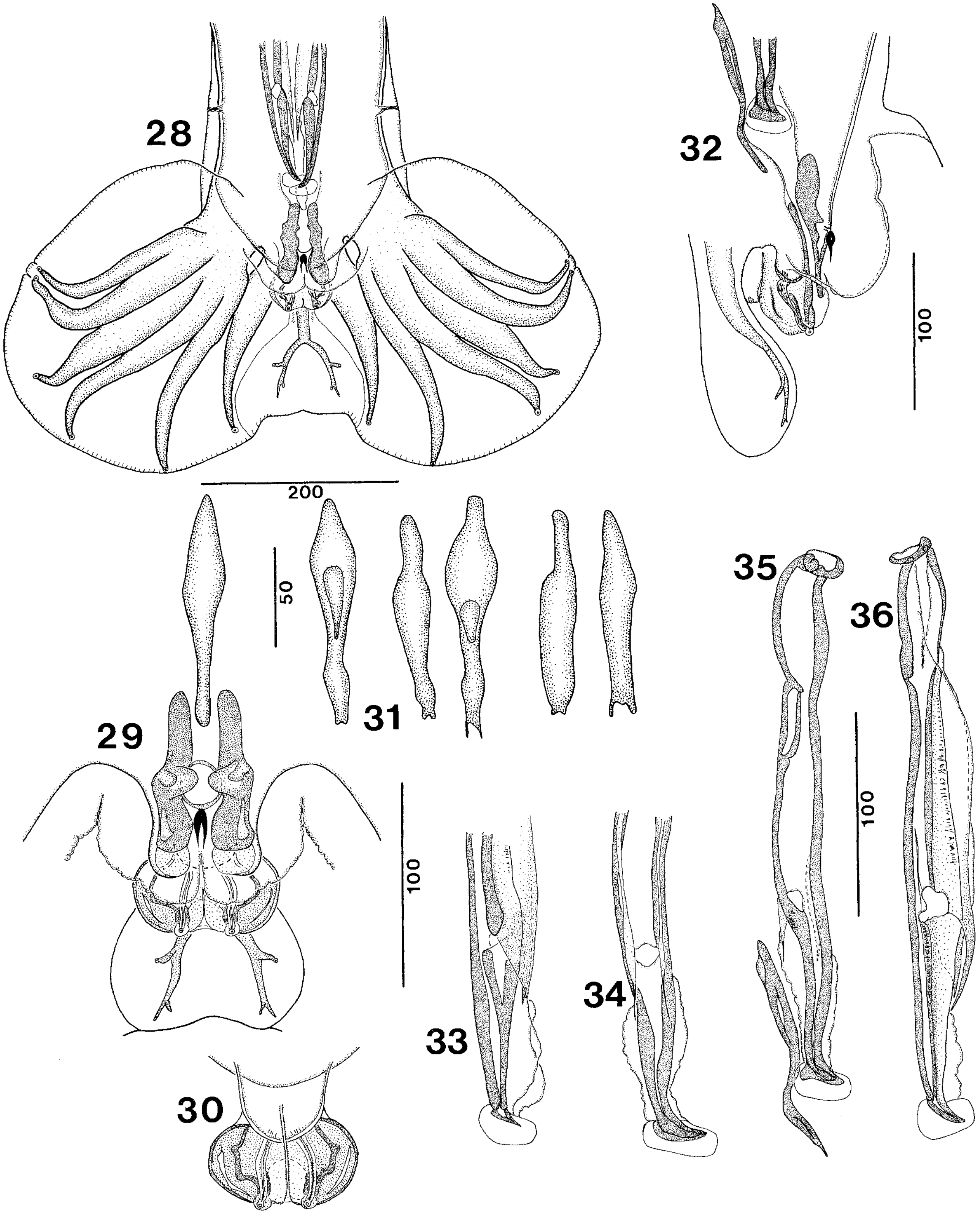
FIGURES 5–10. Synlophe in male (Figs. 5–8) and female (Figs. 9 and 10) specimens of *Teladorsagia boreoarcticus* n. sp. as shown in transverse sections, oriented with dorsal to top (scale bars = 30 μm). Figures 5–8. Structure of synlophe in specimen of minor morphotype male. **5.** Synlophe at the esophageal–intestinal junction (EIJ), showing 40 ridges. **6.** Synlophe at the midbody, showing 45 ridges. **7.** Synlophe at end of the third quarter showing 36 ridges; note the reduction of ridges in the dorsal and ventral fields. **8.** Synlophe in the posterior quarter anterior to the capitulum of the spicules showing 13 ridges; note the restriction of ridges to the lateral fields, and loss of ridges dorsally and ventrally. Figures 9, 10. Synlophe in female specimen. **9.** Synlophe at the EIJ showing 44 ridges. **10.** Synlophe at midbody showing 46 ridges.



FIGURES 11–19. *Teladorsagia boreoarcticus* n. sp. showing structure of cephalic and cervical zone and characters of females; scale bars in micrometers (same scale: 11–13; same scale: 14–16, 18). **11.** Cervical and cephalic regions, showing positions of SVGO, nerve ring, excretory pore, and cervical papillae. **12.** Tail, lateral view. **13.** Tail, ventral view showing pattern of synlophe with ridges extending posterior to anus. **14.** Vulva, lateral view, showing extension of vagina through posteroventrally directed protuberance; note lateral sinuous, cuticular inflation. **15.** Vulva, lateral view, showing transverse vulva, and fully developed flap limited to the ventral surface. **16.** Vulva, lateral view, showing protuberance, and ventral cuticular inflation posterior to vulva. **17.** Vulva, lateral view, showing detail of hypertrophied and cuticularized extension of vagina vera. **18.** Ovejectors, lateral view. **19.** Egg.



FIGURES 20–27. *Teladorsagia boreoarcticus* n. sp. f. major, showing structural characteristics of male; scale bars in micrometers (same scale: 22, 23; same scale: 25–27). **20.** Bursa, ventral view, showing 2-2-1 structure of lateral rays. **21.** Genital cone and dorsal lobe, lateral view, showing hypertrophied bilobed membrane enveloping 0 papillae, and structure of dorsal lobe and ray. **22.** Gubernaculum ventral view, showing variation in form. **23.** Accessory bursal membrane showing divergent position of nerve tracks and 7 papillae; note bilobed form of membrane. **24.** Genital cone and dorsal lobe ventral view, showing relative positions of gubernaculum, telamon, 0 and 7 papillae and dorsal ray. **25.** Spicule (right), lateral view. **26.** Spicule (right), ventral view; note relative length of ventral and dorsal processes. **27.** Spicule (right) and gubernaculum medial view.



FIGURES 28–36. *Teladorsagia boreoarcticus* n. sp. f. minor showing structural characteristics of male; scale bars in micrometers (same scale: 29–31; same scale: 33–36). **28.** Bursa, ventral view, showing 2-2-1 structure of lateral rays. **29.** Genital cone and dorsal lobe, ventral view, showing hypertrophied bilobed membrane enveloping 0 papillae, complex telamon, broad Sjoberg's organ containing 7 papillae, and rounded dorsal lobe. **30.** Sjoberg's organ, ventral view. **31.** Gubernaculum, ventral view, showing variation in form. **32.** Genital cone and dorsal lobe lateral view, showing prominent bilobed, ventral membrane, and cuticularized supports of Sjoberg's organ. **33.** Spicule (left), showing dorsal view of tip; note the broad, triangular, dorsal process. **34.** Spicule (left), medial view of tip. **35.** Spicule (right) and gubernaculum lateral view. **36.** Spicule (right), ventral view; note narrow ventral process.

of spicule terminates in massive hyaline foot. Dorsal, ventral processes near equal in length extending ≤50% of length of spicule tip from trifurcation. Ventral process, narrow, curved, with acute point. Dorsal process, broad, triangular, pointed. Gubernaculum narrow, irregular in form, occasionally broadened in anterior; (n = 53) 98–128 (112 ± 7.6) long.

Genital cone complex, with prominent bilobed membrane disposed ventrally to apex, enveloping 0 papillae. Sjoberg's organ, robust, broader than long, containing divergent dorsally disposed nerve tracks and ventrally directed 7 papillae; situated ventral to dorsal lobe and dorsal to cloaca.

*Female.* Small nematodes, generally straight, with slightly curved caudal extremity. Total length (n = 52) 10,525–15,425 (13,370 ± 985.08); maximum width attained near level of vulva. Cephalic vesicle (n = 39) 90–144 (115 ± 12.59). Esophagus (n = 51) 705–950 (829 ± 58.88) long; 5.3–7.1% of total body length. Esophageal valve (n = 52) 88–128 (105 ± 7.18) long, 42–90 (68 ± 9.02) in maximum width. SVGO (n = 52) 275–358 (322 ± 21.38), nerve ring (n = 46) 288–370 (327 ± 20.42), excretory pore (n = 52) 305–425 (379 ± 25.55), cervical papillae (n = 52) 332–462 (411 ± 29.48) from anterior.

