CHAPTER 2

Parasites in Ungulates of Arctic North America and Greenland: A View of Contemporary Diversity, Ecology, and Impact in a World Under Change

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Abstract

Parasites play an important role in the structure and function of arctic ecosystems, systems that are currently experiencing an unprecedented rate of change due to various anthropogenic perturbations, including climate change. Ungulates such as muskoxen, caribou, moose and Dall's sheep are also important components of northern ecosystems and are a source of food and income, as well as a focus for maintenance of cultural traditions, for northerners. Parasites of ungulates can influence host health, population dynamics and the quality, quantity and safety of meat and other products of animal origin consumed by people. In this article, we provide a contemporary view of the diversity of nematode, cestode, trematode, protozoan and arthropod parasites of ungulates in arctic and subarctic North America and Greenland. We explore the intricate associations among host and parasite assemblages and identify key issues and gaps in knowledge that emerge in a regime of accelerating environmental transition.

List of acronyms

State or province or Country

AK	Alaska (state of the USA)
GL	Greenland
NL	Newfoundland/Labrador
NT	Northwest Territories (territory of Canada)
QC	Québec (province of Canada)
NU	Nunavut Territory (territory of Canada)
YT	Yukon Territory (territory of Canada)

2.1. INTRODUCTION

2.1.1. The Arctic

The Earth's northern circumpolar regions present landscapes of stunning natural beauty – windswept tundra in the north, boreal coniferous forests to the south, mountains, glaciers and ice sheets. Small, isolated settlements are scattered throughout and are inhabited by people of great resilience who maintain close ties to the land. The northern climate is extreme – long cold winters, short cool summers and, at higher latitudes, months of continuous darkness in winter and of continuous sunlight in summer. These regions also support a unique fauna and flora and provide many valuable non-renewable resources for the world.

In the Nearctic, Alaska (AK), Yukon (YT), Northwest Territories (NT), Nunavut (NU) and Greenland occupy almost eight million square kilometres of the Earth's surface (almost sixteen times the size of France), yet they are home to less than one million people. Approximately three quarters of these northern people live in Alaska and one quarter of the total population are aboriginal, with Greenland (88%) and Nunavut (84%) having the highest, and Alaska (15%) the lowest, proportions.

For many northerners, especially aboriginal peoples, wildlife (mammals, birds and fish) are important sources of food through subsistence hunting, generate economic activity through sport hunting and tourism and are vital for the maintenance of many cultural traditions. For example, in the NT, approximately 40% of the residents aged 15 years and above hunted or fished during 2008 and in almost 30% of households >50% of the food consumed had been acquired by hunting or fishing (Anonymous, 2009).

This circumpolar ecosystem has been shaped over time by a variety of complex biotic and abiotic processes. It continues to undergo significant, and in some instances, accelerating change, much of which results from human activity, both local and distant, and which has the potential for global impact (IPCC, 2007).

2.1.2. Parasites in a changing Arctic

Parasites are important components of the arctic ecosystem, influencing health and sustainability of wildlife populations and the health and well-being of the people who depend on wildlife. Beginning in the 1940s, a succession of parasitologists and ecologists have explored parasitism in the Arctic and advanced understanding of the structure and function of northern host–parasite systems (Rausch, 1974; Hoberg et al., 2012). In recent years, the recognition of rapid change in the North has increased these efforts.

Accelerated climate warming and perhaps other anthropogenic landscape perturbations are having measurable biological impacts on the Arctic, including the ecology of ungulates and host–parasite interactions (IPCC, 2007; Kutz et al., 2009a; Post et al., 2009). Ungulates are important components of any ecosystem, serving as food for various carnivores, omnivores and scavengers. They also influence the abundance and diversity of vegetation and affect soil quality (Danell et al., 2002; Bruun et al., 2008). In the Arctic, ungulates are important sources of food and income as well as a focus of traditional activities for indigenous peoples (AMAP, 2002; Nancarrow and Chan, 2010). Additionally, they provide an important habitat for various helminth, protozoan and arthropod parasites (Hoberg et al., 2008a; Kutz et al., 2009b).

Parasites can cause significant clinical and subclinical disease in wildlife and consequently influence the dynamics and trajectory of wildlife populations (Hudson and Dobson, 1997; Hudson and Greenman, 1998; Irvine et al., 2000). The biodiversity, abundance and impacts of macro and micro parasites in arctic wildlife are highly sensitive to climate and climate change as well as to other anthropogenic disturbances at the landscape level (Kutz et al., 2009a,b; Laaksonen et al., 2010a). The current rate of climate and landscape change in the Arctic is expected to alter host–parasite interactions and is a significant concern for the sustainability of arctic ungulates (Hoberg et al., 2008b; Kutz et al., 2009a; Polley et al., 2010). In addition to direct effects on host populations, changes in parasitism in wildlife can also have significant impacts on the people who depend on wildlife. Parasites can affect the quality, quantity and safety of meat and other products of animal origin consumed by people and changes in parasite biodiversity and/or in associated disease processes can influence nutrition, activity levels and the sustainability of cultural activities for northern aboriginal peoples (Davidson et al., 2011).

Although parasitism is often portrayed as a negative process, parasites play important roles and provide unique insights into the historical and current status and health of ecosystems. They reflect trophic interactions in food webs, are often in themselves an important food source in an ecosystem and may modulate the effects of contaminants in hosts (Lafferty et al., 2008; Johnson et al., 2010). Parasites can provide information on the presence of, and direct or indirect interactions with, sympatric species as well as temporal and spatial patterns of habitat use (Hoberg, 2010). Healthy ecosystems typically have a diverse assemblage of parasites, reflecting diversity of definitive and intermediate host species and vectors. Detection of the 'normal' complement of parasites can be indicative of a healthy ecosystem (Hudson et al., 2006). Conversely, detection of non-endemic/invasive parasites or a depauperate parasite community can suggest otherwise. Contemporary arctic host–parasite assemblages have been strongly influenced by dynamic shifts in climate and invasive processes, particularly over the Pleistocene. Parasites can thus also reflect and provide insights into host evolutionary history and the complex historical interactions that have structured ecosystems in space and time (Hoberg and Brooks, 2008; Hoberg et al., 2012c).

To use parasites as indicators, and to track and predict changes in parasitism and animal health, comprehensive data on parasite biodiversity, distribution and lifecycles are required (Hoberg et al., 2003; Hoberg and Brooks, 2008; Hoberg et al., 2008b). Although considerable progress in defining the diversity and ecology of parasites of arctic ungulates has been made, there remain substantial knowledge gaps. In this chapter, we review the current known biodiversity, ecology and impacts of parasites in arctic ungulates of North America, including Greenland. We identify knowledge gaps and emerging issues and suggest future research directions. We define 'arctic' ungulates as those species naturally and consistently found in the subarctic and arctic regions as outlined by *Conservation of Arctic Flora and Fauna* (CAFF) (Fig. 2.1) and focus on caribou (*Rangifer tarandus* ssp.), muskoxen (*Ovibos moschatus* ssp.), moose (*Alces americanus* ssp.) and Dall's sheep (*Ovis dalli dalli*).

2.2. ARCTIC UNGULATE HOSTS

2.2.1. Caribou – *Rangifer tarandus* ssp.

Caribou and reindeer are widespread and abundant across the North American (Figs. 2.2a–c), European and Asian Arctic regions, with a global population of 3.8 million individuals and an estimated North American

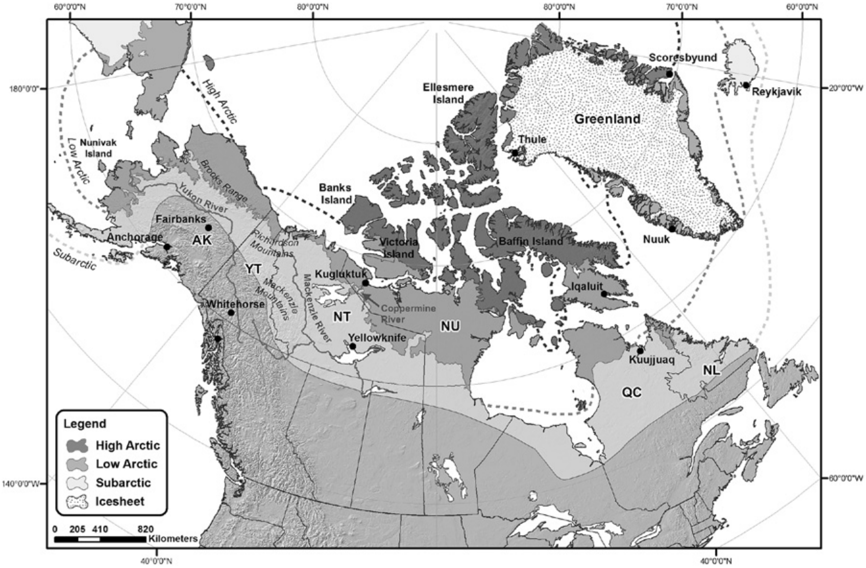

FIGURE 2.1 Map of the North American Arctic showing important political and geographic boundaries, including definition of the Subarctic, low and high Arctic. The latter information adapted from Conservation of Arctic Flora and Fauna (CAFF, 2010). Map created by N. Pamperin, Alaska Department of Fish and Game.

population of approximately 1.5 million (Geist, 1998; Vors and Boyce, 2009; Russell and Gunn, 2010). Through subsistence harvests, sport hunting and tourism, caribou are important sources of food and income for northern aboriginal people as well as a key focus for many traditional activities (Ferguson and Messier, 1997; Jean and Lamontagne, 2004). Meat replacement value for a caribou carcass in the North American Arctic is estimated to be between C$500 and 1,000 and represents a market of tens of millions of dollars per year (Usher, 1976; Ashley, 2000; Tesar, 2007).

Several subspecies and ecotypes of caribou are recognized in North America (Banfield, 1961; Miller, 1998); however, the current classification is likely to be modified by recent genetic studies (McDevitt et al., 2009; Courtois et al., 2010; Festa-Bianchet et al., 2011). Here, we include all extant *Rangifer* subspecies living in the high, low and subarctic and define them based both on ecotype and current subspecies designation. This includes the migratory barren-ground caribou (*R. t. groenlandicus*) occurring in several disjunct populations in Greenland and across most of the mainland tundra in NU and NT, Canada; forest and migratory Grant's caribou (*R. t. granti*) in YT and AK; forest (boreal) and mountain dwelling woodland caribou (*R. t. caribou*) throughout the boreal forest and mountain regions and migratory woodland caribou in northern Quebec (QC) and

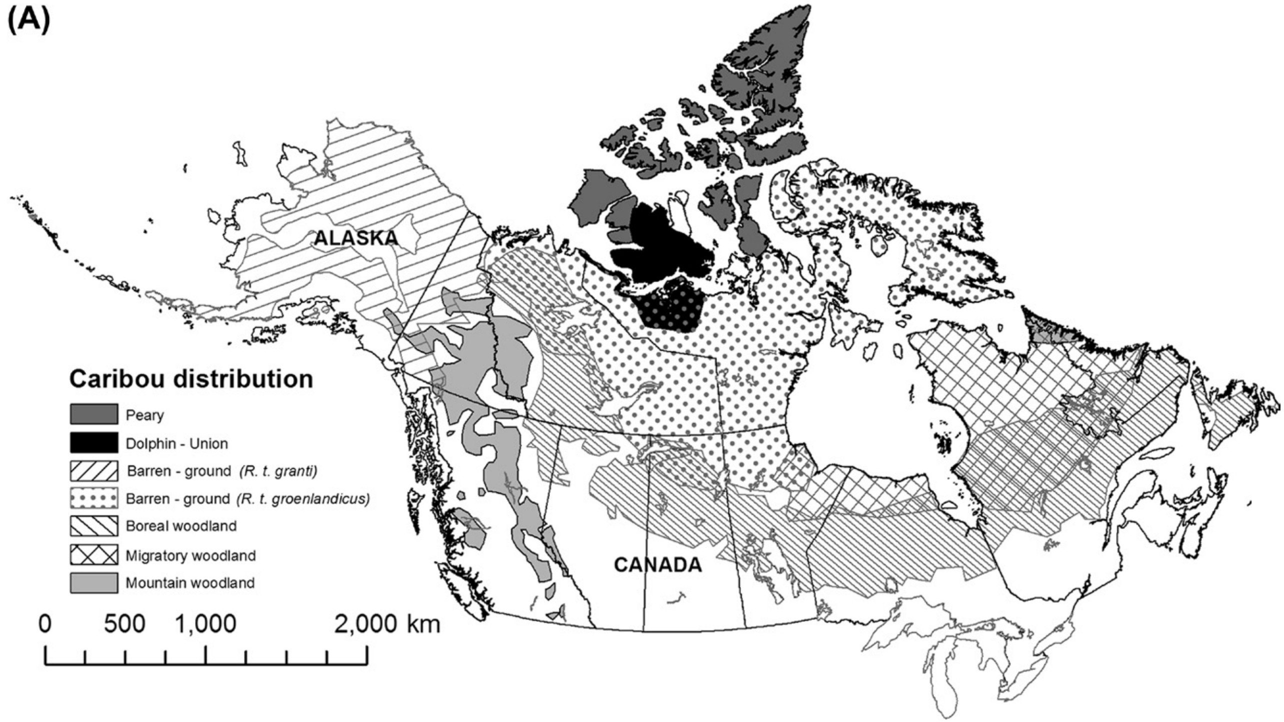

FIGURE 2.2 Distribution of caribou in (A) Canada and Alaska, USA (ecotypes indicated).

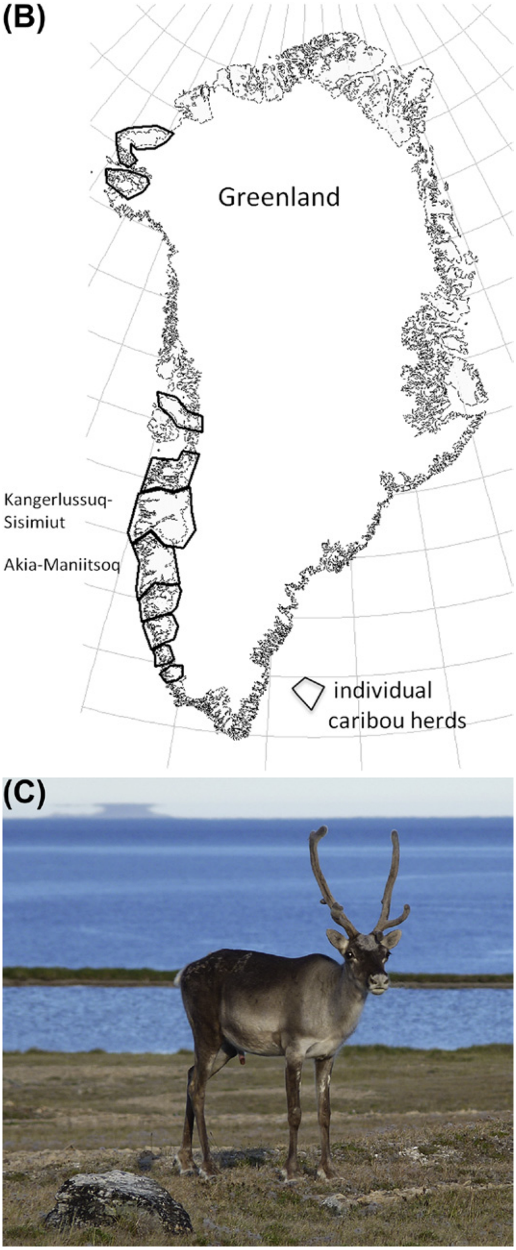

FIGURE 2.2—cont'd (B) Greenland. (C) An adult male Dolphin-Union caribou. Canada/Alaska map created by N. Pamperin and J. Wells, Alaska Department of Fish and Game. Greenland map adapted from that by Christine Cuyler, Greenland Institute of Nature. Caribou photograph by S. Kutz. (For color version of this figure, the reader is referred to the web version of this book.)

Labrador; Peary caribou (*R. t. pearyi*) on the arctic islands and introduced Eurasian semi-domesticated reindeer (*R. t. tarandus*) in western AK, near Tuktoyaktuk, NT, and in various locations in Greenland.

Caribou in North America are thought to have been isolated in two separate glacial refugia during the terminal Pleistocene. *Rangifer t. pearyi*, *R. t. groenlandicus* and *R. t. granti* originated from the Beringian–Eurasian lineage and *R. t. caribou* originated from the North American lineage which was isolated south of the ice sheets and then rapidly spread north and west across the boreal region in the Holocene (Flagstad and Røed, 2003; Cronin et al., 2005; Røed, 2005; McQuade-Smith, 2009). The historical biogeography of *Rangifer* species, together with differences in ecology among 'ecotypes', and multiple introductions and subsequent movements of Eurasian reindeer in the late 1800s and early 1900s (Siem, 1913), no doubt has had an important influence on the contemporary parasite fauna (Lankester and Fong, 1989; Hoberg et al., 2012c).

Migratory caribou herds naturally undergo substantial cyclic fluctuations with more than a 10-fold change in population size (Bergerud, 2000; Couturier et al., 2004). Additive anthropogenic stressors and direct mortality, such as hunting and injury loss, as well as industrial development, roads, climate change and disease, are thought to have significant impacts and may exacerbate the episodic population fluctuations (Forchhammer et al., 2002; Kutz et al., 2009b; Vors and Boyce, 2009; Russell and Gunn, 2010; Festa-Bianchet et al., 2011).

Pronounced population cycles are not recognized for woodland caribou but significant declines in population size and range for this subspecies have been attributed mainly to anthropogenic disturbance and habitat loss (Vors et al., 2007; Festa-Bianchet et al., 2011; Wasser *et al.*, 2011). For Peary caribou on the high arctic islands, periodic events of icing of the snow surface, which prevent access to food, are considered a major cause of starvation-related mortality (Miller and Barry, 2009). Peary caribou and woodland caribou are considered 'endangered' or 'threatened' across most of their range and barren-ground caribou are listed as 'of special concern', by the Species at Risk Act in Canada (http://www.sararegistry.gc.ca/).

2.2.2. Muskoxen – *Ovibos moschatus* ssp.

Muskoxen are the second most abundant ungulate in the Arctic and, as with caribou, they serve as an important source of subsistence food and income for aboriginal people, the latter through commercial and sport hunting and sale of fibre (qiviut) (Nuttal et al., 2010). Unlike caribou, they are relatively sedentary animals and do not undergo extensive seasonal migrations.

There are two recognized subspecies of muskoxen, both of which have been influenced by historical extinction and extirpation as well as recent patterns of introduction. *Ovibos moschatus moschatus* is endemic on mainland NT and NU whereas the 'island' or 'white-faced' muskox, *O. m. wardii*, has ranged historically across most of the arctic islands and eastern Greenland (Fig. 2.3a–c) (Campos et al., 2010). There are approximately 105,000 naturally occurring individuals in the NT and NU (Anonymous, 2011b). They are most abundant on Victoria and Banks Islands, Canada, and have been harvested commercially at these locations since the mid-1970s to provide meat and fibre for sale to the public (Gunn et al., 1991b). The population in east Greenland is over 10,000 (C. Cuyler, pers. comm.).

In addition to these naturally occurring populations, a number of translocated herds are established in AK, YT, northern QC and west Greenland. *Ovibos m. wardi* herds in AK and YT resulted from a series of translocation events that began in 1930 with 34 muskoxen from east Greenland brought to Fairbanks, AK, via the Copenhagen Zoo. In 1935–1936, 31 muskoxen from Fairbanks were introduced to Nunivak Island, AK in the Bering Sea. These animals thrived and created a source population of animals that have since been transplanted to various locations around AK (Paul, 2009). Today, there are approximately 4750 muskoxen in AK (Harper, 2009). Range expansion of a population introduced to northeast AK has resulted in approximately 150–200 muskoxen in YT and NT west of the Mackenzie River (Gunn et al., 1991b; Reynolds, 1998; ADFG, 2011b; Anonymous, 2011a,b).

Ovibos m. wardi were also introduced to northern QC in 1967. Fifteen muskoxen were translocated from Ellesmere Island (NU) and held captive near Kuujjuaq as an agricultural initiative (Le Hénaff and Crête, 1989). Between 1973 and 1983, this herd was gradually released from captive management and the free-ranging population has grown in size to approximately 1500–2000 individuals ranging mainly between the communities of Kuujjuaq and Tasiujaq, QC and gradually expanding into Labrador (Chubbs and Brazil, 2007).

Twenty-seven muskox calves from east Greenland were translocated to the Kangerlussuaq region in west Greenland from 1962–1965 via the Copenhagen Zoo. This population subsequently served as the source population for several more translocations in west Greenland (Clausen, 1993) (Fig. 2.3b). These series of translocations and introductions (in Greenland, Alaska and Canada) has likely influenced the diversity and distribution of parasites in muskoxen, and perhaps sympatric species, in the Arctic (Hoberg et al., 1999; Kutz et al., 2007).

2.2.3. Moose – *Alces americanus* ssp.

Two subspecies of moose are found in the North American Arctic (Fig. 2.4a and b). East of the Mackenzie Mountains are *Alces a. andersoni* and in and to the west of the mountains is the much larger subspecies *A. a. gigas* (Bowyer et al., 1998; Hundertmark and Bowyer, 2004). Approximately 275,000 moose are found in arctic North America with the vast majority of these

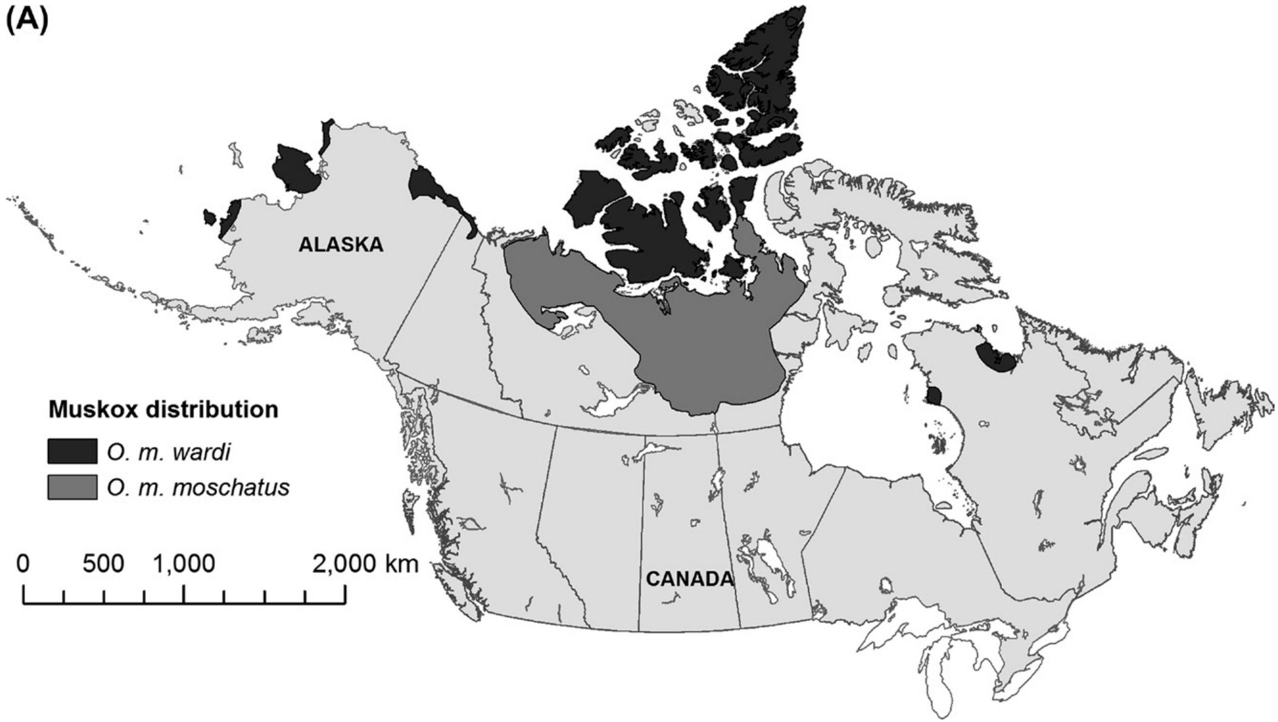

FIGURE 2.3 Distribution of muskoxen in (A) North America.

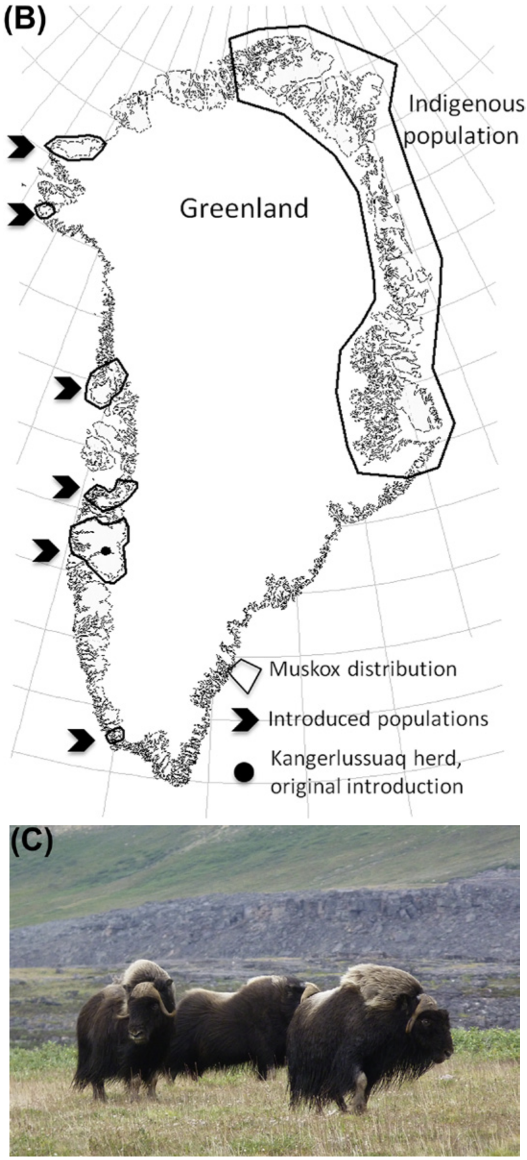

FIGURE 2.3—cont'd (B) Greenland. Translocations of muskoxen to east Greenland indicated. ©. (C) Adult male muskoxen, *O. m. wardi,* from Victoria Island, Nunavut. Canada/Alaska map created by N. Pamperin and J. Wells, Alaska Department of Fish and Game. Greenland map adapted from that by Christine Cuyler, Greenland Institute of Nature. Muskox photograph by S. Kutz. (For color version of this figure, the reader is referred to the web version of this book.)

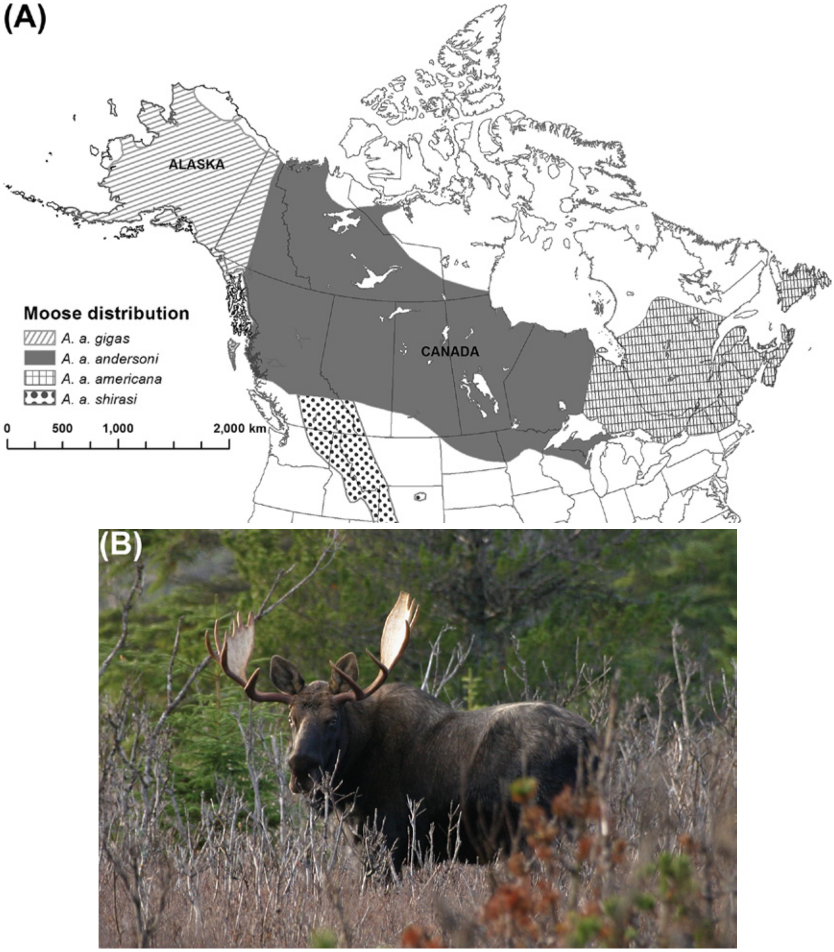

FIGURE 2.4 (A) Distribution of moose in arctic and subarctic North America, (B) Alaskan moose (*A. a. gigas*). Map created by N. Pamperin and J. Wells, Alaska Department of Fish and Game. Moose photograph by J. Jemison, Alaska Department of Fish and Game. (For color version of this figure, the reader is referred to the web version of this book.)

(~200,000) in AK; 65,000 in YT and 10,000 in NT and NU (Franzmann and Schwartz, 1998). Moose are not present in Greenland. There have been moose translocations within AK (Paul, 2009) but no introductions of moose into northern Canada or AK.

Although primarily forest dwelling, both subspecies are found along rivers and lake shores on the tundra extending north to the arctic coast. Moose are an extremely important source of food for people in the boreal forest regions across northern Canada and AK (Lynch, 2006; Larter, 2009).

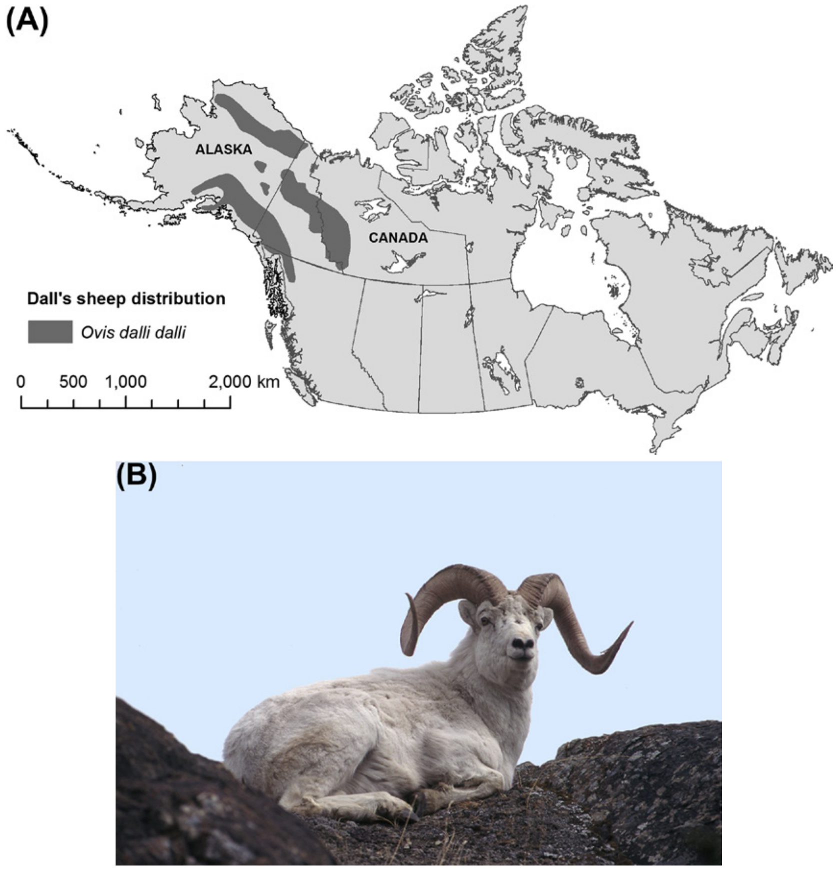

FIGURE 2.5 (A) Distribution of Dall's sheep in arctic and subarctic North America, (B) Adult male Dall's sheep. Map created by N. Pamperin and J. Wells, Alaska Department of Fish and Game. Photograph by S. Arthur Alaska Department of Fish and Game. (For color version of this figure, the reader is referred to the web version of this book.)

2.2.4. Dall's Sheep – *Ovis dalli dalli*

Dall's sheep are common, occurring in disjunct populations throughout the mountainous regions of AK and the western Canadian Arctic and Subarctic (Fig. 2.5b) (ADFG, 2011a; Anonymous, 2011c; ENR, 2011). There are approximately 45,000 in NU and NT and 50,000–64,000 in AK. They are absent from the Arctic islands and Greenland. In general, populations are healthy and stable across their range. Dall's sheep have not been translocated within the Canadian North and only a single unsuccessful introduction has occurred in AK (Paul, 2009). There is some subsistence hunting of Dall's sheep as well as a strong recreational-hunting industry that provides significant income to the northern economy (e.g., ENR, 2011).

2.2.5. Other ungulate hosts

Mountain goats (*Oreamnos americanus*) just barely extend into the subarctic in southern AK, and the Mackenzie Mountains, NT and southern YT, Canada. Population numbers are low and these animals are not used to any significant extent for food or sport hunting. Mountain goats have a distributional history in western North America, which parallels that of wild sheep, with both being represented by strongly disjunct populations across mountainous terrain (Loehr et al., 2006; Shafer et al., 2011). Compared to other arctic ungulates, these ranges indicate relatively limited vagility, which may be expected to have an influence on the distribution of parasites (Hoberg et al., in press-a).

Wood bison (*Bison bison athabascae*), introduced plains bison (*Bison bison bison*), mule deer (*Odocoileus hemionus*), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), occasionally white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*) are found in the Subarctic as defined by CAFF and have distributions that are either parapatric (with minimal overlap) or have some degree of sympatry with the arctic ungulate species described above. These other bovids and cervids are more typical of temperate ecosystems. Although introduced elk populations are established in southern and central YT, these will not be considered in detail in this chapter. They are, however, potentially important in the context of ecological perturbation and northward range expansion and invasion for assemblages of hosts and parasites (e.g. Hoberg and Brooks, 2008; Kutz et al., 2009b; deBruyn, 2010; Hoberg, 2010).

2.3. NEMATODES

Nematodes are important parasites in ungulates globally (Anderson, 2000). Nematodes of the orders Strongylida, Oxyurida, Trichocephalida and Spirurida are found in ungulates of Arctic North America and more broadly across the Holarctic region (Priadko, 1976). Species among these orders are found in a variety of developmental stages in almost all host tissues and maintain a diversity of lifecycles.

2.3.1. Nematodes of the gastrointestinal tract

Gastrointestinal nematodes of arctic ungulates are referred to three orders, including Strongylida, Oxyurida and Trichocephalida. The strongyles, or bursate nematodes, are the most diverse and abundant. Among the stronglyes, members of the subfamilies Ostertagiinae and Nematodirinae are dominant in terms of taxonomic and numerical diversity (Hoberg et al., 2001) (Fig. 2.6). Species richness in these groups is the greatest in the Palaearctic coinciding with a Eurasian centre of origin for the fauna and declines on a longitudinal gradient from west to east into North America

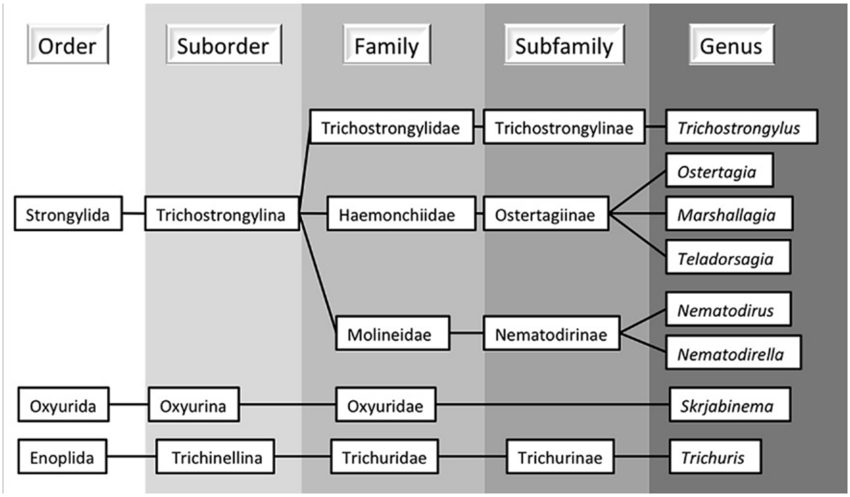

FIGURE 2.6 Gastrointestinal nematodes reported from ungulates of arctic North America, including Greenland. Nomenclature is consistent primarily with Anderson (2000), with some modifications within the Strongylida (Hoberg and Lichtenfels, 1994; Durette-Desset al., 1994, 1999; Carreno and Hoberg, 1999; Chilton et al., 2006).

(Hoberg et al., 2012c). Adult nematodes of most species, including both males and females, generally can be identified on the basis of morphology (e.g. Lichtenfels and Pilitt, 1983a; Lichtenfels and Hoberg, 1993). In contrast, diagnostics at the generic and species level for eggs and larvae remains problematic but is increasingly being addressed through application of DNA-based techniques (reviewed in Lichtenfels et al., 1997; Dallas et al., 2000a,b). Integrated methods incorporating both morphological characters for adults and molecular sequence data for adults and larvae are now considered standard in conducting survey and inventory and for exploring the occurrence of cryptic diversity in ungulate nematode faunas (e.g. Hoberg et al., 2001; Leignel et al., 2002; Jenkins et al., 2005a).

(a) Host and Geographic Range. Knowledge of the diversity and host and geographic distributions of gastrointestinal nematodes in ungulates of arctic North America and Greenland is based primarily on cross-sectional and opportunistic studies focussed on a single host species or at a single location (e.g. Gibbs and Tener, 1958; Nielsen and Neiland, 1974; Samuel and Gray, 1974; Fruetel and Lankester, 1989; Korsholm and Olesen, 1993; Simmons et al., 2001). Ostertagiines (species of *Teladorsagia*, *Ostertagia* and *Marshallagia*) and Nematodirines (species of *Nematodirus* and *Nematodirella*) are found in mixed species infections in individual hosts across most of their range whereas the occurrence of Oxyuridae and Trichuridae is more variable among regions and host species. Many of these parasites can infect

a variety of ungulate species but their relative abundance differs across hosts and geographic regions. For abomasal nematodes, *Ostertagia gruehneri* is most common in caribou; *Teladorsagia boreoarcticus* is most common in muskoxen and *Marshallagia* cf. *marshalli* is most common in Dall's sheep (Nielsen and Neiland, 1974; Fruetel and Lankester, 1989; Hoberg et al., 1999; Simmons et al., 2001). In caribou and muskoxen, *Marshallagia* tends to be restricted to the mountainous regions and arctic islands and is uncommon on the mainland tundra. For the Nematodirinae, species diversity and abundance tend to be greater in muskoxen and Dall's sheep compared to caribou and moose (Nielsen and Neiland, 1974; Hoberg et al., 2001). One exception may be the Kangerlussuaq-Sisimiut caribou herd of west Greenland where faecal examinations revealed an unusually high prevalence of nematodirine eggs in adult females (J. Steele, S. Kutz, C. Cuyler, unpubl. data).

