ARCTIC
VOL. 65, SUPPL. 1 (2012) P. 59–79

Diet and Habitat of Mountain Woodland Caribou Inferred from Dung Preserved in 5000-year-old Alpine Ice in the Selwyn Mountains, Northwest Territories, Canada

JENNIFER M. GALLOWAY,[1] JAN ADAMCZEWSKI,[2] DANNA M. SCHOCK,[3] THOMAS D. ANDREWS,[4] GLEN MacKAY,[4] VANDY E. BOWYER,[5] THOMAS MEULENDYK,[6] BRIAN J. MOORMAN[6] and SUSAN J. KUTZ[3]

(*Received 22 February 2011; accepted in revised form 2 May 2011*)

ABSTRACT. Alpine ice patches are unique repositories of cryogenically preserved archaeological artefacts and biological specimens. Recent melting of ice in the Selwyn Mountains, Northwest Territories, Canada, has exposed layers of dung accumulated during seasonal use of ice patches by mountain woodland caribou of the ancestral Redstone population over the past ca. 5250 years. Although attempts to isolate the DNA of known caribou parasites were unsuccessful, the dung has yielded numerous well-preserved and diverse plant remains and palynomorphs. Plant remains preserved in dung suggest that the ancestral Redstone caribou population foraged on a variety of lichens (30%), bryophytes and lycopods (26.7%), shrubs (21.6%), grasses (10.5%), sedges (7.8%), and forbs (3.4%) during summer use of alpine ice. Dung palynomorph assemblages depict a mosaic of plant communities growing in the caribou's summer habitat, including downslope boreal components and upslope floristically diverse herbaceous communities. Pollen and spore content of dung is only broadly similar to late Holocene assemblages preserved in lake sediments and peat in the study region, and differences are likely due to the influence of local vegetation and animal forage behaviour. The 5000-year legacy of summer use of alpine ice patches by mountain woodland caribou suggests that these small, long-lived features may be important for the health of caribou populations in the Selwyn/Mackenzie Mountain range.

Key words: paleoecology, Late Holocene, ice patches, mountain woodland caribou, food habits, dung, copropalynology, Selwyn Mountains

RÉSUMÉ. Les névés des régions alpines constituent des réserves uniques d'artefacts archéologiques et de spécimens biologiques préservés cryogéniquement. La fonte récente des glaces de la chaîne de Selwyn, dans les Territoires du Nord-Ouest, au Canada, a mis au jour des couches de déjections animales qui ont été accumulées lors de l'usage saisonnier des névés par le caribou des bois des montagnes de la population ancestrale de Redstone au cours des quelques 5 250 dernières années. Bien que les tentatives visant à isoler l'ADN des parasites connus du caribou aient échoué, les déjections ont permis de repérer de nombreux restes et palynomorphes de végétaux bien préservés et variés. Les restes de végétaux qui ont été conservés dans les déjections animales laissent croire que la population de caribou ancestrale de Redstone s'alimentait d'une variété de lichens (30 %), de bryophytes et de lycopodes (26,7 %), d'arbrisseaux (21,6 %), de graminées (10,5 %), de foin plat (7,8 %) et de plantes herbacées non graminoïdes (3,4 %) lorsqu'ils utilisaient la glace alpine pendant l'été. Les assemblages de palynomorphes provenant des déjections laissent entrevoir la croissance d'une mosaïque de peuplements végétaux au sein de l'habitat d'été du caribou, ce qui comprend des composantes boréales en pentes descendantes et des peuplements végétaux herbacés floristiquement variés en pentes ascendantes. La teneur en pollen et en spores des déjections animales est seulement largement similaire aux assemblages de l'Holocène tardif préservés dans les sédiments lacustres et dans la tourbe de la région visée par l'étude. Les différences sont vraisemblablement attribuables à l'influence de la végétation locale et au comportement alimentaire des animaux. L'utilisation estivale des névés des régions alpines par le caribou des bois des montagnes ces 5 000 dernières années laisse entrevoir que ces petites caractéristiques longévives pourraient revêtir de l'importance pour la santé des populations de caribou de la chaîne de Selwyn et des monts Mackenzie.

Mots clés : paléoécologie, Holocène tardif, névés, caribou des bois des montagnes, habitude alimentaire, déjection animale, copro-palynologie, chaîne de Selwyn

Traduit pour la revue *Arctic* par Nicole Giguère.

[1] Corresponding author: Golder Associates Ltd., 48th Street, Yellowknife, Northwest Territories X1A 3S3, Canada; present address: Geological Survey of Canada, Natural Resources Canada, 3303 33rd Street NW, Calgary, Alberta T2L 2A1, Canada; Jennifer.Galloway@NRCan.gc.ca
[2] Environment and Natural Resources, GNWT, Box 1320, Yellowknife, Northwest Territories X1A 2L9, Canada
[3] Faculty of Veterinary Medicine, University of Calgary, 3330 Hospital Drive NW, Calgary, Alberta T2N 1N4, Canada
[4] Prince of Wales Northern Heritage Centre, PO Box 1320, Yellowknife, Northwest Territories X1A 2L9, Canada
[5] Department of Anthropology, University of Alberta, Edmonton, Alberta T6G 2H4, Canada
[6] Department of Geography, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4, Canada

INTRODUCTION

Ice patches are areas of permanent ice that form in northern and alpine regions when the net accumulation of snow is compressed into ice lenses that do not gain enough mass to flow (Farnell et al., 2004). Mountain woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788) in the Northwest Territories (NWT) and Yukon Territory (YT), Canada, are recognized as northern mountain woodland caribou (Environment Canada, 2011). These caribou seek out ice patches for relief from summer heat and insect harassment (Ion and Kershaw, 1989). Their feces are deposited on ice patches in summer and buried subsequently by snow, forming stratigraphically discrete bands of biological remains that include bones, pollen, plant macrofossils, and animal parasites (Farnell et al., 2004). Mitochondrial DNA sequencing of bones contained in dung layers demonstrates that ancestors of the modern Redstone population of mountain woodland caribou in the Selwyn Mountains frequented ice patches throughout the late Holocene and are the most likely source of the caribou dung deposits (Letts et al., 2012).