Ovaries didelphic. Vulva, transverse, ventral, situated at (n = 52) 8,550–12,550 (10,833 ± 790.8), or 79–84% of body length from cephalic extremity. Vulva with clearly defined flap in 51% of specimens (n = 60); with knoblike vulval protuberance containing heavily cuticularized and hypertrophied extension of vagina vera in 27%; lacking flap or enlarged protuberance in 22%. Cuticularized inflations at level of vulva in 60% of specimens; usually disposed laterally. Perivulval pores bilateral, near level of posterior extent of infundibulum, slightly dorsal, 3–4 ridges from lateral; ridges interrupted at level of pore. Ovejectors (n = 42) 716–1,250 (942 ± 112) in length. Anterior infundibulum (n = 44) 150–262 (220 ± 24.6), sphincter + vestibule (n = 49) 190–442 (282 ± 52.49) long. Posterior infundibulum (n = 45) 165–282 (208 ± 26.8), sphincter + vestibule (n = 49) 172–348 (244 ± 42.4) long; anterior ovejector consistently longer than posterior. Eggs, ovoid, (n = 50, from 10 specimens) 81–112 (96 ± 7.05) long, 26–57 (43 ± 7.24) wide. Tail conical, curved ventrally, with 2–5, occasionally more, transverse annulations near apex; (n = 51) 160–250 (201 ± 20.8) long.

## Taxonomic summary

*Host:* Muskox, *O. m. moschatus* (Zimmermann) and *O. m. wardi* Lydekker; also in *R. t. groenlandicus* (Borowski).

*Localities:* Type locality (in *O. m. moschatus*): Cox Lake, mainland, near the settlement of Kugluktuk, NWT, Canada (ca. 67°58′N, 116°45′W); also from Cox Lake (ca. 67°54′N, 116°38′W); the region of the Rae River, mainland, NWT (ca. 68°05′N, 117°15′W); and north of the Rae River, NWT (ca. 68°04′N, 117°04′W); these localities generally in the vicinity of the lower Coppermine, Rae, and Richardson rivers, adjacent to Richardson Bay and the Coronation Gulf, NWT. In *O. moschatus wardi*: Ekalluk River, adjacent to Wellington Bay and the settlement of Cambridge Bay, Victoria Island, NWT (ca. 69°22′N, 106°12′W). Additional locality (in *R. t. groenlandicus*): near Hope Lake, mainland, NWT (ca. 67°34′N, 115°50–58′W).

*Specimens:* Holotype male, major form: Canadian National Museum of Nature (Parasites), CMNP 1998-0062, allotype female, CMNP 1998-0063, paratype male, minor form, CMNP 1998-0065, from type host and locality on 26 March 1996, collected by C. Adjun and S. Kutz; additional paratype specimens from type locality: CMNP 1998-0064, 0066, and USNPC 87905.01, 87905.02, 87905.05 (DNA analysis); and vouchers: USNPC 87905.06, 87905.07. Additional specimens in *Ovibos moschatus*: (1) from Cox Lake (COMX-001, -002), 14 April 1994, collected by A. Niptanatiak, J. Nishi, R. Lamont, E. P. Hoberg; Paratypes—CMNP 1998-0067, -0068, and USNPC 87895.01, 87895.02, and vouchers—USNPC 87895.05, 87895.06; vouchers—USNPC 87894.01, 87894.02; (2) from north of the Rae River (MX-10, -11, -18, -26), 14 November 1994, by C. Adjun, J. Nishi, S. Kutz: Paratypes—USNPC 87896.01, and vouchers—CMNP 1998-0069, 0070 and USNPC 87896.02; vouchers—USNPC 87897.01, 87897.02; vouchers—USNPC 87898.01, 87898.02; and vouchers—87899.01, 87899.02; (3) from Ekalluk River, Victoria Island (C-24, -36, -66, -76), 18 March 1996, by S. Kutz: Vouchers—USNPC 87900.00; paratypes—CMNP 1998-0071, -0072, and USNPC 87901.01, 87901.02, and vouchers—USNPC 87901.06, 87901.07; paratypes—CMNP 1998-0073, -0074, and USNPC 87902.01, 87902.02, 87902.04 (DNA analysis), and vouchers—USNPC 87902.03, 87902.05; vouchers—USNPC 87903.01, 87903.02; and (4) from Rae River (A), 25 October 1996, by A. Niptanatiak: Paratypes—CMNP 1998-0076, -0077, and USNPC 87904.01, 87904.02, 87904.05 (DNA analysis), and vouchers—USNPC 87904.06, 87904.07. Additional specimens in *R. t. groenlandicus*: from Hope Lake (C-186, B), 14 September 1996, by J. Nishi and C. Hokanak: Vouchers—USNPC 87906.01, 87906.02; vouchers—USNPC 87907.01.

*Etymology:* The species name is derived from the Latin, *borealis,* and *arcticus* for northern, polar regions.

## Molecular sequence analysis

Sequences from 11 specimens of presumptive *T. boreoarcticus* n. sp. were substantially different from those generated for 43 specimens of *T. circumcincta* sensu stricto (Fig. 37). The average sequence divergence (distance) between specimens in muskoxen from the Arctic and those in domestic sheep from other regions of North America was 13%; 31 fixed substitutions (out of 99 polymorphic sites) separate the 2 groups. All methods of distance comparison and phylogenetic reconstruction with these sequences yield the same result. Sequences of *T. boreoarcticus* cluster as a distinct group relative to those from nematodes nominally considered to be *T. circumcincta* sensu stricto (Fig. 37).

Specimens of *T. boreoarcticus* f. major and *T. boreoarcticus* f. minor show no distinct divergence and are within the range of variation evident for the cluster that diagnoses the species (Fig. 37). This observation further indicates that the major and minor morphotypes as described above represent a single dimorphic species.

Nucleotide diversity in the population of *T. boreoarcticus* was 4.6 times lower than that observed in *T. circumcincta* sensu stricto ($\pi$ ± standard error = 0.005 ± 0.001 versus 0.023 ± 0.001). Because $\pi = \mathrm{Ne}\,\mu$, where Ne = effective size and $\mu$ = mutation rate (for mtDNA and an equal sex ratio; Li, 1997), these values imply an almost 5-fold difference in effective population size between *T. circumcincta* and *T. boreoarcticus* in the central Canadian Arctic (assuming equilibrium and a constant mutation rate).

Within *T. boreoarcticus* sampled, Nst = 0.05 for the comparison between the regions defined by Victoria Island and the Cox/Rae watershed on the mainland; 1 haplotype was found at both Ekalluk River, Victoria Island, and Cox Lake. Thus, there is no evidence of a strong historical restriction of gene flow between the 2 regions.

## Remarks

*Teladorsagia boreoarcticus* n. sp. is referred to the genus *Teladorsagia* based on the structure of the bursal rays that are in a 2-2-1 pattern, with ray 4 ≥ ray 5 in length, a reduced proconus, and a tapering, Type I lateral synlophe in the cervical region (Gibbons and Khalil, 1982; Durette-Desset, 1983; Lichtenfels and Hoberg, 1993). Currently, the genus is monotypic (disregarding taxonomy proposed by Durette-Desset [1989]) and contains the single species, *T. circumcincta* sensu stricto, with 2 described minor morphotypes (*T. trifurcata*/*T. davtiani*) (Daskalov, 1974; Dróżdż, 1995). Polymorphism within *T. circumcincta* and other ostertagiines (Daskalov, 1974; Dróżdż, 1974, 1995; Lancaster and Hong, 1981) has been strongly corroborated based on comparative morphology (synlophe: e.g., Lichtenfels et al., 1988; Lichtenfels and Hoberg, 1993), biochemical criteria (Andrews and Beveridge, 1990; Gasnier et al., 1993), interbreeding experiments (Suarez and Cabaret, 1992), and molecular sequence data (Stevenson et al., 1996).

*Teladorsagia boreoarcticus,* in contrast to the trimorphic *T. circumcincta,* appears to be dimorphic based on examination of approximately 400 specimens of *T. boreoarcticus* f. minor; but see comments below on specimens from Ellesmere Island, NWT. The minor morphotype of *T. boreoarcticus* occurred at 5–67% of the total male population in each host; in domestic sheep the minor morphotype, *T. trifurcata,* may occasionally exceed 20% of the population (Cabaret et al., 1984).

*Teladorsagia boreoarcticus* is the first polymorphic ostertagiine to be recognized and described since the acceptance of the hypothesis for polymorphism. Although to be treated in detail elsewhere, this has served to reemphasize the currently untenable taxonomy for polymorphic species in the subfamily. There is a necessity to develop a standardized taxonomy for the Ostertagiinae that allows effective recognition of the major and minor forms that represent single species. Such a

FIGURE 37. UPGMA phenogram showing distance relationship between samples of *Teladorsagia boreoarcticus* n. sp. in muskox from the central Canadian Arctic and samples of *T. circumcincta* sensu stricto in domestic sheep from localities in North America. The 2 main branches join at approximately 13% sequence divergence. All other phylogenetic reconstruction methods give congruent results (complete reciprocal monophyly between samples in sheep and muskoxen). Source populations in the Arctic are indicated as follows: V = Victoria Island; C = Cox Lake; R = Rae River. Note the lower overall sequence diversity in the sample of 11 specimens of *T. boreoarcticus.* Also, substantial sequence divergence is not apparent between males representing the major and minor morphotypes for *T. boreoarcticus* (2 of 3 specimens from Victoria Island are the minor form), further corroborating diagnosis of a single dimorphic species. Asterisks indicate specimens of *T. circumcincta* from Saskatoon, Saskatchewan, others are from Blouin et al. (1995); min = minor morphotype.

proposal should (1) preserve taxonomy, (2) promote stability, and (3) allow distinction of morphotypes in which the major form holds the name for the species. The latter would require consensus and presentation of a petition to the International Commission on Zoological Nomenclature (1985).