(b) *Ecology*. The ostertagiine and nematodirine nematodes infecting northern ungulates have direct life cycles. Adults live in the gastrointestinal tract and eggs are shed in the host's faeces. Larval development to the infective third stage (L3) occurs in the external environment and development and survival rates are related to climatic condition (O'Connor et al., 2006). Development of larvae to the infective stage may occur before (Nematodirinae) or after (Ostertagiinae) hatching from the egg. For the Trichuridae, the infective larva remains in the egg. Infective larvae (or eggs with L3) are passively ingested by the final hosts during grazing. Eggs and/or larvae of some species in domestic ungulates can persist in the environment over winter if not ingested by a host within the first year (O'Connor et al., 2006). Once ingested, larvae pass through the digestive tract until they reach their final location in either the abomasum or the intestine. Here, the larvae migrate into the mucosa where they develop to a fourth larval stage (L4). Development to adults is typically completed in the lumen. Under certain environmental and/or host conditions, the L4 of several ostertagiine nematodes may undergo inhibited development in the mucosa, delaying the completion of their life cycle for several months (Eysker, 1993; Sommerville and Davey, 2002).

(b) *Impacts*. The impacts of gastrointestinal nematodes on wildlife species are relatively unstudied, but they can negatively influence body condition, physiology (notably reproductive success) and behaviour of free-ranging ungulates (Albon et al., 2002; Stien et al., 2002; Morgan et al., 2005). In domestic livestock, ostertagiine and nematodirine nematodes are significant pathogens and can cause subtle to severe disease with impacts on food intake, nutrient absorption and body condition, ultimately reducing overall productivity (Holmes, 1987). Some of the most severe disease impacts result from parasites migrating from the mucosa to the lumen of the gastrointestinal tract during development and transition from parasitic larvae to adult stages (Myers and Taylor, 1989). The Trichuridae tend to be parasites of young animals and can cause significant diarrhoea in heavily infected domestic livestock. The Oxyuridae do not appear to cause significant production loss in domestic livestock.

2.3.1.1. Subfamily Ostertagiinae

Nomenclature and Taxonomy

Trichostrongyline nematodes of the subfamily Ostertagiinae are common abomasal parasites of arctic ungulates. Challenges associated with defining species limits within this group have hindered the understanding of the geographic patterns and host associations of these parasites (Dróżdż, 1995). In parallel to most helminth groups, numerous generic and species designations have been assigned over time and evaluation of the literature requires a knowledge of these synonymies. This problem is heightened among the ostertagiines because polymorphism (multiple morphologically distinct forms within a species) occurs among adult males in five of 15 genera of the subfamily (Dróżdż, 1995; Hoberg et al., 2009). For example, historically for some species, discrete differences in structural characters of the genital cone and spicules resulted in identification of individuals as different nominal species, often in separate genera (Gibbons and Khalil, 1982). Only later was it recognized that these morphological differences defined the major and minor morphotypes of single species (Dróżdż, 1995). Since the recognition of polymorphism in the 1970s, the phenomenon has been extensively corroborated based on cross-breeding experiments, morphology, ecological studies and DNA sequence data (Daskolov, 1974; Dróżdż, 1974; Lancaster and Hong, 1981; Lichtenfels and Hoberg, 1993; Dróżdż, 1995; Hoberg et al., 1999, 2001). Major morphotypes are defined by their numerical dominance (relative to minor morphotypes) within infrapopulations of single hosts and appear to represent a balanced polymorphism (Daskolov, 1974; Dróżdż, 1974; Dróżdż, 1995), although seasonal variation in relative abundance has been noted (e.g. Hoberg et al., 1999). The recognition, application and misapplication of polymorphism among males have considerably confused the taxonomy and description of ostertagiinae genera and species over the past century (Dróżdż, 1995; Hoberg et al., 1999). Several arctic ostertagiines, including species of *Ostertagia, Teladorsagia* and *Marshallagia*, are polymorphic (Table 2.1) (Lichtenfels and Pilitt, 1989; Lichtenfels et al., 1990; Hoberg et al., 1999; Hoberg et al., in press-a,b). Throughout the chapter, we adopt the following convention for naming these polymorphic species. When it first appears in the text, the latin binomials are presented for each morphotype, with the major morph given first, for example, *Marshallagia marshalli/M. occidentalis*, *Teladorsagia circumcincta/T. trifurcata/T. davtiani* or *T. boreoarcticus* f. major/f. minor A/f. minor B in the standard notation

TABLE 2.1 Major and minor morphs for ostertagiines recovered from arctic host species

Major morphotype	Minor morphotype
Marshallagia marshalli	*M. occidentalis*
Marshallagia lichtenfelsi	f. minor
Ostertagia gruehneri	*O. arctica*
Teladorsagia boreoarcticus	f. minor A, f. minor B
T. circumcincta[a]	*T. trifurcata/T. davtiani*

[a] Is included here for completeness; however, most, if not all records likely represent *T. boreoarcticus* or an as yet unidentified species (Hoberg *et al.*, 1999, 2001, 2012a, 2012b).

currently adopted (Dróżdż, 1995; Hoberg et al., 1999). Following this first appearance in the text, we dispense with the exhaustive listing and use only the nominal major morphotype to designate the species.

Another more general issue that affects our understanding of diversity for trichostrongyloids is the presence of cryptic species (Pérez-Ponce de Leon and Nadler, 2010). An example is *T. boreoarcticus* described from muskoxen of the central Canadian Arctic in 1999 (Hoberg et al., 1999). Prior to the description of this species, all arctic specimens of *Teladorsagia* were identified as *T. circumcincta* or one of its minor morphotypes, which are common parasites of domestic sheep (Hoberg et al., 2012b). *Teladorsagia circumcincta* was considered to represent a morphologically variable taxon with a considerable host range and broad geographic distribution and as such was an example of a widespread species (Hoberg et al., 1999). This species and *T. boreoarcticus* are similar in appearance but can be distinguished on the basis of morphological characteristics and mitochondrial DNA and it is now known that *Teladorsagia* sp. in muskoxen across their North American range is *T. boreoarcticus* (Hoberg et al., 1999). The discovery of *T. boreoarcticus* may indicate the occurrence of a taxonomically diverse complex of cryptic species within *Teladorsagia* circulating in domesticated and free-ranging ungulates. The species limits for this complex have yet to be adequately explored (Hoberg et al., 1999; Leignel et al., 2002; Hoberg et al., 2012b) but have fundamentally changed our understanding of the history, structure and diversity of ungulate helminth faunas in the Holarctic region (e.g. Hoberg et al., 2008a; Hoberg, 2010). Another cryptic species within the *Teladorsagia* complex has also been proposed at temperate latitudes (Leignel et al., 2002; Grillo et al., 2007) and species complexes may also exist for *Marshallagia* in North American ungulates (Lichtenfels et al., 1997; Hoberg et al., 2012a).

2.3.1.1.1. *Ostertagia gruehneri/O. arctica*

(a) *Host and Geographic Distributions.* Across the Holarctic region, *O. gruehneri* is the most common gastrointestinal nematode of all subspecies of *Rangifer* with prevalence approaching (Table 2.2) 100% both within and

TABLE 2.2 Gastrointestinal nematodes reported from ungulates of arctic North America, including Greenland. The range of prevalence reported is indicated below the parasite name. Only prevalence estimates based on sufficient sample sizes are included. Data compiled from available published and grey literature.

Host, Parasite (range of prevalence)		Herd, region or nearest place name
Caribou		
Marshallagia marshalli	AK	Not specified[a]; Fairbanks[b]
	NT	Banks Island[a,b]
	NU	Dolphin-Union[c]; Kugluktuk[a]
	GL	Kangerlussuaq-Sisimiut[d]
Ostertagia gruehneri	AK	Not specified[e]; Spruce Creek, Mulchatna, Northern Alaska Peninsula[b]
	YT	Chisana[f]
	NT	Beverly[e,g];Bathurst[h]
	NU	Kugluktuk[a]; Dolphin-Union[c]; Not specified[e]; Bathurst Island[b]
	GL	Akia-Maniitsoq[i]
Teladorsagia boreoarcticus	AK	Golovin[j]; Unalakleet[j]; Mulchatna, Northern Alaska Peninsula[b]
	YT	Chisana[f]
	NT	Banks Island[k]; Hope Lake[j]; Bathurst[h]
	NU	Dolphin-Union[k]; Kugluktuk[b]
Teladorsagia circumcincta[w]	AK	Not specified[l]
	NT	Beverly[g]
	NU	Dolphin-Union[c]
	GL	Kangerlussuaq-Sisimiut[e]
Nematodirella longissimespiculata	AK	Not specified[m]; Egavik, Kivalina, Fakotna, Round Up[b]
	NT	Beverly[g]
Nematodirus tarandi	AK	Takotna[b]
	NT	Beverly[g]
Skrjabinema tarandi	AK	Arctic Slope; Barrow; Brooks Range[n]
	NT	Beverly[g,n]
Dall's sheep		
Cooperia spp.	AK	Granite Mountains[o]
Marshallagia marshalli - (18–100%)	AK	Dry Creek, Kenai Peninsula, Interior[o]; Not specified[u]
	NT	Central Mackenzie Mountains[p]
Ostertagia gruehneri	NT	Central Mackenzie Mountains[p]
Ostertagia gruehneri[y] (8%)	AK	Dry Creek, Interior[o]

TABLE 2.2 (*continued*)

Host, Parasite (range of prevalence)		Herd, region or nearest place name
Teladorsagia circumcincta[##] (2–67%)	AK	Dry Creek, Interior, Kenai Peninsula[o]
Nematodirella species	AK	Dry Creek[o]
Nematodirus archari or	AK	Dry Creek[o,q]; Kenai Peninsula[o]
N. andersoni[y] (58–82%)	NT	Central Mackenzie Mountains[p]
Nematodirus davtiani	AK	Dry Creek, Kenai Peninsula[o]
(48–77%)	NT	Central Mackenzie Mountains[p]
Nematodirus oiratianus (13–65%)	AK	Dry Creek, Kenai Peninsula[o]; Not specified[v]
	NT	Central Mackenzie Mountains[o]
Nematodirus spathiger	AK	Dry Creek, Kenai Peninsula[o]
(38–83%)	NT	Central Mackenzie Mountains[p]
Skrjabinema sp. (19,100%)	AK	Windy Gap, South Central; Dry Creek, Kenai Peninsula[o]
Skrjabinema ovis	NT	Central Mackenzie Mountains[p]
Trichuris sp. (25–85%)	AK	Windy Gap, South Central; Dry Creek, Granite Mountains, Kenai Peninsula[o]
Trichuris schumakovitschi	NT	Central Mackenzie Mountains[p]
Moose		
Nematodirella alcidis	AK	Not specified[a,m]; Palmer[b]
Muskoxen		
Marshallagia marshalli	AK	Not specified[a,m,u]
	NT	Banks Island[b]
	NU	Devon and Ellesmere Islands[r]; Victoria Island[c]
Marshallagia species	AK	Nunivak[s]
	NU	Bathurst Island[s]
Teladorsagia boreoarcticus	AK	Barter Island[j]
(100%)	NT	Banks Island[b,h]
	NU	Cox Lake and Rae River near Kugluktuk; Victoria Island (Ekalluk River)[j]; Ellesmere Island[j,r]
Teladorsagia circumcincta[##]	NU	Thelon[t]; Victoria Island[d]
Nematodirella sp.	NU	Cox Lake near Kugluktuk[c]; Ekalluk River, Victoria Island[b]
Nematodirella alcidis	AK	Nunavik Island[b]
	NU	Kugluktuk[a]; Victoria Island[a]

(*continued*)

TABLE 2.2 *(continued)*

Host, Parasite (range of prevalence)		Herd, region or nearest place name
Nematodirella gazelli	NU	Bathurst Island[m,s]
Nematodirella longissimespiculata	AK	Barter Island[a]; College[m]
	NT	Banks Island[b]
	NU	Thelon Game Sanctuary[t]
Nematodirus helvetianus	AK	College[b]
	NT	Banks, Island[b]
	NU	Banks Devon and Ellesmere Islands[b,r]
Nematodirus tarandi	AK	Nunavik Island[b]; College[b]
	NT	Aklavik[b]
	NU	Rae River and Cox Lake[b]; Ekalluk River[b]

[a] Hoberg *et al*. (2001).

[b] USNPC, (2011).

[c] Hughes *et al*. (2009);

[d] Korsholm and Olesen (1993).

[e] Lichtenfels *et al*. (1990).

[f] Hoar *et al*. (2009).

[g] Fruetel and Lankester (1989).

[h] B. Hoar, J. Invik, S. Kutz, E. Hoberg (unpubl. obs.).

[i] J. Steele, S. Kutz, C. Cuyler, E. Hoberg (unpubl obs.).

[j] Hoberg *et al*. (1999).

[k] Hoberg *et al*., (2012b).

[l] Becklund (1962).

[m] Lichtenfels and Pilitt (1983a).

[n] Schad (1959).

[o] Nielsen and Neiland (1974).

[p] Simmons *et al*., (2001).

[q] Rickard and Lichtenfels (1989).

[r] Webster and Rowell (1980).

[s] Samuel and Gray (1974).

[t] Gibbs and Tener (1958).

[u] Lichtenfels and Pilitt (1989).

[v] Lichtenfels and Pilitt (1983b).

[w] *Teladorsagia circumcincta* is an apparent misidentification in the Dolphin-Union Herd and should be referred to *T. boreoarcticus* (Hoberg *et al*., in pressb). Other populations of *T. circumcincta* reported in northern ungulates (with the possible exception of Greenland) are considered to be *T. boreoarcticus* or may be included in a putative complex of species circulating in free-ranging ungulates, which excludes *T. circumcincta* (Hoberg *et al*., 1999, 2001, 2012b).

[x] Records attributed to *Nematodirus archari* in Dall's sheep may be referred to another species endemic to North America, *N. andersoni* according to Durette-Desset and Samuel (1989). Additional studies are required to establish if *N. archari* is a Holarctic species (Rickard and Lichtenfels, 1989).

[y] Nielsen and Neiland (1974) originally reported *O. ostertagi* in Dall's sheep from Dry Creek, AK. These specimens were re-determined as *O. gruehneri* by E.P. Hoberg and A. Abrams. All northern records of *O. ostertagi* in isolated populations of free-ranging hosts are likely referable to *O. gruehneri*.

across most caribou and reindeer herds examined (Bye and Halvorsen, 1983; Bye, 1987; Bye et al., 1987; Irvine, 2000; Irvine et al., 2001; Hrabok et al., 2007; Hoar et al., 2009). The ubiquitous nature of *O. gruehneri* in *Rangifer* may reflect the biogeographic history for these cervids and particularly the history of expansion for host populations linking Eurasia and North America, as well as expansion in the Nearctic (Hoberg et al., 2012b).

Ostertagia gruehneri does appear to be absent from one natural population of caribou in Greenland. In a small survey of the Kangerlussuaq-Sisimiut caribou herd in west Greenland, *O. gruehneri* was not found and other ostertagiines, *Teladorsagia* sp. (reported as *T. circumcincta* but may be *T. boreoarcticus* or both) and *Marshallagia* sp. appeared to dominate the abomasal fauna (Korsholm and Olesen, 1993). Recent post-mortem data support this pattern and also demonstrate that *O. gruehneri* is present in the Akia-Maniitsoq caribou herd immediately to the south of, but physically isolated from, the Kangerlussuaq-Sisimiut herd (J. Steele, S. Kutz, C. Cuyler unpub. obs.). Environmental conditions in the Kangerlussuaq region are relatively mild and generally seem to be suitable for development of *O. gruehneri.* The absence of the parasite in this herd may be because it did not establish with the founding animals or because transmission was not sustained during periods of low host density. The west Greenland caribou herds were established by sporadic natural colonization events by only a few animals, and these populations have undergone periodic crashes (Meldgaard, 1986; Jepsen et al., 2002; Cuyler, 2007). *Ostertagia gruehneri* is also absent in introduced reindeer in Iceland where the contemporary parasite fauna consists almost exclusively of species originating from domestic livestock (Gudmundsdottir, 2006).

Ostertagia gruehneri occurs in muskoxen but at a much lower prevalence and intensity than in caribou or reindeer (S. Kutz, E. Hoberg, unpubl. obs.). In Dall's sheep, *O. gruehneri* is uncommon, with sporadic, low-intensity infections reported primarily in the summer (Nielsen and Neiland, 1974; Simmons et al., 2001). Unusually high counts of 'strongyle-type' eggs were observed in summer faecal surveys of one population of Dall's sheep from the Richardson Mountains, NT (Table 2.3). These eggs were not identified to species but most likely are either *O. gruehneri* or *T. boreoarcticus.* There is substantial sympatry with large numbers of caribou from the Porcupine herd as well as with a small population of muskoxen. Spill-over of *O. gruehneri* from caribou, or *T. boreoarcticus* from muskoxen, is possible. Notably, a high abundance of strongyle-type eggs has not been reported from other Dall's sheep populations sympatric with woodland caribou (Table 2.3).

(b) *Ecology*. Egg production for *O. gruehneri* in *Rangifer* is highly seasonal with faecal egg counts in captive and wild reindeer and caribou increasing in the spring, remaining high throughout the summer and then tapering to very low or negative egg counts from late fall through to the spring (Irvine, 2000; Irvine et al., 2000; Hoar et al., 2009,2012a). On the

TABLE 2.3 Prevalence (%) and intensity of eggs (epg) or oocysts/gram (opg) faeces of parasites detected in faecal samples from North American arctic ungulates from July 2000 to July 2010[a]

			Number of fecals collected each season				*Marshallagia* sp.	
Herd or location	Prov/ State	*N* total[b]	Winter	Spring	Summer	Fall	%	Range epg
Caribou								
Banks Island	NT	341	122	78		141	57.5	1–65
Sahtu	NT	109	73	35	1		0	NA
Chisana Herd	YT	158		158			5.4	1–83
Beverly/Qamanirjuaq	NT NU	25		25			0	NA
Bluenose East	NT NU	51			20		0	NA
Bluenose West	NT	10	10				0	NA
Cape Bathurst	NT	37				37	2.7	77
Dall's Sheep								
Mackenzie Mountains	NT	482	66	194	68	154	86.1	1–117
Richardson Mountains	NT	262		2	177		60.3	1–111
Sheep Mountain	YT	9		9			89.0	1–38
Ivaavik	YT	6			6		83.0	2–43
Tombstone Park	YT	1		1			0	NA
Moose								
Various places	AK	26	6	4	9		0	NA
Mackenzie Mountains	NT	4		4			0	NA
Sahtu	NT	36	27	9			11.1	1–27
Central	YK	27		17		10	29.6	2–16
Yukon	YK	24					0	NA
Muskoxen								
Ellesmere Island	NU	4			4		25.0	4–4
Thelon	NU	2					0	NA
Victoria Island	NU	28	28				42.9	1–2
Banks Island	NT	262			72		10.3	1–13
Sahtu	NT	8		8			50	1–3
North	YT	19		10	9		0	NA

[a] Samples were frozen at −20°C and analyzed by modified Wisconsin double-centrifugation sugar flotation technique (specific gravity 1.26) at the University of Saskatchewan (January 2000–August 2005) and University of Calgary (September 2005–December 2010). Samples collected as part of a wildlife parasitology collaborative monitoring program with the wildlife departments of the governments of the Northwest Territories, Nunavut and Yukon, US Department of Agriculture, and Universities of Calgary and Saskatchewan.

[b] In some cases, season of faecal collection was not specified and '*N*' total is greater than the sum of seasonal '*N*'.

[c] Includes genera of Trichostrongylinae that produce typical 'strongyle' egg. Most likely represents a mixture of *Ostertagia gruehneri* and *Teladorsagia boreoarcticus*, the former most common in caribou and the latter most common in muskoxen.

Strongyle eggs^c		Nematodirinae		*Trichuris* sp.		*Skrjabinema* sp.		Anoplocephalid eggs		*Eimeria* spp.	
%	Range epg	%	Range epg	%	Range epg	%	Range epg	%	Range epg	%	Range opg
23.8	1–19	15.5	1–46	0	NA	0	NA	39.3	1–170	16.4	1–2000
31.2	1–46	6.4	1–7	0.9	1–1	0.9	1–1	0.9	25	8.3	2–1000
60.8	1–247	0	NA	0	NA	9.5	1–7	12.2	2–63	4.7	1–236
8.0	1–1	0	NA	0	NA	0	NA	0	NA	8.0	8–28
5.9	1–4	0	NA	0	NA	0	NA	7.8	17–677	5.9	2–11
0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
0	NA	5.4	4–77	0	NA	0	NA	8.1	39–139	0	NA
1.9	1–23	78.4	1–205	55.6	1–602	2.3	1–105	11.2	1–634	89.4	1–5000
53.8	1–321	62.6	1–207	40.1	1–97	3.8	1–161	24.4	1–3000	70.2	1–6000
0	NA	89.0	1–7	78.0	1–22	0	NA	0	NA	100	5–1000
83.0	1–15	83.0	5–26	67.0	8–40	0	NA	0	NA	50	558–1500
100	3–3	100	11–11	0	NA	0	NA	0	NA	100	13–13
0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
0	NA	25.0	1–39	0	NA	0	NA	2.8	76–76	0	NA
0	NA	18.5	1–4	0	NA	0	NA	3.8	14–14	0	NA
0	NA	79.2	1–41	0	NA	0	NA	16.7	6–247	0	NA
100	24–59	100	1–16	0	NA	0	NA	50	1–6	100	153–704
50	1–1	0	NA	0	NA	0	NA	50	26	0	NA
0	NA	28.6	1–8	0	NA	0	NA	0	NA	96.4	1–325
76.3	1–2236	62.2	1–603	0	NA	0	NA	25.6	1–3745	59.5	1–17,500
87.5	14–66	37.5	1–3	0	NA	0	NA	0	NA	25.0	500–750
57.9	1–187	68.4	1–14	5.3	1–1	0	NA	10.5	7–18	47.4	1–40

Canadian mainland tundra, eggs deposited from early June through to early August can develop to L3 within 3–4 weeks, but exceptionally high mid-summer temperatures (>30°C) may delay development (Hoar et al., 2012b). Although eggs do not survive freezing (deBruyn, 2010), there is high overwinter survival of both L2 and L3 on the tundra (Van der Wal et al., 2000; Hoar et al., 2012b).

Inhibition seems to be a key characteristic of the life history of *O. gruehneri* in barren-ground caribou. Extremely high rates of inhibition were observed in wild barren-ground caribou and in reindeer experimentally infected with L3 cultured from a barren-ground caribou source (Hoar et al., 2012a). Inhibition may be an important strategy of *O. gruehneri* in barren-ground caribou, enhancing survival and transmission of the parasite in a harsh arctic environment where the primary host is migratory. Propensity for inhibition appears to differ across different ecotypes or subspecies of caribou and reindeer (Leader-Williams, 1980; Bye and Halvorsen, 1983; Irvine et al., 2000; Hrabok et al., 2006a; Hrabok et al., 2007) and may be a more common feature linked to migratory behaviour of caribou and highly seasonal environments (Hoar et al., 2012a). Relatively long prepatent periods (PPP) for this family of parasites were observed in three muskoxen infected with *O. gruehneri* L3 from woodland caribou (two muskoxen infected with 2500 L3 each on June 7, monitored daily; PPPs 87 and 93 days) and barren-ground caribou (one muskox infected with 7000 L3 in January, monitored weekly; PPP 61 days) (S. Kutz, B. Hoar, L. Polley, B. Wagner, unpubl. obs.). It is unknown if this reflects a normal maturation rate (no inhibition) for this parasite in muskoxen or if the larvae underwent a short period of inhibition first.

(c) *Impacts*. In reindeer, high intensities of infection with *O. gruehneri* (>5000 adult nematodes/host) can lead to decreased food intake, weight loss and reduced pregnancy rates (Arneberg et al., 1996; Arneberg and Folstad, 1999; Stien et al., 2002).

Using mathematical models, Albon et al. (2002) demonstrated the potential role of *O. gruehneri* in stabilizing population cycles in Svalbard reindeer. Svalbard is an excellent study site to investigate the impact of *O. gruehneri* on its host population because the parasite assemblage of the reindeer is simple, dominated by *O. gruehneri* and *M. marshalli* and the reindeer have no competitors or predators on the archipelago. It is likely that *O. gruehneri* plays a role in the population dynamics of other reindeer and caribou populations but establishing such a link is difficult because of confounding factors, including predation, competition, hunting, development and resource exploration and extraction.

2.3.1.1.2. *Teladorsagia boreoarcticus*

(a) *Host and geographic distributions*. *Teladorsagia boreoarcticus* was originally described as a dimorphic ostertagiine infecting muskoxen and caribou from the central Canadian Arctic and low Arctic islands primarily in the region adjacent to Kugluktuk, NU (Hoberg et al., 1999). Subsequently, a second minor morphotype designated as *T. boreoarcticus* minor B was described based on specimens from Victoria Island and Banks Island, NU and NT, although this form has yet to be demonstrated in mainland populations (Hoberg et al., 2012b). The morphological similarity of *T. boreoarcticus* to *T. circumcincta*, a cosmopolitan nematode of domestic sheep, and the possibility of a cryptic species complex of *Teladorsagia* partitioned among free-ranging northern ungulates complicates a clear understanding of diversity and host associations (Hoberg et al., 1999; Hoberg et al., 2012b). Prior to the description of *T. boreoarcticus*, *Teladorsagia* specimens isolated from caribou, muskoxen and Dall's sheep in the North American Arctic and from mountain goats in western Canada and the US were identified as *T. circumcincta.* It is now known that those from muskoxen and caribou across Canada are *T. boreoarcticus* (Hoberg et al., 1999). A recent study of gastrointestinal parasites of caribou and muskoxen in the central Canadian Arctic reports *T. circumcincta*, not *T. boreoarcticus*, from both host species (Hughes et al., 2009) but this is considered a misidentification (Hoberg et al., 2012b). Unresolved is the identity of *Teladorsagia* sp. reported from a small number of muskoxen in an introduced population near Kangerlussuaq, west Greenland. These animals originated from a natural population in east Greenland and spent time in the Copenhagen Zoo before arriving at their final destination (Clausen, 1993). Korsholm and Olesen (1993) reported *T. circumcincta* in these muskoxen. Although *T. boreoarcticus* would be expected in the source population, it is possible that the animals may have become infected with *T. circumcincta* in the Copenhagen Zoo and maintained that parasite following introduction. Sympatric caribou of the Kangerlussuaq-Sisimiut herd are also host to *Teladorsagia* cf. *boreoarcticus* (J. Steele, S. Kutz, E. Hoberg, C. Cuyler unpubl. data). The possibility of multi-species infections of *Teladorsagia* in Greenland is consistent with the development of mosaic faunas that may be mixtures of endemic and introduced species (Hoberg et al., 2012a; Hoberg, 2010; Hoberg et al., 2012c).

Teladorsagia boreoarcticus is by far the dominant abomasal nematode of free-ranging muskoxen and is also reported in woodland and barren-ground caribou and reindeer (Hoberg et al., 1999; Hoar et al., 2009; deBruyn, 2010). Prevalence and intensity in caribou is generally low, but woodland caribou can maintain *T. boreoarcticus* in the absence of muskoxen (Hoar et al., 2009; deBruyn, 2010). Adults of *T.* cf. *boreoarcticus*, but not *O. gruehneri*, were found in two of the now extirpated caribou in Banff National Park, AB (latitude 51° 8′ 60 N) (deBruyn, 2010), demonstrating a broad latitudinal distribution for *T. boreoarcticus*. *Teladorsagia* sp. is uncommon in Dall's sheep and the few reports of *T. circumcincta* (and morphotypes) in this host, and the more common reports in mountain goats (Cowan, 1951; Kerr and Holmes, 1966; Nielsen and Neiland, 1974; Samuel et al., 1977), may be *T. boreoarcticus* or involve undescribed species in a broad complex that remains to be fully characterized (Hoberg et al., 1999).

The complexity associated with defining species limits and diversity within *Teladorsagia* (and the identification of *T. boreoarcticus*) clearly indicates the potential outcomes of incorrect identifications: (i) erroneous interpretations about evolutionary history and host associations (e.g. Brooks and Hoberg, 2006) and (ii) assumptions about life-history characteristics that may not be applicable to the parasite species in question. Although the extent of this assemblage in free-ranging hosts across the Holarctic remains unresolved, current evidence suggests that *T. circumcincta* sensu stricto, *T. boreoarcticus* and a putative array of cryptic species have been on divergent evolutionary trajectories for a considerable period of time (Hoberg et al., 1999; Leignel et al., 2002). This has implications for parasite development and behaviour in an array of free-ranging ungulate hosts at high latitudes.

(b) *Ecology*. Preliminary investigations on the ecology of *T. boreoarcticus* have revealed some key features of this parasite's life cycle. Based on faecal surveys of free-ranging populations in northern Canada, there is a seasonal pattern of egg production with high egg counts throughout the summer and very low egg production during the winter (S. Kutz, B. Wagner, L. Polley unpubl. obs.; Samuel and Gray, 1974), a similar pattern to that of *O. gruehneri*. Eggs can hatch after short periods of freezing (1–2 weeks at zero to −20°C) (S. Kutz, B. Wagner, L. Polley unpubl. obs.) but freeze tolerance of larval stages has not been investigated. In preliminary laboratory studies, eggs developed to L3 within 8–11 days on the laboratory countertop (estimate 20–22°C) (S. Kutz, B. Wagner, L. Polley unpubl. obs.).

The life cycle of *T. boreoarcticus* has been completed experimentally in three captive muskoxen (S. Kutz, B. Wagner, L. Polley unpubl. obs.). Eggs originated from free-ranging muskoxen on Banks Island. One male castrate muskox was experimentally infected with L3 cultured from eggs that had been frozen for 1–2 weeks. Approximately 950 L3 were given by stomach tube on 21 June and the muskox did not shed eggs until the following spring, on 11 March. Two female muskoxen were each experimentally infected with 23,000 L3 of *T. boreoarcticus* on 7 September of the same year and did not shed eggs until 24 May. These results suggest a strong tendency towards larval inhibition and are particularly surprising for the muskox infected in June when normal maturation of the parasite would have been expected. One domestic sheep infected with 23,000 L3 on 7 September shed small numbers of strongyle eggs intermittently from 5 October to 1 March, when egg production increased significantly for a few weeks and then dropped abruptly (S. Kutz, J. Heath, B. Wagner, L. Polley unpubl. obs.). Data from free-ranging muskoxen indicate that larval inhibition occurs in the wild. Emergence of larvae from the abomasal mucosa occurs in May and causes significant pathology including inflammation and oedema (Kutz et al., 2004b).

(c) *Impacts*. *Teladorsagia boreoarcticus* may play an important ecological role in the population health of muskoxen. High intensities of infection and abomasitis occur in muskoxen on arctic islands in Canada (Tessaro et al., 1984; Wobeser, 1984; Blake, 1985; Rowell, 1987; Kutz et al., 2004a) and it has been suggested that infections in muskoxen may contribute to population cycling through impacts on host body condition and reproduction (Kutz et al., 2004a).

2.3.1.1.3. *Marshallagia marshalli/M. occidentalis*

(a) *Host and Geographic Distributions.* Species of *Marshallagia* are polymorphic abomasal parasites of ungulates across the Holarctic region (Boev et al., 1963; Hoberg et al., 2001). The species in muskoxen, caribou and Dall's sheep across their range has been identified as *M. marshalli*, a presumptive Holarctic species, but may represent a component of a broader cryptic complex (Lichtenfels and Pilitt, 1989; Hoberg et al., 2012a). In caribou and muskoxen from Canada and Greenland, *M. marshalli* appears to be more common in relatively xeric areas, including alpine regions and on the high arctic islands, compared to the low-lying mainland (Table 2.2). *Marshallagia marshalli* is present in the Kangerlussuaq caribou and muskox herds of west Greenland but absent from the Akia–Maniitsoq caribou immediately to the south (Korsholm and Olesen, 1993; Steele et al., 2012). *Marshallagia marshalli* is the dominant abomasal nematode in Dall's sheep across their range. A previously unknown species of *Marshallagia* was recently identified in mountain goats from the western cordillera of North America and appears to be specific to this host species and common across its range (Hoberg et al., 2012a.). The northern extent of the range for this species remains undefined, although it is likely to be in sympatry with populations of *M. marshalli* in areas where Dall's sheep and mountain goats are in contact (Hoberg et al., 2012a).

(b) *Ecology. Marshallagia marshalli* has a direct life cycle with second-stage larvae hatching from eggs and developing to L3 in the environment (Anderson, 2000). Freeze-tolerant eggs make it well suited for the Arctic. In a preliminary study, *Marshallagia* eggs collected from Dall's sheep in the Richardson Mountains, NT, remained viable after being frozen at −10 to −20°C for at least 8 months (S. Kutz, J. Heath, B. Wagner, L. Polley unpubl. obs.). These eggs were isolated and cultured according to Hubert and Kerboeuf, (1984) and L3 were recovered after 13–14 days on the laboratory countertop (estimate 20–22°C). A captive Dall's × Stone (*Ovis dalli stonei*) sheep hybrid infected with 2700 L3 cultured from these eggs became patent at 29 days post-infection (S. Kutz, J. Heath, B. Wagner, L. Polley unpubl. obs.).

Egg production of *Marshallagia* has a seasonal pattern that is the reverse of that for *O. gruehneri* and *T. boreoarcticus*; for muskoxen and Svalbard reindeer, it is higher in the winter/spring than in the summer months (Samuel and Gray, 1974; Irvine et al., 2000) (Table 2.3). Winter transmission is reported for reindeer (Halvorsen et al., 1999; Irvine et al., 2001) and saiga antelope (Morgan et al., 2006) and is probable for muskoxen, caribou and Dall's sheep.

(c) *Impacts*. *Marshallagia* spp. are common, and sometimes numerically dominant, members of the gastrointestinal parasite fauna of arctic ungulates. Despite this, very little is known about the life history or host impacts of this genus. In studies in AK and the Mackenzie Mountains, NT, in the 1970s, adult parasite counts in Dall's sheep ranged to >2000 but most animals tended to have <1000 adult worms (Nielsen and Neiland, 1974; Simmons et al., 2001). The infection intensity of adult *Marshallagia* in Dall's sheep ewes of the Mackenzie Mountains, NT, was negatively correlated with both host body condition and pregnancy rates (S. Kutz, N. Simmons, A. Veitch, L. Polley, E. Hoberg unpubl. obs.). The impacts of *M. marshalli* in muskoxen and caribou remain unknown.

2.3.1.2. Subfamily Nematodirinae

Nematodirines are nematodes of the small intestines of ruminants and lagomorphs (Hoberg, 2005). The subfamily includes species of two genera, *Nematodirus* and *Nematodirella*, which are widespread in arctic ungulates and well adapted to life at these latitudes (Tables 2.2, 2.3).

Host and Geographic Distributions. A minimum of nine species of nematodirines has been reported in free-ranging arctic ungulates from North America and Greenland (Table 2.2). There remain some inconsistencies in the definitive identification of species in this group. For example, *Nematodirus archari* and *N. oiratianus*, both species recognized in Eurasia, have been reported from Dall's sheep (Nielsen and Neiland, 1974) while other studies identify *N. andersoni* and *N. oiratianus interruptus* in bighorn and thinhorn sheep of North America, suggesting that the geographic and host associations for these species be re-evaluated (Lichtenfels and Pilitt, 1983b; Durette-Desset and Samuel, 1989; Rickard and Lichtenfels, 1989). Similarly, in moose, both *Nematodirella alcidis* and *N. longissemispiculata* are commonly reported across most of this host's range (reviewed in Fruetel and Lankester 1988). The latter species probably represents a misidentification in this host and in most cases is likely *N. alcidis* (Lichtenfels and Pilitt, 1983a). Lastly, records of *N. helvetianus* in muskoxen may be in need of examination, assuming that this nematodirine is primarily associated with domesticated cattle and has been widely transported globally with their translocation.

Muskoxen have a diverse nematodirine fauna, including those found in both in moose and caribou, *Nematodirella alcidis*, *N. longissimespiculata* and *Nematodirus tarandi*, as well as *Nematodirella gazelli*, and *Nematodirus helvetianus* (although see comment above re: *N. helvetianus*). Absent from the reported muskox fauna are those species found in Dall's sheep (*N. oiratianus/O. interruptus, N. spathiger*, *N. andersoni/archari* and *N. davtiani*). This may only reflect that muskox populations sympatric with Dall's sheep have not been sampled as opposed to a host barrier. Both *N. filicollis* and *N. spathiger*, parasites typical of domestic sheep, are reported from muskoxen sympatric with domestic sheep in Norway (Alendal and Helle, 1983), and it follows that muskoxen are likely suitable hosts for the nematodirines in Dall's sheep.

In contrast to muskoxen, the reported diversity of nematodirines in caribou and moose is low. For caribou, *Nematodirella longissemispiculata* and *Nematodirus tarandi* are most commonly reported, along with *Nematodirus skrjabini*, which may be a synonym of *N. tarandi* (Dikmans, 1935a; Bergstrom, 1983; Lichtenfels and Pilitt, 1983a; Fruetel and Lankester, 1989; Hoberg et al., 2001). The low diversity may reflect true species barriers and/or sampling limited primarily to barren-ground and island caribou populations. The gastrointestinal nematode fauna in the boreal and mountain woodland caribou ecotypes of the arctic and subarctic is known only through faecal examinations (Table 2.2) (e.g. Hoar et al., 2009; Johnson et al., 2010), which have not allowed differentiation among species of nematodirines. Some of these caribou populations are sympatric with Dall's sheep and/or mountain goats and all are likely to have greater sympatry with moose than do their barren-ground cousins. Captive caribou do harbour a greater diversity of nematodirines (Fruetel and Lankester, 1989), supporting the hypothesis that the apparent low diversity in wild sampled caribou may reflect a combination of ecological isolation and insufficient sampling.

(b) *Ecology.* Nematodirines are core components of the ungulate parasite fauna in arctic and boreal ecosystems in the Holarctic and are well adapted to the environmental conditions at these latitudes (Hoberg, 2005). Larvae develop to the infective L3 within eggs. These eggs are resistant to extreme freezing events, freeze–thaw cycles and desiccation, but direct sunlight and high temperatures may be detrimental (Marquardt et al., 1959; van Dijk and Morgan, 2008).

Nematodirella alcidis is common in moose from temperate regions but its abundance and distribution in the Arctic and Subarctic are not well described. In temperate regions, prevalence ranges from 47 to 100% and infection intensity is typically quite low (Fruetel and Lankester, 1988).