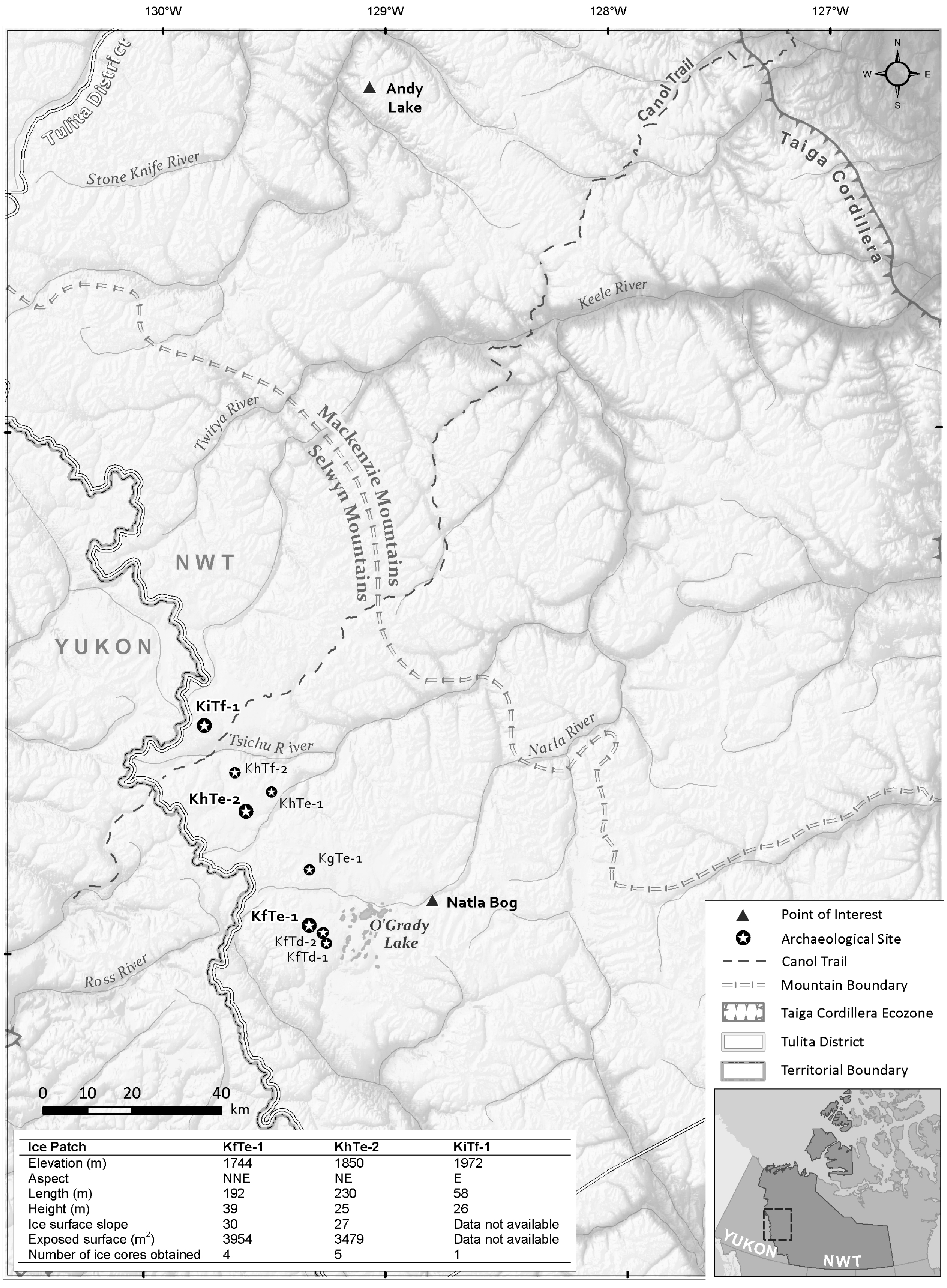
Ancient biological remains yield important information on paleoenvironment and past animal diet (Farnell et al., 2004). DNA of gastro-intestinal parasites (e.g., nematodes of the family Trichostrongylidae) may also be contained in alpine ice and provide information on host body condition and fecundity in domestic and wild ruminants, including caribou (Coyne and Smith, 1994; Albon et al., 2002; Stien et al., 2002; Hughes et al., 2009). Pollen and spores are well represented in caribou dung from ice patches (Farnell et al., 2004) and biogenic deposits recovered from other biological and paleontological contexts (Thompson et al., 1980; Mead et al., 1987; van der Knapp, 1989; Scott and Cooremans, 1992; Akeret et al., 1999; Carrión et al., 2001, 2005, 2007; Scott et al., 2003; Bjune et al., 2005; Kropf et al., 2007; Scott and Woodborne, 2007). Pollen spectra of herbivore feces likely represent a composite of pollen rain deposited onto food items or exposed dung (or both) and palynomorphs sourced directly from ingested food items (Moe, 1983; Mead et al., 1987; Scott and Cooremans, 1992; Gardener et al., 1993; Rasmussen, 1993; Carrión, 2002; Kropf et al., 2007). Biases introduced to fecal pollen spectra through dietary behaviour are unlikely to preclude paleoenvironmental reconstruction because the animal likely foraged on plants within its range. In fact, copropalynology can provide insight on the distribution and ecology of insect-pollinated plants that are commonly under-represented by pollen in sediments deposited by water (Carrión et al., 2001). Indigestible plant fragments, such as epidermal structures, can be identified with greater taxonomic precision than pollen. Microhistological identification of plant fragments preserved in feces is a generally reliable method for reconstructing the diet and habitat requirements of caribou and other large herbivores (Sparks and Malechek, 1968; Todd and Hansen, 1973; Boertje, 1984; Gardener et al., 1993; Fischer and Gates, 2005).

Through examination of palynomorphs and plant fragments, this study assessed the potential of caribou dung preserved in alpine ice patches in the Selwyn Mountains, NWT, to provide a paleoecological context that will improve our understanding of long-term trends in caribou habitat use and foraging habits.

ENVIRONMENTAL SETTING

Twenty-eight alpine ice patches were identified in the Selwyn Mountain complex, a northern part of the North American Cordillera, during aerial surveys conducted between 2005 and 2010 at the time of maximum melt (mid to late August; Andrews et al., 2012). Ice patches occur between 1675 m and 1972 m above sea level and are confined to northwest-, north, or northeast-facing slopes. Ice patches range in size from less than 25 m to over 500 m in length, from 5 m to over 50 m wide, and from less than 1 m to more than 6 m thick. Ice patches all occur above treeline within the Taiga Cordillera Ecozone (TCE; Wiken, 1986; Fig. 1), which spans a diverse area of mountain ranges, rolling hills, high plateaus, depressions, and incised valleys in the northern Rocky Mountain system that covers portions of the YT and southwestern NWT. The climate of the TCE is dry and cold. Average annual precipitation is 300 mm, mean daily January temperatures range from -25˚C to -30˚C across the ecozone, and mean daily July temperatures range from 12˚C to 15˚C (Wiken, 1986).

Vegetation in the study area consists of boreal forest in low-elevation areas such as valley bottoms and depressions and alpine tundra at high altitudes. Alpine tundra in the Selwyn Mountains comprises several communities (Kershaw, 1984; Ion and Kershaw, 1989). Crustose lichen communities occur at highest elevations (> 1900 m), where mineral substrates are exposed. Below this zone, fruticose lichen tundra dominated by *Cladonia stellaris* (Opiz.) Pouz. and Vezda (star reindeer lichen) and *Alectoria ochroleuca* (Hoffm.) A. massal (witch's hair lichen) occurs on well-drained alluvium and colluvium. Cushion plant tundra occurs where winter snow cover is thin and discontinuous; it is dominated by *Dryas integrifolia* Vahl. (mountain avens) with scattered *Silene acaulis* (L.) Jacq. (moss campion), *Saxifraga oppositifolia* L. (purple mountain saxifrage), and *Polygonum viviparum* L. (alpine bistort) and various mosses (e.g., *Hylocomium splendens*). Lichen-grass communities exist on gentle slopes and are dominated by graminoids such as *Deschampsia caespitosa* (L.) P. Beauv. (tussock grass), *Festuca altaica* Trin. (northern rough fescue), *Poa arctica* R. Br. (arctic bluegrass), and *Carex atrofusca* Schk. (darkbrown sedge). *Artemisia arctica* Less. (boreal sagebrush) and *Salix arctica* Pall. (arctic willow) are also present. Lichen-heath tundra occurs at lower elevations on north-facing slopes, where moisture from persistent snow pack is available. This community is dominated by *Dryas integrifolia* and *Cassiope tetragona* (L.) D. Don (white arctic mountain heather) and ericaceous shrubs, including *Vaccinium uliginosum* L. (bog blueberry). Sedge meadow tundra communities are dominated by *Carex podocarpa*



Ice Patch	KfTe-1	KhTe-2	KiTf-1
Elevation (m)	1744	1850	1972
Aspect	NNE	NE	E
Length (m)	192	230	58
Height (m)	39	25	26
Ice surface slope	30	27	Data not available
Exposed surface (m^2)	3954	3479	Data not available
Number of ice cores obtained	4	5	1

FIG. 1. Map showing the location of the study area (inset) and ice patches (✪) in the Selwyn Mountains, Northwest Territories. The three ice patches sampled (KfTe-1, KhTe-2, and KiTf-1, shown with larger stars and bold type) are described in the table at lower left. The Taiga Cordillera Ecozone and other sites mentioned in the text are also shown.

R. Br. (short stock sedge), *Artemisia arctica*, *Polemonium acutiflorum* Willd. Ex Roemer & J.A. Schultes (tall Jacob's-ladder), and various lichens (e.g., *Cladonia arbuscula* (Wallr.) Flotow [reindeer lichen], *Dactylina arctica* (Hook. f.) Nyl. [finger lichen]) occur on flat, poorly drained sites. Shrub tundra communities occur below 1600 m and are dominated by *Betula glandulosa* Michx. (dwarf birch) and *Cladonia stellaris*. On poorly drained sites, willow-forb-moss communities with *Salix barrattiana* Hook. (Barratt's willow) exist. Scattered *Abies* Mill. (fir) grows with an understory of willow and birch at the transition to subalpine. *Picea glauca* Moench (white spruce) and *P. mariana* (P. Mill.) B.S.P. (black spruce) occur farther downslope. In montane regions, spruce-lichen woodlands occur with *Pinus contorta* Dougl. ex Loud. (lodgepole pine). Isolated stands of *Populus tremuloides* Michx. (trembling aspen), *Populus balsamifera* L. (balsam poplar), *Alnus* L. (alder) species, and *Betula papyrifera* (Marsh.) (paper birch) can grow on sheltered lowlands or disturbed sites in the TCE.