Current usage consistent with Lichtenfels and Hoberg (1993) would, for example, result in *T. circumcincta/T. trifurcata/T. davtiani* that designates the trimorphic status for *T. circumcincta* (see Dróżdż, 1995). Alternatively, designation of forma could result in the following: *T. circumcincta* f. circumcincta, *T. circumcincta* f. trifurcata, and *T. circumcincta* f. davtiani, where minor morphotypes are designated as forms of the nominal species. This structure for nomenclature could be adopted for historically recognized and polymorphic ostertagiines where the putative major morphotype consistently carries the species-level designation (based on morphological criteria that have led to recognition of polymorphism ). Future descriptions of polymorphic species could adopt a nomenclature as presented herein that designates the morphotypes as *T. boreoarcticus* f. major and *T. boreoarcticus* f. minor.

*Teladorsagia boreoarcticus* is diagnosable at the species level, relative to its congener *T. circumcincta* sensu stricto, based on consistent differences in sequences of ND4 of mtDNA. Specimens of *T. boreoarcticus* are further distinguished from those of *T. circumcincta* sensu stricto (limited to nematodes distributed in domestic caprine bovids, excluding those in wild ruminants) by a suite of morphometric and consistent but subtle structural characters in both males and females.

In the following diagnosis, morphometric data from reports by Skrjabin et al. (1954), Becklund and Walker (1971), Lichtenfels et al. (1988), and Lichtenfels and Pilitt (1991) are not applicable except where noted. Specimens referred to *T. circumcincta/T. trifurcata* in these studies may represent a composite of more than a single species of *Teladorsagia* and may have included at least some specimens of *T. boreoarcticus* (consistent with the results of the current study).

Overall, male and female specimens of *T. boreoarcticus* are considerably larger than those of *T. circumcincta* sensu stricto (Tables V–IX). Although morphometric variation alone is often insufficient as a species-level diagnostic character, differences in mean values for esophageal valve, spicules, gubernaculum, and bursa in *T. boreoarcticus* f. major and *T. circumcincta* sensu stricto ($P < 0.0008$) and *T. boreoarcticus* f. minor and *T. circumcincta* f. trifurcata ($P < 0.002$), respectively, are statistically significant; measurements of specimens of *T. circumcincta* in domestic sheep and goats (Table VI) are combined for these comparisons. Mean values were from 31% greater for esophageal valve in females to 64% for the bursa in specimens of *T. boreoarcticus* f. major and from 23% greater for the gubernaculum to 44% for the bursa in *T. boreoarcticus* f. minor compared to *T. circumcincta/T. trifurcata.*

Esophageal characters and the synlophe are useful in diagnosis of males and females of *T. boreoarcticus.* Conservatively, the length of the esophageal valve in *T. boreoarcticus* ($\bar{x}$ = 100 and 105 μm for males and females, respectively) is substantially greater ($P < 0.0008$) than that reported for *T. circumcincta* ($\bar{x}$ = 73 and 79 μm in the current study; $\bar{x}$ = 79 μm in Lichtenfels and Pilitt [1991]). Variation was significantly greater for length of esophageal valve in females of *T. boreoarcticus* (SD = 7.04) than for *T. circumcincta* (SD = 4.84). Notably, valve length does not vary significantly between genders; thus, it is not influenced by total length of male or female nematodes. No other measurements were significantly different with respect to variability.

The cervical synlophe in specimens of *T. boreoarcticus* and *T. circumcincta/T. trifurcata* was largely identical, being described by the Type I and Type B patterns defined by Lichtenfels et al. (1988). Hoberg et al. (1993a) and Lichtenfels et al. (1993) showed that the cervical synlophe could be identical in related congeneric species of ostertagiine nematodes (e.g., *Ostertagia mossi* Dikmans, 1931/*O. dikmansi* Becklund and Walker, 1968 and *O. leptospicularis* Assadov, 1953/*O. kolchida* Popova, 1937; and in *Mazamastrongylus odocoilei* (Dikmans, 1931) and *M. pursglovei* (Davidson and Prestwood, 1979)). Although the cervical synlophe does not vary in a definable manner in *T. boreoarcticus* and *T. circumcincta,* there are a greater number of ridges at all levels of the body in both male and female specimens of the former species. Numbers of ridges, a species-level character, is not influenced by size or diameter of the specimen, an observation that has been confirmed with respect to related genera and species of ostertagiines (E. P. Hoberg and A. Abrams, unpubl. obs.). For example, at the midbody in males there are 39–46 ridges in *T. boreoarcticus* versus 26–29 in *T. circumcincta* from North America (based on raw data derived from Lichtenfels et al. [1988] and Lichtenfels and Pilitt [1991]) and 28–29 in *T. circumcincta* from France (Cabaret et al., 1986). In females, there are 37–45 in *T. boreoarcticus* versus 25–31 and 31, respectively, in specimens from North America and France. Additionally, the dorsal and ventral arcuate gaps in the posterior of males are more extensively developed and initiate further to the anterior in males of *T. boreoarcticus.*

Specimens of *T. boreoarcticus* f. major, relative to *T. circumcincta,* have significantly longer spicules ($P < 0.0001$) ($\bar{x}$ = 409 $\mu$m versus $\bar{x}$ = 300 current study; $\bar{x}$ = 333 in Cabaret et al. [1986]; ranges—280–370 by various authors in Sarwar [1956]); gubernaculum ($P < 0.0001$) ($\bar{x}$ = 123 $\mu$m versus $\bar{x}$ = 88 current study; $\bar{x}$ = 83 in Cabaret et al. [1986]); and bursa ($P < 0.0001$) ($\bar{x}$ = 461 $\mu$m versus $\bar{x}$ = 283 current study). In *T. boreoarcticus,* the dorsal process of the spicules is about ≤0.50 the length of the ventral process and relatively short compared to *T. circumcincta* (0.66–0.75); the dorsal process is broader in *T. boreoarcticus.* The spicules overall are strongly concave in lateral profile in *T. boreoarcticus* and less markedly so in *T. circumcincta.*

Specimens of *T. boreoarcticus* f. minor, relative to *T. trifurcata,* have significantly longer spicules ($P < 0.0014$) ($\bar{x}$ = 287 $\mu$m versus $\bar{x}$ 220 current study; $\bar{x}$ = 216 in Cabaret et al. [1986]; $\bar{x}$ = 182 in 15 specimens in Oregon sheep, E. P. Hoberg [unpubl. obs.]; ranges—150–180 in Skrjabin et al. [1954]; 150–220 by various authors in Sarwar [1956]); gubernaculum ($P < 0.002$) ($\bar{x}$ = 112 $\mu$m versus $\bar{x}$ = 91 in current study; $\bar{x}$ = 89 in Cabaret et al. [1986]; range of 70–90 in Skrjabin et al. [1954]); and bursa ($P < 0.0006$) ($\bar{x}$ = 410 $\mu$m versus $\bar{x}$ = 276 current study). The ventral bilobed membrane disposed on the anterior aspect of the genital cone is hypertrophied relative to that observed in nominal *T. trifurcata*; this is also a consistent difference in comparisons of the major morphotypes. The dorsal process of the spicules is equal in length to the ventral process in both *T. boreoarcticus* and *T. trifurcata,* but the ventral process is narrow and the dorsal process is broad and triangular in *T. boreoarcticus* (confirmed in specimens, and see Andreeva [1958], Cabaret et al. [1986], and Lichtenfels and Hoberg [1993]).

Collections from the region surrounding Kugluktuk and those from Ekalluk River, Victoria Island revealed 2 male morphotypes as described and diagnosed. This is consistent with a limited number of specimens examined by Ott (1998) in muskoxen from Banks Island, NWT; specimens identified as *T. circumcincta* had spicules 340–410 $\mu$m, and those of *T. trifurcata* were 260 $\mu$m in length, both morphometrically compatible with *T. boreoarcticus.* Additionally, specimens identified by Webster and Rowell (1980) as *T. trifurcata* in muskoxen from Ellesmere Island (CMNP 1979-419) were examined for comparative purposes. Among 6 specimens we studied, 2 minor morphotypes were identified; 3 were structurally consistent with *T. boreoarcticus* f. minor but at the lower end of the range for morphometric characters (spicule length: 211–239 $\mu$m; bursa length: 300–312 $\mu$m; valve length: 83–91 $\mu$m). Other males were consistent with a *T. davtiani*-like form (spicules: 179–208 $\mu$m; bursa: 299–300 $\mu$m; valve: 83–88). The Sjoberg's organ in these 2 forms was distinctly different and consistent with the primary criterion used for separation of the minor morphotypes associated with *T. circumcincta* sensu stricto (see Becklund and Walker, 1971). This suggests that a third morphotype is associated with *T. boreoarcticus* but is exceptionally rare and has yet to be identified in the central Arctic; or less likely, that specimens from Ellesmere Island do not represent *T. boreoarcticus.*

Among females of *T. boreoarcticus,* variation was evident in the structure and presence of vulval flaps, protuberances, and lateral and dorsal cuticular inflations at the level of the vulva; flaps and inflations occurred in 51% and 60% of specimens examined. The transverse vulva and flap in female *T. boreoarcticus* were similar to those described for *T. circumcincta* by Lancaster and Hong (1990). Some structural characters of the vulva, however, are unique in specimens of *T. boreoarcticus.* The vagina may open through a bulbous vulval protuberance that surrounds a heavily cuticularized and hypertrophied extension of the vagina vera; this is an exclusive character. This vulval structure was also observed in 1 of 7 females in *R. tarandus tarandus* (USNPC 19477 from Alaska) and in a photomicrograph of a female specimen of *Teladorsagia* from Banks Island examined by Ott (1998). Prominent cuticular inflations lateral to the vulva in *T. boreoarcticus* are not observed in *T. circumcincta,* although they have been reported among such ostertagiines as *Mazamastrongylus* Cameron, 1935, *Camelostrongylus* Orloff, 1933 and *Longistrongylus* LeRoux, 1931 (see Hoberg et al., 1993b). Thus, females of *T. boreoarcticus* can be distinguished from those typical of *T. circumcincta* sensu stricto.