In northwestern Ontario, 19 of 20 moose were infected with *N. alcidis* with an average infection intensity of 111 ± 54. Regardless of the time of year sampled, only 21% of the *N. alcidis* population were mature adults and a large proportion of the remaining specimens were 'short' L4. The authors suggested that this may indicate arrested development for this species where inhibited larvae may serve as a reservoir to replace adult nematodes and ensure that eggs are produced throughout the year (Fruetel and Lankester, 1988). In this and other studies, there was no difference between adult and young moose with respect to prevalence or intensity of infection. This pattern is in contrast to that of *N. longissemispiculata* in caribou where large numbers of nematodes, the majority of which are sexually mature, are found in the duodenum of calves in their first summer. Calves produce eggs through the winter and are free of infection the following spring (Fruetel, 1987). Infection of adult caribou with *N. longissemispiculata* is rare, although it is seen in males during the rut. Additionally, nematodirine eggs were common in approximately 50% of adult female caribou of the Kangerlussuaq-Sisimiut herd of west Greenland but have not been identified to species (Steele et al., 2012). Eggs and infective larvae of *N. alcidis* and *N. longissemispiculata* can survive freezing and desiccation and may live for extended periods in the environment (Fruetel, 1987) (Fruetel and Lankester, 1988). In muskoxen, adult animals commonly shed eggs of Nematodirines and egg production tends to increase in the summer and drop off in the fall (Samuel and Gray, 1974) (Table 2.3).

Observations on larval development for *Nematodirus* spp. in domestic animals provide some additional insights into the ecology of these parasites. Hatching of nematodirines occurs within a temperature range specific to the species (11–17°C for *N. battus* but 6–20°C for *N. filicollis*) and, depending on species and geographic location, chilling may be important to trigger hatching. For example, for *N. battus*, the proportion of eggs that hatch without chilling (i.e. in the fall) decreases at more northern latitudes (van Dijk and Morgan, 2008; van Dijk and Morgan, 2010). In the Arctic, it is hypothesized that hatching of nematodirines should be triggered by an extended period of chilling (i.e. the winter) as opposed to no chilling (i.e. hatching in the summer/fall) (van Dijk and Morgan, 2010). Hatching after chilling would synchronize appearance of the majority of the L3 in the spring and allow for transmission throughout the short arctic summer. This strategy may be better than fall hatching for two reasons: 1) the survival of L3 that hatch after chilling is greater than those that have not been chilled (i.e. fall) (van Dijk and Morgan, 2010) and 2) L3 hatching from eggs at the end of a short arctic summer would have a very narrow window for transmission and may not survive the subzero winter temperatures (van Dijk and Morgan, 2010). However, in southern Greenland, *Nematodirus* spp. of sheep, including

N. spathiger, *N. helvetianus* and *N. abnormalis*, may hatch within a month of deposition in the first summer. Development and hatching in this environment is not synchronous and may extend over 37 months (Rose and Jacobs, 1990). Although at high latitude, coastal southern Greenland has a relatively mild maritime climate and the epidemiology of parasites in this environment may not reflect what occurs in a more 'arctic'-type environment.

Differences in development and hatching strategies among *Nematodirus* species infecting a single host may provide a competitive advantage of one species over another depending on ambient conditions (van Dijk et al., 2009) and may partition parasite species over time and space. Those with a lower hatching threshold may be available to infect hosts earlier in the spring while those with a higher hatching threshold may not be available until later in the summer. For example, the developmental threshold for *N. helvetianus* is 3°C whereas development for *N. spathiger* does not occur below 6–7°C (Rose and Jacobs, 1990). Understanding development thresholds and ranges, as well as triggers for hatching, is important as these are key factors influencing the timing and intensity of host exposure and, consequently, the timing and severity of disease. Additionally, such information is essential to understand individual species responses to climatic conditions and climate change.

(c) *Impact*. *Nematodirus* spp. can cause significant disease in domestic livestock, particularly young animals (Samizadeh-Yazd and Todd, 1979), but little is known about the impacts of this group of nematodes in arctic ungulates. *Nematodirella longissemispiculata* was reported from the duodenum and anterior jejunum of a wild muskox and was associated with enteritis characterized by '*petechial haemorrhages, some denuding of the mucosa and a quantity of mucus in the lumen. In addition reddish plaque-like areas were observed on the walls of the duodenum in the area where these worms were found. Microscopic examination…presence of a granulomatous-type lesion*' (Gibbs and Tener, 1958). In caribou, pathology caused by this species is likely limited to calves (Fruetel, 1987). High infection intensities with *N. helvetianus*, *N. longissemispiculata*, and other gastrointestinal nematodes in captive muskoxen in Norway were considered, along with other parasites, as a possible cause of the poor body condition of animals on the farm (Alendal and Helle, 1983). *Nematodirella alcidis* in moose is reported from the anterior third of the small intestine but pathology and clinical disease in this host are not known (Threlfall, 1967; Fruetel and Lankester, 1988). In Dall's sheep, *Nematodirus* species may be partitioned in the small intestine (Nielsen and Neiland, 1974) and species-specific differences in impacts might be expected. Data collected from Dall's sheep in the Mackenzie Mountains, NT, in 1971–1972 suggest a trend for higher infection intensities with *Nematodirus* spp. in non-pregnant compared to pregnant ewes and in ewes in poor body condition compared to those in very good condition (Simmons et al., 2001).

2.3.1.3. Subfamily Oxyurinae

2.3.1.3.1. ***Skrjabinema*** **spp.**

(a) *Host and Geographic Distributions.* Species of *Skrjabinema* are pinworms of the large intestine and caecum. Based on faecal and post-mortem examinations, *Skrjabinema* spp. are present at low to moderate prevalence and intensity in Dall's sheep and mountain goats, are rare in caribou and absent from moose and muskoxen (Tables 2.2 and 2.3) (Cowan, 1951; Kerr and Holmes, 1966; Samuel et al., 1977; Simmons et al., 2001). *Skrjabinema ovis* is common in Dall's sheep and infection intensities are generally low, ranging from 1 to 60+ worms (Nielsen and Neiland, 1974; Simmons et al., 2001). *Skrjabinema* may be underdiagnosed in arctic ungulates as egg shedding can be low and intermittent and few parasitological studies have included thorough examinations of the large intestines and caecum.

(b) *Ecology.* Oxyurids are directly transmitted parasites. In most host species, gravid females migrate to the anus of the host and deposit eggs in the perianal region whence the eggs can be shed in the faeces or, once infective, can be transmitted directly between hosts. Development to the infective stage is species dependent and can take hours to days.

(c) *Impacts*. The Oxyuridae in domestic ungulates are believed to be generally benign with few symptoms (Bowman et al., 2003), but their effects in free-ranging species remain unexplored.

2.3.1.4. Subfamily Trichurinae

2.3.1.4.1. ***Trichuris*** **spp.**

(a) *Host and Geographic Distributions.* Species of *Trichuris* are extremely uncommon in free-ranging caribou and muskoxen but are found in almost all surveyed populations of Dall's sheep (Nielsen and Neiland, 1974; Simmons et al., 2001) (Tables 2.1 and 2.2). The species present in Dall's sheep is believed to be *T. schumakovitschi*. In faecal surveys of Canadian muskoxen, *Trichuris* spp. were found at a low prevalence on the mainland but were completely absent from over 1000 faecal samples examined from Banks Island, NT (Table 2.2). Interestingly, *Capillaria* sp., a parasite common in reindeer in the Palaearctic (Hrabok et al., 2006a), is absent from sampled populations of free-ranging caribou and muskoxen in North America and Greenland (Table 2.3) although it was detected in a captive herd of reindeer in Alberta (S. Kutz, unpubl. data).

(b) *Life Cycle. Trichuris* spp. are directly transmitted nematode parasites of the large intestine and caecum. The L1 is the infective stage and remains within the egg, which is extremely resistant to environmental conditions. This resistance, particularly to desiccation, may be one of the factors allowing these parasites to survive in the Arctic.

(c) *Impacts*. The effects of *Trichuris* spp. infections on free-ranging arctic ungulates are not known but low-intensity trichurid infections in captive muskox calves are often associated with diarrhoea (Seidel and Rowell, 1996).

2.3.1.5. Emerging issues and knowledge gaps

The gastrointestinal nematode fauna of arctic ungulates is generally sparse with the most species diversity represented by the nematodirines, parasites well adapted to arctic climates. In recent years, considerable progress has been made in defining the diversity and host and geographic ranges of the Trichostrongylina in the arctic ungulates of North America, although much remains to be done. Fundamental to this progress is recognition of cryptic species complexes (e.g. *T. boreoarcticus* and *Marshallagia* spp.) and the use of integrated methods that combine diagnostic morphological characters and DNA-based analyses to develop and refine descriptions and phylogenies. Importantly, archived specimens deposited in museum collections (e.g. *Nematodirella, Teladorsagia*) have aided in confirming or re-determining the identity of several species, as well as confirming the presence of cryptic species (Lichtenfels and Pilitt, 1983a; Hoberg et al., 1999). These collections are particularly relevant for arctic parasites because of the cost and logistics of collecting material in the field and the challenges of obtaining specimens from host species that have become endangered or threatened.

Overall, the trichostrongyline parasites in arctic ungulates appear to have broad host ranges but there are host-specific patterns of abundance. For the nematodirines in particular, the role of host species barriers versus ecological barriers to infection requires further investigation. Examining the patterns of host and geographic distribution, and perturbations of these patterns, may provide novel insights into mechanisms of parasite invasion and establishment (Hoberg et al., 2012). For example, the presence of large numbers of ‘strongyle’ type eggs in Dall’s sheep in the Richardson Mountains is unusual and may reflect the unique interactions of sheep with muskoxen and caribou in this region. The absence of *O. gruehneri*, the most common abomasal parasite of *Rangifer*, from caribou colonizing parts of Greenland is particularly surprising and may reflect unique patterns of host and parasite dispersal into these regions, including severe host, and perhaps parasite, bottlenecks. Further exploration of animal movements, natural and anthropogenic, ecological and species barriers and successes and failures of parasite colonization events will contribute to theory on parasite invasion and establishment and provide insight into the potential for new parasite invasions in the Arctic (Hoberg, 2010; Hoberg et al., 2012).

Transmission dynamics of gastrointestinal nematodes will be influenced by the rapidly changing arctic environment (Hoberg et al., 2008b; Kutz et al., 2009a,b). In general, warmer and longer summers are anticipated to facilitate parasite development and transmission, whereas extreme temperatures may have negative impacts (Kutz et al., 2009b; Hoar et al., 2012b). The effects of changing winter conditions are currently speculative – shorter winters may decrease propensity for larval inhibition, increased snow cover that insulates parasites may improve parasite survival whereas increased freeze–thaw cycles will reduce parasite survival. Some endemic parasites may be better equipped to cope and take advantage of changing conditions (e.g. nematodirines), whereas others (perhaps ostertagiines) may not.

There is growing evidence that, at least for some species, the free-living stages of parasites in the North may have sufficiently broad thermal tolerances (e.g. *O. gruehneri*) and/or flexibility in development strategies (e.g. nematodirines and *O. gruehneri*) to persist under these changing conditions (van Dijk and Morgan, 2010; Hoar et al., 2012b). Larval inhibition within the host and overwintering of eggs and larvae in the environment are important strategies for overcoming adverse environmental conditions and can synchronize parasite development with the availability of susceptible hosts, such as spring-borne young (Eysker, 1993; Sommerville and Davey, 2002; Cattadori et al., 2005). The different propensity for larval inhibition in *O. gruehneri* across its geographic range and in different subspecies of *Rangifer* likely reflects selective strategies associated with climatic conditions and host behaviours (Hoar et al., 2012a). Such plasticity within the species may allow it to maximize its fitness (i.e. transmission) under a variety of climatic conditions.

Similarly, research on species of *Nematodirus* in domestic livestock suggests that selection can drive adaptations in patterns of egg hatching under different climatic or latitudinal gradients (van Dijk and Morgan, 2010) such that these nematodes may be very well equipped to survive climate change in the Arctic. The nematodirines are a core, diverse and neglected yet potentially pathogenic component of the gastrointestinal parasite fauna of arctic ungulates. An understanding the ecology of these parasites under the current climate warming conditions is of considerable importance for the health of arctic ungulates and may provide a novel insight into the epidemiology of nematodirines in domestic species. These arctic species remain essentially untouched by the selection pressures of the livestock production industry and may provide a simpler model for exploring concepts of importance for nematodirines of domestic host species.

Invasions of new hosts or parasites to the Arctic may result from a variety of factors including natural range expansion through gradual movements or stochastic events, translocation associated with agriculture or conservation efforts, or anthropogenic change including climate and landscape perturbation (Kutz et al., 2009b; Hoberg, 2010; Hoberg et al., 2012). The gastrointestinal nematode fauna of temperate free-ranging ungulate species in Canada is considerably more diverse than that of arctic ungulates, the former consisting of a mosaic of endemic and introduced parasites (Table 2.4) (Hoberg et al., 2001,2008a; deBruyn, 2010). There is evidence that, given appropriate conditions, some of these species may be able to invade and persist in high latitude ecosystems (e.g. Waller and Chandrawathani, 2005; deBruyn, 2010).

Trichostrongylus axei is one such parasite that may have already established successfully at arctic latitudes. *Trichostrongylus axei* is not known as part of the typical endemic fauna of arctic ungulates in North America or Greenland but it has been reported from a variety of arctic ungulates in captivity at southern latitudes and in Fennoscandia, as well as in domestic sheep in Greenland (Alendal and Helle, 1983; Rose et al., 1984; Bye, 1987; Bye et al., 1987; Fruetel and Lankester, 1989). It was recently found in an introduced population of elk in the Yukon (deBruyn, 2010). Although the original source of *T. axei* in this population is not known (i.e. introduced or naturally present in endemic YT ungulates), its presence in the elk years after their translocation indicates that it is currently able to circulate in this northern environment. It is a host generalist and likely to spill-over to moose and caribou in the region, if it has not already.

A second genus of considerable concern is *Haemonchus.* Some species of *Haemonchus* are pathogenic abomasal nematodes of domestic sheep and cattle that can spill-over into wild ungulates and cause significant disease (Hoberg et al., 2004). Both *H. contortus* and *H. placei* have been reported in wild deer from western Canada (Table 2.4)(deBruyn, 2010). Species of *Haemonchus* and *H. contortus* are considered tropical parasites and the free-living stages are susceptible to both cold and dry conditions and require a mean monthly temperature of 18°C to persist (Gordon, 1948; Hoberg et al., 2004). These attributes may explain the absence of endemic species in North America and current geographic limits of introduced species in the boreal and temperate zones (Hoberg et al., 2012c). Thus, the establishment of *H. contortus* above the Arctic Circle in Sweden is unusual, although these populations are limited to domestic sheep under intense management and confinement (Waller and Chandrawathani, 2005). A high propensity for larval inhibition in the abomasal mucosa, in conjunction with animal husbandry practices, appear to be key features that allow it to persist in domestic livestock at these latitudes (Waller et al., 2004). Semi-domesticated reindeer in Finland have been experimentally

TABLE 2.4 Some gastrointestinal nematode species reported from cervids in western Canada. Adapted from deBruyn (2010)

Parasite[e]	Woodland caribou	Mule deer	White-tailed deer	Black-tailed deer	Elk	Moose
Abomasum						
Haemonchus contortus		AB[f]				
Heamonchus placei			AB, SK			
Marshallagia marshalli	AB	AB				
Mazamastrongylus odocoilei			SK		AB, SK	
Orloffia bisonis (Syn. *Ostertagia bisonis*)		AB[a]	AB[a]			
Ostertagia gruehneri/O. arctica	AB, BC					
Ostertagia mossi/O. dikmansi			SK			
Ostertagia ostertagi		AB[a]	AB[a]			
Ostertagia sp.						AB[b]
Spiculopteragia boehmi		AB	AB		AB	
Teladorsagia boreoarcticus	AB, BC					
Teladorsagia circumcincta		BC		AB, BC[a,d]		
Trichostrongylus axei			AB[a]		AB[b]	
Small intestine						
Cooperia oncophora (Syn. *C. surnabada*)		AB, AB[a]			AB[b]	
Nematodirella alcidis					AB[b]	AB[b]
Nematodirella longissimespiculata						AB[c]
Nematodirus helvetianus		AB, AB[a]			AB[b]	

Nematodirus odocoilei		AB, BC		AB, BC[a,d]		
Nematodirus spathiger	AB					
Skrjabinema					AB[b]	
Trichostrongylus colubriformis			AB			
Trichostrongylus longispicularis						AB[b]

[a] Stock (1978).

[b] Stock and Barrett (1983).

[c] Samuel *et al.* (1976).

[d] Walker and Becklund (1970).

[e] Among the Ostertagiinae, only names for the major morphotype for polymorphic species are included.

[f] AB = Alberta, BC = British Columbia, SK = Saskatchewan.

Records are from DeBruyn (2010) unless otherwise indicated.

infected with *H. contortus* (Hrabok et al., 2006b) and *Haemonchus* sp. has also caused acute disease and death of muskoxen in captivity (Durrell and Bolton 1957) (MacDonald et al., 1976). The absence of *H. contortus* in Greenland sheep may suggest that it was not present in the original sheep brought to Greenland in 1906 and 1915 from the Faroe Islands and Iceland (Rose et al., 1984). The fact that *Haemonchus* is currently absent from Iceland sheep supports this contention (Gudmundsdottir, 2006). Whether *Haemonchus* spp., if introduced, could be maintained in the Arctic by populations of wild ungulates in the absence of domestic livestock or confinement farming is unknown. If established at arctic latitudes, *Haemonchus* could become a serious cause of morbidity and mortality in wild ungulates.

Spiculopteragia boehmi is another potentially pathogenic, invasive parasite of note. It is a Eurasian abomasal nematode of red deer that was translocated to North America (and globally) and is now found in wild deer and elk in geographically disjunct regions of western Canada and the USA (deBruyn, 2010; Rickard et al., 1993). *Spiculopteragia* is well established in game ranched reindeer, and probably elk (*C. elaphus*), in western Canada and appears to have significant impacts on body condition of these animals (S. Kutz, unpubl. obs). Range expansion into temperate caribou populations is expected but establishment at arctic latitudes is uncertain (deBruyn, 2010).

Gastrointestinal nematodes are well established as production limiting parasites in domestic species and are increasingly recognized as having a role in the health and population dynamics of free-ranging hosts (Hudson and Greenman, 1998; Hudson et al., 1998; Albon et al., 2002). While our knowledge of the diversity of gastrointestinal nematodes of arctic ungulates has improved substantially, our knowledge of the ecology and impacts of this group of parasites remains superficial for almost all species except *O. gruehneri*. For some of these parasites, even the very basics of the life cycle remain unknown. For the rest, knowledge of the life cycle and potential impacts is limited to what has been learned from a few pilot studies or extrapolated from related parasites of domestic species.

As parasites with considerable plasticity and resilience in their responses to climatic conditions, some gastrointestinal nematodes of arctic ungulates are likely to continue to thrive under ongoing climate change (e.g. Nematodirines, *Marshallagia*), while others may not be as successful (e.g. *Teladorsagia, Ostertagia*). The transmission dynamics and relative abundance and impacts of these parasites will be sensitive to shifts in diversity, abundance and behaviour of host communities, as well as to invasions of new hosts and parasites. Extirpation of endemic faunas may be a result of competition with such invasive parasites. Parasite-mediated competition among hosts may also occur. A knowledge of how historical ecological conditions have structured the parasite communities and how parasites currently circulate among hosts will allow us to anticipate how these communities may respond to invasions of southern hosts and parasites and ultimately how that will influence the health and sustainability of wildlife populations.

2.3.2. Lung and tissue nematodes: Protostrongylidae and Dictyocaulinae

The Protostrongylidae are pathogenic nematodes of free-ranging and domestic ungulates and lagomorphs around the world. Higher taxonomy for this group was established by Boev (1975), Kontrimavichus et al. (1976) and Carreno and Hoberg (1999). Species of four subfamilies are known in ungulates across North America (Fig. 2.7). Those that live as adults in the lungs belong to the subfamilies Muelleriinae, Protostrongylinae and Varestrongylinae, and those that live as adults in the skeletal muscles or central nervous system are referred to the Elaphostrongylinae. At high latitudes of Canada and AK, various protostrongylid species occur in barren-ground, Grant's, and woodland caribou, thinhorn sheep, moose, muskoxen, and mountain goats (Table 2.5). Protostrongylids have not been reported from caribou or muskoxen in Greenland; however, *Muellerius* sp. (Muelleriinae) is reported from domestic sheep in southern Greenland (Rose et al., 1984). Parasite species diversity, prevalence, and abundance vary with host and geographic location.

Among protostrongylid species with lung-dwelling adults, eggs produced by the females hatch to release first-stage larvae (L1) that move up

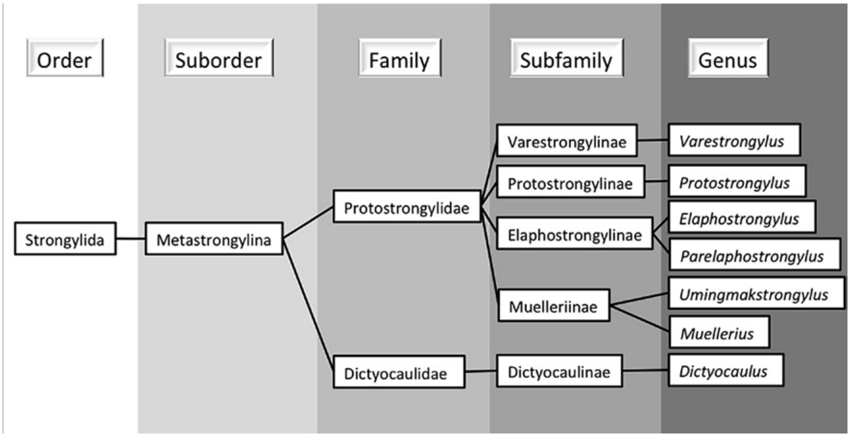

FIGURE 2.7 Tissue and lung Strongylida reported from ungulates of arctic North America, including Greenland.

TABLE 2.5 Tissue and blood nematodes reported from ungulates of arctic North America, including Greenland. Data compiled from available published and grey literature

Host and parasite species	State/ province	Herd, region or nearest place name
Caribou		
Parelaphostrongylus andersoni	AK	Mulchatna[a]; Northern Alaska Peninsula[a]
	YT	Porcupine[a]; Chisana[a]
	NT	Cape Bathurst[a]; Tsiigehtchic[a]; Bluenose West[a]; Beverly[b]
	QC/NL	Rivière-aux-Feuilles[c]; Rivière George[a,b]; Mealy Mountains[a]
Parelaphostrongylus odocoilei	NT	Hay River[d]
Varestrongylus sp. n.	AK	Northern Alaska Peninsula, Mulchatna[a]
	YT	Porcupine[a]
	NT	Beverly[a]; Bluenose East[a]; Cape Bathurst[a]; Godlin Lakes[a]
	NL	Mealy Mountains[a]
Dictyocaulus eckerti[ae]	AK	Western Arctic, Northern Alaska Peninsula and Kenai Peninsula[m]
	QC/NL	Rivière George[e]
	GL	AM herd[f]
Onchocerca cervipedis	AK	Mulchatna[g]
Setaria yehi	AK	College and Cantwell[h] (in reindeer, originally from Nome)
	NT	Not specified[i]
Dall's sheep		
Parelaphostrongylus odocoilei	AK	Central Alaska Range[d]; Chugach Mountains[d]; Wrangel Mountains[d]
	YT	Faro[d]; Kluane National Park[d]; St. Elias Mountains[d]
	NT	Mackenzie Mountains[d,j]
Protostrongylus stilesi	AK	Alaska Range[d,k]; Baird Range[l]; Brooks Range[l]; Chugach Mountains[l]; Wrangel Mountains[d]
	YT	Anvil Mountains[d]; Ivaavik National Park[d]; St. Elias Mountains[d]
	NT	Mackenzie Mountains[d,j]
Moose		
Varestrongylus sp. n.	AK	Tlikakila River, Lake Clark National Preserve[a]

TABLE 2.5 *(continued)*

Host and parasite species	State/ province	Herd, region or nearest place name
Dictyocaulus eckerti	AK	Palmer[m]
Onchocerca cervipedis	AK	Tok River[n]; Palmer[n]
	YT	Various[o]
	NT	Mackenzie Mountains, Mackenzie Valley[p]
Setaria yehi	AK	Unspecified[i]; Fairbanks[q]; Delta Junction[q]
Rumenfilaria andersoni	AK	Interior including Fairbanks, Tanana Flats, Kuskokwim River, Seward Peninsula[q]
Muskoxen		
Umingmakstrongylus pallikuukensis	NT	Sahtu Settlement Region[r]
	NU	West of Kugluktuk[s,t]; Victoria Island (Lady Franklin Point)[u]
Varestrongylus sp. n.	YT	Firth River[k]
	NT	Aklavik[a]
	NU	Cambridge Bay[v]; Thelon Game Sanctuary[a]
Protostrongylus stilesi	AK	Eastern North Slope[w]
	YT	Northern Yukon[x]
	NT	Big Fish River (near Aklavik)[y]
Dictyocaulus eckerti	NU	Kitikmeot region[z]
	QC	Kuujjuaq[aa]
Dictyocaulus sp.[ae]	AK	Eastern North Slope[w]
	NT	Banks Island[ab]
	NU	Bathurst Island[ac]; Thelon[ad]

[a] Kutz *et al.* (2007).
[b] Lankester and Hauta (1989).
[c] Asmundson and Hoberg (pers. comm.).
[d] Jenkins *et al.* (2005a).
[e] Fruetel and Lankester (1989).
[f] C. Cuyler, R. White, S. Kutz (unpubl. data).
[g] G. Verocai, K. Beckmen(i), Hoberg (unpubl. data).
[h] Dieterich and Luick, (1971).
[i] Becklund and Walker (1969).
[j] Kutz *et al.* (2001d).
[k] Neiland (1972).
[l] Jenkins *et al.* (2007).
[m] K. Beckmen (unpubl. data).
[n] K. Beckmen, G. Verocai, E. Hoberg (unpubl. data).
[o] P. Merchant (pers. comm).
[p] S. Kutz, C. Tobac, G. Verocai (unpubl. obs.).
[q] Quist and Beckmen (2011).
[r] S. Kutz, A. Veitch, R. Popko (unpubl. data).
[s] Gunn and Wobeser (1993).
[t] Hoberg *et al.* (1995).
[u] S. Kutz, K. Orsel, G. Verocai (unpubl. obs.).
[v] G. Verocai, S. Kutz, S. Checkley (unpubl. data.).
[w] Afema (2008).
[x] S. Kutz (unpubl. data).
[y] Hoberg *et al.*, (2001).
[z] Hoglund *et al.* (2003).
[aa] USNPC, 2011.
[ab] M. Branigan (unpubl. data).
[ac] Gibbs and Tener (1958).
[ad] Samuel and Gray (1974).
[ae] Reported as *D. viviparus* but most likely *D. eckerti*.

the respiratory tree, are swallowed and passed in the faeces. The adults of tissue-dwelling species (Elaphostrongylinae) produce eggs that are deposited in the blood stream and transported to the pulmonary vasculature where hatching releases the L1. These migrate into the alveoli, then follow the same route as larvae of the lung-dwelling species and are passed in the faeces. First-stage larvae of genera within the Muelleriinae, Elaphostrongylinae and Varestrongylinae have kinked tails with small dorsal spines (dorsal-spined larvae – DSL). It is not possible to reliably differentiate among these genera on the basis of larval morphology alone (Hoberg et al., 2005); therefore, DNA-based methodologies are required for definitive identification (Huby-Chilton et al., 2006; Kutz et al., 2007). The L1 of the Protostrongylinae have straight spike tails, lack dorsal spines and also cannot be reliably distinguished morphologically at either the generic or species level (e.g. Boev, 1975). In general, L1 of northern protostrongylids can survive well in the often-harsh external environment and are characterized by a degree of freeze tolerance but repeated freeze–thaw cycles, shifts in humidity and exposure to high temperatures will reduce viability (Forrester and Lankester, 1998; Shostak and Samuel, 1984; Lorentzen and Halvorsen, 1986).

Gastropod intermediate hosts, which are invaded by L1 from ungulate faeces, are required for continuation of the life cycle for all Protostrongylidae (Anderson, 2000). Development to the infective third-stage larvae (L3) is completed through a variety of terrestrial and aquatic gastropod species, but there is a certain degree of host specificity. Larval development rates and success within the intermediate host vary depending on both parasite and gastropod species and are temperature dependent. Mammalian hosts become infected when they ingest gastropods harbouring L3 or L3 that have spontaneously emerged from the gastropods and are present in the environment (Anderson, 2000; Kutz et al., 2000b).

Adults, eggs and L1 of lung-dwelling species and eggs and L1 of tissue-dwelling species can cause significant pulmonary damage, notably localized or multifocal granulomatous pneumonia. Moreover, the developing larvae and adults of species of the Elaphostrongylinae can cause myositis and neurological disease, with particularly severe disease in ‘aberrant’ host species (Anderson, 2000; Lankester, 2001; Jenkins et al., 2005b).

2.3.2.1. Subfamily Protostrongylinae

The Protostrongylinae is a diverse group of parasites with a cosmopolitan distribution in ungulates and lagomorphs, although the greatest diversity is seen in Eurasia (Boev, 1975). Several species have been reported in cervids and bovids from North America, including *Orthostrongylus macrotis* in mule deer, *Protostrongylus frosti* in bighorn sheep and *P. coburni* in white-tailed deer from northeastern USA (Dikmans, 1935b); only *P. stilesi* and *P. rushi* are present in arctic and subarctic regions.

2.3.2.1.1. *Protostrongylus stilesi*

Protostrongylus stilesi is a small (males 17.55–20.79mm in length, female length not established) (Hoberg et al., 2002) and slender lung nematode found in the lung parenchyma of wild sheep and mountain goats from North America.

(a) *Host and Geographic Distributions. Protostrongylus stilesi* is common in bighorn (*Ovis canadensis*), Stone's and Dall's sheep and mountain goats, across their ranges (Neiland, 1972; Uhazy et al., 1973; Pybus et al., 1984; Kutz et al., 2001d; Jenkins et al., 2005a). Based on post-mortem examinations together with faecal surveys where L1 were presumed to be *P. stilesi* (*P. rushi*, although less likely, was not ruled out), prevalence ranges from 50 to 100% in thinhorn sheep herds and 50 to 78% in mountain goat herds (Jenkins et al., 2006b).

Protostrongylus stilesi is also present at low intensities in an introduced population of muskoxen (*O. m. wardi)* that are sympatric with Dall's sheep in northern YT and northwestern NT (Hoberg et al., 2002), and L1 typical of *Protostrongylus* sp. are present in introduced muskoxen that are sympatric with Dall's sheep in western AK (L. Adams, K. Beckmen, unpubl. obs.). The occurrence of *P. stilesi* in muskoxen is considered a recent host switch associated with anthropogenic breakdown of ecological barriers in conjunction with climate change (Hoberg et al., 2002). Following historical extirpation, muskoxen were introduced to the Arctic Coastal Plain of AK in the late 20th century. Later expansion of this population to the east along the northern shoulder of the Brooks Range has resulted in intermittent sympatry with Dall's sheep and consequent infection with *P. stilesi*. Although infections in muskoxen become patent, larval shedding is low and it is unknown whether *P. stilesi* would be maintained in the absence of Dall's sheep (Hoberg et al., 2002; Kutz et al., 2004b).

(b) *Ecology.* The life cycle of *P. stilesi* is similar to other pulmonary protostrongylids. Larvae of bighorn sheep origin developed to L3 within 11–60 days in several gastropod genera, including *Pupilla*, *Vallonia,* and *Vertigo* (Pillmore, 1956; Monson and Post, 1972) and those of Dall's sheep origin developed to L3 within 34 days in experimentally infected wild-caught pupillid snails (*Vertigo* and *Columella* spp.) at room temperature (mean 22°C) (E. Jenkins and J. Skific pers. comm.). Emergence of small numbers of L3 from gastropod intermediate hosts occurs and although it is not considered an important feature of the parasite's epidemiology in bighorn sheep (Monson and Post, 1972), it may be more important in the Arctic, extending transmission into winter. Third- and fourth-stage larvae have been recovered from foetuses and neonatal bighorn lambs, suggesting that transplacental transmission occurs (Forrester and Senger, 1964; Hibler et al., 1972). The prepatent period in a single experimentally infected Dall's sheep was 45 days (E. Jenkins and J. Skific pers. comm.) and the finding of *P. stilesi* adults in Dall's lambs as young as two months suggests either infection very early in life or that transplacental transmission might also occur in thinhorn sheep (Jenkins et al., 2007). First-stage protostrongylid larvae, not identified to subfamily, were also observed in the bronchi of a wild Dall's foetus from AK at the end of April (K. Beckmen, K. Burek, unpubl. obs.). These may be a result of haematogeneous spread of L1 from the dam, which is unlikely in the case of the Protostrongylinae but perhaps more likely for *Parelaphostrongylus odocoilei* or a patent infection with species of either genus.

In Dall's sheep in the Mackenzie Mountains, NT, larval production tends to be seasonal, with prevalence lowest in August and increasing through the fall and intensity also increasing through fall and winter and peaking in the spring (annual range of 32–1075 LPG) (Jenkins et al., 2006b). Development and transmission of *P. stilesi* under arctic conditions have not been investigated in any detail; however, using a degree–day model for protostrongylid development (Kutz et al., 2002), Jenkins et al. (2005b) suggested that L3 might not develop in a single summer at arctic latitudes. The authors hypothesized that freeze tolerance of L1, overwintering of larvae in gastropods, transplacental transmission and L3 emergence may all contribute to the persistence of this parasite at arctic latitudes (Jenkins et al., 2006b).

(c) Impacts. In naturally infected Dall's sheep, *P. stilesi* can cause severe verminous lesions in the lung parenchyma associated with adults, larvae and eggs. Grossly, there are firm, pale, coalescing lesions of 5–70mm in diameter primarily along the caudodorsal border of the diaphragmatic lobe, but also in other lobes, and it is estimated that, in heavy infections, up to 36% of the lung volume can be compromised (Neiland, 1972; Kutz et al., 2001d). Histologically, there are focal aggregations of inflammatory cells surrounding adult nematodes and immature stages, as well as fibrosis, bronchiolar hyperplasia and mild fibrino-haemorrhagic exudate (Kutz et al., 2001d). In muskoxen, lesions are located in the caudodorsal and diaphragmatic surfaces of diaphragmatic lobes, are round to oval (3–5mm), tan to red brown, extending into the lung parenchyma and contain adults, ova and larvae of the parasite. Histologically, adults are confined to alveolar parenchyma and surrounded by mild to focally marked lymphocyte/macrophage infiltrate (Hoberg et al., 2002). Pathology is not described in mountain goats.

The effects of *P. stilesi* in Dall's sheep at a population level remain unknown. Historically, *P. stilesi* was considered an important pathogen in bighorn sheep and linked to the lungworm–pneumonia complex. Subsequent studies suggest, however, that while lungworms might predispose to other pneumonias, their effects on the individuals and populations of this host species may be more subtle and indirect (Festa-Bianchet, 1991). Of possible significance with respect to Dall's sheep is that, across their central and southern range, they may be co-infected with the muscleworm *P. odocoilei*. Eggs and larvae of *P. odocoilei* cause significant pulmonary damage and co-infections could result in additive or synergistic pulmonary damage (Kutz et al., 2001d; Jenkins et al., 2007).

2.3.2.1.2. *Protostrongylus rushi*

Adults of *P. rushi* are larger (males 18–32mm, females about 38mm in length) than *P. stilesi* and are found in the trachea, bronchi, and larger bronchioles. *Protostrongylus rushi* has been reported in a Dall's sheep from the YT based on a single museum specimen (CMNP 1988-0522) (Kutz et al., 2001d) and in mountain goats at Mt. Juneau and adjacent to Haines, AK (USNPC 100426, 105139). It also occurs in bighorn sheep from the Canadian Rocky Mountains (Uhazy et al., 1973) and mountain goats from central BC (Jenkins et al., 2004). However, the true geographic range of this parasite in the Arctic remains unknown. Although adults of *P. stilesi* and *P. rushi* are easily differentiated, the L1 are morphologically very similar and require DNA-based analyses for identification (e.g. Kutz et al., 2007). Further survey and inventory are necessary to determine the geographic distribution of *P. rushi* in Dall's sheep and mountain goats and its potential significance in these caprines.

2.3.2.2. Subfamily Muelleriinae

Members of the Muelleriinae are a monophyletic group of typically cyst-forming lungworms of the Caprinae and include the genera *Muellerius*, *Cystocaulus*, and *Umingmakstrongylus* (Carreno and Hoberg, 1999). *Umingmakstrongylus pallikuukensis* is the only species of the subfamily endemic to North America. *Muellerius capillaris* is a cosmopolitan parasite of domestic sheep and goats that was introduced to North America with domestic livestock (Anderson, 2000) and has since spilled over to bighorn sheep (Pybus and Shave, 1984; Ezenwa et al., 2010). Species of *Cystocaulus* have distributions in Eurasia and although this genus is the sister of *Umingmakstrongylus*, it has not been reported in North America.

2.3.2.2.1. *Umingmakstrongylus pallikuukensis*

Umingmakstrongylus pallikuukensis is a large (males up to 22cm and females to 65cm long), cyst-forming, pulmonary nematode specific to muskoxen (Kutz et al., 1999). It was first discovered west of Kugluktuk, NU, in 1988 (Gunn and Wobeser, 1993; Hoberg et al., 1995).

(a) Host and Geographic Distributions. In the late 1990s, *U. pallikuukensis* was present at near 100% prevalence in muskoxen on the western Canadian mainland between the Mackenzie and Coppermine rivers and, despite extensive survey, was not found in muskox populations elsewhere (Gunn and Wobeser, 1993; Hoberg et al., 1995; Kutz, 2000). Recently, it has been detected on Victoria Island, NU, and east of the Coppermine River, suggesting significant range expansions (S. Kutz, K. Orsel, M. Dumond, G. Verocai unpub. obs.). It has not been found in sympatric caribou and did not establish in experimentally exposed Dall's/Stone's sheep hybrids or domestic sheep (Kutz et al., 1999 ; Kutz et al., 2004a).

(b) *Ecology. Umingmakstrongylus pallikuukensis* follows a typical protostrongylid life cycle with temperature dependent development in gastropod intermediate hosts. In the core of the parasite's range on the Canadian mainland, the meadow slug, *Deroceras laeve,* appears to be the most abundant intermediate host but larvae can also develop to L3 in at least two (*Catinella* sp. and *Euconulus fulvus*) of the five terrestrial species and one (*Aplexa hypnorum*) of the four aquatic species present in the area. The larval development period in experimentally exposed *D. laeve* ranges from 9 days at 23.4°C, to 42 days at 11.5°C (Kutz et al., 2001c; Kutz et al., 2002) and the prepatent period (PPP) in experimentally infected captive muskoxen is 91–95 days (Kutz et al., 1999).

Umingmakstrongylus pallikuukensis appears to be an exceptionally well adapted, single host, arctic parasite: it is large, long lived (at minimum two years and likely much longer) and highly fecund (up to 3 million L1/day in experimentally exposed muskoxen with adult parasite burdens similar to those observed in the field); L1 are resistant to freezing and desiccation and develop rapidly and efficiently in a gastropod intermediate host species that is relatively abundant and vagile; up to 100% of L3 emerge from the gastropods suggesting the possibility of year-round transmission and infection accumulates with age and causes minimal inflammatory response in muskoxen (Kutz et al., 1999; Kutz, 2000; Kutz et al., 2001b). Where it is present, prevalence approaches 100% in the affected population and calves are infected in their first summer (Gunn and Wobeser, 1993; Kutz et al., 2001b).