Northern mountain woodland caribou are listed as a population of special concern (COSEWIC, 2002) because habitat fragmentation and climate change are adversely affecting populations in northwestern Canada (McLoughlin et al., 2003). The northern mountain woodland caribou ecotype is distinguished from other woodland caribou (e.g., the southern or boreal woodland caribou) by its behaviour and habitat use: northern mountain woodland caribou form discrete groups or herds that range in size from about 200 up to 10 000 individuals in the NWT, YT, and northern British Columbia, where they winter in forested valleys and migrate to alpine mountain habitat during summer months (Olsen et al., 2001; Environment Canada, 2011). The northern mountain woodland caribou in the study region are likely part of the Redstone population, which has been estimated at 5000 to 10 000 animals and is one of the largest woodland groups in Canada (Olsen et al., 2001). Redstone caribou spend winter months in lowland forested habitats in river valleys in the front ranges of the Mackenzie Mountains, which include areas along the Keele, Moose, Horn, and Redstone River basins, where the primary food of caribou is ground lichens. During summer, Redstone caribou migrate to alpine habitat and occupy a range along the border with the YT near Macmillan Pass on the eastern slopes of the Mackenzie Mountains, where their diet may be similar to that of other mountain woodland caribou in northwestern Canada, consisting of a variety of shrubs, forbs, sedges, grasses, lichens, and mosses (Weaver, 2008). Observations at Macmillan Pass in the Selwyn and Mackenzie Mountains indicate that on warm and still days, caribou migrate upslope (> 1600–1700 m) in late morning, seeking cool and windy microclimates of ridge tops and snow and ice patches to avoid insect harassment; they spend much of the afternoon there and descend to elevations below 1600 – 1700 m in late afternoon or evening (Ion and Kershaw, 1989; Quayle and Kershaw 1996). During peak insect season in the early summer, as many as 216 animals have been observed to gather on ice patches and snowdrifts in the study area. By mid August, snow and ice availability decreases, but most insects disappear because of sub-zero night temperatures, and caribou groups rarely exceed 45 animals (Ion and Kershaw, 1989).

METHODS

Field Methods

In 2007 and 2008, 10 ice cores were extracted from three ice patches in the Selwyn Mountains with a Cold Regions Research and Engineering Laboratory coring auger (7.5 cm barrel diameter; Figs. 1, 2). Cores from these ice patches (KfTe-1, KhTe-2, and KiTf-1) were selected for detailed study because they were associated with archaeological remains (Andrews et al., 2012), had a significant amount of ice for geophysical studies, and provided enough biological material for paleoecological analysis (Fig. 2). A sample of modern caribou dung was collected adjacent to ice patch KfTe-1 for comparison to ancient material preserved in alpine ice.

Chronology

Accelerator mass spectrometry (AMS) radiocarbon dates on 72 samples of bone, antler, wood, and bulk caribou dung recovered from multiple cores from multiple ice patches, determined at Beta Analytic Inc., Florida, constrain the chronology of ice patch accumulation in the Selwyn Mountains (Meulendyk et al., 2012). Radiocarbon dates were calibrated to calendar years before present (cal. yr BP) using the computer program CALIB Rev 6.0 (Stuiver et al., 2005) and the IntCal09 dataset (Reimer et al., 2009).

Caribou Parasite DNA

Twelve subsamples (4 g to 8 g) of caribou dung were collected from ice cores from ice patches KfTe-1 and KhTe-2 and the sample of modern feces and stored in molecular grade ethanol in preparation for screening for the presence of Trichostrongylid parasite DNA (Fig. 2). Extraction followed the Gentra PureGene protocol for tissue extractions (Qiagen, Canada). Polymerase Chain Reactions (PCRs) were run using established primers that amplify a diagnostic segment of mammalian mitochondrial DNA to test for the presence of useable DNA in the extracted samples (Cronin et al., 1999). Primers described in Hoste et al. (1995) were used to amplify a diagnostic segment of the internal transcribed spacer region of the genome of nematodes. The positive-control PCR template for mammalian DNA was from a fecal sample from a white-tailed deer (*Odocoileus virginianus*) from southern Alberta extracted using the Gentra PureGene protocol. The positive-control PCR template for Trichostrongylid DNA originated from worms from captive reindeer at the University of Calgary and was also extracted using the Gentra PureGene protocol.

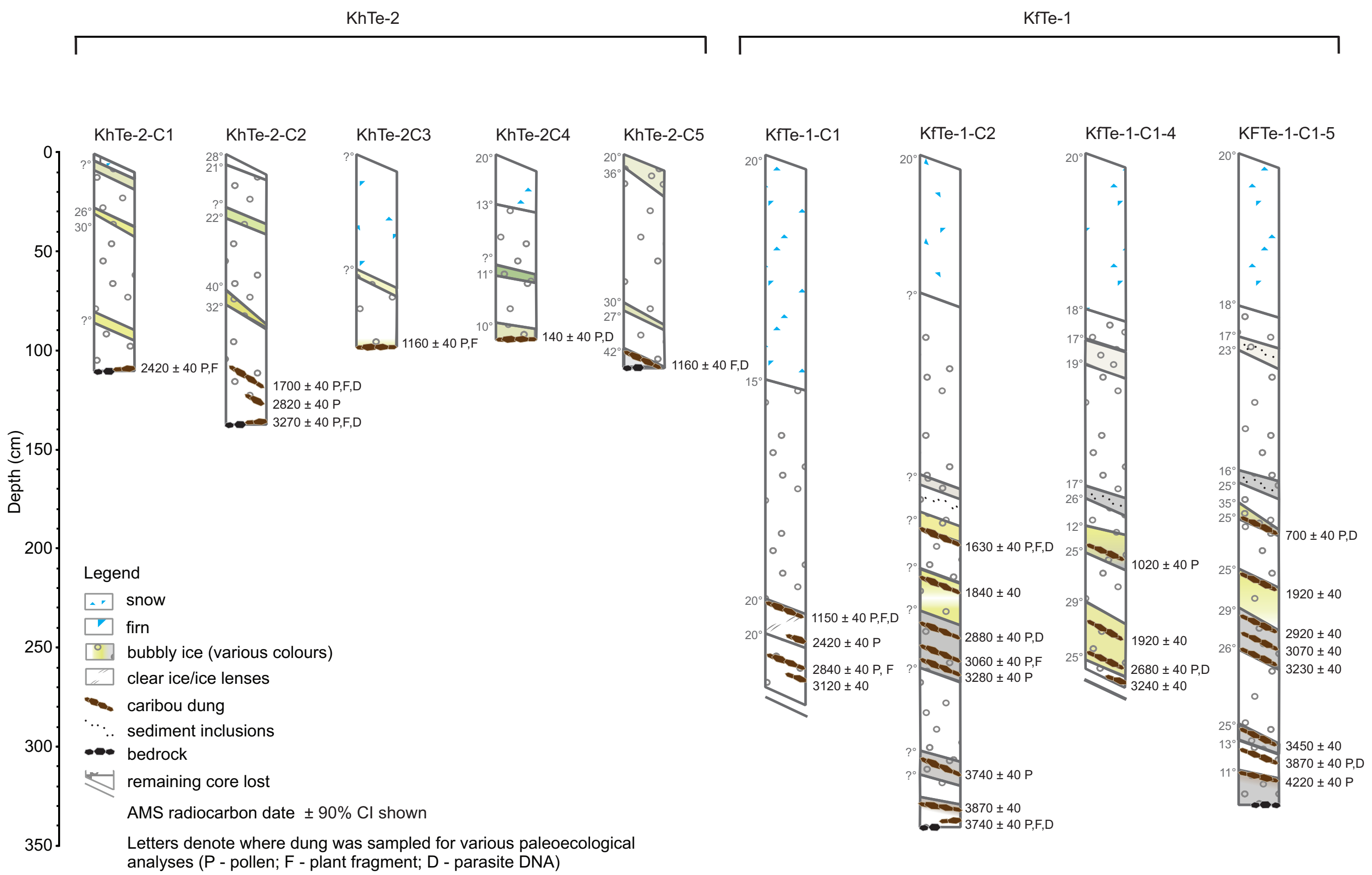


FIG. 2. Stratigraphy of ice cores sampled for paleoecological proxies. Dip is shown to the left of each ice core diagram, and radiocarbon dates to the right. Chronology is from Table 1. Ice core stratigraphy was not compiled for core KiTf-1, where three caribou dung horizons were sampled for pollen. The surface sample of caribou dung collected adjacent to ice patch KfTe-1 is not shown.