Females of most ostertagiines are poorly represented in museum collections, because historically, species-level diagnoses were based largely on characters of males (Lancaster and Hong, 1990). Only recently, with application of studies of the synlophe, has it become possible to identify accurately females for many species (e.g., Lichtenfels et al., 1988). Thus, adequate comparisons of female ostertagiines continue to be hindered by a paucity of specimens.

Sarwar (1956), Becklund and Walker (1971), and Lichtenfels and Pilitt (1991) documented an exceptionally broad range for morphometric characters in *T. circumcincta/T. trifurcata* based on material from both domestic and wild caprine bovids, pronghorn, and cervids. The current study indicates that statistically discrete ranges for some morphometric attributes, e.g., length of esophageal valve, spicules, gubernaculum, and bursa, can be defined within what had been regarded as a continuum (Tables V–VIII). Thus, it is clear that morphometrically, specimens of *T. circumcincta/T. trifurcata* sensu stricto are characterized by a more restricted range in length for some attributes and generally are represented by relatively smaller nematodes. This appears to be indicated uniformly by published values for measurements of specimens in domestic hosts from North America and other regions of the world (Sarwar, 1956; Cabaret et al., 1986; present study); specimens of *T. circumcincta* in domesticated sheep examined from Iceland near the Arctic Circle do not differ from those representing populations at lower latitudes (E. P. Hoberg unpubl. obs.; USNPC 88301, 88302). That morphometric variation at its greatest extent could represent host-induced variation or a cline related to latitude is further refuted by the consistent molecular differences for specimens of *T. circumcincta* sensu stricto and *T. boreoarcticus.*

Species limits relative to the distribution of *T. boreoarcticus* in wild bovids and cervids remain to be elucidated. Specimens of *Teladorsagia* in *O. m. wardi* from Ellesmere Island and Banks Island, and those in *R. t. groenlandicus* from the region of Hope Lake, southeast of the Rae/Richardson drainage, are regarded as conspecific with *T. boreoarcticus* (Table V) but will require sequence analysis for confirmation. Likewise, specimens in *R. t. tarandus,* and *O. m. wardi* introduced to Alaska (based on specimens from Fairbanks and Barter Island, Alaska) from the Palearctic appear consistent with *T. boreoarcticus* (Tables V, VII, VIII); it is clear that multiple populations are represented. Morphometric data indicate that, generally, *Teladorsagia* sp. in wild caprine bovids, caribou, and reindeer are large relative to *T. circumcincta/T. trifurcata* sensu stricto (Tables VI–IX). Populations in *Ovis dalli dalli* Nelson, other caprines, and *R. t. caribou,* as a consequence of historical isolation, may represent a broader complex of sibling species. Definition of the components for this potential complex and the limits for both *T. boreoarcticus* and *T. circumcincta* sensu stricto require additional collections for molecular-level analyses.

# DISCUSSION

## Species limits and the Holarctic fauna

Specimens of *T. boreoarcticus* in muskoxen are diagnosable and differ from *T. circumcincta/T. trifurcata* sensu stricto based on morphological, morphometric, and molecular criteria (Fig. 37). A genetic distance of 13% at the ND4 gene is well within the range of distances that separate other morphologically defined pairs of congeneric nematodes (Blouin et al., 1998). For example, in the sister-group of the Ostertagiinae (see Hoberg and Lichtenfels, 1994), *Haemonchus contortus* (Rudolphi, 1802) and *Haemonchus placei* (Place, 1893) differ by 16% (Blouin et al., 1997). Among the rhabditids, the 4 congeners *Heterorhabditis bacteriophora* Poinar, 1975, *Heterorhabditis megidis* Poinar, Jackson and Klein, 1987, *Heterorhabditis marelatus* Liu and Berry, 1996 and *Heterorhabditis indicus* Poinar, Karunakar and David, 1992, differ by 8–19% at the same region of ND4 (Liu et al., 1999). The large number of fixed differences between *T. boreoarcticus* and *T. circumcincta* sensu stricto also indicates a relatively long history of separation between the 2 gene pools. Thus, the mtDNA data are consistent with the hypothesis that the 2 samples represent discrete species that were on divergent evolutionary trajectories prior to the introduction of *T. circumcincta* into North America 200–300 yr ago (Adams, 1998). In combination with morphometric and structural char-

TABLE V. Comparison of morphometric data for males and females of *Teladorsagia boreoarcticus* n. sp. in *Ovibos moschatus* (including *Ovibos moschatus moschatus* and *Ovibos moschatus wardi*) and morphologically similar nematodes, *T.* cf. *boreoarcticus,* in *Rangifer tarandus groenlandicus* from the Central Canadian Arctic (values in micrometers; range followed by mean ± 1 SD in parentheses).

| Character | *T. boreoarcticus* n. sp. major form, male *O. moschatus* | *T. boreoarcticus* n. sp. minor form, male *O. moschatus* |
|---|---|---|
| Number examined | 53 | 59 |
| Body length | (53)* 8,275–12,240 (10,649 ± 851.6) | (59) 8,425–12,950 (11,228 ± 971.5) |
| Esophagus length | (52) 700–915 (813 ± 40.7) | (59) 675–900 (814–43.3) |
| Esophagus as % total length | (52) 8–9.5 (7.7 ± 0.52) | (59) 6.0–9.1 (7.3 ± 0.5) |
| Valve length | (53) 80–112 (101 ± 6.71) | (59) 80–126 (100 ± 8.28) |
| Valve width | (53) 40–88 (66 ± 8.03) | (58) 42–80 (65 ± 8.02) |
| Cephalic vesicle length | (42) 88–152 (111 ± 11.4) | (51) 94–142 (112 ± 12.0) |
| Subventral esophageal gland† | (51) 288–342 (312 ± 13.26) | (58) 250–348 (310 ± 16.82) |
| Nerve ring† | (46) 234–365 (325 ± 24.7) | (55) 255–362 (332 ± 20.91) |
| Excretory pore† | (53) 258–435 (378 ± 31.1) | (59) 305–440 (391 ± 31.0) |
| Cervical papillae† | (53) 292–480 (410 ± 32.9) | (59) 228–318 (287 ± 18.8) |
| Left spicule length | (52) 350–460 (409 ± 26.3) | (59) 332–490 (426 ± 35.0) |
| Right spicule length | (52) 350–460 (409–26.0) | (58) 225–312 (282 ± 18.3) |
| Left spicule, % trifurcation‡ | (51) 70–78 (74 ± 1.99) | (59) 60–65 (62 ± 1.4) |
| Right spicule, % trifurcation‡ | (52) 70–78 (73 ± 2.12) | (58) 60–66 (63 ± 1.2) |
| Dorsal ray length | (37) 122–170 (145 ± 11.3) | (49) 78–150 (122 ± 13.2) |
| Dorsal ray, % Bifurcation§ | (37) 49–65 (58 ± 3.28) | (49) 42–60 (51 ± 3.16) |
| Gubernaculum | (38) 110–142 (123 ± 8.99) | (53) 98–128 (112 ± 7.6) |
| Bursa length\| | (43) 405–510 (464 ± 32.23) | (59) 300–485 (410 ± 35.28) |
| Vulva position† | | |
| Vulva, % body length | | |
| Anterior infundibulum length | | |
| Anterior sphincter and vestibule | | |
| Posterior infundibulum length | | |
| Posterior sphincter and vestibule | | |
| Ovejector length | | |
| Tail length | | |
| Egg length | | |
| Egg width | | |

* n for individual measurements; for eggs, this represents 50 eggs from 10 individuals.

† Measured from anterior.

‡ Percentage from anterior to trifurcation of spicule tip.

§ Percentage from anterior to bifurcation of dorsal ray.

| Bursa length determined from prebursal papillae.

acters, the 13% divergence in the ND4 gene corroborates the validity of *T. boreoarcticus* and indicates the importance of mtDNA as an important adjunct in the identification of species (Blouin et al., 1998). Also reinforced is the concept of the North American fauna as a mosaic of endemic and introduced elements.

*Teladorsagia circumcincta/T. trifurcata* had been considered to have a broad geographic and host distribution across the Holarctic (Boev et al., 1963; Govorka et al., 1988; Hoberg et al., 2000). The recognition of *T. boreoarcticus* in muskoxen, however, in part corroborates the hypothesis outlined by Hoberg et al. (2000) for the existence of a cryptic species complex of *Teladorsagia* spp. among Caprinae and Cervidae at high latitudes.