The restricted geographic distribution of *U. pallikuukensis* likely reflects a history of near extirpation of muskoxen in the early 1900s as well as limiting historical climatic conditions (Hoberg et al., 1995; Hoberg et al., 2008a). Empirical models suggest that between 1973 and 2002, concurrent with regional warming, larval development within the intermediate host reached a tipping point, shifting from a two- to one-year period. This shift in development rate would have a considerable influence on infection pressure and transmission dynamics and range expansion under the current regime of climate warming was predicted (Kutz et al., 2005). Consequently, the recent finding of *U. pallikuukensis* on Victoria Island, a large arctic island separated from the mainland by Coronation Gulf, is a substantial range expansion (Kutz et al., 2009b). A broadened range reflects a permissive climate, presence of suitable gastropod intermediate hosts and an event for expansion and establishment most likely mediated through infrequent muskox movement between the mainland and the island.

(c) *Impacts.* Adult parasites inhabit spherical to ovoid grey–brown cysts of up to 4cm in greater diameter, containing up to… 5–7 adult worms. Cysts are located throughout the lung parenchyma and some are easily visible and palpable. Histologically, cysts consist of a wall of connective tissue surrounding adult worms, together with numerous eggs, L1 and amorphous debris (Hoberg et al., 1995; Kutz et al., 1999). Some cysts are calcified, which is thought to indicate long-standing infection and some contain no adult parasites. There is little inflammatory reaction outside the region directly adjacent to the cysts. Cysts appear to accumulate with age and naturally infected older bulls may contain up to 250 (Gunn and Wobeser, 1993). On radiographic examination cysts are visible as opacities and are also clearly evident on computed tomography (Kutz et al., 1999).

The population-level impacts of an endemic infection with *U. pallikuukensis*, or the introduction to a naive population such as that on Victoria Island, remain poorly understood. There are anecdotal reports of epistaxis in free-ranging muskoxen that have been stressed by running, and one infected captive muskox demonstrated epistaxis when restrained on a bovine examination tilt table. Conceivably, the parasites may have significant energetic costs for heavily infected muskoxen and the pathology may lead to exercise intolerance and increases in susceptibility to predation.

2.3.2.3. Subfamily Varestrongylinae

The Varestrongylinae is composed of a number of species within the genera *Varestrongylus* and *Pneumostrongylus*. These are small lungworms typically found in the terminal bronchioles of cervids and bovids across the Holarctic (Boev, 1975). In North America, two species are known, *V. alpenae* in white-tailed deer and a recently discovered species, *Varestrongylus* sp. n., in caribou, muskoxen and moose; only the latter species is reported from the Arctic (Kutz et al., 2007).

2.3.2.3.1. *Varestrongylus* sp. n.

Varestrongylus sp. n. is a miniscule lungworm (1–2cm) found deep in the airways or parenchyma of the lungs. Taxonomic description of this parasite is in progress (G. Verocai, E. Hoberg, M. Simard, S. Kutz, unpubl. obs.).

(a) *Host and geographic distributions. Varestrongylus* sp. n. has a broad host and geographic range, naturally infecting muskoxen (*O. m. moschatus* and *O. m. wardi*), woodland, Grant's and barren-ground caribou, and rarely, moose across most of arctic and subarctic North America (Kutz et al., 2007). Unidentified DSL previously found in woodland caribou in several Canadian provinces may also be from this species (Lankester et al., 1976; Gray and Samuel, 1986; Lankester and Fong, 1998; Kutz et al., 2007) but further investigations are required.

Varestrongylus sp. n. occurs in co-infections with *Parelaphostrongylus andersoni* in some barren-ground caribou herds and with *P. odocoilei* in woodland caribou from western Canada (Kutz et al., 2007). Co-infections with *P. stilesi* in muskoxen are probable (Hoberg et al., 2002; L. Adams, K. Beckmen, unpubl. obs.), as are co-infections with *U. pallikuukensis*; however, the latter would be difficult to detect. The substantial lesions caused by *U. pallikuukensis* may obscure the more subtle changes caused by the *Varestrongylus*. Similarly, molecular detection based on DSL from faeces may be confounded by massive larval production from *U. pallikuukensis*, which may obscure the less abundant L1 of *Varestrongylus* (Kutz et al., 2007).

(b) *Ecology*: *Varestrongylus* sp. n. follows the typical protostrongylid life cycle. It was found in a naturally infected slug, *Deroceras laeve*, from the NT (Kutz et al., 2007) and in preliminary studies developed to L3 in both *D. laeve* and *Deroceras reticulatum* (G. Verocai, S. Kutz unpubl. obs.). The prepatent period, pathology and impacts of this parasite in its hosts are not known: gross lesions have not been observed in lungs from a small number of naturally infected muskoxen and caribou (G. Verocai, S. Kutz and M. Simard unpubl. obs.).

2.3.2.4. Subfamily Elaphostrongylinae

The Elaphostrongylinae consist of two genera with a minimum of six species, two of which occur in arctic ungulates of North America. Species of the genus *Parelaphostrongylus* are native to North America whereas *Elaphostrongylus* is a Palaearctic genus. A single species, *E. rangiferi*, introduced to northeastern North America through reindeer translocations from Eurasia is restricted to Newfoundland (Lankester, 2001).

2.3.2.4.1. *Parelaphostrongylus andersoni*

Parelaphostrongylus andersoni is a muscle-dwelling nematode of white-tailed deer (*O. virginianus*) and caribou, with males measuring 19–23mm and females around 30–35mm. It can cause significant muscular and pulmonary disease in these hosts. Despite this pathogenicity and its broad distribution, little is known about the ecology and impacts at the population level in its main arctic host, the caribou.

(a) Host and Geographic Distribution: White-tailed deer are considered the primary hosts, with caribou colonized by host switching during the Pleistocene (Carreno and Lankester, 1994; Asmundsson et al., 2008). Adult nematodes were first found in caribou from central and eastern Canada, including Newfoundland and it was presumed that DSL in caribou across their range were *P. andersoni* (Lankester and Hauta, 1989; Lankester and Fong, 1998; Ball et al., 2001). Recent molecular identification of DSL in several barren-ground and woodland caribou herds has confirmed the presence of *P. andersoni* and supports the hypotheses that this parasite has a continuous distribution in barren-ground caribou across their arctic range (Kutz et al., 2007). Despite sympatry of infected caribou herds with various populations of muskoxen, moose and Dall's sheep, *P. andersoni* has not been detected in these other ungulate species (Jenkins et al., 2005a; Kutz et al., 2007).

(b) *Ecology:* The life cycle of *P. andersoni* is typical of protostrongylids. *Parelaphostrongylus andersoni* successfully developed to L3 in gastropod intermediate hosts *Triodopsis* sp. and *Mesodon* sp. within 3–4 weeks under laboratory conditions at 20–26°C (Pybus and Samuel, 1984a; Lankester and Hauta, 1989) and was reported from wild *Mesodon* spp. and *D. laeve* (Lankester and Fong, 1998; Anderson, 2000). In these studies, however, larval identity was not confirmed using DNA-based techniques. *Deroceras laeve* is considered one of the most important natural intermediate hosts for *P. andersoni* in Newfoundland (Lankester and Fong, 1998) and is found across most, if not all, the mainland North American caribou range (Pilsbry, 1946; Kutz et al., 2000b; Grimm et al., 2009). Emergence of L3 from gastropods has not been investigated for *P. andersoni*. The prepatent period in a single experimentally infected female caribou calf given 385 L3s was 66 days (Lankester and Hauta, 1989) and was within the range of that reported for other cervid hosts (49–75 days) (Prestwood, 1972; Pybus and Samuel, 1984b; Lankester et al., 1990). The migratory path of *P. andersoni* within the ungulate host has not been fully described.

The patent period for *P. andersoni* in experimentally infected caribou and white-tailed deer appears to be quite short. In the only experimentally infected caribou calf (given 295 L3 followed by 85 L3 14 days later), Lankester and Hauta (1989) reported a low peak of 124 LPG of faeces two weeks after patency (66dpi) followed by a significant drop to 7 LPG of faeces by 32 days after patency. A similar pattern was observed in white-tailed deer, with larval shedding peaking in 2–8 weeks post-patency and then declining (Nettles and Prestwood, 1976; Pybus and Samuel, 1981). Higher larval output, longer peaks (12 weeks post-patency) and longer periods of patency were observed in white-tailed deer fawns experimentally infected with higher doses of L3 (1,000L3) (Pybus and Samuel, 1984b). A short patency for *P. andersoni* in caribou was supported by data from naturally infected caribou in Newfoundland, where its co-occurrence with *E. rangiferi* and a putative cross-immunity seem to decrease larval output of both elaphostrongylines. Also, in two caribou herds in which *P. andersoni* occurred alone, larvae were found only in small faecal pellets considered to be from calves and yearlings, and larger pellets were DSL-negative (Ball et al., 2001). These data support the fact that *P. andersoni* has a short patency period in caribou and is primarily in young animals, although association of faecal pellet size with caribou age should be interpreted cautiously. Notably, L1 of *P. andersoni* have been confirmed based on molecular sequence data in adult barren-ground caribou from several different herds (Kutz et al., 2007; G. Verocai, S, Kutz, unpubl. obs.).

(c) *Impacts*: Adult nematodes, eggs and larvae of *P. andersoni* can cause significant pathology in the skeletal muscles and lungs, respectively, and clinical signs can be severe. Adult nematodes are found predominantly in the skeletal muscles, typically in the longissimus dorsus and psoas, but can also be found in other muscles and fat (Prestwood, 1972; Nettles and Prestwood, 1976; Pybus and Samuel, 1981; Lankester and Fong, 1998). Gross pulmonary lesions associated with the presence of eggs and L1 include petechial haemorrhages and whitish nodules and are similar to those found in white-tailed deer (Lankester and Hauta, 1989; Lankester and Fong, 1998). In naturally and experimentally infected caribou, lesions associated with adult parasites include diffuse haemorrhage in the region of the lower neck and back, tight muscles and fasciitis (Lankester and Hauta, 1989).

In deer experimentally infected with a large number of L3 (5000), clinical signs include included pain in the loin muscles, reluctance to stand, weakness, marked discomfort in walking and falling to the ground following light pressure on the loin muscles (Nettles and Prestwood, 1976). Based on clinical signs in experimentally infected deer, this degree of pathology probably compromises the mobility in naturally infected caribou. Moreover, co-infections with other common pulmonary nematodes such as *Varestrongylus* and *Dictyocaulus* might have an additive or synergistic effect leading to more severe verminous pneumonia.

2.3.3.4.2. *Parelaphostrongylus odocoilei*

Parelaphostrongylus odocoilei is a muscle-dwelling protostrongylid common in subspecies of *O. hemionus* (mule, Columbian black-tailed and Sitka black-tailed deer) and Dall's and Stone's sheep and is occasionally reported from mountain goats, bighorn sheep and woodland caribou (Table 2.5). The adult nematodes have a size range from 24 to 33mm for males and 44 to 56mm for females and typically occur in skeletal muscles, primarily of the back, hind limbs, forelimbs and trunk but can be found elsewhere (Hobmaier and Hobmaier, 1934; Pybus and Samuel, 1984b; Kutz et al., 2001d).

(a) *Host and Geographic Distributions: Parelaphostrongylus odocoilei* was described originally in mule deer and it occurs in this species throughout western North America from California to southeastern AK (Hobmaier and Hobmaier, 1934; Brunetti, 1969; Platt and Samuel, 1978; Samuel et al., 1985; Lankester, 2001; Mortenson et al., 2006). It is common and widespread in thinhorn sheep south of the Arctic Circle with prevalence approaching 100% in most infected populations (Jenkins et al., 2005a). It has not been found in Dall's sheep from the Richardson Mountains (YT, NT) or the Brooks Range (YT, AK) despite extensive faecal surveys (Jenkins et al., 2005a ; Jenkins et al., 2007) (E. Hoberg, I. Asmundsson, K. Beckmen unpubl. obs). It occurs in mountain goats in BC, NT and AK (Jenkins et al., 2004). DSL are also reported from this host in AB and Washington State, USA, but have not been conclusively identified (Pybus and Samuel, 1984a).

The distribution of *P. odocoilei* in caribou is less well understood and there exist only two confirmed reports. A single DSL in a woodland caribou from the Hay River region, NT, was identified as *P. odocoilei* by molecular characterization (Jenkins et al., 2005a) and adult nematodes were recovered from skeletal muscles of mule deer experimentally infected with DSL from faeces of mountain woodland caribou from Jasper National Park, AB (Gray and Samuel, 1986). These authors hypothesized that it could be well established in other woodland caribou populations sympatric with mule deer in AB and BC but to date this has not been confirmed despite a moderate level of surveillance using DNA-based techniques (Kutz et al., 2007; G. Verocai, S. Kutz unpubl. obs.).

Moose can be experimentally infected with *P. odocoilei* (Platt and Samuel, 1978), but the parasite has not been found in faecal surveys of moose sympatric with infected deer and/or thinhorn sheep in the YT, the Sahtu Settlement Region NT, northeastern BC, or AK (Kutz et al., 2007). *Parelaphostrongylus odocoilei* has not been reported in muskoxen, but nowhere is this potential host sympatric with infected Dall's sheep or mule deer.

(b) *Ecology:* The life cycle of *P. odocoilei* is similar to that of other tissue-dwelling protostrongylids. Adults in the skeletal muscles are closely associated with blood and possibly lymphatic systems, where females deposit eggs that are carried to the lungs. A number of different arctic gastropod species have been reported naturally or experimentally infected with larvae of *P. odocoilei*, including *D. laeve*, *Catinella* spp. and *Euconulus* cf. *fulvus*, but not members of the Pupillidae (Jenkins et al., 2006a) (Lankester, 2001). As with many other protostrongylids of northern ungulates, *D. laeve* is considered the most important intermediate host because of its abundance, susceptibility and higher prevalence of infection in nature, when compared to other gastropods (Samuel et al., 1985). In the laboratory, development in *D. laeve* occurs in as few as 10 days at approximately 24°C and L3 can develop within a single summer in experimentally infected *D. laeve* in the Mackenzie Mountains, NT (Jenkins et al., 2006a).

Emergence of L3 from *D. laeve* occurs in the laboratory with approximately one-third of the total larvae emerging from days 22 to 60 post-infection at room temperature. Emerged L3 survive up to six months in darkness in water at near-freezing temperatures. Emergence also occurs to a lesser extent in *Catinella* sp. (Jenkins et al., 2006a). Emerged L3 might play an important role in overwinter transmission when gastropods are not available, as postulated for *U. pallikuukensis* (Kutz et al., 2000b; Jenkins et al., 2006a).

The prepatent period in three Stone's sheep and two thinhorn hybrids (*O. d. stonei* × *O. d. dalli*) each given 200 L3 from a Dall's sheep source ranged from 68 to 74 days (Jenkins et al., 2005b), up to 1–3 weeks longer than that reported for mule and black-tailed deer infected with deer-source *P. odocoilei* (Pybus and Samuel, 1984b). Larval shedding early in patency was high, peaking at 14,000–30,000 LPG between 95 and 109dpi. Larval counts remained high (1700–4800 LPG of dry faeces) and patency lasted for a minimum of 180dpi at which point the animals were removed from the study (Jenkins et al., 2005b).

In the Mackenzie Mountains, NT, larvae of *P. odocoilei* were present in 84–100% of Dall's sheep faeces sampled from March 2000 to April 2003. Intensity ranged from 141 to 1350 LPG through the year with larval production peaking from March through May. There was no evidence of age-related immunity (Jenkins et al., 2006b). Experimentally infected *D. laeve* maintained in natural conditions in the Mackenzie Mountains yielded high numbers of L3 by August–September. It is hypothesized that the majority of transmission might happen on the winter range, with infection of gastropods once they emerge from hibernation in spring and definitive host infection when the sheep return during fall (Jenkins et al., 2006b).

The apparent absence of *P. odocoilei* in Dall's sheep and other potential host species from the Richardson Mountains and Brooks Range may result from a combination of historical, climatic, physical and species barriers. The parasite does not appear to have expanded from refugial habitats with its hosts at the termination of the Pleistocene, a factor which may explain current absence at high latitudes north of the Alaska Range (Schafer et al., 2010; Hoberg et al., 2012). Outcomes using a degree–day model for development in gastropod intermediate hosts suggest that temperature-related constraints on development might limit establishment of *P. odocoilei* in naïve Dall's sheep populations at the northern extent of their range (Jenkins et al., 2006b). Under current climate warming scenarios, however, the 'Arctic-adapted' characteristics of *P. odocoilei*, including freeze tolerance of free-living stages, high prevalence and larval production in Dall's sheep, larval emergence, high establishment and development rates in gastropod intermediate hosts, could allow it to persist if introduced into currently non-endemic areas.

Introduction of *P. odocoilei* to the northern sheep ranges is unlikely to be mediated through movement of sheep. Dall's sheep are restricted to mountain ranges and are not likely to disperse across vast expanses of tundra or forest to colonize new mountain habitats, a hypothesis supported by evidence of population fragmentation found in phylogeographic studies (Loehr et al., 2006). Caribou in contrast are much more vagile and conceivably could bridge the gap between mountain ranges during their annual migrations and introduce the parasite to Dall's sheep and muskox populations further north. The potential suitability of caribou as maintenance hosts for this parasite, however, remains enigmatic (see previous discussion). Muskoxen conceivably could also serve a role in maintenance and expansion of *P. odocoilei* between mountain ranges and Dall's sheep populations but susceptibility of this species is unknown. Considerably more research is needed to understand the ecology and transmission dynamics of *P. odocoilei* in this system and the potential for it to emerge further north.

(c) Impacts: Parelaphostrongylus odocoilei is a significant pathogen in Dall's sheep, causing parasitic pneumonia and sporadic mortality events in the wild (Jenkins et al., 2007), as well as weight loss, muscle atrophy and neurological disease following experimental infection (Jenkins et al., 2005b). The neurological symptoms developed two weeks before patency and included ataxia of the hind legs, loss of conscious proprioception and hyperaesthesia, all of which resolved at patency. Pybus and Samuel (1984a,b) found adult nematodes and eggs in epidural fat of the spinal cord in deer and Jenkins et al. (2005b) detected eosinophilic pleocytosis and antibody to *Parelaphostrongylus* spp. in the cerebrospinal fluid of the experimentally infected animals, suggesting that this parasite migrates through the central nervous system of thinhorn sheep. Haematogeneous spread of eggs and larvae of *P. odocoilei* to the lungs during patency causes significant pulmonary pathology manifested as a disseminated granulomatous pneumonia.

The neuromuscular pathology caused by *P. odocoilei* may enhance susceptibility to predation or accidents (e.g. falling off cliffs in the sheep's natural habitat) for animals with moderate to heavy natural infections (Jenkins et al., 2005b). Importantly, the parasite is quite small and difficult to detect, so mortality events associated with the adult stages may be misdiagnosed as accidents or predation. Pulmonary failure due to *P. odocoilei* was the cause of mortality in a 10-month-old, naturally infected Dall's lamb (S. Kutz, E. Jenkins, B. Elkin, A. Veitch unpubl. data) and was a contributing factor in the deaths of other thinhorn sheep in the wild (Jenkins et al., 2007). In Dall's sheep, *P. odocoilei* commonly co-occurs with *P. stilesi*, a pulmonary protostrongylid (Jenkins et al., 2006a).

These two species cause very different pulmonary pathology: *P. odocoilei* diffuse granulomatous pneumonia and *P. stilesi* locally severe granulomatous pneumonia usually in the caudodorsal regions of the lungs. Co-infections, therefore, might lead to additive pathology and more severe disease.

2.3.2.5. Emerging issues and knowledge gaps for the Protostrongylidae

2.3.2.5.1. Potentially invasive protostrongylids

In addition to the protostrongylid fauna discussed above, there are a number of potentially invasive species at temperate latitudes. Shifts in climate and landscape structure, changes in arctic ecosystems, translocations of domestic species and translocations/reintroductions of, and invasions by, free-ranging hosts, might facilitate northward range expansion of some of these species (e.g. Kutz et al., 2009a,b; Hoberg, 2010). Among the species of protostrongylids that are likely to invade and have significant consequences are *O. macrotis* (Protostrongylinae); *M. capillaris* (Muelleriinae); *Varestrongylus alpenae* (Varestrongylinae) and *Parelaphostrongylus tenuis* and *Elaphostrongylus rangiferi* (Elaphostrongylinae).

Orthostrongylus macrotis is found in the trachea and bronchi of mule and black-tailed deer and pronghorn (*Antilocapra americana*) in the western US and southwestern Canada (Boddicker and Hugghins, 1969; Greiner et al., 1974; Pybus, 1990; Belem et al., 1993). It is also reported rarely from moose (Samuel et al., 1976) and elk (Honess and Winter, 1956). Northward range expansion of mule deer may bring this parasite into sympatry with ungulates in subarctic and arctic environments (deVos and McKinney, 2007; Wilson, 2009). The literature on this lungworm is sparse and consequently its ecology, pathology and impacts on hosts, as well as its potential for invasion into northern ungulates, are unknown.

Muellerius capillaris is an important lung nematode of domestic sheep and goats. It has spilled over to bighorn sheep in some regions of Canada and the United States (Ezenwa et al., 2010). It has not been reported in free-ranging Dall's sheep or muskoxen from North America but is found in muskoxen in Norway (S. Kutz, B. Ytrehus, G. Verocai, unpubl. obs.). Suitable gastropod species are present in the Arctic and Subarctic to support development of *M. capillaris*, and this parasite has a lower threshold for development but it has a degree–day requirement similar to *U. pallikuukensis* (Kutz et al., 2001c). It is likely, therefore, that if introduced, environmental conditions and intermediate host diversity and abundance would be suitable for establishment of *M. capillaris*. Ongoing and new commercial or hobby farming activities of sheep adjacent to muskox, Dall's sheep or mountain goat range could lead to spill-over of this parasite to free-ranging hosts.

Varestrongylus alpenae. This is a pulmonary lungworm of white-tailed deer in the eastern USA and southeastern and southcentral Canada, co-occurring with *P. tenuis* and *P. coburni* (Dikmans, 1935b; Cheatum, 1951; Gray et al., 1985). This species was linked to fatal pneumonia white-tailed deer in northwestern USA (Cheatum, 1951). The susceptibility of arctic ungulates to this parasite is not known; examination of woodland caribou and moose in central and eastern Canada that are sympatric with infected white-tailed deer may provide new insights.

Parelaphostrongylus tenuis. This is also a parasite of white-tailed deer and causes severe neurologic disease in several other ungulate species, including reindeer, caribou and moose (Lankester, 2001). This species is widely distributed in white-tailed deer throughout eastern North America; in Canada, the western limit of its range is eastern Saskatchewan. *Parelaphostrongylus tenuis* is considered a significant factor for failure of caribou reintroductions in eastern Canada and Minnesota, USA, where caribou were placed in areas sympatric with, or previously occupied by, white-tailed deer (Trainer, 1973; Dauphiné Jr., 1975; Pitt and Jordan, 1994).

Climate and landscape changes are leading to a northward range expansion of white-tailed deer and their parasites (Thompson et al., 1998; Côté et al., 2004; Latham et al., 2011) but the potential for *P. tenuis* to survive and be transmitted at northern latitudes is currently unknown. This will depend on both deer ecology and densities since white-tailed deer are requisite for its maintenance (all other cervids are essentially dead-end hosts or produce very few larvae that subsequent transmission is unlikely), as well as the ability of larvae to develop and survive in subarctic and arctic environments. *Parelaphostrongylus tenuis* is a risk to existing woodland caribou and moose populations elsewhere in eastern Canada (Lankester et al., 2007) and investigation of host–parasite dynamics at the interface of these species may provide additional understanding of potential risks and implications for invasion of the Arctic.

Elaphostrongylus rangiferi. This is a common parasite of wild and semi-domesticated reindeer (*Rangifer tarandus tarandus*) in Palaearctic regions (Fennoscandia and Russia). It causes cerebrospinal elaphostrongylosis (CSE) in *Rangifer* and experimentally infected moose (Lankester, 1977; Lankester and Northcott, 1979; Stéen et al., 1997; Lankester and Fong, 1998). It is a probable cause of a similar clinical disease in muskoxen in Norway (Holt et al., 1990).

Elaphostrongylus rangiferi was introduced into Newfoundland with infected reindeer from Norway in 1908 and is now well established in woodland caribou across the island. Despite several opportunities for translocation of *E. rangiferi* to North America with multiple other reindeer introductions (e.g. Lankester and Fong, 1989) the parasite has not been detected in extensive faecal-based geographic surveys of caribou and muskoxen on most of Canada's mainland (Huby-Chilton et al., 2006;

Kutz et al., 2007; G. Verocai, E. Hoberg, I. Asmundsson, S. Kutz unpubl. obs.). Nor has it been detected in western AK, where the majority of the introduced reindeer from Russia and Norway were established and are now maintained as a commercial livestock activity (Oleson, 2005; Finstad et al., 2006). Clinical disease has not been detected in the semi-domesticated reindeer or adjacent free-ranging caribou herds; however, clinically affected animals may quickly succumb to predation and with abundant scavengers and a rare human presence carcasses are unlike to be detected. Even the semi-domesticated reindeer are free ranging over a wide geographic, sparsely populated area and are rarely observed except during brief annual handlings for deworming. There have also not been any specific survey with subsequent larval identification for protostrongylids in this area, so the presence of *E. rangiferi* associated with reindeer herds in AK cannot be ruled out.

The possibility remains that *E. rangifer* has established elsewhere in North America but remains undetected. *Deroceras laeve* is a suitable intermediate host (reviewed in Lankester, 2001) and is common and widespread across most of mainland arctic and subarctic Canada (Pilsbry, 1946). The L1 are freeze tolerant, and no clear decrease in larval survival was observed in larvae held at −20°C (Lorentzen and Halvorsen, 1986). Preventing its establishment in arctic North America, however, may be a relatively high threshold temperature as well as a high number of degree days required for development compared to other arctic protostrongylids (Halvorsen and Skorping, 1982; Kutz et al., 2001c).

In order for invasive protostrongylids to successfully establish at subarctic and arctic latitudes, suitable climatic conditions and adequate numbers and density of suitable intermediate and definitive hosts are critical, as is a sufficient founding parasite population. These requirements will differ among species, but some of the parasite characteristics that might be important for establishment include freeze tolerance of immature stages, overwintering ability (transposition of the barrier posed by harsh winter conditions), broad host range, high larval production, and long lifespans. This is applicable to other species in other nematode families and virtually any other metazoan parasite.

2.3.2.5.2. Advances in the identification of parasites and infected hosts

Biodiversity survey and inventory have resulted in significant advances in a knowledge of the distribution of Protostrongylidae species infecting ungulates in high latitudes of North America (Hoberg et al., 1995; Kutz et al., 2001b; Jenkins et al., 2005a; Kutz et al., 2007; Hoberg et al., 2008b). Less than two decades after the recognition of a new genus of protostrongylid in muskoxen from the Central Canadian Arctic (Hoberg et al., 1995), the definition of new host and geographic ranges for two other protostrongylids and discovery of yet another previously unknown species that is widespread through northern North America (Kutz et al., 2001d; Hoberg et al., 2002; Kutz et al., 2007) show us that there remains much to be revealed. Recent and substantial advances in the knowledge of protostrongylid faunas are partially due to the development and use of molecular techniques that permit species identity based on single L1s in faeces. These methods supplant laborious bioassay trials and equivocal assessments of larval morphology, which were impediments to definitive identification of parasites and infected hosts (Jenkins et al., 2005a; Huby-Chilton et al., 2006; Kutz et al., 2007). Importantly, previous records of protostrongylids not validated with either adult specimens or sequencing of larval DNA remain suspect. Application of molecular-based diagnostics has already facilitated large-scale studies, both geographically extensive and site intensive, on parasite biodiversity which have eliminated the need for necropsy and examination of adult nematodes (Jenkins et al., 2005a; Kutz et al., 2007; Asmundsson et al., 2008). The development and application of new and affordable molecular diagnostics approaches that permit rapid identification of high numbers of protostrongylid larvae has immediate value for screening ungulate populations prior to management and conservation activities such as translocations.

2.3.2.5.3. Ecology

In general, protostrongylid species appear highly adapted to inhospitable arctic environmental conditions. Arctic adaptations include a series of ecological traits such as cold and freeze tolerance in both L1 and L3, emergence of L3 from the gastropod host, extended patency (e.g. *U. pallikuukensis, P. odocoilei*) and cumulative infections in some species of long-lived hosts. Not all arctic protostrongylids display all of these traits but they persist nonetheless. For example, despite a relatively short period of patency and low larval production, *P. andersoni* has a vast geographic range across the mainland Arctic and Subarctic. Its distribution mirrors that of its only known arctic host, the caribou. Strategies used by this parasite that allow it to persist across such a large area in a single host species, when the closely related elaphostrongyline, *P. odocoilei*, cannot, may be linked to a combination of historical host–parasite associations and colonization events as well as tolerance and resilience to contemporary ecological conditions (e.g. Hoberg et al., 2012c).

The protostrongylid species in arctic ungulates appear to have varying degrees of host specificity, ranging from apparently absolute with *U. pallikuukensis*, parasitic only in muskoxen, to generalists such as *P. odocoilei* which is found naturally infecting caribou, Dall's sheep and mountain goats and experimentally can infect moose. In some cases when obvious ecological barriers have been removed, such as when muskoxen were introduced or expanded onto Dall's sheep range, parasites have successfully colonized new hosts (e.g. *P. stilesi* in muskoxen, although persistence in muskoxen in the absence of sheep has not been demonstrated). In other cases where there are no obvious ecological barriers, parasites retain apparent host specificity. For example, despite caribou being sympatric with Dall's sheep and muskoxen across large parts of their range, *P. andersoni* has not been detected in these latter two species (see also Asmundsson et al., 2008). Some of these species cross taxonomic boundaries of hosts, infecting both cervids and bovids (e.g. *P. odocoilei, Varestrongylus*) while others remain within subfamily or family boundaries (e.g. *Protostrongylus* in Caprinae, *P. andersoni* in cervids). In the case of moose, this species appears to be an accidental host, only naturally and rarely infected with *Varestrongylus* sp. n. in the Arctic. Understanding how this mosaic of protostrongylids circulates among arctic ungulates requires an integrative approach examining deep historical events of host and parasite colonization of North America, population genetics and phylogenetic and phylogeographic studies of the parasites and contemporary ecological studies (e.g. Hoberg et al., 2012b).

A major and essential component of the protostrongylid life cycle that remains poorly defined for the Arctic is the ecology of the gastropod intermediate hosts. The literature on arctic gastropods is sparse and limited to a few species distributions (Pilsbry, 1946; Kutz et al., 2000b; Grimm et al., 2009). This aspect of the life cycle has the potential to be very dynamic and responsive to climate, with changing temperature and hydrological conditions in the Arctic likely to have substantial impacts on the biodiversity and population dynamics of gastropods. The role of aquatic gastropods as intermediate hosts deserves further investigation. These intermediate hosts may become increasingly important under climate change scenarios where a warmer environment together with increased precipitation and flooding events may favour parasite species capable of infecting aquatic gastropods (reviewed in Morley, 2010). Intricately linked to studies on gastropods are those on host movement, habitat use and grazing behaviour. Such knowledge provides information on environmental contamination and sources and rates of exposure. Understanding this complexity may help tease out some of the ecological features which determine apparent host and geographic distributions.

Climate change is a major feature of arctic landscapes and protostrongylids are repeatedly demonstrated as being highly responsive to climate warming (Handeland and Slettbakk, 1994; Ball et al., 2001; Jenkins et al., 2006b). Current climate warming conditions are likely to decrease development times and increase survival rates for protostrongylids endemic to ungulates in the North, extend the period of the year when parasite transmission is possible and lead to expansion of geographic ranges of endemic and invasive protostrongylids (Kutz et al., 2005; Hoberg et al., 2008a, 2008b; Kutz et al., 2009b). Disease outbreaks may be triggered by unusually warm summers such as has occurred in reindeer in northern Europe infected with *E. rangiferi* (Handeland and Slettbakk, 1994) or by invasions of new protostrongylids into naïve host populations (Ball et al., 2001).

Mechanistic models have been developed and validated for predicting the development and response to climate of two key arctic protostrongylids (*U. pallikuukensis* and *P. odocoilei*) in gastropods on the tundra. These have served as useful tools for examining the past, current and future distribution of these parasites and can provide an insight into the ecology of other protostrongylids if basic life cycle information (development thresholds and heating constants) is available. These models require further development to move into a more quantitative predictive realm that will allow identification of the key stages of the life cycle that are sensitive to change.

2.3.2.5.4. General effects

Protostrongylids can cause significant multi-systemic pathology. Exacerbating the effects on the individual is the fact that caribou, muskoxen, Dall's sheep and mountain goats are each susceptible to at least three separate species of protostrongylids, and co-infections with at least two species are confirmed in all hosts. While the basic pathology has been described for most (but not all) northern protostrongylids, the potential additive effects of co-infections require further investigation. Similarly, while there is a small literature that demonstrates potentially subtle population-level effects of protostrongylids in bighorn sheep and snowshoe hares (Festa-Bianchet, 1991; Murray et al., 1997), the role of protostrongylids in the population dynamics of arctic ungulates in North America is yet to be examined.

2.3.2.6. Subfamily Dictyocaulinae

2.3.2.6.1. Dictyocaulus spp.

Dictyocaulus spp. are large (up to several centimetres long) white nematodes found typically with a dorsal distribution in the bronchi and bronchioles of the lungs. A number of species are found in a broad range of free-ranging ungulate hosts across the Holarctic (Hoglund et al., 2003). There are varying degrees of host specificity.

(a) *Host and Geographic Distributions:* At least one species – *Dictyocaulus eckerti* – is recorded in moose and caribou in AK, and muskoxen from the Kitikmeot region of NU and northern QC. *Dictyocaulus viviparus* has been reported from muskoxen on the arctic islands and mainland NT and NU, Canada, as well as AK but these records should be considered suspect (Table 2.5) (Gibbs and Tener, 1958; Samuel and Gray, 1974; USNPC, 2011). Records of *D. viviparus* have often been based uncritically on adult and/or larval morphology and in light of recent genetic and morphological work it is more likely that these are *D. eckerti* (Divina et al., 2000; Hoglund et al., 2003). There are no published reports for *Dictyocaulus* in Dall's sheep or mountain goats but *D. filaria* has been reported in bighorn sheep from the USA (USNPC, 2011). In Greenland, *Dictyocaulus* sp. was observed in one of five caribou calves of the Akia-Maniitsoq herd examined in April 2008 (C. Cuyler, S. Kutz, unpubl. data).

(b) *Ecology:* Adult nematodes produce eggs that pass up the trachea and, depending on the species, larvated eggs or larvae are excreted in the faeces. The life cycle is direct and infection is by ingestion of infective L3. The development from eggs or L1 in the environment is temperature and humidity dependent. Data on larval development in the environment are not available for *D. eckerti*, but for *D. filaria* of domestic sheep, development of L1 to infective L3 in northeast England took approximately 4–9 days in spring and summer, 1.5–4 weeks in autumn and 5.5–7 weeks in winter (Gallie and Nunns, 1976). The persistence of *Dictyocaulus* in muskoxen as far north as Bathurst Island at 75° latitude (Samuel and Gray, 1974) suggests that it can develop to infective L3 in the short high arctic summer. Extended survival of L3 in the arctic environment is unlikely. Whether dispersal of the infective larvae of *Dictyocaulus* spp. in the Arctic is facilitated by spores of the faecal fungus *Pilobolus* released from the sporangia, as occurs for at least some species (e.g. *D. viviparus* in cattle) (Eysker, 1991), is not known.

Inhibited development is an important phenomenon in the life cycle of *D. filaria*, with a large proportion of the eggs and larvae ingested in the autumn inhibiting until the following spring (Ayalew et al., 1974). A similar pattern of inhibition is expected for *Dictyocaulus* in muskoxen. In commercial muskox harvests on Banks Island, NT, adult nematodes are most common in yearling animals in early winter (typically November) and are rare or absent in February (M. Branigan, pers. comm), suggesting that *Dictyocaulus* at this latitude may overwinter as inhibited larvae.

(c) *Impacts*: In general for *Dictyocaulus* spp., developing pre-adult larvae, adults, eggs and hatched larvae can cause significant pulmonary damage and respiratory disease in their hosts. In muskoxen on Banks Island, NT, *Dictyocaulus* infections were associated with emaciation and mortality in yearlings on at least one occasion (Gunn et al., 1991b). *Dictyocaulus eckerti* can also cause significant disease in reindeer and histopathological findings in this host are consistent with those described in domestic livestock (Rahko et al., 1992).

The biodiversity of *Dictyocaulus* circulating in ungulates at high latitudes remains poorly defined. There exist only a few patchy reports where species identifications have been confirmed in North America. Where this has occurred, the species has been designated as *D. eckerti*, refuting previous records of *D. viviparus*. Anecdotal evidence suggests that *Dictyocaulus* may be a significant cause of morbidity and mortality of young muskoxen

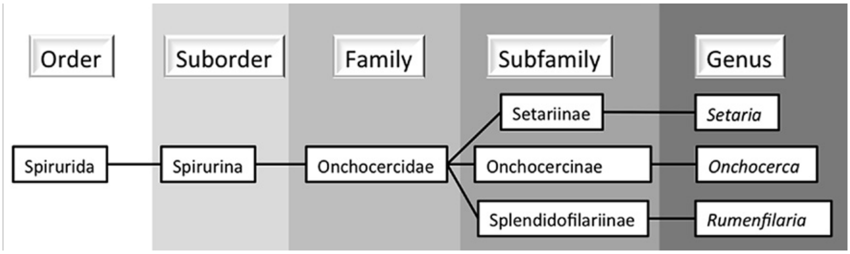

FIGURE 2.8 Tissue and lymphatic Spirurida reported from ungulates of arctic North America, including Greenland.

and perhaps also caribou. That it persists in the harsh high Arctic environment in low-density host populations is perhaps surprising and further exploration of the ecology of the free-living and parasitic stages of this parasite is warranted.

2.3.3. Other tissue nematodes: Onchocercidae

There is a minimum of three genera of Onchocercidae nematodes circulating in ungulates of arctic Canada and AK; none have been reported from Greenland (although see Fielden, 1877) (Fig. 2.8). Depending on genus and species, adult nematodes may be found in the abdominal cavity, connective tissue or lymphatic system of their hosts, whereas larval forms are found in the blood or lymph. These larval forms, named microfilariae (L1), are typically transmitted by haematophagous dipteran insect intermediate hosts in which development to infective L3 occurs.

2.3.3.1. Subfamily: Setariinae

2.3.3.1.1. ***Setaria*** spp.