Samples that produced appropriately sized bands were prepared for sequencing using ExoSAP-IT® (USB) according to manufacturer's specifications and subjected to sequencing in both directions on an ABI 3730xl DNA sequencer.

Palynology

Twenty-three subsamples (50 mm^3) of caribou dung were obtained from ice cores recovered from ice patches KfTe-1, KhTe-2, and KiTf-1 for palynological analyses (Fig. 2). Two pellets of the modern dung sample were also processed. Processing for palynological analysis followed standard procedures except that hydrofluoric acid treatment and sieving were not performed (Fægri and Iversen, 1989). To calculate pollen concentration, we added a known quantity of polystyrene microspheres to each sample (1 mL per sample; LacCore pollen spike suspension Batch No. 3; concentration 5×10^4 spheres/mL ± 7%; Stockmarr, 1971). Palynomorphs were identified and enumerated using light microscopy. Identification was aided by the keys of McAndrews et al. (1973) and Kapp et al. (2000). Cupressaceae pollen was not identified to the genus level; however, judging by modern plant distributions in northwestern Canada, this pollen type is likely attributable to *Juniperus* L. (Rowe, 1972). Small (~8 µm), psilate spores with a sigmoid germination pore that occur as solitary cells or in chains were identified as *Sporormiella* Ellis & Everh. (Kapp et al., 2000; Aptroot and van Geel, 2006). *Sporormiella* is a coprophilous ascomycete fungus that is widely distributed but has a preference for boreal regions (Aptroot and van Geel, 2006). Pollen counts were converted to relative abundance using a main pollen sum that included all pollen and spores of terrestrial vascular and non-vascular plants. Data were explored using Q-mode cluster analysis (Ward minimum variance linkage and Euclidean distance). To determine whether pollen and spore spectra vary between ice cores and ice patches, we arranged samples spatially by ice core and ice patch. To examine spectra changes over time, we developed a composite chrono-paleoecological diagram using samples from multiple ice cores from three ice patches. Pollen diagrams were generated using Tilia and TiliaGraph (Grimm, 1993).

Plant Remains

Ten subsamples (2.38 g to 9.58 g) of caribou dung were obtained from cores from ice patches KfTe-1 and KhTe-2 (Fig. 2). Samples were submitted to Washington State University's Wildlife Habitat and Nutrition Lab in Pullman, Washington, for microhistological identification (Putman, 1984). Plant fragments were identified to the lowest taxonomical level possible during 200 slide views per sample. No adjustments were made for different digestibility of plant species, and results are presented as relative abundances of the total number of identifications. Q-mode cluster analysis using a Ward minimum variance linkage method and Euclidean distance was used to explore relationships between samples. To determine whether plant fragment composition of dung samples varies between ice cores or ice patches, we plotted data spatially. A composite chrono-paleoecological diagram was developed using samples from multiple ice cores from two ice patches and arranged in chronologic order to observe if any trends in plant fragment composition occur over time. Diagrams were generated using Tilia and TiliaGraph (Grimm, 1993).

RESULTS

Chronology

The ice patch chronology is constrained by 72 calibrated AMS radiocarbon ages (Table 1), 34 obtained from bulk caribou dung taken from the three sampled ice patches (KfTe-1, KhTe-2, and KiTf-1) and 38 obtained from other types of biological material (including bone, antler, and wood associated with archaeological remains) recovered from all ice patches. Radiocarbon dating shows that ice patch formation began in the Selwyn Mountains by at least 4580 ± 40 ^{14}C yr BP (ca. 5250 ± 200 cal. yr BP) and corresponds to a period of regional cooling in northwestern Canada and resumed ice patch growth in the YT (MacDonald, 1983; Ritchie, 1984; Ritchie et al., 1987; Farnell et al., 2004). The radiocarbon dates also demonstrate that the ice patches in the NWT have been used almost continuously by caribou and humans since their formation in the mid-Holocene.

Layers of caribou dung preserved in alpine ice could represent the feces of an individual or a few animals during a short period of time, or homogenized annual summer deposits of many animals that visited ice patches over the summer, or even "super-layers" that are amalgamations of multiple annual deposits formed during periods of melt or hiatuses in ice growth (Farnell et al., 2004; see Meulendyk et al., 2012, for details on ice accumulation).

Caribou Parasite DNA

DNA of known caribou parasites was not detected in any samples of caribou dung. Only mammalian DNA, confirmed by sequencing to be caribou DNA, was amplified from the modern caribou fecal sample. Positive and negative control samples performed as expected, including sequencing results from the positive control samples.

Palynology

All 24 caribou dung samples yielded pollen and spores, and most samples have good preservation of palynomorphs. An average of 82 ± 44 SD pollen and spores were enumerated per sample because of low palynomorph abundance in some samples. Total concentrations of pollen and spores in caribou dung samples range from 18 635 to 192 008 grains per gram. Concentrations are similar to those reported for lake sediments in the western NT (Slater, 1985) and comparable to the recovery of pollen and spores from the dung of other animals (Scott and Woodborne, 2006; Yll et al., 2006). Twenty-three plant taxa from 27 families were identified, and as in previous copropalynological studies, a remarkable diversity of pollen from herbaceous plants was observed (Carrión et al., 2001; Table 2; Fig. 3A, B). Forbs are the most abundant plant group in all caribou dung samples (mean 34.1% ± 16.3 SD) and are dominated by *Artemisia* L. pollen (mean 22.9% ± 14.3). Pollen from coniferous plants is abundant (mean 29.2% ± 14.1) and dominated by *Picea* A. Dietr. (mean 17.6% ± 11.5 SD). Shrubs are the next most abundant group (mean 9.7% ± 8.5) and include *Betula* L. (mean 3.5% ± 3.7 SD), *Salix* L. (mean 2.0% ± 2.9 SD), and *Alnus* (mean 1% ± 1.3 SD) pollen. Pteridophyte spores, Poaceae and sedge pollen, and bryophyte and moss spores are also present. In general, pollen from anemophilous plants (e.g., *Picea*, *Artemisia*) is well represented in dung samples, while pollen from entomophilous plants (e.g., *Polemonium* L.) is less common. Pollen spectra of dung samples have a great deal of variability, particularly in the relative abundance of *Artemisia* pollen, but samples do not cluster by ice patch or radiocarbon age (Fig. 4), and sustained trends over time in the relative abundance of individual pollen or plant types (conifers, deciduous shrubs, forbs, grasses, ferns, bryophytes and lycopods, and other) are not observed (Fig. 3B).