In the Canadian Arctic, *Teladorsagia* has been reported in *O. moschatus* from Thelon Sanctuary (Gibbs and Tener, 1958), Ellesmere Island (Webster and Rowell, 1980), and Banks Island (Ott, 1998). These apparently represent natural and isolated host populations and indicate the historical presence of *T. boreoarcticus* in muskoxen from the Nearctic. Alendal and Helle (1983) reviewed records for *Teladorsagia* in muskoxen; there are few from North America and none listed for Greenland. It is apparent, however, that nematodes were introduced to Nunivak Island, Alaska, and later to the Arctic coastal plain near Barter Island (based on specimens from this latter locality, UAM 2572) with muskoxen translocated from East Greenland in 1935. Specimens of nematodes from Ellesmere Island, Banks Island, and those introduced from East Greenland to Alaska appear to be consistent with *T. boreoarcticus.*

Korsholm and Olesen (1993) reported on abomasal nematodes in muskoxen and barren ground caribou from West Greenland and found *T. circumcincta/T. trifurcata.* The origin of these parasites is problematic, and none was available for examination. Muskoxen were transplanted to West Greenland from East Greenland, after wintering in the Copenhagen Zoo in 1962 and 1965. Thus, current evidence for the presence and endemic nature of *T. boreoarcticus* in East Greenland is circumstantial (based on putative introductions to Alaska). Additionally, these muskoxen were introduced onto range occupied by *R. t. groenlandicus* in West Greenland, which further com-

TABLE V. extended.

| *T. boreoarcticus* n. sp.<br>female<br>*O. moschatus* | *T.* cf. *boreoarcticus* n. sp.<br>major form, male<br>*R. t. groenlandicus* | *T.* cf. *boreoarcticus* n. sp.<br>minor form, male<br>*R. t. groenlandicus* |
|---|---|---|
| 52 | 13 | 3 |
| (52) 10, 525–15,425 (13,370 ± 985.08) | (12) 9,950–11,150 (10,591 ± 408.89) | (3) 10,600–11,710 (11,147 ± 555.20) |
| (51) 705–950 (829 ± 53.88) | (11) 798–905 (836 ± 33.61) | (2) 806–860 |
| (51) 5.3–7.1 (6.2 ± 0.37) | (11) 7.2–8.3 (7.8 ± 0.31) | (2) 7.2–7.3 |
| (52) 88–128 (105 ± 7.18) | (8) 95–110 (102 ± 4.75) | (2) 92–105 |
| (52) 42–90 (68 ± 9.02) | (8) 40–80 (64 ± 13.00) | (2) 55–72 |
| (39) 90–144 (115 ± 12.59) | (11) 98–128 (114 ± 9.37) | (2) 112–125 |
| (52) 275–358 (322 ± 21.38) | (11) 282–342 (313 ± 20.24) | (2) 300–318 |
| (46) 288–370 (327 ± 20.42) | (10) 308–368 (339 ± 18.94) | (2) 350–355 |
| (52) 305–425 (379 ± 25.55) | (12) 358–422 (391 ± 20.51) | (2) 390–412 |
| (52) 332–462 (411 ± 29.48) | (12) 388–458 (423 ± 22.94) | (2) 425–448 |
| | (13) 370–450 (411 ± 23.71) | (3) 270–302 (289 ± 16.82) |
| | (13) 365–455 (411 ± 24.10) | (3) 265–300 (285 ± 18.03) |
| | (13) 71–77 (75 ± 1.99) | (3) 60–64 (62 ± 2.08) |
| | (13) 71–77 (75 ± 2.02) | (3) 61–64 (63 ± 1.53) |
| | (8) 132–162 (143 ± 10.52) | (3) 125–135 (129 ± 5.13) |
| | (8) 50–58 (54 ± 2.82) | (3) 52–57 (54 ± 2.52) |
| | (6) 108–135 (118 ± 11.6) | (2) 112–115 |
| | (13) 400–475 (443 ± 27.51) | (3) 405–418 (409 ± 7.51) |
| (52) 8,550–12,550 (10,833 ± 790.8) | | |
| (52) 79–84 (81 ± 0.91) | | |
| (44) 150–262 (220 ± 24.6) | | |
| (49) 190–442 (282 ± 52.49) | | |
| (45) 165–282 (208 ± 26.8) | | |
| (49) 172–348 (244 ± 42.4) | | |
| (43) 716–1,250 (944 ± 108.86) | | |
| (51) 160–250 (201 ± 20.8) | | |
| (50)* 81–112 (96 ± 7.05) | | |
| (50)* 26–57 (43 ± 7.24) | | |

plicates elucidation of the history for distribution of *Teladorsagia* and other nematodes. It is notable that Rose et al. (1984) reported remarkably large specimens of ostertagiine nematodes, including males identified as *T. circumcincta* in domestic sheep from West Greenland.

On Spitsbergen in the Svalbard Archipelago, various ruminants have been introduced over the past century, and an endemic caribou, *Rangifer tarandus platyrhynchus* Vrolik, is present (see Bye et al., 1987). Small populations of muskoxen (from East Greenland), semidomestic reindeer (from Norway), and cattle were established. Muskoxen are considered to have had some influence on parasite biodiversity in endemic caribou (see Bye and Halvorsen, 1983; Bye et al., 1987). It is possible that both *T. circumcincta* sensu stricto and *T. boreoarcticus* could be present in the archipelago.

Species limits and the geographic distribution for *T. boreoarcticus* in wild bovids and cervids other than muskoxen and caribou from the central Canadian Arctic remain largely unresolved. Potentially, *T. boreoarcticus* is a Holarctic species distributed in *O. moschatus* ssp. in the Nearctic and Greenland and in *R. tarandus* ssp. at high latitudes from Greenland across the Nearctic and Palearctic. Current data indicating a substantial morphological and morphometric similarity among populations of *Teladorsagia* in muskoxen (Canadian Arctic; and Alaska, via a source from East Greenland), barren ground caribou, woodland caribou (from the northern Nearctic), and reindeer (introduced to western Alaska from the Palearctic) at high latitudes would not refute this hypothesis (Tables V–IX). Corroboration, however, is dependent on new collections from Alaska (including *R. t. granti*), Canada (including *R. t. caribou* and *R. t. pearyi*), Siberia, and Greenland (*Rangifer tarandus* ssp.) in which mtDNA sequences can be evaluated.

Based on a limited number of specimens, *Teladorsagia* sp. in Dall's sheep (*O. d. dalli*) are morphometrically most similar to *T. boreoarcticus* (Tables V, VII, VIII). In contrast, major morphotypes of those in mountain goat (*Oreamnos americanus*) and bighorn sheep (*O. canadensis*) appear to be most similar to *T. circumcincta* (Tables V, VI); minor morphotype males in mountain goats are most similar to *T. boreoarcticus* (Tables V, VIII). This range of variation for *Teladorsagia* sp. in wild Caprinae and a history of geographic isolation for hosts (addressed below) further suggest the presence of a broader complex of cryptic species across the Holarctic.

The concept for *T. circumcincta* as a widespread cosmopolitan species (e.g., Skrjabin et al., 1954; Dróżdż, 1965; Lichtenfels et al., 1988; Lichtenfels and Pilitt, 1991) has in part been refuted in the current study. Consequently, the overall geographic and host distribution for *T. circumcincta* sensu stricto

TABLE VI. Comparison of morphometric data for major morphotype males: *Teladorsagia circumcincta* sensu stricto in domestic caprine bovids and *T. circumcincta*-like nematodes in wild hosts (values in micrometers; range followed by mean ± 1 SD in parentheses).

| | *Ovis aries* | *Capra hircus* | *Oreamnos americanus* | *Ovis canadensis* |
|---|---|---|---|---|
| Character | 39 | 10 | 5 | 23 |
| Body length | (33)* 5,925–10,575 (8,324 ± 978.77) | — | (5) 8,132–9,482 (8,684 ± 551.69) | (10) 6,167–10,150 (8,120 ± 1,221.90) |
| Esophagus length | (30) 545–675 (605 ± 40.61) | — | (5) 582-685 (639 ± 37.32) | (20) 562–698 (617 ± 38.57) |
| Esophagus as % total length | (29) 6.3–8.2 (7.2 ± 0.51) | — | (5) 6.7–7.7 (7.4 ± 0.4) | (19) 6.1–10.3 (7.8 ± 1.28) |
| Valve length | (34) 60–92 (73 ± 6.87) | — | (5) 75–90 (80 ± 6.28) | (18) 55–95 (72 ± 10.7) |
| Valve width | (34) 35–58 (45 ± 5.24) | (4) 42–48 (45 ± 2.45) | (5) 50–60 (55 ± 4.12) | (18) 42–60 (51 ± 5.33) |
| Cephalic vesicle length | (11) 78–115 (94 ± 10.80) | — | — | (6) 98–112 (108 ± 5.67) |
| Subventral esophageal gland† | (29) 208–292 (240 ± 19.76) | — | (5) 212–260 (242 ± 18.19) | (20) 215–265 (239 ± 12.63) |
| Nerve ring† | (25) 242–302 (270 ± 14.28) | — | (4) 235–300 (258 ± 29.96) | (7) 240–300 (278 ± 21.22) |
| Excretory pore† | (30) 180–395 (320 ± 38.04) | — | (4) 262–358 (312 ± 39.56) | (20) 282–382 (336 ± 34.29) |
| Cervical papillae† | (31) 208–432 (350 ± 39.68) | — | (5) 290–402 (336 ± 44.24) | (20) 308–422 (364 ± 38.73) |
| Left spicule length | (39) 242–355 (297 ± 28.86) | (10) 300–340 (318 ± 15.77) | (5) 315–342 (330 ± 12.66) | (23) 305–355 (329 ± 13.10) |
| Right spicule length | (39) 240–355 (296 ± 28.36) | (10) 300–340 (318 ± 15.66) | (5) 310–338 (328 ± 12.28) | (23) 305–350 (329 ± 13.54) |
| Left spicule, % trifurcation‡ | (37) 68–79 (74 ± 2.78) | (10) 71–77 (74 ± 1.94) | (4) 72–73 (72 ± 0.58) | (23) 71–78 (74 ± 1.76) |
| Right spicule, % trifurcation‡ | (37) 68–77 (74 ± 2.47) | (10) 71–77 (74 ± 1.95) | (4) 71–72 (72 ± 0.5) | (23) 71–77 (74 ± 1.70) |
| Dorsal ray length | (26) 62–101 (80 ± 9.57) | (10) 65–90 (78 ± 7.63) | — | (14) 84–112 (97 ± 6.93) |
| Dorsal ray, % bifurcation§ | (26) 48–59 (53 ± 2.88) | (10) 49–58 (53 ± 2.94) | — | (14) 48–61 (54 ± 4.54) |
| Gubernaculum | (20) 75–105 (89 ± 8.18) | (9) 79–92 (86 ± 4.66) | — | (17) 80–108 (96 ± 6.58) |
| Bursa length\| | (30) 240–400 (288 ± 33.91) | (4) 222–248 (235 ± 10.89) | (3) 275–325 (305 ± 26.46) | (17) 225–390 (337 ± 40.58) |

* n for individual measurements.