Setaria spp. are robust nematodes 10–90mm long and 1–3mm thick found in the peritoneal cavity of a variety of ungulates (Becklund and Walker, 1969; Laaksonen et al., 2007). Two species have been identified in North American wild ungulates: *S. yehi* and *S. labiatopapillosa. Setaria yehi* is considered distinct from *S. tundra*, the main species parasitizing cervids in Fennoscandia (Becklund and Walker, 1969). According to Nikander et al. (2007), however, the morphological differences between these nominal species are less than the intraspecific variation demonstrated within *S. tundra.* The potential synonymy for *S. yehi* and *S. tundra* requires further exploration; the occurrence of a single holarctic species may be consistent with the recent history for moose or caribou at high latitudes (Rehbinder et al., 1975; Laaksonen et al., 2007; Nikander et al., 2007; Hoberg et al., 2012).

(a) *Host and Geographic Distributions. Setaria yehi* is found in cervids across a broad geographic range, documented in reindeer, caribou and moose from AK and caribou in the NT (Table 2.5) (Becklund and Walker, 1969; Dieterich and Luick, 1971; A. Quist, K. Beckmen unpubl. obs.). *Setaria labiatopapillosa* is typically a parasite of bovids but has been reported from caribou and moose at temperate latitudes (Becklund and Walker, 1969; USNPC, 2011); at least some of the records from moose may actually be of *S. yehi*. There are no reports of *Setaria* in muskoxen, Dall's sheep or mountain goats but *S. labiatopapillosa* has been reported from bighorn sheep (Becklund and Walker, 1969), indicating that North American caprines may harbour *Setaria* species. *Setaria* sp. are also common in wood bison in the NT (B. Elkin, unpubl. obs.).

(b) *Ecology:* The ecology of *S. yehi* in the Arctic has not been investigated. A series of studies on *S. tundra*, however, provide valuable insight into the ecology of these species in ungulates at arctic and subarctic latitudes. Adult nematodes live in the peritoneal cavity and produce microfilariae that circulate in the blood stream (Laaksonen et al., 2009b). Haematophagous insects including mosquitoes (Culicidae, especially *Aedes* spp. for *S. tundra*) and horn flies (*Haematobia* spp.) are intermediate hosts (Laaksonen et al., 2009a). Development of microfilariae to L3 in the insect is temperature dependent and for *S. tundra* takes 14 days at 21°C but does not occur at a mean temperature of 14.1°C (Laaksonen et al., 2009a). Animals are exposed to *S. tundra* during the summer and the prepatent period in reindeer is approximately four months, with microfilaria first detected in calves in early November. Thus, in arctic environments, animals infected one summer will not contribute to transmission until the following year.

Patterns of microfilariae in the peripheral blood vary with age, season and activity levels. Prevalence and density of microfilariae tend to be higher in calves than in adults for *S. tundra* in reindeer and moose (Laaksonen et al., 2007; Laaksonen et al., 2009b) and similar results were reported for *Setaria* sp. in black- and white-tailed deer from southern latitudes of North America (Weinmann et al., 1973; Prestwood and Nettles, 1977). Density of microfilaria in the peripheral blood is the highest during the summer. Microfilarial density also increases with host activity and may enhance transmission during periods of insect harassment, when hosts are more active due to the discomfort caused by bites and presence of insects (Laaksonen et al., 2009b). In six captive reindeer, microfilariaemia peaked from June to mid-September, then decreased and disappeared by January ($n = 3$) or remained very low until the following summer ($n = 3$), suggesting a one-year lifespan for the adult parasite and/or evidence of acquired immunity. Patterns of disease outbreaks in reindeer in Finland – emerging initially in the south and then moving to the north while disease in the south decreased – also support an acquired immunity in reindeer. There is no evidence for transplacental transmission in reindeer.

Moose sympatric with infected reindeer populations have a very low prevalence of *S. tundra* (1.4–1.8%) suggesting that they are not good hosts for this parasite (Laaksonen et al., 2007; Laaksonen et al., 2009b). However, in some regions of AK, *S. yehi* appears to be well established in moose with prevalence of microfilariae up to 100% (A. Quist, K. Beckmen unpubl. obs.).

Setaria is highly sensitive to climatic conditions and disease outbreaks and range expansions of *S. tundra* in Fennoscandia are linked to unusually warm climatic conditions. In Finland, disease outbreaks in reindeer have occurred following two consecutive summers with warmer than average temperatures. Models developed to describe these outbreaks suggest that disease emergence results from increased development rates and abundance of the parasites in vectors as well as the herding behaviour and habitat use of the reindeer (Laaksonen et al., 2009a; Laaksonen et al., 2010a).

(c) *Impacts:* Unlike the situation in Fennoscandia with *S. tundra*, *S. yehi* does not currently seem to be an important cause of morbidity and mortality in wild caribou of North America. Clinical disease is not reported in caribou and it was not found in post-mortem examinations of several hundred wild caribou during International Polar Year activities (S. Kutz and CARMA, 2011). In AK, infections of 5–20 adult *S. yehi* in captive adult reindeer caused a mild to moderate peritonitis but no clinical signs (Dieterich and Luick, 1971). In contrast, and much more recently, intense inflammation, a secondary bacterial peritonitis and mortality in nine free-ranging moose calves were attributed to migrating *S. yehi* and massive numbers of microfilaria (A. Quist, K. Beckmen unpubl. obs.).

2.3.3.2. Subfamily Onchocercinae

2.3.3.2.1. Onchocerca spp.

In North America, *Onchocerca cervipedis* (syn. *Wehrdikmansia cervipedis*), commonly known as 'legworm' or 'footworm', is a common parasite of cervids, including moose and woodland caribou of the boreal regions of AB, BC and southern AK (Ritcey and Edwards, 1958; Williams and Babero, 1958; Low, 1976; Samuel et al., 1976). Adult nematodes range from 5.5 to 6cm (males) and 1.8 to 2.0cm (females) and are found in nodules within subcutaneous tissues (Wehr and Dikmans, 1935). Parasite identification is based mainly on gross morphology and the presence of subcutaneous nodules containing intra-lesional adult nematodes and/or microfilariae (Samuel et al., 1976). In Eurasia, *Onchocerca skrjabini* (Synonym *O. tarsi-*

cola), is present in reindeer and moose (Bylund et al., 1981). Nodules in reindeer are mainly present under the skin of the muzzle, hocks and to a lesser extent elsewhere on the body including the brisket and shoulder (Lisitzin, 1964).

(a) *Host and Geographic Distributions.* Until recently, there were only anecdotal reports of *O. cervipedis* in moose from AK and the YT (Table 2.5) (P. Merchant, pers. comm.) Recent findings, based on combined parasite identification, including molecular and histopathological methods, have confirmed that *O. cervipedis* occurs in moose and Grant's caribou from AK and moose from the NT (G. Verocai, K. Beckmen, S. Kutz, E. Hoberg unpubl. obs.). The occurrence of this parasite in muskoxen, Dall's sheep and mountain goats is unknown. *Onchocerca cervipedis* may be much more widespread in ungulates of arctic North America, however, and the need for targeted survey is apparent.

(b) *Life Cycle:* The microfilariae produced by female parasites remain in the skin and are ingested by the vectors during feeding. Blackflies (Diptera: Simuliidae) act as intermediate hosts, with microfilariae developing to L3. Pledger (1978) demonstrated that *Simulium decorum* and *Simulium venustum* serve as intermediate hosts of *O. cervipedis* in northeastern AB, although other simuliids were found feeding on moose. Intermediate hosts species involved in the epidemiology of this parasite in high latitudes of North America are not known but species that serve as intermediate hosts in AB, and related species, are widely distributed in AK, YT, NT and NU (Currie, 1997; Currie and Adler, 2000; Currie, 2006; Adler and Currie, 2008).

(c) *Impacts*: *Oncocherca cervipedis* rarely causes significant clinical signs. There are occasional reports of massive infections resulting in swelling, ulceration and hoof damage in *Odocoileus* spp. (Rush, 1935; Herman and Bischoff, 1946). De Nio and West (1942) postulated that clinically affected animals would be more susceptible to predation and an easier target to hunters. In contrast, in moose and caribou, this parasite is generally found along the metatarsus and metacarpus (DeNio and West, 1942). Clinical disease has not been described in caribou but infections in moose from YT were associated with open sores in the lower legs (P. Merchant, pers. comm.). The impacts of *O. cervipedis* on cervid populations in high latitudes of North America are unknown. Some species of *Onchocerca* can be zoonotic, and a recent study reported that *Onchocerca jakutensis*, a species that normally infects wild cervids from Eurasia, causes nodular dermatological disease in people (Koehsler et al., 2007).

2.3.3.3. Subfamily: Splendidofilariinae

2.3.3.3.1. *Rumenfilaria andersoni*

Rumenfilaria are nematodes located in the subserosal lymphatic vessels or veins of the rumen. Males are up to 62mm long and females up to 205mm long and may be visible to the naked eye in older and/or thin animals (Lankester and Snider, 1982; Laaksonen et al., 2010b).

(a) *Host and Geographic Distributions: Rumenfilaria andersoni* was first described in moose from northwestern Ontario in 1982 (Lankester and Snider, 1982) and until recently was only known from the original description. Surveys have now detected microfilariae consistent with *R. andersoni* in the blood of up to 70% of Alaskan moose (A. Quist, K. Beckmen unpubl. obs.). *Rumenfilaria* has not been documented in muskoxen, Dall's sheep, mountain goats or caribou from North America. *Rumenfilaria andersoni* tends to be common in other regions where there has been targeted survey, for example, in Finland (Laaksonen et al., 2010b), and the absence of reports in caribou, and perhaps other ungulates, in arctic North America may reflect a lack of search effort as opposed to true absence. Conspecificity of populations in Fennoscandia and North America remains to be determined.

Life Cycle: Microfilariae are easily detected in the blood of infected animals (Laaksonen et al., 2010b), and based on what is known for related genera it is probable that transmission is by haematophagous arthropods.

Impacts: Adults obstruct the lymphatic vessels of the rumen leading to dilatation, lymphaedema, lymphangitis, granulomatous inflammation and fibrosis (Laaksonen et al., 2010b). The occurrence of clinical disease in wild ungulates remains unknown.

2.3.3.4. Emerging issues and knowledge gaps for the Onchocercidae

Until recently, the Onchocercidae were a completely neglected component of the helminth fauna of arctic ungulates of North America. Recent mortality events for moose calves in AK, new observations of *Onchocerca* in moose and caribou in northern Canada and major mortality events in Fennoscandia linked to *S. tundra* highlight the possibility that these could become, or may be becoming, important emerging pathogens under current scenarios for climate change. In particular, the work in Fennoscandia has demonstrated that these parasites are highly responsive to climatic conditions and that small changes in summer temperatures can lead to significant disease outbreaks. Members of the Onchocercidae are also important pathogens of humans in the tropics and knowledge gained from studying their ecology in the Arctic may provide insights into management of this group of parasites in other regions (Laaksonen et al., 2010a; Davidson et al., 2011). Further research on the biodiversity, definitive host

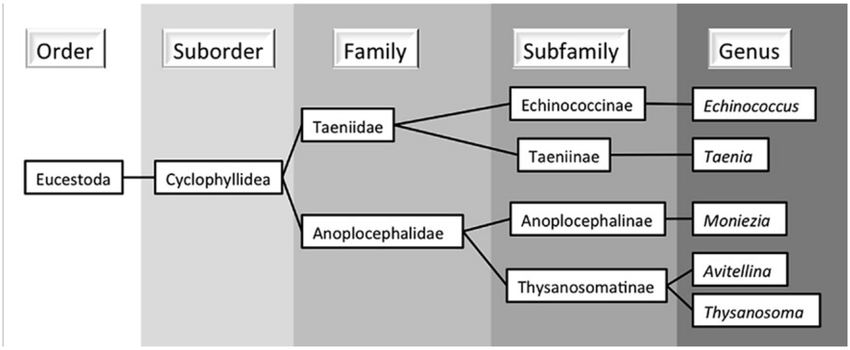

FIGURE 2.9 Cestoda reported from ungulates of arctic North America, including Greenland.

TABLE 2.6 Cestodes reported from ungulates of arctic North America, including Greenland. The range of prevalence reported is indicated below the parasite name. Only prevalence estimates based on sufficient sample sizes are included. Data compiled from available published and grey literature

Host, Parasite		Herd, region or nearest place name
Caribou		
Echinococcus granulosus (1.3-20%)	AK	Not specified[a]; Teshekpuk, Northern Alaska Peninsula, Mulchtna, Western Arctic[b]
	NT	Mackenzie Delta[c–e]; Beverly[f]
	QC/NL	Rivière George[g]
Taenia hydatigena (15-60%)	AK	Teshekpuk[b]; Not specified[a,c,h]
	NT	Mackenzie Delta[c,e]; Beverly[f]
	NU	Kitimeot Region[i]
	QC	Rivière-aux-Feuilles[j]
Taenia krabbei	AK	Northwest, Southcentral, Interior[k]
Taenia cf. *krabbei* (13–20%)	AK	Teshekpuk, Northern Alaska Peninsula, Mulchatna[b], Not specified[a,h]
	NT	Mackenzie Delta[e,w]
	NU	Kitikmeot Region[i]
	QC	Rivière-aux-Feuilles[j]
	GL	Kangerlussuaq[l]
Moniezia cf. *expansa*	GL	Kangerlussuaq[l]
Avitellina arctica	NT/NU	Thelon Game Sanctuary[m]
	QC	Rivière George[n]
Dall's sheep		
Taenia hydatigena (35%)	AK	Not specified[h]
	NT	Mackenzie Mountains[o]
Moniezia sp. (10–16%)	NT	Mackenzie Mountains[o]

TABLE 2.6 *(continued)*

Host, Parasite		Herd, region or nearest place name
Moose		
Echinoccocus granulosus (24%)	AK	South Central[p]; Tanana Flats, Fairbanks, Palmer[b]
	NT	Mackenzie Mountains[q]
Taenia arctos	AK	Interior and South Central[k]
Taenia krabbei	AK	Interior[k]
Taenia cf. *krabbei*	AK	Not specified[h]
	NT	Mackenzie Mountains[q]
Muskoxen		
Echinoccocus granulosus	NT/NU	Thelon Game Sanctuary[r]
Taenia cf. *hydatigena*	AK	Not specified[h]
	NT/NU	Not specified[q]; Thelon Game Sanctuary[r]
	GL	Hurry Inlet[s]
Taenia cf. *krabbei*	AK	Not specified[h]
	GL	Kangerlussuaq[t]
Taenia sp.	NU	Ellesmere Island[u]
	GL	east Greenland[v]
Anoplocephalidae egg	NU	Bathurst Island and Devon Island[u,w]
Moniezia expansa	NU	Ellesmere Island[q]; Thelon Game Sanctuary[r]
Moniezia sp.	AK	Nunivak Island[w]
	NU	Ellesmere Island[x]

[a] Hadwen (1922).
[b] K. Beckmen (unpubl. data).
[c] Broughton *et al.* (1967).
[d] Sweatman and Williams (1963).
[e] Choquette *et al.* (1957).
[f] Thomas (1996).
[g] Parker (1981).
[h] Dieterich (1981).
[i] Gunn *et al.* (1991a).
[j] Ducrocq and Lair (2007).
[k] Lavikainen *et al.* (2011).
[l] Clausen *et al.* (1980).
[m] Gibbs (1960).
[n] USNPC, (2011).
[o] Simmons *et al.*, (2001).
[p] Rausch (1959).
[q] S. Kutz, C. Tobac (unpubl. obs.).
[r] Gibbs and Tener (1958).
[s] Alendal and Helle (1983).
[t] Raundrup *et al.* (2012).
[u] Webster and Rowell (1980).
[v] Fielden (1877).
[w] Samuel and Gray (1974).
[x] Tener (1954).

and geographic range of Onchocercidae in arctic ungulates, together with research on the life cycle, intermediate host species, transmission patterns and response to climate change are required (Fig. 2.8).

2.4. CESTODES

The cestodes present in arctic ungulates are from two families, the Taeniidae, for which ungulates are intermediate hosts, and the Anoplocephalidae, for which ungulates are definitive hosts. Members of Taeniidae include species of *Taenia* and *Echinococcus*, whereas the Anoplocephalidae is represented by *Moniezia*, *Avitellina* and perhaps *Thysanosoma* (Figure 2.9, Table 2.6).

2.4.1. Ungulates as Intermediate hosts: Taeniidae

2.4.1.1. Subfamily Taeniinae

2.4.1.1.1. ***Taenia hydatigena*****,** ***Taenia krabbei*** **and** ***Taenia arctos***

(a) *Host and Geographic Distributions.* The three species of *Taenia* recognized at high latitudes in North America, *T. hydatigena*, *T. krabbei* and *Taenia arctos* all have apparently Holarctic distributions in arctic ungulates, canids and ursids (Table 2.6) (Loos-Frank, 2000; Haukisalmi et al., 2011). Larvae are simple cysticeri that commonly occur in the liver and omentum, or elsewhere in the peritoneal cavity (*T. hydatigena*) or in the heart, tongue, oesophagus and skeletal musculature, and less commonly the brain (*T. krabbei* and *T. arctos*) (Broughton et al., 1967; Choquette et al., 1957; Gibbs and Eaton, 1983; Lavikainen et al., 2011).

Taenia krabbei is often listed as a subspecies of *T. ovis*, a designation now refuted by molecular evidence (Lavikainen et al., 2010). A recent report of *T. ovis krabbei* in a muskox from west Greenland (Raundrup et al., 2012) should be referred to *T.* cf. *krabbe*i; however, it is also possible that this represents *T. arctos* instead (see Haukisalmi et al., 2011). *Taenia arctos* is morphologically similar to, but genetically distinct from, *T. krabbei*. It was recently described to be circulating in moose from AK and Finland and brown bears (Ursus arctos) in Finland (REFS) (Haukisalmi et al., 2011; Lavikainen et al., 2011). Consequently, all previous species-level identifications of *T. krabbei* require re-evaluation by both morphological and molecular criteria to establish identity. In particular, current records of *T. krabbei* in non-canid hosts may not represent this species (e.g. Rausch, 1994; Hoberg et al., in press-a). *Taenia arctos* and *T. krabbei* are considered phylogenetically quite distant, with the former as a putative sister species to *T. solium* and *T. krabbei* as a sister to *T. multiceps*. Since both species had been reported to infect moose, previous records of *T. krabbei* in these intermediate hosts should be revisited (Lavikainen et al., 2011). We refer historical records of *T. krabbei* as tentative and use the designation of *T.* cf. *krabbei* in further discussions below. We treat *T. hydatigena* similarly, since limited morphological and molecular confirmation of species identity in arctic ungulates has been done.

Taenia cf. *hydatigena* is reported in caribou, muskoxen, moose and Dall's sheep across their arctic ranges (Table 2.6) (Gibbs and Tener, 1958; Tener, 1965; Webster and Rowell, 1980). *Taenia* cf. *krabbei* is known in caribou, moose and muskoxen but has not been reported in Dall's sheep. *Taenia arctos* was recently described to be circulating in moose and brown bears (*Ursus arctos*) from AK and Finland (Haukisalmi et al., 2011; Lavikainen et al., 2011). *Taenia parenchymatosa*, a taeniid typical in Eurasian reindeer, was reported in the liver of reindeer from Alaska (Pushmenkov, 1945 cited in Choquette et al., 1957) and was probably introduced with these cervids from Chukotka in the last century. It is unknown as to what extent this parasite established in North America. Infections may be pathogenic as indicated experimentally where one reindeer died following rupture of the liver (Pushmenkov 1945 cited in Choquette et al., 1957; Jones and Pybus, 2001).

(b) *Ecology: Taenia* spp. have a predator–prey life cycle with adult cestodes occurring in the small intestines of carnivores or omnivores and larval stages found as cysts in tissues of herbivore hosts (Loos-Frank, 2000; Jones and Pybus, 2001). Infection of the definitive hosts is by ingestion of protoscolices from cysticerci in infected ungulates, and intermediate hosts are infected by ingestion of eggs from the faeces of carnivores. Transplacental transmission of *T.* cf. *hydatigena* was observed in a wild muskox foetus on the mainland of western Nunavut, Canada (S. Kutz, J. Nishi unpubl. data). Taeniid eggs are robust, can survive for extended periods (>200 days) at cool temperatures (Gemmel, 1977) and are likely to persist for extended periods in the Arctic. Infection prevalence and intensity increases with age for *T.* cf. *hydatigena* in moose and caribou (Addison et al., 1979; Thomas, 1996, although see Pollock et al., 2009) and for *T.* cf. *krabbei* (possibly *T. arctos*) in moose (Addison et al., 1979). Viable and degenerate cysts are found across a wide age range of animals, suggesting both a finite lifespan for the cysticerci as well as ongoing infection (Addison et al. 1979). In caribou, prevalence of *T.* cf. *hydatigena* tends to decrease from December to March (Thomas, 1996).

A series of experiments on *T.* cf. *krabbei* and *T. hydatigena* by Sweatman and Henshall (1962) provide some important insights into characteristics of the lifecycles of *Taenia* spp. in the context of arctic systems. For *T.* cf. *krabbei*, the prepatent period in two dogs given cysticerci that originated from reindeer from northern Canada was 34 and 37 days. This is short compared to that for *T. ovis* in the same study (~60 days) (Sweatman and Henshall, 1962). The prepatent period of *Echinococcus multilocularis* is similarly short (Rausch and Schiller, 1956) and Sweatman and Henshall (1962) suggested that both these species appeared to have evolved at high latitudes and that the short prepatent periods could be adaptations to the short arctic summers, allowing carnivores to maximize egg production during the seasonal period when successful transmission to the intermediate host is more likely. These species have extended histories at high latitudes (e.g. Hoberg et al., 2012) and have been influenced by increasingly cold environments since the Pliocene.

Establishment of cysticerci of *T.* cf. *krabbei* as adult cestodes in experimentally infected dogs was high, with 7 of 7 cysticerci maturing to adult worms in one dog. An average of 9.2–9.3 proglottids, with an average of 19,300 eggs each, were shed per day throughout patency that lasted at least 131 days. Ten sheep, seven goats, one domestic calf and two pigs were refractory to experimental infection with *T.* cf. *krabbei* of reindeer origin, suggesting host specificity of this parasite (Sweatman and Henshall, 1962).

Sweatman and Plummer (1957) conducted similar studies on the life history of *T. hydatigena*. The prepatent period in dogs experimentally infected with cysticerci from sheep or moose was 51–76 days and patency lasted 4.5–11.5 months. During that time, proglottids were excreted regularly with one dog infected with five worms excreting an average of 3.7 proglottids per day. Excreted proglottids contained from 6000–23,000 eggs and some remained active for a day or so post-excretion and were highly mobile, moving up to three feet from the faeces (Sweatman and Plummer, 1957). In contrast to *T. krabbei*, *T. hydatigena* of moose origin, passaged through a dog, was infective to domestic sheep, suggesting no species barriers between the sylvatic and domestic cycle for this species (Sweatman and Plummer, 1957).

In contrast to domestic sheep, cysticerci in moose, reindeer and muskoxen can mature in the parenchyma of the liver (Choquette et al., 1957; Sweatman and Plummer, 1957; Gibbs and Tener, 1958). Cysticerci in the liver parenchyma of moose remain viable for up to 48 hours at subzero temperatures in northern Ontario, considerably longer than those on the liver surface or in the omentum. Thus, development to mature, viable cysticerci deep in the hepatic parenchyma may be a mechanism that enhances transmission potential during the arctic winter in the sylvatic cycle (Sweatman and Plummer, 1957).

Adult stages of both *T.* cf. *hydatigena* and *T.* cf. *krabbei* have been reported in domestic dogs (*Canis familiaris*), wolves (*Canis lupus*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*) and arctic fox (*Vulpes alopex*) (Kapel and Nansen, 1996; Lavikainen et al., 2011). *Taenia* cf. *krabbei* has also been reported in black (*Ursus americanus*), brown (*U. arctos*) and polar (*U. maritimus*) bears (Choquette et al., 1969; Pence et al., 1983; USNPC, 2011). To date, *T. arctos* has been described only from brown/grizzly bears (Haukisalmi et al., 2011) but previous records of *T. krabbei* in ursids need to be revisited. It is probable that the contribution of each intermediate and definitive host species to the circulation of these cestodes in arctic environments differs. For example, in west Greenland and Svalbard where wolves are absent and domestic dogs are few, it is the arctic fox that is responsible for maintaining *T. krabbei* (Bye, 1985; Kapel and Nansen, 1996; Stien et al., 2010) whereas wolves may play a more important role elsewhere.

(c) *Impacts*: *Taenia* species are relatively common in arctic ungulates at low intensities and in general do not seem to cause significant pathology. There are, however, occasional hunter reports of animals in poor condition that are severely affected with *T.* cf. *krabbei* (Kutz, 2007). Migrations of *T. hydatigena* through the liver can also cause tissue damage (Sweatman and Plummer, 1957). In cross-sectional studies, there was no relationship between the number of cysts of *T.* cf. *hydatigena* in the livers of caribou and kidney fat index (Pollock et al., 2009) and no detectable impact of *T.* cf. *hydatigena* or *T.* cf. *krabbei* on body condition in moose (Addison et al., 1979).

Taenia hydatigena, *T. krabbei* and *T. arctos* are not known zoonoses; however, *T. krabbei* and *T. arctos* are sister species of *T. multiceps* and *T. solium*, respectively, both of which can infect people, leading to uncertainty concerning the zoonotic potential for these arctic taeniids (Lavikainen et al., 2008). Meat or livers with high intensities of cysticerci may be discarded by harvesters (Kutz, 2007; B. Elkin, S. Kutz, unpubl. obs.).

2.4.1.2. Subfamily Echinococcinae

2.4.1.2.1. Echinococcus granulosus

(a) *Host and Geographic Distributions: Echinococcus granulosus* occurs in the larval stage (hydatid cysts) in the lungs of reindeer, caribou, moose and muskoxen across North America (Table 2.6) (Gibbs and Tener, 1958; Rausch, 1967; Choquette et al., 1973; Barrett and Dau, 1981; Rausch, 2003). It is reported in mountain goats from temperate regions (Foreyt et al., 2009) but has not been found in Dall's sheep nor is it known from Greenland (OIE, 1998; Smith, 1957 in Rausch, 2003). Two strains circulate in ungulates of arctic Canada, G8 and G10, and these differ from other forms of *E. granulosus* with respect to pathogenicity to people, infectivity to domestic ungulates, serology and genetics (reviewed in Thompson, 2008). Whether these strains represent a different species of *Echinococcus*, that is, *E. canadensis*, is unresolved (Thompson, 2008; Knapp, 2011).

(b) *Ecology.* Wolves (*Canis lupus*) are the primary definitive hosts in the Arctic and coyotes (*Canis latrans*) and domestic dogs can also be infected (Rausch, 2003). The prepatent period is 56–65 days in dogs, maximum egg production occurs as early as 76 days post-infection, and the lifespan of the adult parasite is 8 months to a year (Sweatman and Williams, 1963; Rausch, 1993). Individual dogs can acquire hundreds to tens of thousands of adult parasites following ingestion of hydatid cysts (Rausch, 1993). Ungulates are infected by ingestion of eggs from the faeces of infected canids. Like species of *Taenia*, these eggs can persist in the environment under cool moist conditions (Gemmel, 1977). In caribou and moose prevalence, intensity and cyst size increase significantly with age and up to 167 cysts have been reported in a single moose (Addison et al., 1979; Thomas, 1996). *Echinococcus granulosus* is zoonotic, and exposure to faeces from infected dogs that have consumed cysts in wild game is a potential risk in arctic communities (Choquette et al., 1973; Rausch, 2003; Himsworth et al., 2010). Skinning wolves and foxes are also potential zoonotic risks for trappers.

(c) *Impacts*. In arctic ungulates, hydatid cysts are found predominantly in the lungs and less frequently in the liver where they are usually abnormal and sterile (Rausch, 2003; Broughton et al., 1967). In moose, they can also occur in the spleen, heart or kidneys (Addison et al., 1979). Thomas (1996) was unable to detect a significant impact of *E. granulosus* on pregnancy, weight or kidney fat in caribou although there were trends towards poorer body condition and lower pregnancy rates. Infection in moose may lead to increased mortality; those with high burdens of cysts in their lungs are more susceptible to hunting and predation than are those with low burdens or no infection (Rau and Caron, 1979; Joly and Messier, 2004). The impacts in other arctic ungulates are unknown.

2.4.2. Ungulates as definitive hosts: Anoplocephalidae

2.4.2.1. Subfamilies Anoplocephalinae and Thysanosomatinae

2.4.2.1.1. Moniezia, Avitellina, Thysanosoma

(a) *Host and Geographic Ranges: Moniezia* and *Avitellina* are large, long cestodes reaching several metres in length and found in the small intestine of ruminants. Eggs of anoplocephalid tapeworms have been recovered from faeces of muskoxen, Dall's sheep, caribou and mountain goats throughout most of their range (Table 2.6). Adult specimens of *Moniezia expansa* have been reported from muskoxen in NU and NT (Gibbs and Tener, 1958; Tener, 1965; Samuel and Gray, 1974). Anoplocephalid eggs are present in the faeces of muskoxen in Nunavik, QC, and may differ morphologically from those recovered from muskoxen in the western Canadian Arctic (S. Kutz, M. Simard, unpubl. data). *Thysanosoma actinoides* and *M. expansa* are reported in moose from temperate regions of North America (Samuel et al., 1976; Stock and Barrett, 1983; Hoeve et al., 1988) and anoplocephalid eggs are common in moose from the arctic and subarctic regions (Table 2.6). *Moniezia* sp. is reported from Dall's sheep of the Mackenzie Mountains (Simmons et al., 2001) and *M. benedeni*, *Avitellina* sp. and *Thysanosoma actinoides* are reported in mountain goats from western Canada (Cowan, 1951; Samuel et al., 1977).

The diversity of anoplocephalid cestodes in subspecies of *Rangifer* is not well documented in North American and Greenland. *Avitellina arctica* was reported in a caribou from the Thelon Game Sanctuary, NT (Gibbs,

1960) and the Rivière-George caribou herd in QC in 2006 (USNPC, 2011) and is commonly reported from reindeer in Eurasia. Several species of *Moniezia* including *M. benedeni*, *M. taimyrica* and *M. rangiferina* have been described in reindeer from Russia, Norway and South Georgia Island (Semenova, 1967; Zelinskii, 1973; Leader-Williams, 1980; Bye, 1985); however, there are no confirmed reports of *Moniezia* sp. in free-ranging arctic and subarctic North American caribou. Diversity of anoplocephalids, and particularly species of *Moniezia* at high latitudes, requires further investigation including the application of new molecular-based methods to unequivocally resolve identity and host associations for these otherwise widespread species.

(b) *Ecology.* Anoplocephalids have an indirect life cycle. Eggs in the faeces of infected ungulate definitive hosts are ingested by arthropod intermediate hosts where they develop to the infective cysticercoid stage. The life cycle is completed when cysticercoids are ingested by the definitive hosts. *Moniezia* spp. are generally transmitted by oribatid mites (Samuel and Gray, 1974; Elliott, 1986; Denegri, 1989; Xiao and Herd, 1992) and in Russia *Avitellina arctica* develops in at least two species of Collembola, *Onychiurus taimyricus* and *O. furcifera* (Kozlov, 1986). Development to fully formed cysticercoids is temperature dependent, for example, ranging from 27 (28°C) to 97 (18–20°C) days for *M. expansa* in oribatid mites (Narsapur and Prokopic, 1979). The long development time at these relatively warm temperatures (18–20°C) is perhaps surprising for an arctic parasite and suggests that climatic conditions may play an important role as determinants of geographic range and epidemiology of this group of parasites.

Anoplocephalids are generally parasites of young animals and are uncommon in adults (Kirilenko, 1975; Bye, 1985). There is some evidence of host specificity, for example, *A. arctica* does not infect 'horned' species that are sympatric with infected cervids in Russia (Gibbs, 1960). Similarly, caribou that are sympatric with infected muskoxen in the Thelon Game Sanctuary, NU, were infected with *A. arctica* while M. *expansa* was identified from muskoxen (Gibbs and Tener, 1958; Gibbs, 1960).

(c) *Impacts*. Anoplocephalid tapeworms can cause diarrhoea and reduced weight gain in domestic lambs (Narsapur, 1988). In reindeer in Russia, *A. arctica* causes sufficient pathology in calves to warrant treatment and *M. baeri*, *M expansa* and *M. benedeni* are reported to cause unthriftiness and emaciation (Polyanskaya, 1961; Kirilenko, 1975). For muskoxen, there is some evidence of pathology induced by *Moniezia* spp. Translocated muskox calves that grazed on pasture previously occupied by domestic sheep and cattle in Iceland died with heavy tapeworm infections and scouring in captive muskoxen in Norway was attributed to *Moniezia* spp. (Samuel and Gray, 1974). The specimens of *Moniezia* were not identified to species in either of these cases.

TABLE 2.7 Trematodes reported from ungulates of arctic North America, including Greenland. The range of prevalence reported is indicated below the parasite name. Only prevalence estimates based on sufficient sample sizes are included. Data compiled from available published and grey literature

Host and Parasites	Herd or location	
Caribou		
Fascioloides magna (15–60%)	QC	Rivière-aux-Feuilles[a]; Rivière George[b–d]
Paramphistomum cervi	AK	Cantwell[e]; Northern Alaska Peninsula, Mulchatna[f]
Muskoxen		
Fascioloides magna (87%)	QC	Kuujjuak, Tasiujaq[g]
Moose		
Paramphistomum cervi	AK	Anchorage[h]; Fairbanks, Tanana Flats[f]

[a] Ducrocq and Lair (2007).

[b] Choquette *et al*. (1971).

[c] Parker (1981).

[d] Lankester and Luttich (1988).

[e] Dieterich, (1981).

[f] K. Beckmen (unpubl. obs.).

[g] M. Simard (pers. comm.).

[h] USNPC, (2011).

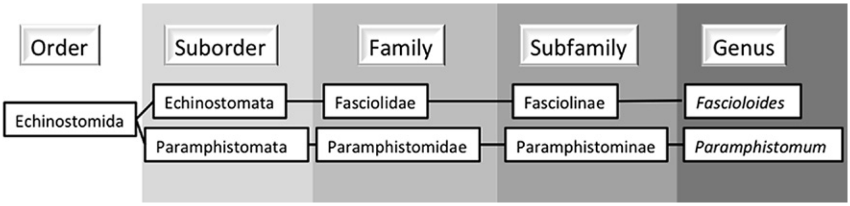

FIGURE 2.10 Trematoda reported from ungulates of arctic North America, including Greenland.

2.4.3. Emerging issues and knowledge gaps for the Cestoda

Cestoda, although widespread in ungulates of arctic North America and Greenland, are not well characterized. Recent phylogenetic work on the taeniids, together with discovery of a new species of *Taenia* circulating in moose across the Holarctic, highlights the possibility of additional cryptic species and complexes circulating in ungulates from the Arctic and Subarctic (Lavikainen et al., 2008; Lavikainen et al., 2010; Haukisalmi et al., 2011; Lavikainen et al., 2011).

Similarly, for the anoplocephalids, the Russian literature suggests that there may be considerable hidden diversity within *Moniezia*, that anoplocephalids may have significant impacts on their hosts and that they may be influenced by climate changes (Priadko, 1976; Narsapur and Prokopic, 1979). That there has been no recent work on biodiversity or impacts of this family in North America is perhaps surprising. Further characterization of the cestode fauna of arctic ungulates is warranted and will strongly benefit from molecular approaches in defining species limits, diversity and epidemiological patterns. There is also a need to more critically explore the impacts of these parasites in arctic hosts, their potential zoonotic risk, particularly for taeniids, and how they circulate among the various definitive and intermediate hosts.

2.5. TREMATODES

The trematode fauna of ungulates in arctic North America is very simple, consisting of only two known species: *Fascioloides magna*, the giant liver fluke, and *Paramphistomum cervi*, the rumen fluke (Table 2.7, Figure 2.10). Both parasites require aquatic snails as intermediate hosts for transmission.

2.5.1. Family Fasciolidae

2.5.1.1. Subfamily Fasciolinae

2.5.1.1.1. Fascioloides magna

(a) *Host and Geographic ranges:* The arctic distribution of *F. magna* is limited to caribou and muskoxen from northern Quebec and Labrador (Choquette et al., 1971; Lankester and Luttich, 1988; Pollock et al., 2009: M. Simard pers. comm) (Table 2.7). Both hosts become patent and prevalence is high, often approaching 100%. Moose are dead-end hosts for *F. magna* (Pybus, 2001), and it has not been reported in mountain goats or Dall's sheep nor has it been reported in Greenland.

(b) *Ecology:* Aquatic snails of the family Lymnaeidae are intermediate hosts for *F. magna* (Pybus, 2001; Králová-Hromadová et al., 2011). Lymnaeid snails are present across the Arctic (Hershey, 1990) and various stages of the parasite have been demonstrated to overwinter in snails (Pybus, 2001). In caribou, prevalence and intensity tend to increase with age (Lankester and Luttich, 1988). The life cycle in muskoxen is undescribed.

(c) *Impacts*: *Fascioloides magna* causes substantial liver pathology in normal and aberrant hosts (Pybus, 2001). In caribou, adult flukes are associated with lesions that include fibrous capsules typically containing two flukes and copious amounts of viscous grey–brown/black fluid. Migrating immature flukes are associated with blood filled tunnels up to 1.5cm wide (Lankester and Luttich, 1988). Similar lesions are present in muskoxen (CCWHC, 2011). Despite the significant hepatic damage, there is no evidence that *F. magna* has negative effects on body condition of caribou (Lankester and Luttich, 1988; Pollock et al., 2009). In moose, the flukes do not mature and the continued migration of immature flukes through the liver can lead to mortality (Pybus, 2001). Flukes also did not mature in three bighorn sheep experimentally infected with 50 or 100 metacercariae. All three sheep died from the effects of the flukes within 104–197 days post-infection. Post-mortem findings included multifocal pyogranulomatous hepatitis, necrotizing haemorrhagic pneumonia, pleuritis and peritonitis (Foreyt, 1996). Three, 18 and 21 flukes were recovered from the sheep indicating a low lethal dose. A similar outcome might be expected in other bovids, specifically Dall's sheep and mountain goats. The introduction of *F. magna* into areas where hosts had not been previously exposed is related to mortality events in European cervids (Balbo et al., 1989; Slavica et al., 2006).

Fascioloides magna is present in wild cervids of northern BC, AB and SK (Wobeser et al., 1985; Pybus, 2001) but its distribution is patchy. Range expansion for this parasite has been associated with natural migration or translocation of infected hosts into non-endemic areas (Wobeser et al., 1985; Pybus, 2001; Slavica et al., 2006; Králová-Hromadová et al., 2011). Development in snail hosts is temperature dependent which may limit its northward range expansion; however, it is well established in arctic Quebec, and the ability to overwinter in snails may facilitate its maintenance in this environment.