Plant Remains

Plant fragments of 40 taxa representing 23 families are present in dung samples (Tables 3 and 4; Fig. 5). Forbs are the most diverse group (12 taxa), followed by shrubs (eight taxa). Also identified were seven members of Poaceae, six bryophyte/lycopod taxa, four Cyperaceae taxa, and six lichen taxa from five families. Lichens are the most abundant type of plant fragment identified in dung samples (mean 30% ± 8.9 SD), followed by bryophyte/lycopods (mean 26.7% ± 5.1 SD) and shrubs (21.6% ± 6.4 SD). Lichens reach a maximum relative abundance of 45.8% in sample KfTe-1 Core 2 bottom and are dominated by *Cladina* (Nyl.) Nyl., *Cladonia* P. Browne, or both (up to 26.8% of total plant fragments). Bryophytes are dominated by *Dicranum*-type (up to 20.1% of total plant fragments in sample KhTe-2 Core 3 bottom). Shrub fragments are dominated by *Salix* stems (mean 7.4% ± 2.9 SD) and leaves (mean 4.3% ± 1.9 SD). Grasses also occur (mean 10.5% ± 4.5 SD) and are dominated by *Poa* L. (mean 4.8% ± 2.8 SD). Sedges (mean 7.8% ± 4.1 SD), dominated by *Carex* L. (mean 5.7% ± 2.4 SD), and forbs (mean 3.4% ± 1.9 SD), dominated by *Equisetum* L. (mean 1.2% ± 0 SD) and *Saxifraga* L. (mean 1% ± 0.6 SD), are also important. As with the palynological

TABLE 1. Accelerator mass spectrometry radiocarbon ages on material recovered from ice patches in the Selwyn Mountains, Northwest Territories.

Site and sample no.	Stratigraphic horizon (cm)	Lab No.	Item	Material	Conventional age (^{14}C yr BP ± 90% CI)	^{13}C/^{12}C ratio (‰)	Calibrated age (2σ range)[1]	Median calibrated age cal. yr BP ± 95% CI)[2]	^{15}N/^{14}N ratio (‰)
KhTe-1-14	–	Beta-216915	shed antler	collagen[3]	133.2 ± 0.9 pMC	-18.7			2.5
KhTe-1-6	–	Beta-216914	long bone	collagen	930 ± 40	-17.8	744–927	840 ± 90	1.5
KhTe-1-Z2	–	Beta-241809	rib	collagen	3270 ± 40	-17.3	3395–3606	3500 ± 110	–
KhTe-1-15	–	Beta-216916	self bow	*Salix*	340 ± 50	-23.8	306–497	400 ± 100	–
KhTe-2-Z3	–	Beta-241810	atlas	collagen	1090 ± 40	-17.1	928–1070	1000 ± 70	–
KhTe-2-Z4	–	Beta-241811	axis	collagen	1140 ± 40	-17.1	963–1171	1070 ± 100	–
KhTe-2-Z5	–	Beta-241812	left mandible	collagen	800 ± 40	-16.6	672–783	730 ± 60	–
KhTe-2-Z6	–	Beta-241813	1st phalanx	collagen	880 ± 40	-17.6	699–915	810 ± 110	–
KhTe-2-Z14	–	Beta-255287	left rib	collagen	990 ± 40	-17.9	795–964	880 ± 80	2
KhTe-2-Z12	–	Beta-255286	left ulna-radius	collagen	108.1 ± 0.4 pMC	-20			2.8
KhTe-2-C1-1	base	Beta-240112	caribou dung	dung	2420 ± 40	-24.2	2348–2700	2520 ± 180	-–
KhTe-2-C2-1	107–110	Beta-240113	caribou dung	dung	1700 ± 40	-25.1	1531–1703	1620 ± 90	–
KhTe-2-C2-2	120–124	Beta-240114	caribou dung	dung	2820 ± 40	-25.4	2803–3064	2930 ± 130	–
KhTe-2-C2-3	136–142	Beta-240115	caribou dung	dung	3270 ± 40	-25.3	3395–3606	3500 ± 110	–
KhTe-2-C3-1	bottom	Beta-240116	caribou dung	dung	1160 ± 40	-25.3	971–1175	1070 ± 100	–
KhTe-2-C4-1	bottom	Beta-240117	caribou dung	dung	140 ± 40	-25.1	0–282	140 ± 140	–
KhTe-2-C5-1	bottom	Beta-240118	caribou dung	dung	1160 ± 40	-25.5	971–1175	1070 ± 100	–
KhTe-2-1	–	Beta-240097	arrow shaft	*Betula*	340 ± 40	-23.7	308–488	398 ± 90	–
KfTe-1-Z28	–	Beta-255284	lumbar vertebra	collagen	2530 ± 40	-17.7	2473–2747	2610 ± 140	2.7
KfTe-1-Z18	–	Beta-255283	thoracic vertebra	collagen	2490 ± 40	-18	2365–2729	2550 ± 180	1.9
KfTe-1-10	–	Beta-248993	snare	*Salix*	970 ± 40	-24.1	791–955	870 ± 80	–
KfTe-1-11	–	Beta-256287	arrow shaft	*Picea*	850 ± 40	-21.4	684–904	790 ± 110	–
KfTe-1-C1-1	224.5–228.5	Beta-240100	caribou dung	dung	1150 ± 40	-25	970–1172	1070 ± 100	–
KfTe-1-C1-2	242–244	Beta-240101	caribou dung	dung	2420 ± 40	-25.8	2348–2700	2520 ± 180	–
KfTe-1-C1-3	254–256	Beta-240102	caribou dung	dung	2840 ± 40	-24.6	2852–3074	2960 ± 110	–
KfTe-1-C1-4	262–264	Beta-240103	caribou dung	dung	3120 ± 40	-25.4	3246–3443	3340 ± 100	–
KfTe-1-C2-1	189–191	Beta-240104	caribou dung	dung	1630 ± 40	-26	1410–1682	1550 ± 140	–
KfTe-1-C2-2	213–214	Beta-240105	caribou dung	dung	1840 ± 40	-25.2	1638–1875	1760 ± 120	–
KfTe-1-C2-3	238–240	Beta-240106	caribou dung	dung	2880 ± 40	-24.6	2879–3157	3020 ± 140	–
KfTe-1-C2-4	248–250	Beta-240107	caribou dung	dung	3060 ± 40	-25.4	3162–3374	3270 ± 110	–
KfTe-1-C2-5	256–258	Beta-240108	caribou dung	dung	3280 ± 40	-25.1	3403–3613	3510 ± 110	–
KfTe-1-C2-6	309–316	Beta-240109	caribou dung	dung	3740 ± 40	-25.6	3979–4233	4110 ± 130	–
KfTe-1-C2-7	331–332	Beta-240110	caribou dung	dung	3870 ± 40	-24.4	4157–4416	4290 ± 130	–
KfTe-1-C2-8	bottom	Beta-240111	caribou dung	dung	3780 ± 40	-25	3990–4291	4140 ± 150	–
KfTe-1 Core1-4-161-162	161–162	Beta-255263	caribou dung	dung	1020 ± 40	-25	798–1052	930 ± 130	–
KfTe-1 Core1-4-203	203	Beta-255274	caribou dung	dung	1920 ± 40	-25.5	1736–1967	1850 ± 120	–
KfTe-1 Core1-4-218-223	218–223	Beta-255264	caribou dung	dung	2680 ± 40	-25.1	2745–2855	2800 ± 60	–
KfTe-1 Core1-4-231	231	Beta-255265	caribou dung	dung	3240 ± 40	-24.9	3382–3560	3470 ± 90	–
KfTe-1 Core1-5-118-125	118–125	Beta-255266	caribou dung	dung	700 ± 40	-25.2	559–721	640 ± 80	–
KfTe-1 Core1-5-156-161	156–161	Beta-255267	caribou dung	dung	1920 ± 40	-25.2	1736–1967	1850 ± 120	–
KfTe-1 Core1-5-180	180	Beta-255268	caribou dung	dung	2920 ± 40	-25.5	2955–3210	3090 ± 130	–
KfTe-1 Core1-5-189	189	Beta-255269	caribou dung	dung	3070 ± 40	-25.3	3166–3378	3270 ± 110	–
KfTe-1 Core1-5-199	199	Beta-255270	caribou dung	dung	3230 ± 40	-25.6	3377–3557	3470 ± 90	–
KfTe-1 Core1-5-247-249	247–249	Beta-255271	caribou dung	dung	3450 ± 40	-24.1	3616–3834	3730 ± 110	–
KfTe-1 Core1-5-258-266	258–266	Beta-255272	caribou dung	dung	3870 ± 40	-25.1	4157–4416	4290 ± 130	–
KfTe-1 Core1-5-273-278	273-278	Beta-255273	caribou dung	dung	4420 ± 40	-25.4	4867–5276	5070 ± 200	–