† Measured from anterior.

‡ Percentage from anterior to trifurcation of spicule tip.

§ Percentage from anterior to bifurcation of dorsal ray.

| Bursa length determined from prebursal papillae.

TABLE VII. Comparison of morphometric data for major morphotype males: *Teladorsagia boreoarcticus* n. sp.-like nematodes in wild caprine bovids and *Rangifer tarandus* (values in micrometers; range followed by mean ± 1 SD in parentheses).

| Character | *Ovis dalli* 4 | *Ovibos moschatus wardi* 11 | *Rangifer tarandus tarandus* 9 | *Rangifer tarandus caribou* 3 |
|---|---|---|---|---|
| Body length | (4)* 8,590–10,260 (9,448 ± 807.52) | (11) 7,383–12,150 (9,619 ± 1,491.2) | (7) 7,488–9,215 (8,314 ± 686.27) | (3) 9,005–9,950 (9,427 ± 480.63) |
| Esophagus length | (4) 745–782 (763 ± 15.46) | (11) 705–875 (777 ± 53.38) | (7) 670–815 (735 ± 50.74) | (3) 805–825 (817 ± 10.79) |
| Esophagus, % total length | (4) 7.3–8.8 (8.2 ± 0.8) | (11) 7–10 (8.2 ± 1.1) | (7) 8.6–9.2 (8.9 ± 0.23) | (3) 8.3–8.9 (8.6 ± 0.30) |
| Valve length | (4) 85–106 (94 ± 9.6) | (11) 88–108 (96 ± 5.99) | (7) 72–100 (84 ± 8.60) | (3) 95–98 (96 ± 1.73) |
| Valve width | (4) 45–58 (52 ± 5.91) | (11) 52–70 (64 ± 5.78) | (7) 48–58 (55 ± 4.08) | (3) 40–60 (52 ± 10.4) |
| Cephalic vesicle length | — | (1) 112 | (2) 98–110 | (3) 82–105 (96 ± 12.1) |
| Subventral esophageal gland† | (4) 272–316 (299 ± 19.07) | (11) 262–348 (297 ± 22.58) | (7) 258–302 (280 ± 16.98) | (3) 280–318 (301 ± 19.31) |
| Nerve ring† | (3) 300–308 (302 ± 4.62) | (10) 285–358 (312 ± 23.09) | (7) 258–320 (290 ± 23.22) | (2) 282–300 |
| Excretory pore† | (4) 342–368 (355 ± 13.9) | (11) 280–425 (364 ± 40.43) | (7) 325–388 (345 ± 24.57) | (3) 325–335 (331 ± 5.13) |
| Cervical papillae† | (4) 372–402 (388 ± 12.48) | (11) 302–460 (397 ± 46.9) | (7) 355–422 (376 ± 28.54) | (3) 362–370 (367 ± 4.16) |
| Left spicule length | (4) 392–440 (415 ± 20.23) | (10) 338–430 (392 ± 29.41) | (9) 305–440 (387 ± 38.82) | (3) 355–450 (396 ± 48.95) |
| Right spicule length | (4) 392–442 (415 ± 21.47) | (11) 332–432 (388 ± 30.96) | (9) 305–440 (386 ± 38.57) | (3) 350–450 (394 ± 51.07) |
| Left spicule, % trifurcation‡ | (4) 74–76 (75 ± 0.96) | (9) 72–77 (74 ± 1.72) | (9) 70–77 (74 ± 2.67) | (3) 77–78 (77 ± 0.58) |
| Right spicule, % trifurcation‡ | (4) 73–76 (74 ± 1.29) | (10) 72–76 (74 ± 1.4) | (9) 70–77 (74 ± 2.65) | (3) 76–77 (77 ± 0.58) |
| Dorsal ray length | (4) 150–188 (175 ± 18) | (2) 125–128 | — | (1) 145 |
| Dorsal ray, % bifurcation§ | (4) 50–57 (54 ± 3.3) | (2) 56–58 | — | (1) 65 |
| Gubernaculum | (2) 122–127 | (8) 88–138 (116 ± 15.2) | (3) 100–110 (106 ± 5.29) | (3) 95–120 (108 ± 12.6) |
| Bursa length‖ | (3) 395–425 (410 ± 15) | (6) 315–435 (379 ± 53.52) | (7) 278–395 (349 ± 49.92) | (3) 305–445 (367 ± 71.47) |

* n for individual measurements.

† Measured from anterior.

‡ Percentage from anterior to trifurcation of spicule tip.

§ Percentage from anterior to bifurcation of dorsal ray.

‖ Bursa length determined from prebursal papillae.

TABLE VIII. Comparison of morphometric data for minor morphotype males: *Teladorsagia trifurcata* sensu stricto in domestic sheep and *Teladorsagia boreoarcticus* n. sp.-like nematodes in wild hosts (values in micrometers; range with mean ± 1 SD in parentheses).

| Character | *T. trifurcata* sensu stricto *Ovis aries* | *T. boreoarcticus*-like *Oreamnos americanus* | *T. boreoarcticus*-like *Ovis dalli* | *T. boreoarcticus*-like *Ovibos moschatus wardi* | *T. boreoarcticus*-like *Rangifer t. tarandus* |
|---|---|---|---|---|---|
| Number examined | 20 | 9 | 4 | 5 | 2 |
| Body length | (16)* 6,100–9,125 (8,058 ± 805.9) | (6) 8,440–11,220 (9,866 ± 983.4) | (2) 11,593–11,980 | (1) 12,055 | (2) 8,400–8,800 |
| Esophagus length | (17) 522–675 (601 ± 41.24) | (8) 622–720 (678 ± 34.03) | (3) 780–820 (806 ± 22.54) | (3) 825–835 (828 ± 5.77) | (2) 700–775 |
| Esophagus as % total length | (14) 6.7–8.6 (7.4 ± 0.5) | (6) 6.4–8.2 (7.1 ± 0.69) | (2) 6.5–7.1 | (1) 6.9 | (2) 8.3–8.8 |
| Valve length | (18) 55–95 (73 ± 9.57) | (8) 75–100 (88 ± 7.86) | (3) 104–125 (114 ± 10.6) | (5) 85–105 (96 ± 8.02) | (1) 85 |
| Valve width | (17) 38–52 (44 ± 4.31) | (8) 55–72 (63 ± 6.34) | (3) 50–52 (51 ± 1.16) | (5) 50–60 (54.4 ± 4.34) | (1) 55 |
| Cephalic vesicle length† | (13) 80–108 (91 ± 7.66) | (2) 112–122 | (3) 112–118 (114 ± 3.46) | — | (1) 115 |
| Subventral esophageal gland† | (14) 198–260 (239 ± 15.74) | (7) 240–278 (259 ± 14.31) | (3) 302–320 (311 ± 9.02) | (3) 308–315 (312 ± 3.51) | (2) 270–285 |
| Nerve ring† | (11) 256–300 (281 ± 14.12) | (8) 275–328 (306 ± 18.86) | (2) 312–320 | (2) 300–342 | (2) 292–302 |
| Excretory pore† | (17) 278–385 (329 ± 29.79) | (8) 330–385 (366 ± 17.89) | (3) 375–422 (392 ± 26.31) | (2) 405–462 | (2) 348–355 |
| Cervical papillae† | (18) 298–422 (356 ± 31.64) | (8) 350–412 (393 ± 22.01) | (3) 405–450 (428 ± 22.5) | (2) 348–448 | (2) 382–390 |
| Left spicule length | (19) 188–280 (219 ± 22.12) | (9) 245–315 (286 ± 21.13) | (4) 290–328 (310 ± 19.77) | (5) 245–290 (268 ± 16.11) | (2) 208–235 |
| Right spicule length | (19) 182–280 (217 ± 22.65) | (9) 245–305 (281 ± 19.49) | (4) 282–322 (303 ± 19.97) | (5) 238–278 (263 ± 14.86) | (2) 204–230 |
| Left spicule, % trifurcation‡ | (19) 60–66 (62 ± 1.48) | (9) 62–65 (63 ± 1.13) | (4) 62–64 (63 ± 0.96) | (4) 60–64 (62 ± 1.71) | (2) 61–64 |
| Right spicule, % trifurcation‡ | (19) 60–67 (63 ± 1.78) | (9) 62–67 (64 ± 1.62) | (4) 62–65 (63 ± 1.41) | (4) 63–64 (63 ± 0.5) | (2) 62–63 |
| Dorsal ray length | (7) 68–91 (80 ± 7.35) | (6) 105–130 (119 ± 8.70) | (3) 116–135 (125 ± 9.5) | (2) 76–125 | (1) 88 |
| Dorsal ray, % bifurcation§ | (7) 50–60 (54 ± 4.06) | (6) 50–57 (54 ± 3.01) | (3) 50–51 (51 ± 0.58) | (2) 46–56 | (1) 51 |
| Gubernaculum | (14) 75–105 (91 ± 10.61) | (5) 90–125 (108 ± 14.84) | (4) 106–125 (115 ± 8.77) | (1) 92 | (1) 80 |
| Bursa length\| | (17) 208–345 (276 ± 35.15) | (8) 300–425 (366 ± 43.24) | (4) 345–400 (375 ± 24.83) | (4) 240–375 (340 ± 66.42) | (1) 258 |

* n for individual measurements.