2.5.2. Family Paramphistomidae

2.5.2.1. Subfamily Paramphistominae

2.5.2.1.1. Paramphistomum spp.

(a) *Host and Geographic ranges: Paramphistomum* spp. are rumen flukes that are pear-shaped worms characterized by a large terminal ventral sucker. Numerous genera and species within the Paramphistominae have been described but the genus was redefined and restricted with only nine species being retained (Eduardo, 1982). In North America, *P. cervi* is reported in Alaskan caribou and moose (Dieterich, 1981; USNPC, 2011; K. Beckmen, unpubl. data) and *P. cervi* and *P. liorchis* are known in moose from temperate Canada (Lankester et al., 1979; Kennedy et al., 1985). *Paramphistomum* has not been observed in muskoxen, Dall's sheep or mountain goats. *Paramphistomum leydeni* is documented in reindeer from Eurasia (Nikander, 1992).

(b) *Ecology*: The life cycle of species of *Paramphistomum* requires aquatic snail intermediate hosts of which members of the Lymnaeidae and Planorbidae are suitable (DeWaal, 2010). Miracidia develop in eggs, hatch, infect aquatic snails and develop to cercaria. This process is temperature dependent, and in one experimental study on *P. cervi*, miracidia developed in 20 days in eggs maintained at 20°C but did not hatch at temperatures below 13°C. When infected snails were maintained at 20°C, cercaria were shed by 50 days post-infection (reviewed by Lankester et al., 1979). Snails can shed cercariae for up to one year (Dinnik and Dinnik, 1957). Based on the seasonal variation in size of adult *P. cervi* throughout the year, Lankester et al. (1979) proposed a one-year life cycle for parasites in moose from Ontario. Animals are infected in the summer and flukes mature by the following spring, breed and die by autumn. Maturation of flukes in moose appears to be much slower than that in cattle, sheep and roe deer in Germany and may be related to changing seasonal diet as well as a strategy to synchronize egg production with availability of intermediate hosts in the summer (Lankester et al., 1979). In moose in Ontario, prevalence increased from calves (14%) to yearlings (50%) to adults (82%) (Lankester et al., 1979).

Little is known about the effects of rumen flukes in wild cervids. Heavy infections have been noted in severely debilitated adult moose and caribou in AK (K. Beckmen, unpubl. obs.). There is one report of severe denudation of rumen villae in heavily infected moose calves (Seyfarth, 1938 cited in Lankester et al., 1979). In general, clinical signs are uncom-

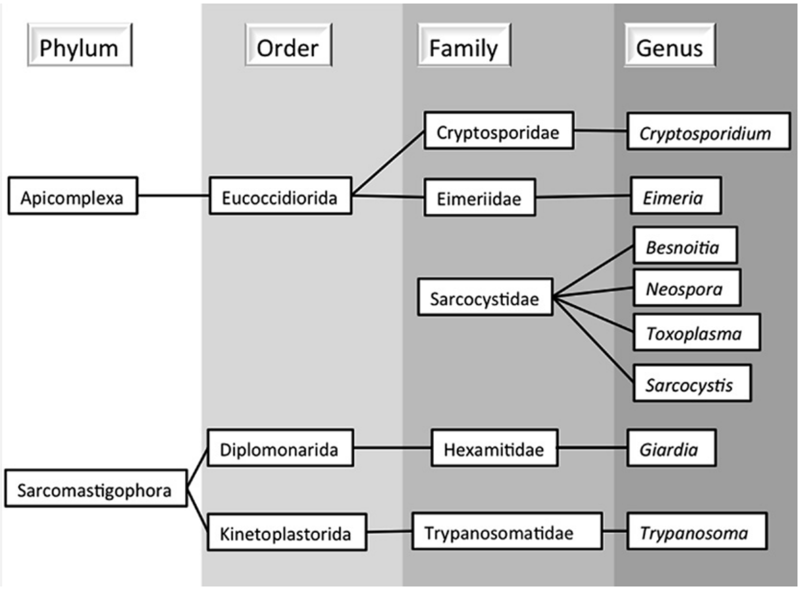

FIGURE 2.11 Protozoa reported from ungulates of arctic North America, including Greenland.

mon in domestic livestock but juvenile parasites in the small intestine may cause a severe enteritis and profuse diarrhoea (DeWaal, 2010).

The host and geographic distribution of *Paramphistomum* flukes in ruminants from the Canadian and Greenlandic Arctic remains virtually unexplored, and the life cycle and effects are not well understood. Some features of the life cycle for *P. cervi*, hatching only over 13°C, and long development time for cercaria at 20°C in the snail intermediate hosts may limit the abundance and distribution of this parasite at northern latitudes (note though *Paramphistomum* spp. are widespread in reindeer of the Russian taiga). Species of *Paramphistomum* are typically considered parasites of tropical regions, and recent increased occurrence in domestic livestock at more northern latitudes (DeWaal, 2010) may reflect changes in geographic distribution, perhaps linked to climatic changes. Further survey and inventory in the Arctic should be pursued.

2.6. PROTOZOA

Arctic ungulates are host to a broad array of gastrointestinal and tissue protozoa (Figure 2.11).

2.6.1. Protozoa of the gastrointestinal tract

2.6.1.1. Family Hexamitidae

2.6.1.1.1. Giardia duodenalis

Giardia is a genus of intestinal protozoa that infects a variety of vertebrate hosts, including people and wildlife (Thompson, 2004). *Giardia duodenalis* (synonyms: *G. intestinalis* and *G. lamblia*) infects a wide range of free-ranging and domestic animals, and people (Thompson, 1998). A minimum of seven assemblages (A–G) and many subgroups are recognized (Thompson, 2004; Lasek-Nesselquist et al., 2010). Some subgroups of assemblage A and B are zoonotic (Sprong et al., 2009). Other assemblages (C–G) are considered host specific and non-zoonotic (Lebbad et al., 2010).

(a) *Host and Geographic Distributions: Giardia* species are reported with a patchy distribution and low prevalence and intensity in caribou and Dall's sheep from North America (Table 2.8) (Samuel and Gray, 1974; Roach et al., 1993; Siefker et al., 2002; Kutz et al., 2008; Kutz et al., 2009c). *Giardia duodenalis* assemblage A is common in muskoxen on Banks Island, NT, (Kutz et al., 2008) but absent from over 200 muskoxen tested on Victoria Island, NT and NU (S. Kutz, J. Wu, S. Checkley, M. Dumond unpubl. obs.). In a broad survey of frozen faeces from 520 barren-ground caribou from twelve herds in North America, only seven sample(s) tested by immunofluorescent antibody (Waterborne Inc.) were positive for *Giardia* (S. Kutz

TABLE 2.8 Gastrointestinal protozoa reported in ungulates of arctic North America, including Greenland. The range of prevalence reported is indicated beside the parasite name. Herds or locations where the parasites were tested for but were absent are indicated by a '0' following the location/herd with the number of animals tested following in parentheses. Data compiled from available published and grey literature

Host and parasite species (range of prevalence)		Herd, region or nearest place name
Caribou and reindeer		
Cryptosporidium sp. (1.3–12%)	AK	Teshekpuk and Western Arctic[a]
	NT	South Slave region[b]; Banks Island[c]
Giardia sp. (3%)	AK	Teshekpuk and Western Arctic[a]
	NT	Banks Island[c]
Eimeria sp.	YT	Chisana[d]
	NT	South Slave[b]
Moose		
Cryptosporidium sp.	AK	Colville River area 0(32)[a]
Giardia sp.	AK	Colville River area 0(32)[a]
Muskoxen		
Cryptosporidium sp.	NT	Banks Island 0(72)[e]
Giardia duodenalis Assemblage A	NT	Banks Island[e]
Eimeria sp.	NU	Devon Island[f]
Eimeria moshati (75–100%)	AK	Nunavik Island[g]
E. faurei (43–100%)	NU	Bathurst Island[g]
E. ovina (93–100%)	QC	Kuujjuaq and Tasiujaq[g]
Eimeria granulosa (21 and 24%)	AK	Nunavik Island[g]
	NU	Bathurst Island[g]
Eimeria oomingmakensis (14.3%)	NU	Bathurst Island[g]
Dall's sheep		
Cryptosporidium spp.	YT	Not specified 0(5)[h]
Giardia (40%)	YT	Not specified[h]
Eimeria ahsata	NT	Mackenzie Mountains[i,j]
Eimeria crandallis	NT	Mackenzie Mountains[i,j]
Eimeria dalli	AK	Kenai Peninsula[k]
	NT	Mackenzie Mountains[i,j]
Eimeria ninakohlyakimovae	NT	Mackenzie Mountains[i,j]
Eimeria parva	NT	Mackenzie Mountains[i,j]

[a] Siefker *et al.* (2002).
[b] Johnson *et al.* (2010).
[c] Nagy *et al.* (1998).
[d] Hoar et al. (2009).
[e] Kutz *et al.* (2008).
[f] Samuel and Gray (1974).
[g] Duszynski *et al.* (1977).
[h] Roach *et al.* (1993).
[i] Uhazy *et al.* (1971).
[j] Simmons *et al.*, (2001).
[k] Clark and Coldell (1974).

and CARMA, unpubl. obs). *Giardia* was not found in a survey of 92 caribou from two herds in western Greenland (S. Kutz, C. Cuyler, unpubl. obs.) nor is it reported for other Greenland wildlife, but it was found in Greenlandic people (Babbott et al., 1961; Krasilnikoff and Gudmand-Hoeyer, 1978). *Giardia* sp. have not been documented in moose from the North American Arctic but are reported in moose from northern Saskatchewan (Heitman et al., 2002) and *G. duodenalis* assemblage A are reported from moose in Norway and Sweden and in reindeer in Norway (Heitman et al., 2002; Siefker et al., 2002; Hamnes et al., 2006; Lebbad et al., 2010).

(b) *Impacts*: Clinical disease associated with *Giardia* spp. has not been described in free-ranging arctic ungulates. In people and domestic animals, clinical signs can include diarrhoea, dehydration, abdominal pain and weight loss (Thompson, 2004; Collinet-Adler and Ward, 2010). In cattle, *Giardia* spp. infections and disease mainly affect calves and can decrease herd performance (Naciri et al., 1999; Olson et al., 2004).

(c) *Ecology: Giardia* is typically considered a waterborne parasite but transmission may be equally likely through contaminated vegetation (Thompson, 2004). *Giardia* cysts are immediately infective and in general are thought to be environmentally resistant (Thompson, 2004) but multiple freeze–thaw cycles may cause high mortality (Robertson and Gjerde, 2004; Robertson and Gjerde, 2006).

The high prevalence of *G. duodenalis* in muskoxen on Banks Island, NT, demonstrates that it is capable of persisting in a true arctic environment. The mechanisms for this persistence are unknown but could include overwinter survival in both the hosts and the environment; cysts are documented in muskox faeces in winter (Kutz et al., 2008).

It is enigmatic that *Giardia* appears to be absent from muskoxen on the adjacent Victoria Island while it is so well established on Banks Island. Muskoxen on these islands presumably originated from a common Beringian population; however, they have undergone bottlenecks in more recent times (Gunn et al., 1991b) that may have led to regional extirpation of *Giardia* in small sub-populations. Recognizing that the source of infection could be people, the historical movements of Inuit, whalers and explorers, and more recently tourists, must also be considered. A point source introduction of *Giardia* by people to Banks Island, with subsequent establishment and spread in the muskox population, is plausible. Contemporary ecological conditions on the islands also differ, with historically a higher density of muskoxen on Banks Island and perhaps a higher concentration of animals around key water and food sources such as river valleys.

Our understanding of the epidemiology and transmission pathways for *Giardia* spp. on Banks Island and elsewhere in the Arctic is limited by patchy surveys and absence of ecological studies. Of particular interest is the potential interaction among people, wildlife and domestic animals for the circulation of *Giardia* in northern ecosystems (Kutz et al., 2008; Kutz et al., 2009c). *Giardia* occurs in people, particularly the young, in arctic communities (Babbott et al., 1961; Eaton and White, 1976) and has been isolated from water sources for rural villages in Alaska (Pollen, 1996). Further survey and strain characterization, in animals and people, are essential to better understand the ecology and potential impacts of this zoonotic pathogen in wildlife and people in the Arctic.

2.6.1.2. Family Cryptosporidae

2.6.1.2.1. Cryptosporidium spp.

Cryptosporidium spp. are gastrointestinal protozoa that are important causes of diarrhoea in people and a wide variety of animals (Fayer et al., 2010). There are multiple species and genotypes and a range of host specificities.

(a) *Host and Geographic Distribution: Cryptosporidium* spp. are occasionally reported from muskoxen and caribou in the North American Arctic and Subarctic (Table 2.8). They were not detected in over 80 caribou from the Kangerlussuaq-Sisismiut and Akia-Maniitsoq caribou herds of west Greenland (S. Kutz, C. Cuyler, unpubl. obs.) nor in faecal surveys from moose in AK or Dall's sheep in the YT (Roach et al., 1993; Siefker et al., 2002; Kemper et al., 2004; Kutz et al., 2008). However, clinical disease associated with *Cryptosporidium* was recently observed in one of two orphaned moose calves in AK (K. Beckmen, R. Gerlach, unpubl. obs.) (Table 2.8). A novel caribou genotype was reported from one herd of caribou in AK (Siefker et al., 2002) and the isolates from the AK moose calves are currently being described (L. Ballweber, K. Beckmen, unpubl. obs.).

(b) *Ecology:* Based on fairly extensive faecal survey, *Cryptosporidium* is not a common parasite of caribou, moose or muskoxen. Freezing can kill *Cryptosporidium* spp. oocysts in laboratory conditions (Fayer et al., 2000) and in colder aquatic and terrestrial environments; thus, transmission may be temperature limited in the Arctic (Robertson and Gjerde, 2004; Robertson and Gjerde, 2006).

(c) *Impacts*: *Cryptosporidium* is generally considered a disease of neonatal and young animals and tends to be self-limiting in immunocompetent hosts (Naciri et al., 1999; Hamnes et al., 2006; Petry et al., 2010). Clinical disease in wild arctic ungulates, other than a single moose calf in AK, has not been reported, but *Cryptosporidium* spp. infection was the cause of severe diarrhoea and lethargy in captive muskox calves in Saskatchewan, Canada (Western College of Veterinary Medicine, Saskatoon, Saskatchewan medical records). The caribou genotype described from AK is closely related to *C. andersoni*, an abomasal species associated with decreased milk production and lower weight gains in cattle (Ralston et al., 2011); similar effects may be anticipated in caribou (Siefker et al., 2002).

2.6.1.3. Family Eimeriidae

2.6.1.3.1. Eimeria spp.

The Eimeriidae consists of a broad diversity of protozoal parasites of the gastrointestinal tract. There have been some recent advances in knowledge of species diversity in the Palaearctic ungulates, but little is known about the ecology of this group of parasites in arctic ungulates.

(a) *Host and Geographic Distributions: Eimeria* species are found in almost all examined caribou, muskoxen and Dall's sheep populations throughout their ranges in North America, including Greenland (Tables 8, 11). There is a minimum of six species of *Eimeria* described from muskoxen and three from Dall's sheep (Uhazy et al., 1971; Clark and Coldell, 1974; Duszynski et al., 1977; Korsholm and Olesen, 1993).

Perhaps surprisingly given the presumed host specificity of most *Eimeria* species, three species from muskoxen, *E. granulosa*, *E. ovina* and *E. faurei*, are also reported from bighorn sheep (Duszynski et al., 1977). The species of *Eimeria* in caribou of North America and Greenland have not been identified, but *Eimeria mayeri* (prevalence 2.6%; $n=195$), *E. rangiferis* (1.0%; $n=195$) and *E. hreindryria* (1.8%; $n=56$) have been described in Icelandic reindeer (Gudmundsdottir and Skirnisson, 2005; Gudmundsdottir and Skirnisson, 2006), and *E. arctica*, *E. mühlensi*, *E. tarandina* and *Isospora rangiferis* (the latter species identification may be suspect) have been described in Russian reindeer (Yakimoff 1936, 1937 and 1939, cited by Gudmundsdottir and Skirnisson, 2006). There are no reports of *Eimeria* species in moose from northern BC, YK and NT but *Eimeria* sp. and associated diarrhoea in calves is a chronic problem in a captive, research herd of moose in AK (K. Beckmen, unpubl. obs.) and *E. alces* has been described in Russian moose (Soshkin, 1997).

(b) *Ecology: Eimeria* spp. of arctic ungulates have a direct life cycle with oocysts shed in faeces, sporulation in the environment and infection through ingestion. In muskoxen, *Eimeria* oocysts are present in the faeces year round, including throughout the winter (Table 2.11). Samuel and Gray (1974) reported increased shedding of oocysts from muskoxen in the high Arctic from March to June. At least some species of *Eimeria* from muskoxen are freeze tolerant and sporulate after several months storage at −20°C (R. Rember, S. Kutz, E. Greiner, unpubl. obs.). Sporulation after extended freezing at −7°C or colder is rare for most *Eimeria* spp. (Landers, 1953; Marquardt et al., 1960; Rind and Brohi, 2001) but ability to withstand freezing may be related to environmental conditions under which the species exist. For example, Landers (1953) demonstrated sporulation of three species of *Eimeria* (*E. arloingi, E. ninakohlyakintovi* and *E. parva*) from domestic sheep in Wyoming after freezing at −19 to −25°C as well as repeated freeze–thaw cycles. These temperatures were similar to the extreme minimums for that region in winter. Other *Eimeria* of cattle, *E. bovis* and *E. zuernii* sporulated after 24h of freezing at −20°C but not when maintained for a longer time period (Rind and Brohi, 2001). Freeze tolerance for *Eimeria* spp. from caribou and Dall's sheep has not been investigated.

The abundance of *Eimeria* spp. is low in barren-ground caribou but quite high in both muskoxen and Dall's sheep and the parasites tend to be present year round in these latter species (Table 2.11). Such differences may reflect the different behaviour of these host species. Barren-ground caribou have massive home ranges, migrate over vast distances (over 1000 km) and are moving constantly throughout the summer (Nagy et al., 2005). This behaviour may remove caribou spatially from contaminated regions and reduce opportunities for exposure to infective oocysts. In contrast, muskoxen and Dall's sheep are more sedentary with much smaller home ranges and a build-up of the parasites in their immediate environment and ongoing exposure may be more likely.

(c) *Impacts*: Clinical disease associated with *Eimeria* spp. is not common in free-ranging arctic ungulates. The highest oocyst count reported in faecal surveys of >1000 Dall's sheep, caribou, moose and muskoxen in northern Canada is 17,500 oocysts per gram (opg) of previously frozen faeces in a muskox from Banks Island (NT) (Table 2.2). Oksanen et al. (1990) found up to 350,000 *Eimeria* opg of faeces in reindeer calves and suggested that clinical disease would be related to higher numbers of oocysts (>800,000 opg faeces) (Oksanen et al., 1990). In Greenland, extremely high oocyst counts (up to 990,000 opg) were recorded from calves during a mortality event. The proximate cause of mortality was an *E. coli* septicaemia and the role of *Eimeria* was not determined (Clausen et al., 1980).

(d) *Issues and future research:* Knowledge of *Eimeria* spp. in ungulates of arctic North America is limited to primarily cross-sectional faecal surveys and a few species descriptions. Survey data, a few case reports, and preliminary laboratory experiments suggest differing patterns of infection and abundance among host species, possibly significant pathology and arctic adaptations such as sporulation of oocysts after freezing. New DNA-based technologies and morphological studies, together with further observational (seasonal faecal surveys and characterization of parasite diversity and abundance among host species and age/sex classes) and experimental research are necessary to describe the species diversity, host range, ecology and significance of *Eimeria* in the Arctic.

2.6.2. Tissue and blood protozoa: the Sarcocystidae, Trypansomatidae and Babesiidae

2.6.2.1.Family Sarcocystidae

Besnoitia tarandi, *Neospora caninum*, *Sarcocystis* spp. and *Toxoplasma gondii* are tissue-dwelling obligatory intracellular parasites of a variety of vertebrate species, including arctic ungulates. The life cycle of these Sarcocystidae family members typically relies on predator–prey linkages with predators as the definitive hosts. For some of these species, however, vertical and horizontal transmission in the absence of definitive hosts is possible. Diagnosis is by histological identification of cysts, immunohistochemistry, DNA-based techniques or serological tests (Dubey and Odening, 2001; Leighton and Gajadhar, 2001).

2.6.2.1.1. Besnoitia tarandi

Besnoitia tarandi is a tissue cyst-forming parasite first described in Alaskan reindeer in 1922 (Hadwen, 1922). Cysts are located in the skin, subcutaneous tissue, conjunctiva, sclera, periosteum of long bones and skull, muscle fascia, testicles and occasionally other soft tissues (Ayroud et al., 1995; Wobeser, 1976). There are three other species of *Besnoitia* reported from 'large mammal' hosts and these include *B. besnoiti*, primarily from cattle, *B. bennetti* primarily from domestic equids, and *B. caprae* primarily from goats (Olias et al., 2011). No significant genetic differences between *B. tarandi* and *B. besnoiti* were identified in one study, but morphological and biological differences suggested that further investigation with more precise genetic markers is needed (Olias et al., 2011). Subsequent work suggests the utility of microsatellite markers in discriminating among such taxa. Significant sampling has identified a stable multilocus genotype for *B. tarandi* across the Arctic not precisely replicated in any of several specimens of *B. besnoiti* heretofore examined (B. Rosenthal, pers. comm.). Broader application of this and related methods might prove useful in determining the duration and consequences of evolutionary differentiation between these and related parasite taxa.

(a) Host and Geographic Distributions: Besnoitia tarandi has a circumarctic distribution in *Rangifer.* In North America, it is present in semi-domestic reindeer and free-ranging woodland and migratory barren-ground caribou populations from AK to Labrador (Table 2.9). Prevalence on the mainland tends to be higher than on nearby arctic islands and it is absent from Greenland (Gunn et al., 1991a; Ducrocq, 2011). *Rangifer* species are the primary intermediate hosts; however, it has also been reported in muskoxen on mainland Nunavut, Canada, but not in over 100 muskoxen sampled on Victoria Island immediately to the north (Gunn et al., 1991a; J. Wu, S. Kutz, S. Checkley, unpubl. obs.). It also occurs in reindeer in Fennoscandia and Russia (Nikolaevskii, 1961; Rehbinder et al., 1981; Dubey et al.,

TABLE 2.9 Tissue and blood protozoans reported from ungulates of arctic North America, including Greenland. The range of prevalence reported is indicated below the parasite name. Only prevalence estimates based on sufficient sample sizes and reliable diagnostic techniques were included (e.g. data from cursory visual assessment for *Sarcocystis* and *Besnoitia* were excluded but histological assessment included). Locations/herds where the parasites were tested for but were absent are indicated by a '0' following the location/herd and sample size 'n' following in parentheses. Data compiled from available published and grey literature

Host and parasite species (range of prevalence)		Herd, region or nearest place name
Caribou or reindeer (rd)		
Besnoitia tarandi (5–78%)	AK	Various[a]; Western Arctic or Teshepuk[b]; Porcupine[c]
	NT	Mackenzie River Delta (rd)[d]; Not specified(rd)[e]; Cape Bathurst[f]; Bluenose West[c]
	NU	Bathurst[c]; Dolphin-Union[g]; Southampton Island[c]
	QC	Riviere-aux-Feuilles[c]; Riviere George[c]
Sarcocystis sp. (37.5–100%)	AK	Adak, Delta, Izembek, Nelchina, Porcupine, Western Arctic, Wrangell Mountain[h], Various[a,b,i]
	NT	Bluenose West[n]
	NU	Victoria Island[g]; Bathurst[c]
	QC	Riviere George and Feuilles[c]; Goose Bay and Hopedale[j]
Toxoplasma gondii (0.7–62.5%)	AK	North Slope and Alaska Peninsula[k]; Various, Porcupine, Western Arctic[l]
	YT	Chisana[m]
	NT	Bluenose and Beverly[n]; southern NT[ac]
	NU	Bathurst, Dolphin-Union, and North Baffin Island[n]
	QC	Riviere George and Feuilles[o,p]
	GL	Akia-Maniitsoq 0(49); Kangerlussuaq-Sisimiut 0 (50)[q]
Neospora caninum (1.4–15.7%)	AK	North Slope and Alaska Peninsula[k]; Porcupine, Western Arctic, Various[l]
	YT	Chisana[m]
	NT	Bathurst[r]
Trypanosoma sp.	AK	Fairbanks (reindeer from Nome)[a]
	YT	Porcupine[ab]
	NT	South Slave[ac]
	NU	Bathurst[ab]
	GL	Akia-Maniitsoq, Kangerlussuaq-Sisimiut[ab]

(*continued*)

TABLE 2.9 *(continued)*

Host and parasite species (range of prevalence)		Herd, region or nearest place name
Dall's sheep		
Sarcocystis spp. (14–77.4%)	AK	Alaska Range, Brooks Range, McCumber Creek, Sheep Creek, Tok, Wrangell Mountains[h]; Various[i]
	NT	Mackenzie Mountains[s]
Toxoplasma gondii (6.9%)	AK	Interior[k]
Neospora caninum	AK	Various 0 (52)[b]
Trypanosoma sp.	NT	Mackenzie Mountains[ae]
Moose		
Sarcocystis spp.	AK	Interior, Holitna River and Nelchina, McKinley Park, Seward Peninsula, Stikine River, Unit 13, White River[h]; Various[i]
Toxoplasma gondii (1.3–22.7)	AK	North Slope, Interior and South Central regions[k]; South Central and Interior regions 0(201)[l]
Neospora caninum (0.5–2.5)	AK	South Central and Interior regions 0(201)[l]; Not specified[t]
	NT	Mackenzie Valley Sahtu Settlement Region[u]
Trypanosoma sp.	AK	Not specified[ad]
Muskoxen		
B. tarandi (32%)	NU	Kugluktuk[g]; Victoria Island 0(153)[v]
Sarcocystis spp 80%	AK	Nunivak Island[h]
	NT	Banks Island[w]
	NU	Ellesmere Island[x]
Toxoplasma gondii (4.6–40%)	NT	Victoria Island (Holman)[y]
	NU	Kugluktuk and Victoria Island (Cambridge Bay)[y]
Neospora caninum (6–8%)	AK	Eastern North Slope[b]; Not specified[t]
	NU	Victoria Island (Cambridge Bay)[v]

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[a] Hadwen (1922).
[b] Beckmen (2010).
[c] Ducrocq and Lair (2007), J. Ducrocq, S. Lair, CARMA (unpubl. obs).
[d] Choquette *et al.* (1967).
[e] Lewis (1992).
[f] Larter (1999).
[g] Gunn *et al.* (1991a).
[h] Neiland (1981).
[i] Dau (1981).
[j] Khan and Evans (2006).
[k] Zarnke *et al.* (2000).
[l] Stieve *et al.* (2010).

TABLE 2.9 *(continued)*

[m] M. Oakley, S. Kutz, R. Farnell (unpubl. obs.).
[n] Kutz *et al*. (2001d).
[o] Leclair and Doidge (2001).
[p] McDonald *et al*. (1990).
[q] P. Curry, Susan Kutz, 2012 S. Kutz, C. Cuyler (unpubl. obs.).
[r] P. Curry, S. Kutz, CARMA (unpubl. obs.).
[s] Kutz *et al*. (2001a).
[t] Dubey and Thullez (2005).
[u] C. Kashivakura, S. Kutz, A. Veitch, J. Invik (unpubl. obs.).
[v] J. Wu, S. Kutz, M. Dumond, S. Checkley (unpubl. obs.).
[w] Tessaro *et al*. (1984).
[x] Samuel and Gray (1974).
[y] Kutz *et al*. (2000a).
[aa] Kingston *et al*. (1982).
[ab] D. Schock, S. Kutz, CARMA (unpubl. obs.).
[ac] Johnson *et al*. (2010).
[ad] Kingston (1985).
[ae] S. Kutz, A. Veitch (unpubl. obs.).

2004; Ducrocq, 2011), and the status of free-ranging reindeer from Iceland is unknown (R. Thorarinsdottir pers. comm.).

Diagnosis in free-ranging ungulates is typically through gross and histological examination. In caribou, histological evaluation of skin from the mid-cranial metatarsus for cysts provides a sensitive measure for prevalence and intensity of infection (Ducrocq et al. 2012). In the live animal, hosts with high infection intensities can be identified by visual observation of parasitic cysts on the ocular conjunctiva but this method significantly underestimates the true prevalence (sensitivity of 0.29 and specificity of 0.98) (Ducrocq, 2011). A commercial serological assay is available for *B. besnoiti* in domestic livestock (Schares et al., 2011) but has not been validated for *B. tarandi* or arctic ungulates.

(b) *Ecology*: The transmission cycle for *Besnoitia* spp. remains poorly understood (see Olias et al. 2011 for a review). Feline definitive hosts have been confirmed for some of the *Besnoitia* spp. that have small animal intermediate hosts (e.g. *B. darlingi*, *B. wallacei*, *B. oryctofelisi*, *B. neotomofelis*); definitive hosts have not been identified for those with large animal intermediate hosts (*B. besnoitia*, *B. benneti*, *B. tarandi*) (Olias et al., 2011; Basso et al., 2011). Specifically for *B. tarandi*, experimental infections of a limited numbers of dogs, domestic cats, raccoons and an arctic fox were unable to establish these species as definitive hosts (Glover et al., 1990; Ayroud et al., 1995; Dubey et al., 2004). Possible alternate definitive hosts that are present across the range of most affected herds include arctic fox (*Vulpes lagopus*), wolverine (*Gulo gulo*), lynx (*Lynx lynx*) and wolf (*Canis lupus*).

Transmission of *Besnoitia* sp. by insect vectors has also been hypothesized and tabanids, mosquitoes, tse tse and stable flies were experimentally demonstrated to be competent for mechanical transmission of *B. besnoiti* among cattle and between cattle and rabbits (Bigalke, 1968; Olias et al., 2011). Epidemiological evidence for *B. tarandi* supports the possibility of vector-borne transmission but does not rule out carnivore definitive hosts. A study of risk factors associated with *B. tarandi* infection in two herds in QC, Canada, demonstrated that the prevalence and intensity of *Besnoitia* cysts in the metatarsal skin increased from summer to fall of the same year suggesting summer transmission (Ducrocq, 2011). This could have occurred as a result of vector-borne transmission but could also be explained by the presence of a definitive host, which may be more abundant, and contribute to more environmental contamination on the summer range compared to the winter range. Vector-borne transmission was also hypothesized in an outbreak in captive zoo animals that demonstrated similar temporal patterns of occurrence (Glover et al., 1990).

Importantly, transmission of *Besnoitia* sp. through insects and definitive hosts are not exclusive of each other. Other modes of transmission have also been suggested, including migratory birds and the possibility that large mammals are aberrant hosts and the parasite is really maintained by small mammalian intermediate hosts (Olias et al., 2011). The finding of *Besnoitia* cysts in tundra mice sympatric with infected reindeer herds is interesting and raises a question as to how *Besnoitia* may be circulating in these tundra systems (Nikolaevskii, 1961).

In a recent study of North American migratory caribou herds, *Besnoitia* prevalence, based on histological examination of metatarsal skin, was estimated between 5.5 and 44.2% and maximum cyst density was 13.1 cysts/mm^2 (Ducrocq, 2011). Prevalence in males was higher than in females, and prevalence of infection increased in the first years of life and then decreased with age (Ducrocq, 2011). Decreases in *B. tarandi* cyst density over the winter were observed and may be the result of either the elimination of *B. tarandi* cysts from the dermis during the winter, or of a lower winter survival rate of caribou heavily infected by *B. tarandi* (Ducrocq, 2011). Complete cyst elimination, however, is not known for other *Besnoitia* sp. and there is little evidence to support this from histological examination of more than a thousand caribou where only a few necrotic cysts with associated inflammatory cells were observed (Ducrocq, 2011).

Although *B. tarandi* has a wide geographic distribution, significant disease outbreaks in free-ranging caribou have only been reported recently in the Rivière-George and Rivière-aux-Feuilles caribou herds in QC and Labrador, Canada (Kutz et al., 2009b; Ducrocq, 2011). The cause of this disease emergence is not understood, but possible hypotheses include a recent introduction of *B. tarandi* to a naïve population, changing environmental conditions that have allowed increased transmission rates or an increase in animal susceptibility. Prior to 2007, there was only a single report of *Besnoitia* in caribou in QC and this was in 1960 from a herd of unknown geographical origin (CCWHC, 2011). There were no subsequent records in the Canadian Cooperative Wildlife Centre (CCWHC) database until 2007 when clinical besnoitiosis emerged in the Quebec herds (Ducrocq and Lair, 2007). Although the CCWHC data are based on passive surveillance, *Besnoitia* is routinely reported as an incidental finding in caribou in other regions of arctic North America and previous lack of detection in QC suggests absence or very low prevalence. *Besnoitia tarandi* isolates from North America apparently do not differ genetically from those in Fennoscandia (B. Rosenthal, pers. comm.) and may have been introduced relatively recently to North America through multiple reindeer importations, primarily to AK, at the turn of the 20th century. Alternatively, this uniformity may reflect the continuous distributions for *Rangifer* between Eurasia and Beringia most recently during the Pleistocene and rapid geographic expansion in North America during the Holocene. The Rivière-George and the Rivière-aux-Feuilles herds originate from the North American lineage, south of the glaciers during the last ice age, and are physically separated from other migratory caribou herds by Hudson Bay. Thus, these herds may have been isolated from *Besnoitia* in both evolutionary and ecological time.

(c) *Impacts*: Clinical signs caused by *B. tarandi* in caribou range from asymptomatic to significant clinical illness (Wobeser, 1976; Rehbinder et al., 1981; Ducrocq and Lair, 2007). Severe pathology in captive caribou, reindeer and mule deer (*O. hemionus*) was observed in an outbreak at the Winnipeg Zoo where the naive status of the animals may have contributed to the severity of the infection (Glover et al., 1990). Alopecia, skin thickening, decreased mobility and resistance to movement are reported for captive and free-ranging caribou with high infection intensities (Wobeser, 1976; Rehbinder et al., 1981; Ducrocq, 2011), and this may increase susceptibility to predation and reduce thermoregulatory abilities. In males, *B. tarandi* cysts can cause severe inflammation and obstruction of blood vessels in the pampiniform plexus of the testicles (Choquette et al., 1967; Wobeser, 1976; Ayroud et al., 1995). Decreased or impaired fertility is reported in bovine and caprine besnoitiosis and this may also be the case in *Rangifer* (Kumi-Diaka et al., 1981; Njenga et al., 1999). Testicular pathology can alter testosterone levels, causing antler malformation and abnormalities (Blake et al., 1998) that may influence social interactions (Clutton-Brock, 1982) and reproductive success (Thomas and Barry, 2005). Velvet retention and broken antlers have been reported in caribou infected with *Besnoitia* (Rehbinder et al., 1981; Ducrocq and Lair, 2007) and further investigation of this association is warranted. Given the impact on both survival and reproductive success, this parasite may play an important role in population dynamics. Recent population surveys have shown substantial declines in the Rivière-aux-Feuilles and Rivière-George herds within the past decades and the potential contribution of *Besnoitia* to these declines is not known.

Besnoitia infection in muskoxen is rare but can cause severe pathology including laminitis and ulcerative dermatitis (Gunn et al., 1991a). Limited data suggest that infection in muskoxen is more prevalent on the mainland compared to on arctic islands (Gunn et al., 1991a; J. Wu, S. Kutz, M. Dumond, S. Checkley unpubl. obs.). The role of caribou in the epidemiology of the parasite in muskoxen and other contributing factors for transmission to muskoxen remain unknown.

(d) *Issues and future research: Besnoitia tarandi* is a common and widespread parasite among subspecies of *Rangifer* across most of the Arctic. Recent emergence of this parasite as a significant disease-causing agent was surprising and highlighted the fact that we know very little about its life cycle and epidemiology. The emergence of disease in Canadian caribou coincided with emergence of *B. besnoiti* and associated disease in domestic and wild animals in Europe (Mehlhorn et al., 2009), perhaps raising the question of the possibility of a larger scale driver for the ecology of this group of parasites. The lifecycles and epidemiology for both *B. tarandi* and *B. besnoiti* remain virtually unknown, yet given the genetic similarity between these two species, it follows that information gained from one may guide the understanding of the other.

Priorities for future research on *B. tarandi* should include establishing the parasite's life cycle, likely a challenge considering that the life cycle of *B. besnoiti*, a species with a much higher profile, has not yet been determined. Experimental studies together with epidemiological modelling applied to existing data (e.g. Ducrocq, 2011) can be used to elucidate the lifecycle of this parasite, evaluate the relative contribution of different transmission pathways and understand the potential impacts of changing environmental conditions and animal communities on transmission and disease. Apparent differences in disease occurrence and severity in caribou and muskoxen across the Arctic, possibly related to differences between individual hosts and/or host population susceptibility, and ecological conditions, require further exploration. Impacts on individuals, and how these translate to population-level effects, are important.

2.6.2.1.2. Neospora caninum

Neospora caninum is best known as a parasite of agricultural economic importance, causing abortion and neonatal mortality in cattle (Dubey et al., 2007; Andreotti et al., 2010). In livestock, it is transmitted horizontally through a canid-ungulate predator–prey life cycle and vertically from mother to foetus. Its occurrence and potential significance in wildlife are increasingly recognized.

(a) *Host and Geographic Distributions:* Caribou, muskoxen and moose seropositive for *Neospora caninum* are reported from AK, YT, NT and NU (Table 2.9) but the parasite has not yet been isolated from these species. None of 52 Dall's sheep tested in AK between 1998 and 2004 were serologically positive (K. Beckmen, unpubl. obs.). Wolves (*n* = 324, 9.0%) and coyotes (*n* = 12, 16.7%), but not red foxes (*n* = 9), were seropositive in one survey in AK (Stieve et al., 2010).

(b) *Life Cycle:* Canids are definitive hosts for *N. caninum* and a wide variety of ungulates serve as intermediate hosts. Dogs and wolves are considered natural hosts, coyotes are demonstrated as suitable hosts experimentally and *N. caninum* DNA, but not viable organisms, has been isolated from the faeces of free-ranging coyotes and foxes (McAllister et al., 1998; Gondim et al., 2004; Wapenaar et al., 2006; Dubey and Schares, 2011).

Seropositivity in remote caribou, moose and muskox populations in various remote locations across the Arctic (Table 2.9), and competency of wolves and coyotes as definitive hosts, provides compelling evidence that *N. caninum* is a common parasite of sylvatic systems, perhaps primarily, with spill-over to domestic agricultural systems. In many regions of NT and NU, there are currently no domestic livestock and previous introductions were limited to very few animals that were maintained in the settlements by missionaries or traders for very short periods. Historically, working sled dogs may have been important in the life cycle as they travelled extensively on the land and were fed wild game. Today, there are very few working dogs and although these and non-working dogs are still fed wild game (Salb et al., 2008; Brook et al., 2010), dog travel 'on the land' is not as common and opportunities for significant environmental contamination may not be substantial. The few dogs that are brought into the communities are typically small breeds that are (i) unlikely to have been exposed to *N. caninum* previously and (ii) are unlikely to have any significant travel outside the northern communities and limited opportunities, therefore, to be a source of *N. caninum* for wildlife. Seropositive dogs have been detected in two northern communities where wild game is a large component of the diet for more than half of the dogs (Salb et al., 2008).