TABLE 1. Accelerator mass spectrometry radiocarbon ages on material recovered from ice patches in the Selwyn Mountains, Northwest Territories – *continued:*

Site and sample no.	Stratigraphic horizon (cm)	Lab No.	Item	Material	Conventional age (^{14}C yr BP ± 90% CI)	$^{13}C/^{12}C$ ratio (‰)	Calibrated age (2σ range)[1]	Median calibrated age cal. yr BP ± 95% CI)[2]	$^{15}N/^{14}N$ ratio (‰)
KfTd-1-2	–	Beta-241808	antler	collagen	1240 ± 40	-19.4	1068 – 1270	1170 ± 100	–
KfTd-1-Z3	–	Beta-255262	right mandible	collagen	330 ± 40	-17.4	305 – 484	390 ± 90	4.5
KfTd-2-01	–	Beta-256285	foreshaft	*Betula*	570 ± 40	-24.2	521 – 651	590 ± 70	–
KhTf-1-1	–	Beta-256286	Snowshoe	*Picea*	70 ± 40	-25.7	0 – 267	130 ± 130	–
KiTf-1-Z6	–	Beta-241815	lumbar vertebra	collagen	370 ± 40	-17.9	315 – 504	410 ± 90	–
KiTf-1-Z8	–	Beta-241816	shed antler	collagen	30 ± 40	-19.8	0 – 257	130 ± 130	–
KiTf-1-Z12	–	Beta-255288	right maxillary	collagen	1640 ± 40	-18.4	1413 – 1687	1550 ± 140	4.9
KiTf-1-Core1-167	167	Beta-255275	caribou dung	dung	1740 ± 40	-23.9	1541 – 1774	1660 ± 120	–
KiTf-1 Core1-218	218	Beta-255276	caribou dung	dung	3900 ± 40	-24.5	4160 – 4428	4290 ± 130	–
KiTf-1 Core1-245-249	245 – 249	Beta-255277	caribou dung	dung	4580 ± 40	-24.4	5053 – 5448	5250 ± 200	–
KiTf-1-1	–	Beta-240098	dart shaft	*Betula*	2410 ± 40	-22.7	2345 – 2699	2520 ± 180	–
KgTe-1-Z7	–	Beta-255285	right rib	collagen	400 ± 40	-19.1	318 – 518	420 ± 100	3.5
KgTe-1-3	–	Beta-240096	arrow shaft	*Betula*	270 ± 40	-23.5	0 – 464	230 ± 230	-
KhTf-2-5	–	Beta-241814	antler	collagen	1030 ± 40	-18.1	800 – 1055	930 ± 130	-
KhTf-2-1	–	Beta-240099	foreshaft	*Amelanchier* sp. cf. *A. alnifolia*	2310 ± 40	-24.2	2157 – 2452	2300 ± 150	-
KhTf-2-3	–	Beta-256356	shaft	*Betula*	2350 ± 40	-23	2211 – 2676	2440 ± 230	-
7T1-Z1	–	Beta-241801	scapula	collagen	2520 ± 40	-17.6	2466 – 2745	2610 ± 140	-
7T1-Z8	–	Beta-255278	right mandible	collagen	520 ± 40	-17.6	503 – 634	570 ± 70	4.4
7T2-Z6	–	Beta- 255279	left innominate	collagen	1830 ± 40	-18.5	1631 – 1871	1750 ± 120	3.1
7T9-Z1	–	Beta-241802	antler	collagen	3510 ± 40	-17.8	3650 – 3892	3770 ± 120	–
7T9-Z2	–	Beta-241803	left mandible	collagen	570 ± 40	-18.3	521 – 651	590 ± 70	–
7T10-Z2	–	Beta-241804	innominate	collagen	1050 ± 40	-18.1	916 – 1058	990 ± 70	–
7T10-Z3	–	Beta-241805	lumbar vertebra	collagen	1080 ± 40	-17.8	929 – 1061	1000 ± 70	–
7T10-Z17	–	Beta-241806	rib	collagen	710 ± 40	-17.2	562 – 726	640 ± 80	–
7T10-Z20	–	Beta-241807	thoracic vertebra	collagen	910 ± 40	-17.5	740 – 918	830 ± 90	–
8T1-Z3	–	Beta-255280	left humerus	collagen	3520 ± 40	-19.3	3692 – 3899	3800 ± 100	0.7
8T2-Z5	–	Beta-255281	thoracic vertebra	collagen	2550 ± 40	-18.2	2489 – 2754	2620 ± 130	2
8T3-Z1	–	Beta-255282	right calcaneous	collagen	2950 ± 40	-17.2	2975 – 3247	3110 ± 140	2.1

[1] Calibrated with CALIB 6.0 (Stuiver et al., 2005) and the IntCal09 dataset (Reimer et al., 2009).

[2] Rounded to the nearest 10 years.

[3] The bone collagen dates are all identified as *Rangifer*, except for the right rib from KgTe-1-Z7, which is identified to Order Artiodactyla, and the left humerus from 8T1-Z3, identified as *Alces alces*.

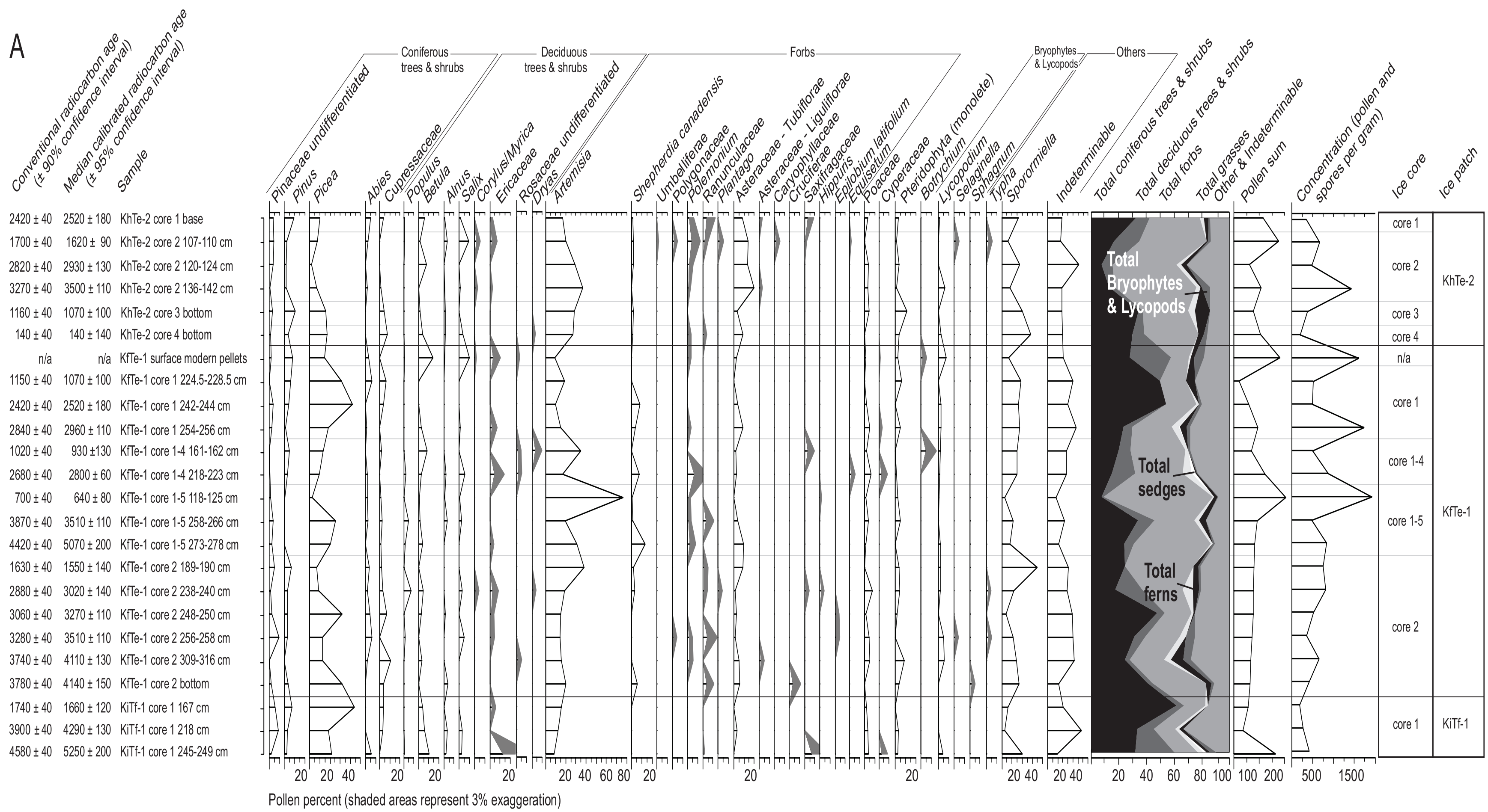


FIG. 3. Relative abundance of palynomorphs preserved in ice patch caribou dung in the Selwyn Mountains, Northwest Territories. Samples are arranged spatially by ice core and ice patch (A). A composite diagram including samples from all ice cores from all ice patches is arranged in chronological order (B). Area graph of plant types whose pollen is identified is also shown. Relative abundances are based on the main pollen sum, which excludes pollen from aquatic plants and fungal spores. Chronology is from Table 1.