† Measured from anterior.

‡ Percentage from anterior to trifucation of spicule tip.

§ Percentage from anterior to bifurcation of dorsal ray.

| Bursa length determined from prebursal papillae.

TABLE IX. Comparison of morphometric data for females of *Teladorsagia circumcincta* sensu stricto in domestic caprine bovids, *Teladorsagia boreoarcticus* n. sp.-like nematodes in *Rangifer tarandus*, and *T. circumcincta*-like nematodes in *Oreamnos americanus* (values in micrometers; range followed by mean ± 1 SD in parentheses).

| Character | *T. circumcincta* sensu stricto *Ovis aries* | *T. boreoarcticus*-like *Rangifer tarandus tarandus* | *T. circumcincta*-like *O. americanus* |
|---|---|---|---|
| Number examined | 34 | 7 | 8 |
| Body length | (34)* 9,050–14,750 (11,258 ± 1,282.26) | (7) 9,000–10,900 (10,000 ± 640.79) | (8) 11,000–13,025 (12,165 ± 695.73) |
| Esophagus length | (34) 568–725 (639 ± 37.02) | (7) 720–818 (776 ± 36.84) | (8) 645–720 (669 ± 28.09) |
| Esophagus as % total length | (34) 4.9–7.1 (5.7 ± 0.5) | (7) 7.1–8.8 (7.8 ± 0.58) | (8) 5–5.9 (5.5 ± 0.34) |
| Valve length | (33) 65–98 (79 ± 8.05) | (7) 88–98 (91 ± 3.96) | (8) 80–92 (86 ± 4.60) |
| Valve width | (33) 35–66 (52 ± 6.18) | (7) 45–60 (52 ± 4.8) | (8) 58–70 (64 ± 4.56) |
| Cephalic vesicle length | (13) 80–118 (96 ± 10.68) | (4) 112–118 (114 ± 2.87) | (5) 110–125 (117 ± 6.30) |
| Excretory pore† | (32) 255–375 (330 ± 32.99) | (7) 309–352 (330 ± 15.78) | (7) 345–380 (361 ± 13.63) |
| Cervical papillae† | (34) 288–408 (360 ± 34.7) | (7) 338–395 (364 ± 19.87) | (8) 375–418 (391 ± 14.97) |
| Subventral esophageal gland† | (28) 219–290 (250 ± 17.33) | (6) 282–322 (296 ± 14.61) | (8) 250–287 (269 ± 13.56) |
| Nerve ring† | (24) 215–320 (274 ± 29.16) | (7) 252–305 (282 ± 18.43) | (7) 286–320 (302 ± 12.93) |
| Vulva position† | (34) 7,400–12,100 (9,226 ± 1,054.69) | (7) 7,415–8,925 (8,161 ± 512.59) | (8) 8,975–10,575 (9,924 ± 552.83) |
| Vulva, % body length† | (34) 80–84 (82 ± 0.98) | (7) 81–82 (82 ± 0.53) | (8) 80–84 (82 ± 1.19) |
| Anterior infundibulum length | (24) 125–225 (170 ± 21.31) | (5) 180–200 (191 ± 7.54) | (6) 155–225 (189 ± 27.77) |
| Anterior sphincter and vestibule | (34) 132–330 (209 ± 53.53) | (7) 190–320 (263 ± 48.44) | (8) 178–280 (233 ± 33.36) |
| Posterior infundibulum length | (27) 122–206 (155 ± 19.12) | (4) 155–212 (182 ± 23.9) | (6) 162–202 (181 ± 18.27) |
| Posterior sphincter and vestibule | (34) 103–275 (185 ± 49.44) | (7) 180–280 (232 ± 37.26) | (8) 182–235 (204 ± 17.21) |
| Ovejector length | (22) 583–976 (731 ± 113.12) | (3) 733–954 (827 ± 113.99) | (6) 738–880 (804 ± 51.61) |
| Tail length | (34) 142–220 (169 ± 21.42) | (7) 145–178 (161 ± 12.67) | (8) 185–225 (206 ± 13.90) |

* n for individual measurements.

† Measured from anterior.

in wild and domestic caprines (and other hosts) still remains to be resolved in Eurasia and more generally in the Palearctic and Nearctic. Current concepts would suggest that sibling species are common, but generally unrecognized, components of nematode faunas in vertebrate hosts (Anderson et al., 1998). Among ruminants, this may be of particular consequence in areas of sympatry for domestic and wild caprines and cervids, on natural ecotones, or on the interface between natural and agricultural ecosystems.

### Parasite population biology

In North America, *T. circumcincta* in sheep show a high level of nucleotide diversity and very little differentiation among populations. This pattern likely results from very large effective population sizes and from anthropogenic influences that promote a high rate of gene flow via long distance movement of livestock (Blouin et al., 1995). In contrast, the nucleotide diversity for *T. boreoarcticus* in the central Arctic is 4–5 times lower than that observed for *T. circumcincta* sensu stricto in sheep, indicating a much lower long-term effective population size. Muskoxen are less abundant than sheep, population densities are lower, and historical bottlenecks related to extirpation in the Arctic are apparent (see Gunn, 1982).

A small effective population size for *T. boreoarcticus* may result from (1) small dispersed host populations (a contrast to caribou); (2) disjunct winter and summer foraging zones (Gunn, 1982) that would result in dispersion of larvae over an extensive area and across sites that are only visited seasonally; (3) a short summer season in which ambient temperatures act to define a narrow window for larval development (S. Kutz, unpubl. obs. for protostrongylid nematodes), thus dampening the potential for amplification of the parasite population (an influence that would be modified with increasing global temperatures, see Hoberg et al. [2000]); and (4) low overwinter survival in harsh Arctic conditions, although it recognized that subnivial habitats can be substantially buffered from surface ambient temperatures (S. Kutz, unpubl. obs.), wind, and desiccation. Seasonal restrictions in larval availability could represent environmentally driven bottlenecks or narrow windows for transmission that act synergistically as controls on patterns of parasite prevalence and abundance. Consequently, the lower effective population size for *T. boreoarcticus* probably results from a smaller host population and a limited reservoir of infective larvae in habitats utilized for foraging.

Additionally, there is no evidence for geographic segregation for parasite populations between Ekalluk River, Victoria Island and the region of the Rae/Richardson rivers despite isolation by distance across the Coronation Gulf (Fig. 1). Indeed, the presence of similar haplotypes on the mainland in the region of the Rae/Richardson rivers and Victoria Island at Ekalluk River is indicative of extensive gene flow. Muskoxen, however, are relatively sedentary and are not known to cross the straits during the winter (Case et al., 1989). This suggests that barren ground caribou that do cross during annual migrations to Victoria Island (Manning, 1960; Gunn et al., 1997) are hosts for *T. boreoarcticus* (as implied from morphometric data). Dispersal with caribou may account for the degree of cohesion apparent between mainland and insular populations of *T. boreoarcticus* that have been examined; southerly dispersal of caribou from Victoria Island could also influence parasite distribution. The pattern recognized is clearly indicative of widespread movement for parasites mediated by hosts, at least historically.

### Historical biogeography for parasites and hosts

The biogeographic history for the Holarctic and North American fauna is intricate. Periods of intense isolation for host–parasite populations within this assemblage since the late Pliocene and extending through the Quaternary have been mediated by climatic variation and habitat perturbation. Such periodic, sequential and historically defined isolation events occurred at different scales: (1) across the Beringian nexus during interglacials, (2) among refugia in the Nearctic and Palearctic during glacial maxima, (3) north and south of the continental glaciers in North America during stadials, and (4) by secondary range restriction in postglacial habitats since the Pleistocene. Sequential periods of isolation during the Pleistocene in glacial and postglacial refugia and subsequent expansion from refugial centers for hosts are postulated as primary controls on faunal structure for parasites. These have been suggested as the principal determinants for parasite biogeography and biodiversity for Holarctic faunas (Hoberg and Lichtenfels, 1994; Hoberg et al., 1995, 2000). Subsequent introductions and translocation of wild artiodactyls and helminths in the past century are also viewed as a potential factor determining faunal diversity at some localities (e.g., Bye et al., 1987).

Species of *Teladorsagia* are widespread in bovids of the subfamily Caprinae, and it is likely that early diversification of these nematodes was associated with the Caprini and Rupicaprini in Eurasia, with secondary colonization of cervids (see Zarlenga et al., 1998). This appears compatible with the observation that *Teladorsagia* is relatively rare in cervid hosts, or when it does occur, is at a lower prevalence and intensity. A putative basal association with caprines (see Groves and Shields, 1996) and a complicated history for range expansion and geographic segregation both within the Palearctic and Nearctic (e.g., Kurtén and Anderson, 1980; Guthrie, 1982, 1984; Geist, 1985; Groves, 1997) suggest that parasite populations have been repeatedly partitioned by isolation events since at least the late Pliocene. Periodic allopatry associated with small effective populations, and some degree of cospeciation and host-switching, in part may have been the driving mechanism for genealogical diversification of parasites. This history could be consistent with discrete species of *Teladorsagia* in pachycerine sheep and mountain goats in the Nearctic, among wild Caprini and Rupicaprini in the Palearctic, and among muskoxen and caribou across the Holarctic. Mechanisms involved in isolation and speciation of the parasite fauna, however, may not be entirely apparent based on contemporary ecological assemblages because late Pleistocene mammalian communities do not have modern analogues (FAUNMAP Working Group, 1996). In the case of *Teladorsagia,* domestication of sheep over the last 10,000 yr (Ryder, 1984) may also have resulted in intense selection pressure with rapid divergence of parasites in domestic and wild hosts.