In caribou from YT and AK, there was no difference in *Neospora* seroprevalence between calves and animals aged one year or older, suggesting transplacental transmission (Stieve et al., 2010). Such a transmission route may be important in maintaining the parasite under sub-optimal climatic conditions and in regions with low densities of definitive and/or intermediate hosts. In one serological study on moose, exposure to *Neospora* was detected but not common (Table 2.9) (Stieve et al., 2010). The low prevalence in moose was attributed to their feeding habits: they tend to browse and eat aquatic vegetation, which could limit exposure to oocysts from carnivore faeces (Stieve et al., 2010).

(c) *Impacts*: Clinical signs associated with *N. caninum* have not been reported in arctic ungulates, but this may reflect a lack of detection rather than an absence of disease. The parasite was the cause of mortality in a wild Californian black-tailed deer fawn (*O. h. columbianus*), causing lesions in the lungs, liver and kidney (Woods et al., 1994), and transplacental infection with *N. caninum* was reported in a stillborn captive Eld' deer (*Cervus eldi siamensis*) in Europe (Dubey et al., 1996). In domestic cattle, *N. caninum* reduces fertility and causes abortion (Dubey and Lindsay, 1996; Andreotti et al., 2010) and similar impacts are hypothesized in free-ranging cervids (Dubey et al., 1996). There is anecdotal evidence that *Neospora* may be linked to abortion in captive reindeer. Ninety-two percent seroprevalence for *Neospora* was observed in a captive reindeer herd approximately five months after a severe late-term abortion storm. Of the 39 animals (25 females, 14 males) in the herd, only three (two males, one female) were found to be seronegative (Curry, 2010). The herd also had a history of multiple pasture intrusions by coyotes during the summer preceding the abortion storm. Unfortunately, no sera were available from before the abortion storm to evaluate *Neospora* exposure (S. Kutz, K. Orsel, P. Curry unpubl. obs.). Also, seroprevalence for *Neospora* was 15.8% in adult females of a declining woodland caribou herd in the YT where poor early calf survival was considered a major cause of the decline (M. Oakley, S. Kutz, A. Seller, R. Farnell unpubl. obs.). There were anecdotal reports of a late-term foetus/stillborn calf and additional weak calves in the herd in the same year, but the potential contribution of *Neospora* was not determined.

(d) *Issues and future research*: Serological investigation for *N. caninum* in arctic ungulates has only been done in recent years and the full extent of its host and geographic distribution in the Arctic is not well defined. Isolation of the parasite from definitive and intermediate hosts should be a priority in order to further characterize and compare these isolates to those circulating in domestic cycles. It is probable that *N. caninum* has reproductive impacts on caribou and other arctic ungulates that could lead to substantially reduced productivity (i.e. abortion and stillbirths) but low detectability of carcasses, thus resulting in 'silent' population declines.

Finally, the relative role of different definitive host species (coyotes, wolves and perhaps foxes and domestic dogs) as well as the contribution of vertical transmission to maintenance of the parasite in wild host populations in the Arctic requires further exploration. Climate and landscape change-related shifts in carnivore communities, such as northern range expansion of coyotes, may alter the transmission dynamics of the parasite depending on relative suitability of each of these definitive hosts. The potential role of red and arctic foxes should also be considered.

2.6.2.1.3. Toxoplasma gondii

Toxoplasma gondii is a pathogenic tissue cyst-forming protozoan with a global distribution (Dubey and Beattie, 1988). It can cause abortions, foetal abnormalities and neurological disease in a wide range of intermediate hosts, including people (Dubey and Beattie, 1988). Felids are the only known definitive hosts for *T. gondii* but there is a broad range of intermediate hosts (Sibley et al., 2009). Infection of intermediate hosts can be through ingestion of sporulated oocysts that are shed in the faeces of felids, transplacental transmission or carnivory. *Toxoplasma gondii* cysts develop predominantly in neural and muscular tissues of intermediate hosts. Most *T. gondii* isolates can be genotyped into three major clonal lineages (types I, II, and III) (Sibley et al., 2009).

(a) *Host and Geographic Distributions: Toxoplasma gondii* appears to be well established in the Arctic. It has been reported from a variety of terrestrial and marine mammals and birds, as well as people, around the Arctic (Table 2.9) (McDonald et al., 1990; Oksanen et al., 1998; Zarnke et al., 2000; Kutz et al., 2001a; Dubey et al., 2003; Prestrud et al., 2010; Stieve et al., 2010; Elmore et al., 2011).

Seropositive barren-ground and woodland caribou, muskoxen, Dall's sheep and moose are reported from AK to Labrador and from the subarctic to the arctic islands but not in Greenland (Table 2.9). Similar to *Neospora*, the actual parasite has not yet been isolated from arctic ungulates. Prevalence of infection in muskoxen and caribou decreases at higher latitudes, from the mainland to the Arctic Archipelago (Kutz et al., 2001a), and a similar latitudinal gradient is reported for polar bears on Svalbard, Norway (Jensen et al., 2010). The lineages circulating in North American arctic ungulates have not been defined.

(b) *Ecology:* The transmission of *T. gondii* in Arctic ungulates remains somewhat enigmatic. Domestic cats are rare and those that are present are almost exclusively indoors (Prestrud et al., 2010; Stieve et al., 2010). Thus, with the possible exception of occasional environmental contamination from kitty litter (e.g. landfills or sewage), it is unlikely that the domestic cat contributes significantly to the life cycle of the *T. gondii* in the Arctic (Zarnke et al., 2000; Prestrud et al., 2010). Lynx (*Lynx canadensis*) are present in the low Arctic and the Subarctic and seroprevalence for *Toxoplasma* in this species ranges from 15% to 44% in AK, NT, BC and QC (Zarnke et al., 2000; (Labelle et al., 2001; Philippa et al., 2004; S. Kutz, R. Mulders, B. Elkin, JP Dubey, unpubl. obs.). Thus, lynx may serve as definitive hosts in these regions.

The presence of seropositive caribou and muskoxen on arctic islands where domestic and wild felids are absent suggests an alternate mode of transmission at higher latitudes. On the arctic island of Svalbard, a high seroprevalence in arctic foxes in the absence of definitive hosts is attributed to predation on infected migratory geese (Jensen et al., 2010; Prestrud et al., 2010).

Reindeer have been known to eat lemmings, and active or passive exposure to cysts through contaminated vegetation or ingestion of carrion may be possible sources of infection for arctic ungulates (Oksanen et al., 2000). Vertical transmission, as can occur in domestic goats and sheep (Dubey, 1982; Rodger et al., 2006; Camossi et al., 2010), is another potentially very important means of infection in arctic ungulates that may allow persistence of *Toxoplasma* for multiple generations in the absence of a definitive hosts.

Seroconversion to *Toxoplasma gondii* increases with age in many wild animal species (polar bears, arctic fox, wolves and cervids) indicating cumulative exposure or age-dependant behaviours (Kutz et al., 2000a; Prestrud et al., 2007; Ankerstedt et al., 2010; Jensen et al., 2010; Jokelainen et al., 2010). Risk factors for *T. gondii* exposure in arctic ungulates remain undefined, but for other species variations in diet and behaviour are important (Aubert et al., 2010; Jensen et al., 2010).

(c) *Impacts*: Overt disease caused by *T. gondii* has not been reported in free-ranging arctic ungulates, but clinical disease is observed in captive settings. Two experimentally infected reindeer developed signs of depression, decreased appetite and haemorrhagic diarrhoea leading to fatal enteritis in one animal (Oksanen et al., 1996). Transplacental transmission of *T. gondii* and subsequent abortion have been reported for a captive muskox and a captive reindeer (Crawford et al., 2000; Dubey et al., 2002). The impacts of *Toxoplasma* at the population level remain unknown; however, if abortion/stillbirth is a consistent feature of this parasite in arctic ungulates, then it may have a significant impact on populations by reducing lifetime reproductive success. As with *Neospora*, such an impact would be subtle and difficult to detect (poor calving rates but no visible carcasses littering the tundra) yet could have major consequences for population growth and/or stability.

Toxoplasma in subsistence species may pose a significant zoonotic risk to aboriginal people, particularly with some traditional food preparation methods where meat is eaten raw or undercooked and cysts may not be inactivated. In the past, when wild game formed the core of the diet, primary exposure to cysts in meat probably occurred at a young age and continued throughout life. More recently, consumption of wild game is not as common or consistent, and for some may occur only on special occasions, meaning that many individuals may not be exposed to the parasite until later in life. Such shifts in behaviour could increase the chances of primary exposure occurring during pregnancy with subsequent risk of congenital toxoplasmosis.

(d) *Issues and future research:* Although *T. gondii* may be an important pathogen of wildlife and people in the Arctic its transmission and impacts in arctic ungulates, and potential transmission risks from ungulates to people, are very poorly understood. In particular, its presence at high arctic latitudes in the absence of typical definitive hosts suggests alternate transmission pathways that need to be explored (Prestrud et al., 2010). To further elucidate the life cycle of *T. gondii* in the Arctic, parasite isolation and genotyping, together with studies on virulence and ecology are needed. Such activities will also provide an insight into the worldwide circulation of strains and their virulence (Aubert et al., 2010; Prestrud et al., 2010).

Recent evidence from the marine system suggests that *T. gondii* is increasing in prevalence (Jensen et al., 2010). Similar studies tracking trends of *T. gondii* in arctic ungulates do not exist, although widespread survey did occur during International Polar Year (Parkinson, 2008). Emerging threats that may shift the transmission dynamics for *T. gondii* include a growing human presence in the Arctic that is coupled with increased environmental contamination through sewage, including ballast from cruise ships, waste disposal and increased numbers of domestic cats (Prestrud et al., 2010). Additional threats under a warming climate include northern range expansion of possible definitive hosts such as lynx and cougars (*Felis concolor*) (Anderson et al., 2010).

2.6.2.1.4. Sarcocystis spp.

(a) *Host and Geographic Distributions: Sarcocystis* spp. are common in Dall's sheep, caribou, moose, muskoxen, and mountain goats in the North American Arctic, and were detected by gross examination in caribou of Greenland (Orsel, Cuyler pers. comm). Species diversity in the Nearctic is poorly defined (Table 2.9), with only *Sarcocystis alceslatrans* and *S. ovalis* described in moose from AB, Canada (Colwell and Mahrt, 1981; Dahlgren and Gjerde, 2008). The biodiversity of this genus is much better described for arctic ungulates of the Palaearctic. *Sarcocystis ovalis*, as well as *S. alces*, *S. scandinavica* and *S. hjorti* have been described in moose in Norway, and *S. gruehneri*, *S. rangi*, *S. tarandivulpes*, *S. hardangeri*, *S. rangiferi* and *S. tarandi* have been described in reindeer in Norway and Iceland (Gudmundsdottir and Skirnisson, 2006; Dahlgren and Gjerde, 2007; Dahlgren et al., 2008a). The extent of these species in ungulates of arctic North America is not known.

(b) *Ecology: Sarcocystis* spp. use carnivore definitive hosts and herbivore intermediate hosts. Sexual reproduction occurs in the gastrointestinal tract of the definitive hosts, and asexual reproduction in the vascular endothelium of the intermediate hosts, leading to tissue cysts in skeletal and cardiac muscle and the nervous system (Herbert and Smith, 1987). A single intermediate host can be infected by several different species of *Sarcocystis* at the same time (Dubey and Odening, 2001; Dahlgren and Gjerde, 2007).

Canids are definitive hosts of *S. alceslatrans* found in North American moose and of at least two and three of the species found in Norwegian moose and reindeer, respectively (Fayer et al., 1982; Colwell and Mahrt, 1983; Dahlgren et al., 2008b; Dahlgren and Gjerde, 2010a). Potential definitive hosts in the North American Arctic include arctic and red foxes, wolves, coyotes, black bears, grizzly bears, cougars, lynx, wolverine and dogs (Neiland, 1981; Mahrt and Colwell, 1980; Dau, 1981; Foreyt, 1989; Khan and Evans, 2006; Dahlgren and Gjerde, 2010b) Avian scavengers such as corvids, which are common in the Arctic, may also act as definitive hosts for some species (Gjerde and Dahlgren, 2010). *Sarcocystis* spp. in arctic ungulates are not considered zoonotic, but this aspect of their biology has not been adequately investigated (Tessaro et al., 1994).

(c) *Impacts*: The impact of *Sarcocystis* for most arctic ungulates has not been investigated, but clinical disease associated with *Sarcocystis* spp. has been reported in other naturally and experimentally infected cervid species. A captive white-tailed deer died, after a week of lethargy, from an acute necrotizing pneumonia caused by *Sarcocystis* sp. infection (Duncan et al., 2000). In Oregon, an epizootic in free-ranging mule deer fawns reduced growth rate (Dubey and Kistner, 1985). Experimental infections of elk fawns with *Sarcocystis* spp., including *S. sybillensis* and *S. wapiti*, resulted in weight loss (Foreyt et al., 1995) and experimental infections of mule deer fawns with *S. hemionilatrantis* led to anorexia, weight loss, pyrexia, weakness and death (Hudkins and Kistner, 1977).

In semi-domestic reindeer, infection with *Sarcocystis* is a cause of meat condemnation in Fennoscandia and thus a source of production loss (Dahlgren and Gjerde, 2007). Changes in protein, moisture and fat content, as well as increased bacterial contamination, were reported for buffalo meat infected with sarcocysts (Mostafa and Yasein, 2010), but no changes in meat quality were reported for bovine meat infected with *S. cruzi* (Daugschies et al., 2000). To date, *Sarcocystis* infection has not been a cause of meat condemnation in commercial caribou harvests in northern Canada (B. Elkin, unpubl. obs.).

(d) *Issues and future research:* The knowledge on *Sarcocystis* spp. in ungulates of arctic North American and Greenland is scant. The zoonotic potential and effects of *Sarcocystis* spp. on the quality and safety of meat from game animals in the Arctic is of considerable local importance and requires further work. The biodiversity, life cycles, host specificity and impacts are poorly described. Similarly, the potential impacts and consequences of northern range expansion of definitive and intermediate host species and their *Sarcocystis* spp. require exploration.

2.6.2.2. Family Trypanosomatidae

2.6.2.2.1. Trypanosoma spp.

Trypanosoma spp. are blood-borne protozoans that parasitize a wide range of vertebrates globally. They are transmitted by blood-feeding arthropods. In tropical regions some species, for example, *T. congolense*, and *T. cruzi* can cause severe clinical disease in livestock and people, respectively, whereas those species in ungulates of temperate and arctic North America are not considered significant pathogens.

(a) *Host and Geographic Distributions. Trypanosoma* spp. are widespread and common in free-ranging ungulates in North America (Kingston, 1981). They have been morphologically identified as *T. cervi*, but differences in biology and infectivity for different hosts, together with absence of molecular characterization of the parasite from various hosts, raises some uncertainty as to whether more than one species circulates in cervids across North America. *Trypanosoma* cf. *cervi* have been detected in the blood of reindeer, woodland caribou, moose (culture and PCR) and Dall's sheep in AK, NT, NU and Greenland (Table 2.9) (Bequaert, 1942; Kingston, 1981 ; Kingston et al., 1982; Kingston et al., 1985; Lefebvre et al., 1997; Johnson et al., 2010). *Trypanosoma* sp., consistent with *T. cervi*, was detected in a mountain goat from Montana (Kingston, 1985) and, using amplification and sequencing of a 550 base pair segment of the 18SrRNA gene, *Trypanosoma* sp. has been found in mule deer (SK), ranched elk (AB), Rocky Mountain bighorn sheep (BC) and wood bison (NT) (D. Schock, S. Kutz unpubl. obs., methods as per Noyes et al., 1999). Based on blood cultures or microhaematocrit centrifugation concentration, the prevalence of *Trypanosoma* sp. in free-ranging caribou is quite high 72–84% (Lefebvre et al., 1997; Johnson et al., 2010). There are no reports in muskoxen, which might reflect a lack of surveillance, or could be real and reflect reduced rates of attack on muskoxen by potential vectors. *Trypanosoma* sp. in caribou is morphologically similar to *T. cervi,* but experimental exposure of two elk to trypanosomes from Alaskan reindeer did not result in infection (Kingston et al., 1982).

(b) *Ecology.* In North America, *Trypanosoma* spp. have been isolated from deer flies, ticks (*Amblyomma americanum*) and horse flies (reviewed in Lefebvre et al. 1997). At least 33 species of tabanid flies are reported in the Arctic (Teskey, 1988) although the species transmitting *Trypanosoma* in this region are unknown. *Trypanosoma* spp. are present in Greenland where arthropod diversity is likely quite poor, and investigation of potential vectors in this relatively simple system may provide valuable insight into transmission (D. Shock, S. Kutz, C. Cuyler unpubl. obs.). Transplacental transmission of *T. cervi* in mule deer is documented, but the frequency and significance of this mode of transmission is not known (Kingston, 1982).

Prevalence of infection appears to be seasonal in reindeer and elk with highest prevalence based on direct examination, not culture, during midsummer and much lower prevalence in the mid to late autumn (Kingston, 1981; Kingston et al., 1982). This summer peak may coincide with vector abundance and thus enhance opportunities for transmission.

(c) *Impacts*. No clinical disease has been reported associated with *Trypanosoma* in arctic ungulates or wild North American cervids (Kingston et al., 1982; Kingston and Nikander, 1985).

2.6.2.3. Invasive protozoa

Babesia spp. are apicomplexan protozoans transmitted by ticks, and in the mammalian hosts, they invade red blood cells to replicate. Natural infections with *Babesia* have not been reported in free-ranging arctic ungulates of North America or Greenland; however, natural infections with *Babesia* and significant disease are common in eastern Russia (Rehbinder, 1990). *Babesia odocoilei* has been reported from captive woodland caribou, farmed reindeer and captive muskoxen in the USA (Holman et al., 1994; Holman et al., 2003; Schoelkopf et al., 2005). It is transmitted by Ixodid ticks but other possible vectors have been hypothesized in Russia (Zhilyaev, 1977).

In its mammalian hosts, *Babesia* spp. can cause intravascular haemolysis, anaemia, haemoglobinuria and occasionally a secondary toxic nephritis (Petrini et al., 1995). It almost invariably causes severe disease in captive *Rangifer*, with all cases of untreated babesiosis reported in North American acute and fatal (Holman et al., 1994; Schoelkopf et al., 2005; Bartlett et al., 2009). It is not known if subclinical babesiosis occurs in caribou and reindeer (Schoelkopf et al., 2005), as has been observed in farmed elk (Gallatin et al., 2003) and free-ranging white-tailed deer (Holman et al., 1994; Petrini et al., 1995; Holman et al., 2000). Two acute, fatal cases of babesiosis have been reported in muskoxen in a zoo in Minnesota. *Babesia odocoilei* was identified in these animals using DNA-based techniques (Schoelkopf et al., 2005). There are no published reports of *Babesia* in Dall's sheep, mountain goats or moose (Fig. 2.11).

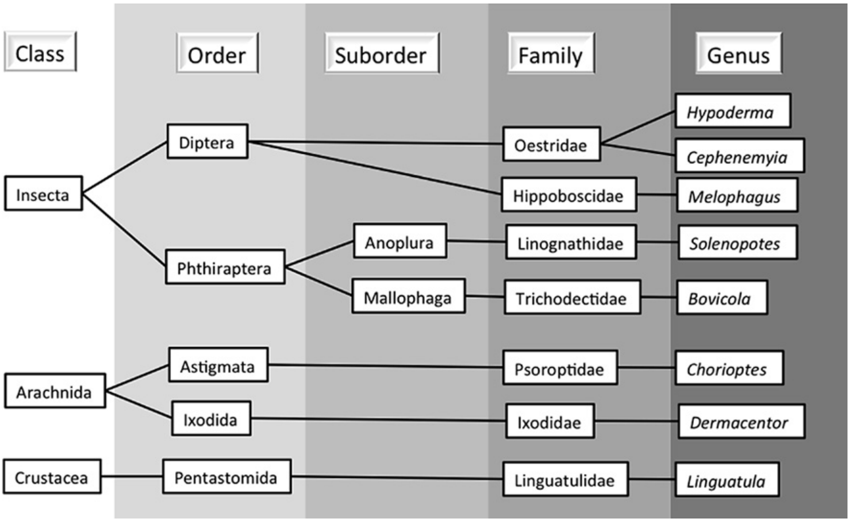

FIGURE 2.12 Arthropoda reported from ungulates of arctic North America, including Greenland.

TABLE 2.10 Arthropod parasites in ungulates of arctic North America, including Greenland. Data compiled from available published and grey literature

Host and Parasite species	Location	Herd, region or nearest place name
Caribou or reindeer		
Hypoderma tarandi	AK, NT, NU	All sampled herds and locations[a–g] (Note: latitudinal gradient – reduced prevalence at higher latitudes[c])
	YT	Porcupine[b,e], Chisana[e]
	QC/NL	Rivière-George herd[b,i]
	GL	Kangerlussuaq-Sisimiut[b,j,k]; Akia-Maniitsoq[b]
Cephenemyia trompe	AK	Western Arctic[b,d]; Mulchatna[d], Northern Alaska Peninsula[d], Nelchina[d], Teshepuk[d]; Various tundra[l]
	NT	Bathurst[b]
	NU	Baffin[n], Keewatin[l]; Bernard Harbor[l]
	GL	Kangerlussuaq-Sisimiut[b,j]; Akia-Maniitsoq[b]
Bovicola sp.	NT	Bluenose East[o]
Solenoptes tarandi	AK	Anaktuvuk Pass of Brooks Range and Utukok River south of Barrow[a]
Chorioptes texanus	NT	Mackenzie Delta reindeer[p]
Dermacentor albipictus	YT	Various[q]
	NT	Woodland caribou North Slave[f,q]
Linguatula arctica	AK	Unimak Island[r]
	NU	Baffin Island[n]
Dall's sheep		
Bovicola jellisoni	AK	Kenai Peninsula[s]
Melophagus ovinus	AK	Unspecified[t]; Chugach Mtns[d]; Alaska Range[d]
Moose		
Dermacentor albipictus	YT	Various[q]
	NT	Sahtu, South Slave, Deh Cho[f,q]
Muskoxen		
Hypoderma tarandi	AK	Seward Peninsula[d]
	NU	Victoria Island[g,h]
	QC	Kuujjuaq[u]

[a] Weisser and Kim (1973).

[b] CARMA, (2011).

[c] Thomas and Kiliaan (1990).

[d] K. Beckmen (unpubl. data)

[e] S. Kutz, M. Oakley (unpubl. data).

[f] B. Elkin (unpubl. obs.).

[g] Hughes *et al.* (2009).

[h] Gunn *et al.* (1991a).

[i] Parker (1981).

[j] Korsholm and Olesen (1993).

(*continued*)

TABLE 2.10 *(continued)*

[k] Clausen *et al.* (1980).
[l] Bennett and Sabrosky (1962).
[m] Downes *et al.* (1985).
[n] Ferguson (2003).
[o] C. Kashivakura, B. Kenny, G. Verocai, S. Kutz, A. Veitch (unpubl. obs.).
[p] Sweatman (1958).
[q] Kutz *et al.*, (2009b).
[r] Murie (1926).
[s] Kim (1977).
[t] Bequaert (1942).
[u] M. Simard, S. Kutz (unpubl. obs.).

Despite its potential importance as a significant cause of morbidity and mortality in caribou and muskoxen, there are no published studies on *Babesia* in wild caribou or other arctic ungulates in North America. The ixodid tick, *Dermacentor albipictus*, is found on moose and woodland caribou in the subarctic (Kutz et al., 2009b) but is a one-host tick and its competence as a vector for *Babesia* is unknown. *Ixodes scapularis*, the known vector of *B. odocoilei*, is common in white-tailed deer in temperate regions. In Canada, the currently non-contiguous ranges of this tick are expanding but the northern boundaries of their range are still a considerable distance from the Subarctic and Arctic (Steiner et al., 2008; Ogden et al., 2009). Thus, although white-tailed deer are expanding their range northwards and may eventually become an important reservoir for *B. odocoilei* species in the North (Waldrup et al., 1990), it may be some time before this tick species and *Babesia* appear in subarctic and arctic regions.

2.7. ARTHROPODS

The known diversity of ectoparasites of arctic ungulates is relatively simple and includes only one or two representatives in each of the following families: the Oestridae (bots), the Linognathidae and Trichodectidae (lice), the Psoroptidae (mites) and Ixodidae (ticks), and the Lingulatidae (Fig. 2.12, Table 2.10). In addition, a number of flies, including members of the Muscidae, such as moose flies (*Haematobosca alces*), members of the Tabanidae such as horse flies, members of the Hippoboscidae such as the sheep ked (*Melophagus ovinus*) (Bequaert, 1942) and members of the Simulidae and Culicidae (blackflies and mosquitoes, respectively) are reported across much of the Arctic but are not discussed here. Caribou have the greatest diversity of ectoparasites whereas muskoxen have the least and appear to be primarily accidental hosts.

2.7.1. Diptera

2.7.1.1. Family Oestridae

The Oestridae, nose/throat bots (*Cephenemyia trompe*) and warbles (*Hypoderma tarandi*) are the most abundant and extensively studied ectoparasites of arctic ungulates. They are parasites primarily of *Rangifer* spp. and rarely infest other ungulate species. They have a Holarctic distribution and are found in most, but not all, extant *Rangifer* populations. It is thought that both species were introduced to west Greenland with reindeer imported from Norway in 1952 (Clausen et al., 1980). Also, the presence of *C. trompe* on Baffin Island, NU, appears to be a more recent phenomenon with it first detected on the southern part of the island in 1997 (Ferguson, 2003). Both species are absent from translocated reindeer populations in Iceland and South Georgia Island.

Adults of *Hypoderma* and *Cephenemyia* are large, robust flies characterized by a dense covering of golden and black hairs (Colwell et al., 2006) in patterns that make them Batesian mimics of several species of bumble bee (Nilssen et al., 2000; Anderson, 2006). Mimicry of bumblebees presumably protects the flies from predation by birds (Anderson, 2006). Adults are nonfeeding and must complete all activities using fat reserves built up during larval development within the host. Females are strong fliers, capable of flight speeds between 29 and 36km/hr and theoretical flight distances of up to 330 km (based on flight mill studies) (Nilssen and Anderson, 1995).

First instars are small, translucent white, muscomorph larvae (≈1mm in length), uniformly covered with small spines (*H. tarandi)* or slightly dorso-ventrally flattened and covered with a number of thin spines primarily on the ventral and lateral surfaces (*C. trompe*). The first instars of *H. tarandi* grow to approximately 1cm in length during development beneath the skin. Second instars are translucent white of up to 1.5cm in length with widely disbursed short spines on all body surfaces. Third instars are large (up to 3cm in length) creamy white with all body surfaces having short, stout, sparsely distributed spines (Colwell et al. 2006). As third instars near completion of their development, the cuticle becomes increasingly melanized and mature third instars are almost completely black.

Third instars that have exited the host bury themselves in the surface litter prior to pupariation. These larvae and the puparia are likely to encounter freezing temperatures and presumably exhibit cold hardiness similar to other oestrids (Nilssen, 2006). Development within the puparium is highly temperature dependent, occurring from 10°C to 35°C with the maximum development rate at approximately 25°C and not increasing between 25°C and the upper limit (Nilssen, 2006). Overall duration of the pupal period will range from 7 to 80 days. This exquisite temperature dependence will result in dramatic variation in the timing of adult fly eclosion between regions and years with differing temperature regimes.

Harassment by oestrid flies can reduce feeding time and lead to reduced feed intake, reduced summer weight gain, decreased lactation, reduced calf weights and poorer overall condition that may influence reproductive success for reindeer (Weladji et al., 2003). The effect of larval stages on the host, particularly for *C. trompe*, is less well understood.

2.7.1.1.1. *Cephenemyia trompe*

(a) *Host and Geographic Ranges. Cephenemyia trompe* is found throughout most of the Holarctic, coincident with the distribution of *Rangifer*. It is considered host specific to *Rangifer* although there are reports of this species from *Odocoileus hemionus* in central Ontario, (Bennett and Sabrosky, 1962). Larvae have been reported from most subspecies of *Rangifer* (Table 2.10).

(b) *Ecology. Cephenemyia trompe* are ovoviviparous and females emerge from the puparia with a compliment of 500–1500 fully developed eggs (Anderson, 2006). Males aggregate at ecologically characteristic sites, usually treeless hilltops (Downes et al., 1985; Anderson, 2006) to await passing females with which to mate. Newly mated females rest for several days, in order for the larvae to develop within a specialized segment of the oviduct. When larval development is complete, the females must quickly search for a suitable host as they do not feed and do not supply nutrient to their larvae. Individual caribou respond to fly approach by dropping their head to get their nose as close to the ground as possible which may prevent the accurate deposition of larvae. Harassment by adult *Cephenemyia* is thought to induce stress responses similar to those induced by blood-feeding flies. The fly activity period in southern YT extends from June through August (Downes et al., 1985). Temperature, wind and cloud cover are the prime regulators of fly activity with the flies remaining inactive during cool, windy and inclement weather (Anderson and Nilssen, 1996). In the YT, males were active at temperatures >6°C (Downes et al., 1985).

Females approach the host from below the head and forcibly eject small groups of first instars precisely on to the upper lip of reindeer hosts (Anderson and Nilssen, 1990). Larvae migrate along the roof of the mouth or tongue to the upper respiratory tract where first instar development is completed. Second instars move to the pharyngeal region where they develop within the retropharyngeal recesses or pouches. Third instar development takes place in the same region and at the completion of this last stage the larvae are coughed up by the host and expelled. The rate of larval development may be affected by crowding in the host, where at high intensities development may not be synchronous (Nilssen and Haugerud, 1994). This often leads to hosts with all three larval stages present simultaneously. In general, the second instars are first present in mid-January and third instars will be found from early March. Departure of third instars from the host begins in late April and may continue until late June (Nilssen and Haugerud, 1994).

(c) *Impacts*. Larviposition behaviour alters the normal activity patterns of caribou (Hagemoen and Reimers, 2002; Anderson, 2006) resulting in reduced grazing time (Colman et al., 2003) and increased energy expenditure associated with avoidance behaviours. Coupled with the harassment by *Hypoderma tarandi*, these flies are a major factor in reduced summer weight gain, which is crucial to fertility and winter survival, and can have serious consequences for caribou populations (Hughes et al., 2009). A model quantifying weather conditions suitable for fly activity has been developed (Weladji et al., 2003) and could prove useful for predicting the impact of these flies on caribou at various localities. The impact of larval stages of *Cephenemyia* in caribou is not known.

2.7.1.1.2. *Hypoderma tarandi*

(a) *Host and Geographic Distributions. Rangifer* spp. are the primary hosts for *H. tarandi* although there are a few reports of larvae found in muskoxen in QC and NU and a moose in Sweden (Zumpt, 1965; Gunn et al., 1991a; Agren and Chirico, 2005; M. Simard, S. Kutz, unpubl. obs.). Host selection by ovipositing *H. tarandi* has not been extensively studied, but indications from other species in the genus suggest that a combination of visual, olfactory and chemosensory evaluations by the fly restrict the host range. For example, female cattle grubs, *H. lineatum*, are very selective as to the diameter of hair shaft to which they will attach eggs (Jones, 2000). The ability of first instars of *H. tarandi* to penetrate and survive in hosts other than caribou is likely limited based on the observation that *H. lineatum* larvae are incapable of penetrating >1–2mm into mouse skin (D. Colwell unpubl. obs.) and by failure of the same species to either penetrate or survive in goats under experimental conditions (Colwell and Otranto, 2006). However, oviposition and limited larval survival does occur in non-primary hosts, as exemplified by *H. lineatum* infestations in bison and horses (Scharff, 1950).

(b) *Ecology. Hypoderma tarandi* are oviparous and females emerge from the puparia with a fully developed set of eggs (300–800/ female, Anderson, 2006) and are thus ready to mate almost immediately. Males, which tend to emerge a few days ahead of females, aggregate at ecologically characteristic sites, usually flat graveled areas with sparse plant growth located along rivers or streams (Anderson, 2006). Mating occurs at these sites and females depart in search of suitable hosts. Three factors affect oestrid fly activity with the requirement that ambient temperature be >10°C, wind or air speed be <6m/s and cloud cover be <40%. These factors have been used to successfully predict insect harassment (Moerschel, 1999; Weladji et al., 2003). Females land on the host and thrust their ovipositors into the pelage, to near the skin surface, where eggs are attached individually to the hair shaft using ‘glue’ that reduces loss of the eggs. Development of larvae within the eggs takes place within 7–10 days and larvae migrate quickly to the skin surface. Larvae penetrate the skin and reside in the subcutaneous tissues where they become surrounded by a granuloma referred to as a 'warble'. Unlike the species that infest cattle, *H. tarandi* first instars do not undergo migrations in the connective tissues deep within the body. The warble provides a nutrient-rich environment where the larvae complete three instars prior to exiting the host. Larval departure from the host generally begins in early May and is complete by early to mid-July (Nilssen and Haugerud, 1994; Nilssen, 2006). Larvae that have exited the host and the puparia are likely to encounter freezing temperatures; they presumably exhibit cold hardiness similar to other oestrids (Nilssen, 2006).

(b) *Impacts.* Adult and larval stages may impact the health of caribou. Individual animals respond to oviposition activities by vigorous leg stamping, presumably to deter or dislodge the flies. This harassment is thought to induce stress responses similar to those induced by blood-feeding flies. Additional impact on the host results from the developing larval stages during winter. The cost to the host results from the energy cost of development and maintaining the granuloma (warble) surrounding the larvae as well as the cost associated with the development and maintenance of an immune response (e.g. antibody production). Research on west Greenland caribou suggests that infestation with *H. tarandi* is a significant drain on the energy budget of the host and could threaten the survival of calves and severely reduce fat deposition in pregnant cows (Cuyler, et al. 2012) and work on Dolphin-Union caribou, NU, suggests that increasing warble burdens are negatively associated with the likelihood of pregnancy (Hughes et al., 2009). In other natural systems, it has been demonstrated that in a situation where food resources are restricted the larvae can have a major impact on host survival (Milton, 1996). These observations suggest that, together, adult and larval stages of oestrid flies may have substantial impact on caribou populations in the Arctic.

Hypoderma tarandi is becoming of increasing concern as a zoonosis (Lagace-Wiens et al., 2008); in people, it can cause a serious ophthalmomyiasis interna, which often leads to loss of the eye. While the condition has been reported throughout the range of *H. tarandi*, there is an increasing occurrence in the Canadian Arctic. Larvae recovered from affected individuals have been early first instars, but the actual mode of infestation is not clear. Possible routes include oviposition on the human subjects by errant flies or accidental transfer of newly hatched larvae from the hide of caribou.

2.7.2. Phthiraptera

Blood-feeding and chewing lice are described from caribou, Dall's sheep and mountain goats but not from muskoxen or moose (Durden, 2001). There is, however, little information available on the specific features of their biology, epizootiology and impact on their hosts. In addition, there are few published data on the prevalence and intensity of infestation for any of these hosts. The following details on biology are derived from information on lice affecting domestic livestock (Price and Graham, 1997).

2.7.2.1. Family Linognathidae

2.7.2.1.1. Solenopotes tarandi

(a) *Morphology*. Sucking lice are small (usually 1–2mm in length), often blue or blue–grey in colour, with narrow, pointed heads. They have highly adapted legs with tarsi modified for grasping hairs on the host's body. These grasping 'claws' help the lice hold their position close to the skin while feeding.

(b) *Host and Geographic Distributions.* The distribution of *S. tarandi* is presumably Holarctic as the original description of this species was from reindeer in Sweden and it was subsequently identified in barren-ground caribou in AK (Weisser and Kim, 1973). *Solenoptes* sp. has not been reported in moose, muskoxen or Dall's sheep in the North American Arctic.

(c) *Life Cycle.* Lice are hemi-metabolous insects with incomplete metamorphosis, that is, nymphal stages appear superficially similar to the adult stages. All life cycle stages are closely associated with their hosts and they will not survive off the host for long periods. Transmission of lice occurs by direct contact, although transfer between hosts can occur on inert objects. Young animals may become infected through transfer from their dams within a short time after birth.

Both sexes are obligate blood feeders, using small, highly modified mouthparts that are concealed within the head capsule to obtain numerous small meals from capillaries in the upper layers of their skin. Data from cattle feeding species suggest females lay 2–6 eggs per day, which are attached to the host hair shafts (D. Colwell, unpubl. obs). Eggs complete embryonation and hatch within 8–11 days of deposition. Lice have three nymphal stages, which bear a morphological similarity to the sexually mature adult stage. Each nymphal stage will take 2–4 days to complete. Louse development rate, at all stages, is highly temperature dependent but is optimal at a narrow temperature range. Temperatures >41°C and 46 °C are lethal for eggs and adults, respectively, of *Linognathus vituli* of cattle. Optimal development takes place between 33 °C and 37 °C. Lice therefore show a seasonal periodicity with very low numbers in the summer when conditions are hot. Populations begin to increase as temperatures and solar radiation decline, reaching maximum levels in late winter. Lice preferentially occupy sites where the host is unable to groom effectively, but the distribution will become more generalized as the pelage become thicker during fall and winter.

Knowledge on the ecology of *S. tarandi* from caribou is limited. In one study, 36 and 74 lice were found exclusively on the head, predominantly around the ears and cheeks and anterior part of the neck of two of three caribou sampled in AK in June 1971. With the exception of *H. tarandi*, no other ectoparasites were recovered from total hide digests of these animals (Weisser and Kim, 1973). The authors suggested that the predilection for the head region could be due to the microclimate in this region. Fur on the head is much shorter than on most of the rest of the body and lacks the dense underfur, thus providing a unique temperature and humidity regime that may be preferred by the lice (Weisser and Kim, 1973). Predilection for the head may also be a result of the difficulty in individuals grooming that region effectively.

(d) *Impacts*. Generally, lice do not cause severe problems in large ungulate hosts and given the limited literature available it does not appear that the blood-feeding lice are of serious concern in ungulates in the Arctic. Rare cases of host disease have been noted in non-arctic ungulates (Foreyt et al., 1986) where a species of louse has switched host species.

2.7.2.2. Family Trichodectidae

2.7.2.2.1. Bovicola spp.

(a) *Morphology*. Chewing lice (*Bovicola tarandi*, *Bovicola jellisoni* and *Bovicola oreamnidis*) are generally small, <2mm in length. These lice are highly mobile, usually brown or reddish-brown in colour with a characteristically dorso-ventrally flattened body and broad, rounded head.

(b) *Host and Geographic Distributions. Bovicola tarandi* are described from woodland caribou and reindeer, suggesting a Holarctic distribution (Low,

FIGURE 2.13 Dall's sheep ewe with fur loss. Sheep Mountain, Yukon Territory Canada. (photograph by S. Kutz, 7 May 2006). (For color version of this figure, the reader is referred to the web version of this book.)

1976). *Bovicola jellisoni* is described as infesting Dall's sheep (Kim, 1977) but was originally described from bighorn sheep (Emerson, 1962).

(c) *Life Cycle.* These lice feed on dead skin cells, hair and oil secretions, which they abrade from the surface using their chewing mouthparts. There may be some abrasion of the upper skin layers and there has been demonstration that sheep develop antibodies to salivary sections of *Bovicola ovis* (James et al., 1998). Sex ratios are highly female biased and parthenogenesis is a common occurrence in many species (Price and Graham, 1997). Females deposit less than one egg per day. Embryonation is completed in 7–10 days producing nymphs, which molt three times before reaching sexual maturity. As with the sucking lice, development is highly regulated by temperature with a narrow range for optimal development and survival. Chewing lice can survive off the host for up to two weeks under ideal conditions. Transmission of lice occurs by direct contact, although phoretic transfer of chewing lice between hosts by flies occurs occasionally (Mertins et al., 2011).