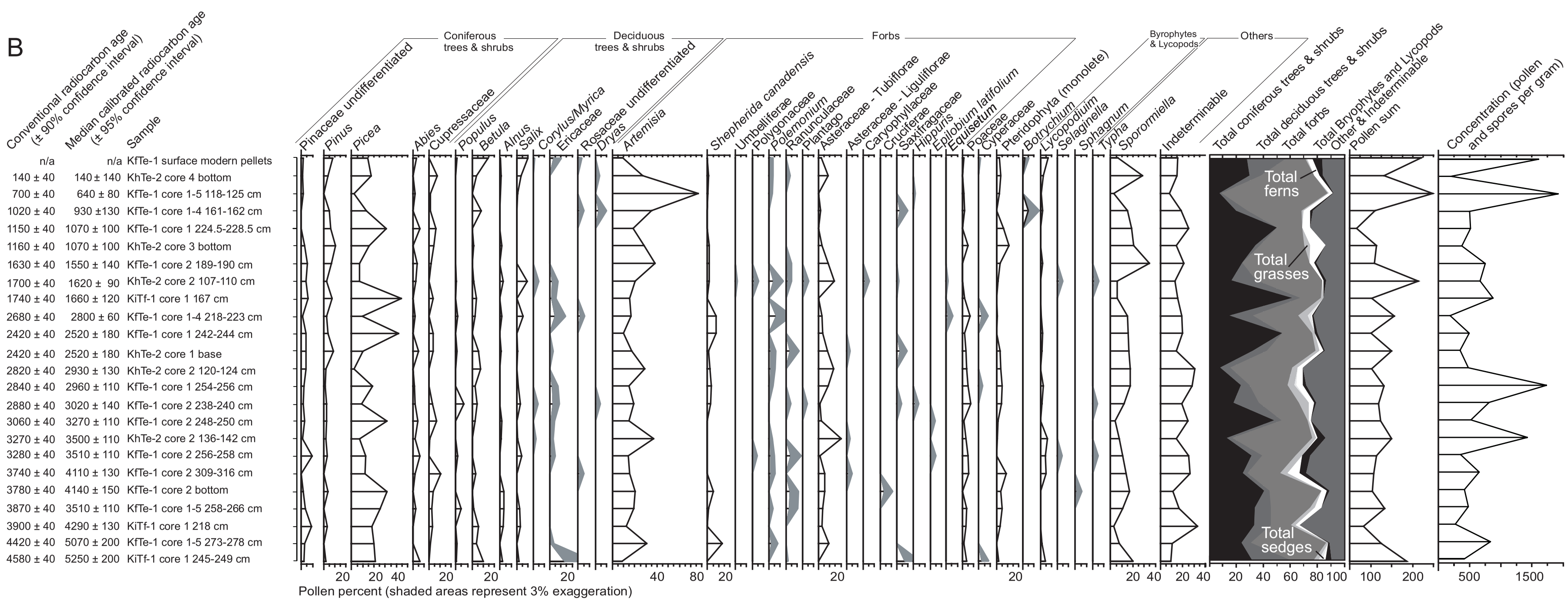


FIG. 3. Relative abundance of palynomorphs preserved in ice patch caribou dung in the Selwyn Mountains, Northwest Territories. Samples are arranged spatially by ice core and ice patch (A). A composite diagram including samples from all ice cores from all ice patches is arranged in chronological order (B). Area graph of plant types whose pollen is identified is also shown. Relative abundances are based on the main pollen sum, which excludes pollen from aquatic plants and fungal spores. Chronology is from Table 1. – *continued:*

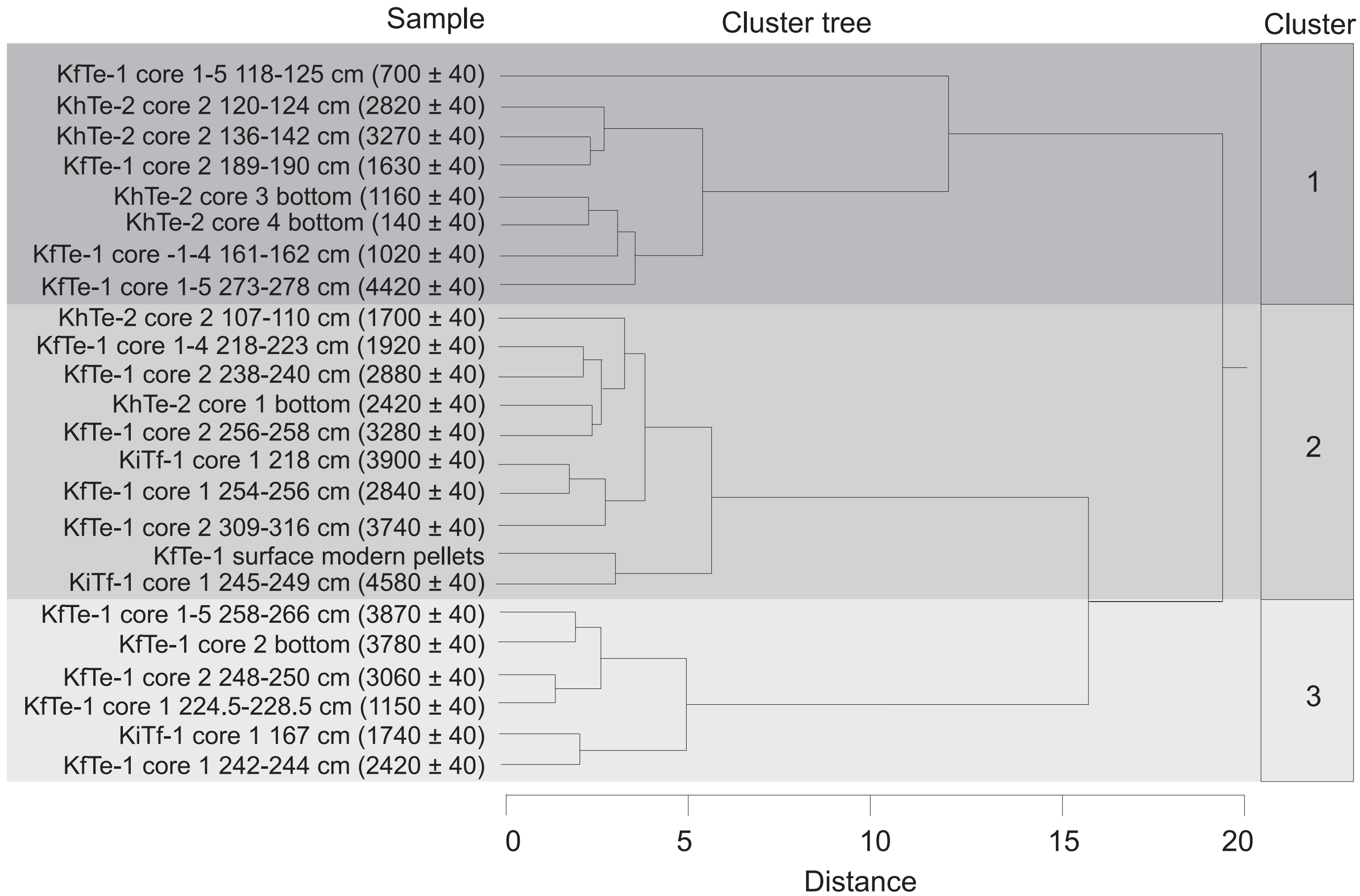


FIG. 4. Hierarchical Q-mode cluster analysis (Ward's dissimilarity measure and Euclidean distance) of relative abundances of pollen and spores preserved in ice patch caribou dung in the Selwyn Mountains, Northwest Territories, shows that samples do not cluster by ice patch or radiocarbon age.

data, cluster analysis of plant remains did not group samples by ice patch or radiocarbon age (Fig. 6), and no sustained trends in the relative abundances of plant types are observed when caribou dung samples are arranged in chronological order (Fig. 5B). Pollen and plant histological datasets contained few similarities (Table 5).