The concept of a mosaic fauna in North America and a putative coevolutionary association between *Teladorsagia* and caprines indicates that the ancestor for what may be an assemblage of cryptic species in wild sheep, muskoxen, and goats occurred in Eurasia. It also suggests an origin for *T. boreoarcticus* in the northern Palearctic and subsequent movement across Beringia into the Nearctic with muskoxen or caribou. Further, it is predicted that *T. circumcincta* sensu stricto and *T. boreoarcticus* are not sister-species and otherwise may not be closely related. The latter contention follows from the observation that *Teladorsagia* occurs in geographically disparate and historically isolated host species and populations across the Holarctic (e.g., Kurtén, 1968; Kurtén and Anderson, 1980). For example, *T. circumcincta* was reported in muskoxen, Dall's sheep, bighorn sheep, mountain goat, pronghorn, and some cervids from North America and such hosts as snow sheep, mouflon, argali, other wild sheep, rupicaprines, and cervids from Eurasia and Siberia (Boev et al., 1963; Govorka et al., 1988; Hoberg et al., 2000). Thus, sylvatic faunas endemic to Eurasia, eastern Siberia (Chukhotka), and the arctic, subarctic, and boreal-montane regions of North America may eventually be recognized. A preliminary indicator of broader faunal diversity within *Teladorsagia* and *T. circumcincta* is the discovery of *T. boreoarcticus.*

The history for *T. boreoarcticus* as a component of an Arctic fauna must be examined within the context of biogeography for muskoxen and caribou. Muskoxen originated in Eurasia and are known from the Early Pliocene. In the Late Pliocene and Pleistocene they were represented by a diverse assemblage of now extinct genera and species (Kurtén and Anderson, 1980; Harington, 1987). In the Nearctic, muskoxen entered Alaska as *O. moschatus* about 200 Ka BP or earlier (thousand years before present) and had attained an extensive Holarctic range during the Pleistocene (Kurtén, 1968; Kurtén and Anderson, 1980). In the Palearctic, *O. moschatus* became extinct by 3 Ka BP (Stuart, 1991) but was continuous in the Nearctic and Greenland. Currently, 2 subspecies are recognized, *O. m. moschatus,* on the mainland of Canada and *O. m. wardi,* with a distribution extending across the Arctic archipelago to Greenland. The origin of the extant subspecies may be linked to isolation in Pleistocene glacial refugia north and south of the Laurentide ice during the Wisconsin (Harington, 1961). In the Holocene, populations of muskoxen in the Nearctic were extirpated in Alaska and areas of mainland Canada during the 19th century (Gunn, 1982). Since the 1930s, white-faced muskoxen from East Greenland have been successfully introduced to Alaska and now occur on the Arctic coastal plain following translocation from an original population established on Nunivak Island in 1935–1936 (Bell, 1931; Spencer and Lensink, 1970; Reynolds, 1998). Thus, severe population bottlenecks have characterized the recent history for muskoxen on the mainland of Canada (Groves, 1997).

Caribou probably originated in the Beringian region in the late Pleistocene (Kurtén and Anderson, 1980; Groves and Grubb, 1987). In North America, 4 subspecies are recognized: *R. t. groenlandicus, R. t. granti, R. t. pearyi,* and *R. t. caribou* (Miller, 1982). In the central Arctic, caribou migrate between the mainland and Victoria Island (Gunn et al., 1997), but such movement apparently ceased between 1900 and about 1980 coinciding with declining populations of *R. t. groenlandicus* (Miller, 1982; Gunn, pers. comm.); this represents a population bottleneck for caribou. Populations of caribou in the Nearctic remained historically isolated until the late 19th centry, when semidomesticated reindeer were introduced from Siberia and Norway to Alaska.

Reindeer were first introduced to Alaska in 1890 from eastern Siberia and Norway and by 1920 occupied the entire Seward Peninsula, the coastal plain north to Point Hope and south across the deltas of the both the Yukon and Kuskokwim Rivers. Stock were also introduced to Nunivak Island and St. Matthew Island (see Hadwen and Palmer, 1922; Syroechkovskii, 1995); by 1950 populations were greatly reduced (Elton, 1958). In western Alaska, reindeer were largely parapatric relative to populations of *R. t. granti.* Attempts to introduce reindeer into Canada (to central Yukon; Newfoundland; Fort Smith, NWT; Lake Harbour, Amadjuak Bay, Baffin Island, NWT) from Lapland and Alaska were largely unsuccessful, and reindeer are considered extinct at these localities (Miller and Kellogg, 1955; Scotter, 1972; Graves, 1989). A herd was established on the Mackenzie River Delta based on introductions from Alaska in 1935 and escapes and interbreeding with barren ground caribou may have subsequently occurred (Scotter, 1972; J. Nishi and A. Gunn, pers. comm.). Additionally, in Greenland reindeer of European origin were introduced and released primarily to West Greenland where they exist in geographically isolated pockets confined by natural barriers; populations present are diverse in their origins (Syroechkovskii, 1995).

*Teladorsagia boreoarcticus* concurrently may have a temporally deep and relatively recent history in the Arctic. Both muskoxen and caribou were components of a mammalian megafauna that existed in the Beringian region and across the Holarctic during the Pleistocene (e.g., Vereschchagin and Baryshnikov, 1982; Guthrie 1982, 1984). In Beringia, a diverse artiodactyl community was characterized by extensive sympatry among muskoxen, wild sheep and goats, bison, caribou, and other cervids. This suggests that helminth faunas, particularly those involving trichostrongyloids with direct life cycles, may have been widely shared among ruminant hosts. At the termination of the Pleistocene, climatic variation resulted in habitat discontinuity and the disruption of this community, eventually leading to heightened allopatry (Guthrie, 1984). Extinction of some ruminants and increased allopatry may have constituted limiting factors on parasite faunal diversity or acted as determinants of postglacial isolation for helminths.

Subsequent and more recent population bottlenecks have influenced the distribution of muskoxen and caribou in the Nearctic over the past century (e.g., Gunn, 1982; Miller, 1982; Groves, 1997). These would be expected to have exerted an influence on populations of dependent parasites. If *T. boreoarcticus* is determined to have a Holarctic distribution across Siberia, this would imply that nematodes continued to circulate in *Rangifer* following the extinction of muskoxen. Additionally, it is possible that this species persisted in *Rangifer* from Alaska following extirpation of *Ovibos* in the last century.

These deep historical determinants and recent factors such as local extinctions and introductions of muskoxen and reindeer complicate elucidation of the history for *T. boreoarcticus.* The species may have been introduced with white-faced muskoxen to Alaska (USNPC 41345, 41346; Table III) and probably was established on Nunivak Island and secondarily distributed across the Arctic coastal plain (e.g., at Barter Island, UAM 2572). *Teladorsagia* also appears to have been introduced with reindeer probably from Siberia, in the late 19th century to Alaska (USNPC 19477, 26175, 31435; Table III). It is probable that parasites were introduced with the Mackenzie Herd as indicated by records of "*Teladorsagia trifurcata*" in reindeer from Aklavik, NWT (Choquette et al., 1957). We do not, however, know the population history for these parasites or the degree to which there has been interaction with an endemic fauna or exchange from barren ground caribou to reindeer.

It is clear, however, that *T. boreoarcticus* was historically present in the Canadian Arctic as indicated by its distribution on the mainland near Kugluktuk, at Ekalluk River on Victoria Island and by specimens from Ellesmere Island (Webster and Rowell, 1980) and Banks Island (Ott, 1998). The degree to which subsequent and putative introductions of *Teladorsagia* have influenced the structure and distribution of the fauna remains to be evaluated.

Historical isolation of *T. boreoarcticus* may afford the opportunity to examine the phylogeographic history for parasites and hosts (Avise, 1994). Parasites then become independent adjuncts to elucidating the biogeographic history of their hosts (Hoberg, 1997b) and in this case could be applied to an examination of the biogeographic history for muskoxen in the Canadian Arctic Islands and Greenland. This would assume that parasite populations have effectively been isolated and that there has not been substantial gene flow, but either scenario would be worthy of evaluation.

Discovery of *T. boreoarcticus* and the protostrongylid lungworm, *Umingmakstrongylus pallikuukensis* Hoberg, Polley, Gunn and Nishi, 1995 in *O. moschatus* serves to highlight the paucity of knowledge about the genealogical and numerical diversity of nematode faunas characteristic of artiodactyls at high latitudes across the Holarctic (Hoberg et al., 1995, 2000; Hoberg, 1997a). Discovery of a previously unrecognized species of *Teladorsagia* in muskoxen has additional implications and clearly indicates (1) our knowledge is incomplete relative to those potentially pathogenic parasites that could be exchanged among domestic and wild caprines; (2) we do not have sufficient knowledge of the fauna to understand the ecological control mechanisms (limitations) on dissemination and host range; and (3) poor documentation of faunal diversity hinders development of predictions about global change (climatologically and anthropogenically driven) and potential impacts of emergent parasites and pathogens on populations of large ruminants on which subsistence cultures are dependent in the Arctic (Hoberg 1997a; Hoberg et al., 2000). Examination of these concepts will serve to broaden and define our understanding of historical and geographical influences on the genealogical, ecological and numerical diversity and distribution of nematode faunas in domestic and wild ruminants and the interface between agricultural and natural ecosystems across the Holarctic.

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