Bovicola jellisoni was described from two of three Dall's ewes collected 27 April 1971 from the Kenai Peninsula, AK. One animal had 18 lice, and the second had approximately 19,300 lice, with 85% of the population distributed on the sides and belly and 13% around the anus (Kim, 1977). A high proportion (88%) of the louse population were nymphs, 9% female adults, and the sex ratio was 3:1 female:male.

(d) *Impacts*. Chewing louse populations tend to be small on individual hosts and they have little impact on the host, although there are descriptions of hair loss associated with louse infestation on horses (Larsen et al., 2005). Occasional reports of hair loss on Dall's sheep occur (Figure 2.13) (R. Popko, Mackenzie Mountains, pers. comm.; S. Kutz, Sheep Mountain Yukon, unpubl. obs.), but aetiology has not been determined. Reports of skin lesions and hair loss in caribou, with the exception of those associated with *Besnoitia* are not common (Kutz, 2007).

There is concern that the potential exists for severe impact on naive hosts when lice are exchanged between host species that have only recently come into contact. A severe hair loss syndrome has been described in black-tailed deer resulting from the transfer of *Tricholipeurus parallelus* from white-tailed and mule deer (Bildfell et al., 2004; Foreyt et al., 2004). On black-tailed deer, the populations of *T. parallelus* were uncharacteristically high and the severity of hair loss lead to death in some cases. Whether the syndrome was the result solely of the lice or a combination of factors is not entirely clear, but the consequences for the affected deer were serious. The problem has become of more concern with the report by Mertins et al. (2011) describing the impact of *Bovicola tibialis*, a louse brought to North America with *Dama dama* (fallow deer), on native species of deer. It appears that the louse has switched to several native cervids with some ease and is causing severe hair-loss syndrome in many populations and is thought to be impacting the well-being of the affected populations. A potential explanation of the hair-loss syndrome could be the exposure to a new allergen produced by lice to which the host was not adapted. Pfeffer et al. (2010) have described an allergen produced by sheep lice (*Bovicola ovis*) that is responsible for small reactions seen on the skin of infested sheep and on non-adapted hosts the reactions could be more severe.

2.7.3. Acari

2.7.3.1. Family Psoroptidae

2.7.3.1.1. Chorioptes spp.

(a) *Morphology*. *Chorioptes* mites are very small, adults being approximately 0.5mm long. The body is oval with legs bearing single stalked pulvilli that terminate in a cup-like structure.

(b) *Host and Geographic Distributions*. *Chorioptes texanus* is considered to be relatively non-host specific and capable of infesting a wide range of wild cervids and domestic livestock. It has been reported from reindeer (*Rangifer tarandus*) in Canada (Sweatman, 1958), where it was collected from the ears, but the distribution is likely Holarctic. *Chorioptes* has not been reported from moose in North America, but *Chorioptes texanus* was reported from moose in Poland (Kadulski, 1996) and a previously uncharacterized pathogenic species has been described from the outer ear canals of moose in Sweden (Hestvik et al., 2007). *Chorioptes* sp. was observed from the lower legs of captive muskoxen (B. Wagner, S. Kutz, unpubl. obs.).

(c) *Life Cycle*. The life cycle comprises five distinct stages, including egg, larva, protonymph, tritonymph and adult. Based on information from *C. bovis* of domestic livestock, the entire life cycle requires from 19 to 28 days to complete on the host (Baker, 1999). Larval and nymph stages feed on skin debris.

(d) *Impacts*. In moose, *Chorioptes* sp. causes significant epidermal and dermal inflammatory lesions in the outer ear canals (Hestvik et al., 2007). In captive muskoxen pruritus, mild scaling and hair loss were observed on the lower legs (S. Kutz, unpubl. obs.). In cattle, an allergic dermatitis occurs occasionally leading to focal hair loss around the tail-head while in other domestic animals the predilection site varies (Yeruham et al. 1999).

2.7.3.2.Family Ixodidae

2.7.3.2.1. Dermacentor albipictus

(a) *Morphology*. These are medium-sized ticks (3–6mm long) with eyes, festoons (folds in the posterior margin of the idiosoma), short mouthparts and palps with a rectangular basis capitulum. Members of this Family are characterized by the presence of a dorsal shield, or scutum, which covers nearly all of the body of males but is confined to the anterior portion in females and immature stages. The openings of the respiratory system are associated with near tear-drop-shaped spiracular plates (also known as stigmal plates) that are characteristic for the species (Gregson, 1956).

(b) *Host and Geographic Distributions. Dermacentor albipictus* is broadly distributed in temperate North America and is reported from a wide range of hosts including moose, woodland caribou, mountain goat and bighorn sheep (Allan, 2001). Recently, *D. albipictus* appears to be expanding its geographic range north in moose, woodland caribou and elk in NT and YT, and the potential invasion of barren-ground caribou herds is a significant concern under current climate warming conditions (Kutz et al., 2009b).

(c) *Life Cycle. Dermacentor albipictus* is a one-host tick with all blood-feeding stages occurring on the same host. Gravid females, once having mated on the host, drop off in April and March. Oviposition begins in June. Survival of females, eggs and larvae is reduced by exposure to high temperatures (Drew and Samuel, 1985). Larvae develop over the course of the summer and may enter a diapause. Diapause is influenced by photoperiod (Wright, 1969; Wright, 1971) and larvae are found questing at the tips of vegetation in September and October (Drew and Samuel, 1985). There is a high degree of cold tolerance in the larvae allowing persistence during often hostile periods (Gregson, 1956; Samuel and Welch, 1991). Once on the host, larvae feed and nymphs can be found within three weeks. This latter stage does not feed until some time later, often January (Drew and Samuel 1985). The feeding can take place over a long period, extending to March, in northern latitudes (Samuel and Barker, 1979). Adult ticks are found on hosts from March through early June.

(d) *Impacts*. Feeding by *D. albipictus* has a range of effects on the host that may be linked to the host susceptibility, grooming behaviour and intensity of infection. Moose tend to have the highest burdens, infested by many thousands of ticks (Samuel and Welch, 1991), caribou and elk can have moderate infections, and deer tend to support very few ticks (Welch et al., 1990). The feeding activity of ticks induces an intense itching that stimulates grooming activity. The grooming can result in dramatic hair-loss in some host species such as moose, which can culminate in adverse effects leading to death. Moose die-offs have been associated with heavy infestations (Allan, 2001). Other species show only mild alopecia.

High intensities of infestation of captive reindeer and woodland caribou are associated alopecia, although the confined nature of the animals may have contributed to the high tick burdens (Welch et al., 1990; Kutz et al., 2009b). Small numbers of winter tick have also been reported from a few free-ranging woodland caribou in northern AB and NT (Welch et al., 1990; Kutz et al., 2009b).

2.7.4. Crustacea, Pentastomida

2.7.4.1. Family: Linguatulidae

2.7.4.1.1. Linguatula arctica

(a) *Morphology*. Adult females are large (6–13cm long), dorso-ventrally flattened with numerous pseudo-segments (annuli). In the anterior half, the annuli are broader than in the caudal half giving the parasites a paddle-shaped appearance (Riley et al., 1987; Nikander and Saari, 2006). Males are smaller (3–4cm long) with a slightly smaller number of annuli. The number of annuli is a diagnostic feature used to separate *L. arctica* from the common species infecting canids *L. serrata* (Riley et al., 1987).

(b) *Host and Geographic Distributions.* The sinus worms have been thought of as primarily parasites of semi-domesticated reindeer in the Palaearctic; however, there are two reports from North America. It was reported from a caribou (misidentified as *L. serrata*, a cosmopolitan parasite of carnivores) on Unimak Island, the easternmost Aleutian island in Alaska (Murie, 1926), and more recently from Baffin Island caribou (Ferguson, 2003). Based on oral histories from indigenous hunters, Ferguson (2003) suggests that the sinus worms were present on Baffin Island prior to the introduction of Norwegian reindeer in 1921. These reports may suggest a Holarctic distribution for the parasite, but the apparent discontinuous distribution across the North American Arctic is enigmatic.

(c) *Life Cycle.* The reindeer sinus worm has a direct life cycle; an unusual feature for this group that often utilizes intermediate hosts for the completion of larval development. Adult sinus worms are found in the nasal cavity of their hosts where they produce embryonated eggs that are shed from the host in mucous. The eggs are immediately infective to grazing calves.

(d) *Impacts*. Most infections with the sinus worm are found in calves and animals under two years of age suggesting the development of protective immunity (Riley et al. 1987). There has been no reported effect on infected animals (Haugerud, 1989) despite the presence of significant pathology in some animals.

2.7.5. Emerging issues and future research for the Arthropoda

With the exception of the Oestridae, the diversity, host and geographic distribution and impacts of ectoparasites in ungulates of the North American Arctic are very poorly defined, consisting primarily of a few case reports from a few hosts and locations. Caribou appear to have the most and muskoxen the least diverse faunas.

The majority of research on host–parasite interactions and on biology of adult stages has been conducted in the Palaearctic, primarily with the semi-domesticated reindeer hosts (e.g. *C. trompe*, *H. tarandi* and *L. arctica*). For the oestrid flies, there is a paucity of data on the biology of the pupal stages and their response to changes in environment, for example, studies of the freeze tolerance of mature third instars and pupae are needed. In the case of *H. tarandi*, variation in the susceptibility of the various subspecies of caribou present in North America requires research particularly in light of the demonstration by Rødven et al. (2009) that the intensity of infestation was higher in lighter coloured individuals (Nørwegian et al., 2009).

The effects of lice and mites on arctic ungulate hosts remain unknown. Evidence of high infestation intensities (e.g. *B. jellisoni* in Dall's sheep), hair loss of unknown etiologies, and recent recognition of *Chorioptes* as an important pathogen in Scandinavian moose suggest that these parasites may play an important role in host health.

The lifecycles and transmission dynamics of all the ectoparasites described above are limited or accelerated by ambient climatic conditions, in particular temperature and relative humidity, but also wind speed and cloud cover. Defining current faunal diversity, including host and geographic distributions, together with establishing thermal tolerances, thresholds and tipping points, are essential steps to understanding the potential response of these host–parasite systems to ephemeral climatic events and long-term climate trends.

2.8. DISCUSSION

2.8.1. Parasites alive and well in arctic ungulates

We have defined and reviewed patterns of biodiversity for a complex, successful and geographically widespread parasite fauna in caribou, muskoxen, Dall's sheep and moose of the North American Arctic, including Greenland. At minimum, this fauna consists of 60 described species of helminths, arthropods and protozoans yet there remains considerable undescribed biodiversity and probable cryptic species complexes. For the few parasites that have been studied in some detail, there is strong evidence that they can have significant impacts on individual health and host population dynamics. Most of these arctic parasites are highly responsive to climate and climate change and many have important consequences for the safety, security (sustainability and availability of wildlife populations) and quality of country foods on which many northern aboriginal peoples continue to depend. So what have we learned and where do we need to go?

2.8.2. Parasite biodiversity

It is abundantly clear that, despite the fact that ungulate species are charismatic components of northern ecosystems, there remain many basic questions regarding the biodiversity and faunal structure for their parasites. Much of the endemic fauna across the high latitudes of the Nearctic was established through geographic expansion and colonization from Eurasia under the influence of various biotic and abiotic filters ovet the last 3 million years (Hoberg et al., 2012). This historical perspective sets the stage for understanding the current diversity and also provides a foundation to explore biological systems under dynamic change. We are now defining the faunal assembly and patterns of distribution, recognizing that species richness tends to decrease at high latitudes and on a west to east gradient, perhaps coinciding with expansion and invasion from Eurasia into North America.

Recent and ongoing descriptions of new species and cryptic complexes, diagnoses of new genera and definition of new host or geographic distributions highlight the significant but hidden diversity of helminths (Hoberg et al., 1995, 1999; Kutz et al., 2001d; Hoberg et al., 2002; Kutz et al., 2007; Laaksonen et al., 2010b; Haukisalmi et al., 2011; Hoberg et al., in press-a,b) and enteric and tissue cyst-forming protozoans (Gudmundsdottir and Skirnisson, 2005; Gudmundsdottir and Skirnisson, 2006; Dahlgren et al., 2008a; Kutz et al., 2008; Kutz et al., 2009c) in arctic ungulates. Although diversity for ectoparasites has been explored minimally, hidden diversity is probable. Ectoparasites may be highly responsive to climatic changes and also can be important vectors or intermediate hosts for a variety of pathogens; thus, there is some urgency to understand this fauna much better in an Arctic undergoing substantial climate change.

Essential to documenting biodiversity are permanent specimen-based and archival collections that provide historical baselines for contemporary systems and allow comparison across regions and over time (Hoberg et al., 2003, 2009). Museum archival collections (specimens and associated informatics) are the critical foundations for documenting change in northern systems (Hoberg, 2010). Importantly, archival collections are ‘self-correcting’ records, that is, specimens can be re-examined and identifications re-determined as new information and new technology develops. Such collections have been essential for redescriptions of species, identification of cryptic species, and correction of historical records (e.g. Hoberg et al., 1999; Lichtenfels and Pilitt, 1983a). They have also been key resources for the development of this manuscript where specimens from previously published records could be re-examined and reported with the most up to date taxonomic designations.

2.8.3. Characteristics of arctic parasites – New insights

Parasites of ungulates in the Arctic demonstrate a variety of attributes that facilitate their persistence in an environment characterized by high seasonality, extremes of climate and weather (temperature and humidity), and a generally low abundance and diversity of hosts that varies over space and time. These factors have operated over both evolutionary and ecological time, playing critical roles in structuring of the contemporary parasite fauna (Hoberg, 2012b). Freeze tolerance, arrested development, overwintering in/on the hosts, large size and high fecundity, long life spans and defined seasonal characteristics are some of the features that have ensured the success and often extensive distributions of arctic parasites.

2.8.3.1. Freeze tolerance

A key feature of many arctic parasites is their ability to withstand extended freezing events. Nematodirines and *Marshallagia* have eggs that are resistant to environmental extremes and subzero temperatures for extended periods. Both L2 and L3 of *O. gruehneri* have high overwinter survival on the arctic tundra. For at least some of the protostrongylids, for example, *U. pallikuukensis* and *P. odocoilei*, both the first-stage larvae in the environment and developing larvae in gastropod intermediate hosts are able to overwinter at subzero temperatures; this is predicted also for *P. stilesi* and *P. andersoni*. The cysticerci of *T. hydatigena* mature within the liver parenchyma of arctic ungulates, thus surviving subzero ambient temperatures longer than more superficial cysticerci that are typical in domestic animals infected with this cestode. This feature is not described in domestic hosts and may indicate a behavioural adaptation to subzero temperatures in sylvatic cycles. At least some species of *Eimeria* from muskoxen have the ability to sporulate after extended freezing, an uncommon characteristic for the Apicomplexans. Freeze tolerance for a number of other parasites including the tissue forming protozoans (*Besnoitia*, *Toxoplasma*, *Sarcocystis* and *Neospora*) and the pupae of *Hypoderma* and *Cephenemyia* is unknown but would certainly be an advantage in the arctic environment.

2.8.3.2. Arrested larval development

Whereas some parasites are able to overwinter in the environment, others use a different strategy to survive the extreme cold. Observational and experimental data demonstrate that arrested larval development is a dominant feature of the lifecycles for both *O. gruehneri* and *T. boreoarcticus*.

Similarly, observational data suggest that *Dictyocaulus* in muskoxen may overwinter as fourth-stage larvae in the lungs of calves or yearlings. In these situations, arrested development over the winter effectively maintains the parasites during extended periods of poor environmental conditions and in a hypobiotic state, which conceivably minimizes the energetic costs to the hosts during periods of possible nutritional stress. Inhibited development may thus reduce parasite-mediated morbidity and mortality that would be detrimental to persistence of these directly transmitted helminths.

Nematodirus alcidis in moose, however, appears to maintain an arrested larval population throughout the year and this may serve as a ready reservoir to replenish the adult population (Fruetel and Lankester, 1988). Such a strategy may be particularly important in environments where exposure to infective larvae is erratic and unpredictable, for example, where host density is low or climatic conditions are variable.

2.8.3.3. Seasonality

Several arctic parasites display very strict seasonal patterns that coincide with features of host lifecycles and appear to promote their persistence in the Arctic. For example, the arrested development of *O. gruehneri* limits egg production, and subsequent availability of infective larvae, to the spring and summer, a time when parasites are most likely to develop in the external environment and be transmitted within migratory caribou populations. In addition, adult nematodes persist in the abomasa of caribou throughout the winter but are not gravid during this time. Quiescence of these adult nematodes may minimize the parasite cost to the host at a time when any eggs produced would not likely survive. Preliminary studies on *T. boreoarcticus* suggest similar patterns.

2.8.3.4. Prepatent periods, fecundity and lifespans

Prepatent periods in arctic helminth parasites differ across taxa and many appear to be finely tuned to the seasonality of the arctic environment. The short prepatent period for *Taenia krabbei* in the definitive host is considered a potential adaptation to the short summers, where high rates of predation on ungulate intermediate hosts during the summer would then lead to egg production throughout the summer (Sweatman and Henshall, 1962). In contrast, *P. cervi*, the rumen fluke, and *S. tundra*, the peritoneal nematode, have very long prepatent periods where infection in one summer results in peaks in eggs/microfilaria production the following summer when arthropod intermediate hosts are available and transmission is most likely to succeed.

Several arctic-adapted nematode parasites tend to have long prepatent periods, are larger in body size and longer lived than their temperate and southern relatives. For example, *U. pallikuukensis*, which appears to have indeterminate growth (Kutz et al., 1999), is very large-bodied and long lived relative to other Muelleriinae lungworms (Hoberg et al., 1995; Kutz et al., 2001b). Similarly, specimens of *T. boreoarcticus* are generally considerably larger than those of the closely related *T. circumcincta* (Hoberg et al., 1999). Jacobs and Rose (1990) observed large *T. circumcincta* in domestic sheep in Greenland and, through experimental studies and cross-infections, concluded that the large size was more likely a result of environ-

TABLE 2.11 Checklist of parasites confirmed from ungulates of arctic North America, including Greenland. 'X' indicates parasite present in the host in the Arctic and/or Subarctic

Type of Parasite	Caribou (reindeer)	Dall's sheep	Moose	Muskoxen
Nematoda (enteric) (15)				
Trichostrongylina				
Ostertagia gruehneri	X	X		X
Teladorsagia boreoarcticus	X	X		X
Marshallagia marshalli	X	X		X
Nematodirella sp.		X		
Nematodirella alcidis			X	X
Nematodirella longissimespiculata	X			X
Nematodirella gazelli				X
Nematodirus archari/andersoni		X		
Nematodirus davtiani		X		
Nematodirus helvetianus				X
Nematodirus oiratianus/o. interruptus		X		
Nematodirus spathiger		X		
Nematodirus tarandi	X			X
Oxyurina				
Skrjabinema tarandi	X			
Skrjabinema ovis		X		
Trichinellina				
Trichuris spp.	X			X
Trichuris schumakovitschi		X		
Total species 15	**7**	**10**	**1**	**9**
Nematoda (tissue)				
Metastrongylina				
Dictyocaulus sp.	X		X	
Dictyocaulus eckerti			X	X
Parelaphostrongylus andersoni	X			
Parelaphostrongylus odocoilei	X	X		

(continued)

ment in the host (in particular, low host immunity) rather than a species

TABLE 2.11 *(continued)*

Type of Parasite	Caribou (reindeer)	Dall's sheep	Moose	Muskoxen
Protostrongylus stilesi		X		X
Protostrongylus rushi		X		
Varestrongylus sp. nov.	X		X	X
Umingmakstrongylus pallikuukensis				X
Spirurina				
Rumenfilaria andersoni			X	
Setaria sp.	X			
Setaria yehi	X		X	
Onchocerca cervipedis	X		X	
Total species 10	**7**	**3**	**6**	**4**
Cestoda				
Taenia hydatigena	X	X	X	X
Taenia krabbei	X		X	
Taenia arctos			X	
Echinococcus granulosus	X		X	X
Anoplocephalidae	X	X	X	X
Avitellina sp.				
Avitellina arctica	X			
Moniezia sp.		X		
Moniezia benedeni				
Moniezia expansa				X
Total species 7	**4**	**2**	**5**	**4**
Trematoda				
Fascioloides magna	X			X
Paramphistomum sp.	X		X	
Total species 2	**2**	**0**	**1**	**1**
Protozoa (gastrointestinal)				
Giardia sp.	X	X		
Giardia duodenalis assemblage A				X
Cryptosporidium sp.	X		X	X
Eimeria sp.	X		X	X
E. ahsata		X		
E. crandallis		X		
E. dalli		X		
E. faurei				X
E. granulosa				X
E. moshati				X
E. ninakohlyakimovae		X		
E. oomingmakensis				X
E. ovina				X

TABLE 2.11 *(continued)*

Type of Parasite	Caribou (reindeer)	Dall's sheep	Moose	Muskoxen
E. parva		X		
Total species 12	**3**	**6**	**2**	**8**
Protozoa (tissue) (5)				
Besnoitia tarandi	X			X
Neospora caninum	X		X	X
Sarcocystis spp.	X	X	X	X
Toxoplasma gondii	X	X	X	X
Trypanosoma sp.	X	X	X	
Total species 5	**5**	**3**	**4**	**4**
Arthropod ectoparasites				
Cephenemyia trompe	X			
Hypoderma tarandi	X			X
Melophagus ovinus		X		
Bovicola tarandi	X			
Bovicola jellisoni		X		
Solenoptes tarandi	X			
Chorioptes texanus	X			
Dermacentor albipictus	X		X	
Linguatula arctica	X			
Total species 9	**7**	**2**	**1**	**1**
Total parasite species 60	**35**	**26**	**18**	**31**

difference from *T. circumcincta* elsewhere. It is possible that large size may be a product of both parasite intrinsic characteristics (e.g. genetics) and host factors. Certainly, reduced host immunity may be an important factor for arctic ungulates, in particular muskoxen, which appear to be particularly susceptible to most parasites and parasite-induced disease (e.g. Alendal and Helle, 1983).

The lifespans of for both *O. gruehneri* and *T. boreoarcticus* appear to be extended, at least two years, an exceptionally long time for this subfamily of nematodes. Larvae ingested one summer mature the following spring, produce eggs throughout the summer and persist in the host through the following winter. Whether they then die or continue to produce eggs the next summer remains uncertain; however, evidence from experimental infections suggests that adults of *O. gruehneri* may survive and produce eggs for at least two summers. Two reindeer experimentally infected with a low dose of *O. gruehneri* and with very minimal opportunity for re-infection had similar egg counts for two consecutive summer seasons (Hoar et al., 2012a).

In general, for nematodes, prepatent period is frequently positively correlated with body size and body size is positively correlated with egg production (Gemmill et al., 1999; Rowe et al., 2008). Large size and longevity in the Arctic may allow pulses of high egg/larval production over short seasonal periods but multiple years. Multi-year lifespans may ensure maintenance of the parasites over years where environmental conditions are inadequate to support development in the environment or when host densities or behaviour reduce transmission potential. Indeterminate growth, large body size and extended fecundity for infections in highly vagile ungulates are expected to be correlated with a capacity for invasion and geographic colonization (Hoberg, 2010; Hoberg, in press b).

2.8.3.5. Generalist life history

Another mechanism for survival in the arctic environment may be a propensity for a generalist life history. The ability to parasitize several different host species may provide a buffer if one species declines or is seasonally unavailable. In our study, of 60 parasites that were identified to the species level, 26 are able to parasitize more than one species of arctic ungulate (Table 2.11). Caribou, however, generally the most abundant ungulate across the Arctic, may maintain a few more host-specific parasites. For example, *Besnoitia*, *Hypoderma*, and *Cephenemya*, are essentially host specialists. Although they spill-over into muskoxen on occasion, it is highly unlikely that they could be maintained in this host.

2.8.4. Exploring characteristics of arctic parasites in a broader framework

Our review has highlighted that differences among arctic ungulate species or ecotypes may be very important determinants of parasite community diversity and transmission patterns. For example, transmission of parasites among the highly vagile, migratory caribou may differ substantially from patterns among the highly philopatric Dall's sheep. Even within a host species, biodiversity of parasites and patterns of transmission are likely to differ, for example, between relatively solitary, low-density and non-migratory Peary and boreal woodland caribou compared to migratory barren-ground caribou. As our knowledge of the biodiversity and distribution of parasites among these hosts expands, we can use meta-analyses to explore how host behaviour and ecology influence parasite distributions within the relatively simple arctic ecosystem. Such new investigations should include landscape level assessments of genetic diversity using appropriate fine-scale markers to explore patterns of historical and contemporary isolation and expansion for both hosts and parasites.

Similarly, we are also at a point where broader comparisons among parasites of arctic, temperate and tropical systems are needed. In particular, phylogenetically corrected meta-analyses comparing parasite life-history patterns and characteristics such as direct versus indirect lifecycles, arrested development, freeze tolerance, body size, length of prepatent periods and patency, accumulation of parasites and patterns of age prevalence/intensity, host associations and host specialists versus generalists across broad latitudinal gradients are now becoming possible. Such comparisons will provide new insights into host–parasite associations and adaptations and potential responses to different climatic conditions and environmental perturbations. Clearly, essential for such meta-analyses is an understanding of diversity and history for ungulate parasite faunas both in the Arctic and in temperate and tropical zones.

An exciting area of research that remains virtually unexplored in the Arctic is the biomass of parasites in the ecosystem and their role in food webs. Parasites are responsible for a complex array of linkages within the arctic food web (Kutz, 2012) and understanding how they cycle nutrients through the environment and the relative importance of this in an arctic ecosystem that is nutrient poor compared to a tropical or temperate system is an important issue. For example, the biomass of warble larvae in caribou is substantial. These larvae are composed entirely of nutrients derived from the caribou host. When they pupate in the environment they may become important components of the food chain as prey for rodents, birds and other invertebrates, thus translating caribou biomass into a potentially wide array of terrestrial vertebrates and invertebrates.

2.8.5. Changing polar environments and host–parasite interactions

Polar environments today are changing at an unprecedented rate in response to climate change and effects of these changes are now evident in the biosphere (Callaghan et al., 2004; Post et al., 2009). Accelerated climate change and extreme weather events are influencing the ecology, impacts and geographic distribution of endemic parasites in the Arctic (Kutz et al., 2005; Hoberg, 2010; Laaksonen et al., 2010a) and leading to the expanding ranges and emergence of new parasites at high latitudes (Kutz et al., 2009b).

Responses of host–parasite systems to climatic changes will vary and will be linked to the specific history of faunal assembly, species diversity, life-history characteristics, and particular tolerances, thresholds and resilience of parasites and hosts (e.g. Kutz et al., 2009b; Hoberg et al., 2008a; Hoberg et al., 2012). For example, we may expect arthropod transmitted parasites to respond rapidly, and for the most part positively, to warming climatic conditions (e.g. Laaksonen et al., 2010a) whereas directly transmitted parasites may be positively or negatively influenced depending on their thermal tolerances (Kutz et al., 2009b; Hoar et al., 2012b). Additionally, parasites transmitted by gastropod, and perhaps arthropod, intermediate hosts may be sheltered from climatic extremes because of behavioural thermoregulation by these intermediate hosts and therefore will respond to a warming climate in a more moderated manner (Kutz et al., 2009b).

Photoperiod at arctic latitudes may be an important factor influencing the phenology of parasites (Hueffer et al., 2011). While warming climate may push the potential for more rapid development rates, photoperiod may temper these responses. For example, the diapause, and consequently the questing by larvae of the tick *D. albipictus*, is strongly influenced by light regime. Under a constant photoperiod of 8h, larvae attached to hosts at 4 weeks post hatching whereas larvae maintained at 12 and 16 hours remained in diapause for 10 and 12 weeks, respectively (Wright, 1969, 1971). Thus, photoperiod has a significant impact on larval questing and, depending on how climate and photoperiod interact, may limit, or accelerate, range expansion of this parasite at in the Arctic. Further exploration of the interaction between climate and photoperiod with respect to parasite transmission dynamics is important at high latitudes where both these abiotic features have a very broad range.

2.8.5.1. The breakdown of ecological barriers

Episodic changes in climate and habitat have historically influenced the assemblage of arctic ungulates and their parasites (Hoberg, in press b). Ongoing and increasing anthropogenic changes in the Arctic, including rapid climate warming, landscape perturbation associated with human activities and animal translocations, can lead to the breakdown of ecological barriers that previously may have separated different host species and/or restricted the movement of parasites either within the North or between temperate and arctic species (Hoberg, 2010; Hoberg et al., 2012). Such invasions could lead to shifts in parasite communities and parasite transmission pathways (e.g. through new intermediate/definitive host species and/or vectors). Given the general pattern for low host specificity among parasites of arctic ungulates, emergence of new host–parasite interactions are expected. This is exemplified by muskox translocation and subsequent expansion leading to sympatry with Dall's sheep and infection of muskoxen with *P. stilesi* acquired from sheep. With northward range expansion of southern host and parasite species, disease emergence in naive northern species and parasite-mediated competition are potential outcomes. Importantly though, invasion and establishment of new parasites under warming climatic conditions is not a foregone conclusion. For each individual parasite species, numerous ecological conditions, including but not limited to sufficient densities and spatio-temporal distributions of definitive and intermediate hosts, suitable climate and appropriate thermal tolerances of the parasite, need to be met before an invasion could succeed.

Other climate-related changes that may influence the parasite fauna, and subsequently the health and sustainability of wildlife populations, include increased colonization of northern regions by people and their domestic animals and thus the potential for rapid invasions by new parasites. Tourism and dumping of ballast water may also influence systems by introducing new parasites, such as *Giardia*, which may be transmissible to wildlife.

2.8.5.2. Loss of parasite biodiversity

Another important potential outcome of climate change for parasites in the Arctic that has received little attention is that of parasite extinctions. As environmental conditions change and southern species invade, competition among invasive and endemic parasite species could lead to displacement, extirpation and even extinction of arctic-adapted parasite species. Similarly, if arctic host species are threatened by extinction, co-extinction of any host-specific parasites is a reality. Globally, despite the fact that many host-specialist parasites are anticipated to go extinct with the extinction of their hosts, there is currently only one parasite listed on the IUCN red list – the pygmy hog sucking louse (Hematopinidae: *Haematopinus oliveri*) (Whiteman and Parker, 2005). Loss of endemic parasites may reduce cross-immunity to invasive species and would reduce interspecific competition for invading parasites; thus, it may facilitate establishment of new parasites. Such losses would also have downstream effects on food webs as well as consequences for host health. Finally, extirpation of endemic parasite species would remove a key element of biodiversity and a window into the evolutionary past of their hosts (Brooks and Hoberg, 2000; Hoberg et al., 2003, in press b; Whiteman and Parker, 2005).

2.8.6. Directions forward

In the last 15 years, there has been substantial progress in understanding the biodiversity and ecological interactions of parasites in arctic ungulates yet there remain significant knowledge gaps. The relative simplicity of the Arctic makes it extremely enticing to explore host–parasite interactions much more thoroughly – a perhaps tangible and achievable goal.

2.8.6.1.Climate change

Climate-driven emergence of new parasites and parasite-induced disease syndromes in the Arctic have heightened our awareness of the sensitivity of these systems and the value of the Arctic as a model system for investigating the impacts of climate change (Hoberg et al., 2003; 2008a; Kutz et al., 2009b). The development of empirical models for the transmission patterns of protostrongylids has provided predictive tools for anticipating potential effects of climate change on distribution and transmission rates of this group of parasites (Kutz et al., 2005;Jenkins et al., 2006b). Similarly, the determination of a temperature 'tipping point' for emergence of *Setaria* has provided a measurable climate indicator that can be used to predict disease outbreaks for this parasite (Laaksonen et al., 2010a). Initial research on impacts of directly transmitted nematodes suggests that responses to climate change may differ substantially from those of the indirectly transmitted protostrongylids and upper temperature thresholds may become important (Kutz et al., 2009b; Hoar et al., 2012b).

An additional consideration is that directional climate change results in cumulative or incremental processes over a range of time periods (years to decades) and on regional scales. These processes may interact with extreme or idiosyncratic (short-term) climatic events, which can influence the emergence of pathogens and disease across landscapes (Hoberg et al., 2008a). Further modelling of these systems, integrating climate-related impacts on free-living parasite stages, together with life-history parameters of parasites and hosts, is essential for better understanding potential similarities and differences in the response of these systems to a shifting climate.

2.8.6.2. Parasite ecology

Limiting our understanding of the ecology of parasites in Arctic ungulates is our incomplete understanding of many of their lifecycles. In some cases, transmission pathways remain completely unknown and we currently draw on what is known for related species to infer possible transmission routes. For example, *Besnoitia* may have two divergent transmission routes – through arthropod vectors or through carnivore definitive hosts – and the response of the host–parasite system to a changing landscape will differ depending on the transmission route. For other parasites, the basic transmission cycle may be known; however, the specific development and survival parameters, thermal tolerances, thresholds and tipping points, and alternate, intermediate, and paratenic hosts and vectors are undescribed. Clearly, knowledge of the transmission route(s), biotic and abiotic factors influencing the success of these routes and relative contribution of different pathways when they exist is necessary to understand the drivers of disease and anticipate pathogen impacts under a changing landscape and different climate scenarios.

2.8.6.3. Impacts

The consequences of parasite infections and the emergence of parasitic diseases for the sustainability of arctic ungulates are still not well understood.

As we look further and in more depth, however, there is increasing evidence to suggest that these changes may be detrimental to individuals and host populations (Jenkins et al., 2005b; Irvine, 2006; Laaksonen et al., 2010a). The studies that have provided the most robust information on impacts on individuals have been those that are longitudinal experimental studies where parasites have either been removed (i.e. Svalbard reindeer) or animals have been experimentally exposed (e.g. *P. odocoilei*). Coupling these studies with modelling of host population dynamics (e.g. Svalbard) has provided an insight into potential impacts at the population level.

While experimental manipulations are extremely useful for exploring impacts of parasites on individuals and populations, the frequently complex logistics and finances have limited the number of such studies on free-living populations. Also, the components of host–parasite relationships generating disease are often complex and intricately linked. It is important to recognize that sometimes the parasites' adverse effects on hosts are not obvious and frequently can be very difficult to detect and quantify. Also, most ungulates are infected with multiple genera and species, and synergies among these might be important in generating disease.

In fact, most data on host–parasite systems in arctic ungulates comes from cross-sectional post-mortem examinations. Despite inherent constraints, such studies can be particularly valuable when they are large, standardized, and repeated on a regular interval to monitor changes over time and over geographically disparate regions (e.g. Nielsen and Neiland, 1974; Simmons et al., 2001; Kutz et al., 2012). Data from these studies can provide robust measures of parasite diversity trends, associations with other biotic and abiotic conditions and host factors (e.g. population size, trajectory, demographics, sympatric species). They can also help to identify associations between parasite diversity and abundance and indicators of host health, age, sex, pregnancy and other physiological parameters. While it is difficult to irrefutably determine cause and effect, such studies can lead to important insights and can be used to recognize new ecological processes and generate new hypotheses.

2.8.6.4. Monitoring programs

Key to successful, monitoring programs are standardized protocols, efficient field techniques, reliable laboratory assays, user-friendly centralized and comprehensive databases that have adequate and long-term IT support, and physical archives of whole specimens and specimen DNA (e.g. Hoberg et al., 2008a). Additionally, it is crucial that any data released be sufficient to allow meaningful comparisons within and between studies, for example, date of sampling (to allow for possible seasonal effects), host age or age class (to allow for age effects), and sample history (to allow for storage effects such as freezing). For arctic ungulates, the CircumArctic

Rangifer Monitoring and Assessment network (CARMA) developed such protocols for *Rangifer* sampling during International Polar Year (Kutz et al., 2012). Different levels of field sampling protocols with an increasing degree of complexity were designed depending on the expertise of the collector (from lay person through to experienced wildlife disease experts) and protocols were made publically available on a website. Techniques for sampling were refined to facilitate scientifically robust and comprehensive sampling. For example, Nobuto filter paper strips were validated for infectious disease serology and then implemented in the field, thus removing the need for whole-blood collection and serum separation under field conditions (Curry 2010; Curry et al., 2011). Application of these protocols during defined time period across circumpolar *Rangifer* herds has led to a much deeper insight into the parasite biodiversity in the Holarctic and has provided a relatively comprehensive baseline (S. Kutz, J. Ducrocq and CARMA, 2011, unpubl. obs.). Perhaps limiting the potential future value of these collections is the absence of a single centralized database that can manage the data long term, limited capacity of some museums for archiving specimens and no central repository for archiving of parasite DNA. The most appropriate collections will involve a large number of specimens subsampled for both definitive morphospecies identification and molecular characterization tied to informatics resources for phylogeny, ecology and biogeography (Hoberg et al., 2003).

2.8.7. Conclusions

In this review, we have highlighted the current state of knowledge of the contemporary parasite fauna infecting arctic ungulates of North America and Greenland. Contemporary systems do not exist in an historical vacuum and understanding the structure of these systems in ecological time has been, and continues to be, guided by a robust historical foundation. Parasites are key components of arctic ecosystems, bridging trophic levels and influencing the health and dynamics of wildlife populations. Although much has been learned, many knowledge gaps remain, related particularly to parasite faunal structure, the dynamics of the complex interactions within and among parasite and host communities (including invasive fauna) and the population-level impacts on free-ranging ungulates.

Of equal importance, however, is the very real fact that ungulates play a key role in the lives of northern aboriginal peoples and changing host–parasite dynamics across the North may negatively impact northern residents. Parasite-mediated population declines could limit availability of arctic ungulates for subsistence or commercial use. Parasitism in individual animals may be a food safety concern (e.g. *Toxoplasma*), decrease the quality of the hides (e.g. warbles) and the meat (e.g. decrease body condition and reduce amount of highly valued fat), and may make meat aesthetically unpleasing (e.g. animals with high intensities of *Taenia* cysts are often discarded) (Kutz et al., 2009b). In a land where the individual hunter must serve as his/her own meat inspector, emergence of new disease syndromes can w significant concerns and uncertainties, resulting in the loss of confidence in country foods, the loss of cultural traditions, and a reduction in community health.

Arctic ecosystems are undergoing significant perturbations, many of which have the potential to affect ungulates and other wildlife. Critical among these is climate warming, which is more marked in the Arctic than in many other areas of the world. The possible consequences of this warming for the health and sustainability of the region's wildlife and people are difficult to detect, measure and predict. We can take a lesson from the past across the Arctic, a region strongly influenced by episodic shifts in climate and where host–parasite systems have diversified under cycles of dynamic and rapid change. Invasions, accompanied by geographic and host colonization have shaped the structure of diversity that we have documented. We anticipate that such processes will continue to have a substantial influence on high latitude systems. Further, it is possible that some effects of new climate regimes might be mediated through parasites, for many of which host and geographic distributions, transmission, abundance and health impacts depend on local and regional environmental conditions.

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