DISCUSSION

Caribou dung from ancestral Redstone populations that frequented the Selwyn Mountains throughout the late Holocene contains abundant and generally well preserved pollen, spores, and plant remains. While examination of the composition of plant fragments in herbivore feces is a well-established and generally accepted method for determination of animal diet (Sparks and Malechek, 1968), the use of copropalynology in paleoenvironmental reconstruction and animal behaviour studies is relatively new and demands a consideration of modes of palynomorph inclusion in fecal samples. Pollen could have been incorporated into ice-patch caribou dung via (1) deposition from the air, (2) ingestion of pollen in anthers of forage, (3) ingestion of pollen that has settled on forage or water, or (4) settlement of pollen on the hair of animals (Carrión et al., 2005; Bowyer, 2011).

Pollen and spore assemblages of ice patch caribou dung were broadly similar to spectra preserved in caribou feces in alpine ice in the southwest YT, where a parallel study has taken place (Bowyer et al., 1999; Farnell et al., 2004; Bowyer, 2011). Detailed comparison between palynomorph assemblages in NWT and YT ice patches will be forthcoming. Assemblages were also broadly similar to the ranges of relative abundance of pollen and spores present in late Holocene (past 5000 years) spectra of regional lakes and modern pollen rain (Fig. 7; Ritchie, 1984; MacDonald and Ritchie, 1986; Ritchie et al., 1987; Szeicz et al., 1995). However, several important differences are observed. First, a high degree of sample-to-sample variability is observed in dung samples relative to late Holocene lake sediment records. This variability may be due to differences in time recorded in the two types of deposits. Radiocarbon dating shows that lake sediment or peat samples in the NWT often represent several years of sediment accumulation (MacDonald, 1983) whereas dung samples could represent as little as a few days of grazing or a single season of exposure to regional pollen rain (Bowyer, 2011). Second, over-representation of local vegetation is known to bias sedimentary records deposited by water, but likely also applies to biogenic deposits (Wilmshurst and McGlone, 2005). In lake sediment and peat samples from tundra lakes in the NWT,

TABLE 2. Scientific and common names of pollen and spore taxa identified in ice patch caribou dung in the Selwyn Mountains, Northwest Territories.

Life form	Family	Genus	Common name
Coniferous trees and shrubs	Pinaceae	Undifferentiated	Pine family
		Pinus L.	Pine
		Picea A. Dietr.	Spruce
		Abies Mill.	Fir
	Cupressaceae	Undifferentiated	Cypress family
Deciduous trees and shrubs	Betulaceae	*Betula* L.	Birch
		Alnus Mill.	Alder
		Corylus L.	Hazel
	Salicaceae	*Salix* L.	Willow
		Populus L.	Poplar
	Myricaceae	*Myrica* L.	Myrtles and Gales
	Ericaceae	Undifferentiated	Heath family
	Rosaceae	Undifferentiated	Rose family
		Dryas L.	Mountain-aven
Forbs	Elaeagnaceae	*Shepherdia canadensis* (L.) Nutt.	Soapberry
	Umbelliferae	Undifferentiated	Carrot family
	Polygonaceae	Undifferentiated	Knotweed family
	Polemoniaceae	*Polemonium* L.	Jacob's ladder
	Ranunculaceae	Undifferentiated	Buttercup family
	Plantaginaceae	*Plantago* L.	Plantain
	Asteraceae	Undifferentiated	Aster family
		Artemisia L.	e.g., Wormwood, Sagebrush
		Subfamily Tubuliflorae	n/a
		Subfamily Liguliflorae	n/a
	Cruciferae/Brassicaceae	Undifferentiated	Mustard family
	Saxifragaceae	Undifferentiated	Saxifrage family
	Hippuridaceae	*Hippuris* L.	Mare's tail
	Oragraceae	*Epilobium latifolium* L.	Dwarf fireweed
	Caryophyllaceae	Undifferentiated	Carnation family
	Equisetaceae	*Equisetum* L.	Horsetail
Grasses	Poaceae	Undifferentiated	Grass family
Sedges	Cyperaceae	Undifferentiated	Sedge family
Ferns	Pteridophyta (phylum)	Undifferentiated	Fern
	Ophioglossaceae	*Botrychium* Sw.	Moonwart
Bryophytes and Lycopods	Lycopodiaceae	*Lycopodium* L.	Clubmoss
	Selaginellaceae	*Selaginella* L.	Spikemoss
	Sphagnaceae	*Sphagnum* L.	Peatmoss
Aquatic plants	Typhaceae	*Typha* L.	Cattail
Fungi	Sporormiaceae	*Sporormiella* Ellis & Everh.	(common dung fungus)

the abundance of *Betula* pollen is commonly very high (up to ~50%; MacDonald, 1983; MacDonald and Ritchie, 1986) compared to caribou dung samples (Fig. 7). *Betula* is a common shrub in riparian habitats surrounding water bodies in the NWT, but it does not grow above 1600 m in the Selwyn Mountains, where alpine ice accumulates (Kershaw, 1984; Ion and Kershaw, 1989). In contrast, *Artemisia* is common in alpine lichen-grass and lichen heath communities above 1600 m in the Selwyn Mountains and has been observed growing in the immediate vicinity of ice patches in the study area (Ion and Kershaw, 1989). Growth of *Artemisia* near or immediately next to alpine ice may be partially responsible for the higher proportion of this pollen type in caribou dung samples than in regional sediments deposited by water because *Artemisia* is a copious pollen producer, is wind-pollinated, but does not appear to have been a popular forage item: plant fragments of *Artemisia* occur in only one dung sample and at a low frequency (0.2%; Table 4). Animal behaviour (e.g., migration routes, food habits) is also likely to influence pollen spectra of dung (Scott and Cooremans, 1992; Bjune et al., 2005; Bowyer, 2011). Pollen types enriched in caribou dung samples relative to sediment samples from regional lakes and bogs include *Artemisia*, Asteraceae – Tubiflorae, Cupressaceae, *Shepherdia canadensis*, and *Polemonium* (Fig. 7). Pollen from zoophilous plants not known to grow in the immediate vicinity of ice patches (e.g., *Polemonium*) may have been concentrated in dung through selective grazing and subsequently deposited on alpine ice by caribou. A lack of similarity in the palynological assemblages and plant remains identified in ice patch caribou dung samples provides little additional insight into the provenance of palynomorphs (Table 5). Dissimilarity

TABLE 3. Scientific and common names of plant fragments identified in ice patch caribou dung in the Selwyn Mountains, NWT.

Life form	Family	Genus	Common name
Shrubs	Betulaceae	*Betula* L.	Birch
	Salicaceae	*Salix* L.	Willow
	Ericaceae	*Cassiope* D. Don	Cassiope
		Empetrum L.	e.g., Crowberry
		Kalmia L.	e.g., Sheep-laurel, Lambkill
		Rhododendron L. subsect. *Ledum* L.	Labrador tea
		Vaccinium L.	e.g., Cranberry
		Undifferentiated Ericaceae	
	Rosaceae	*Dryas* L.	Mountain-aven
Forbs	Asteraceae	Undifferentiated	
		Antennaria Gaertn.	e.g., Catsfoot, Pussytoes, Everlasting
		Artemisia L.	e.g., Sagebrush, Wormwood
	Polemoniaceae	*Polemonium* L.	Jacob's ladder
	Fabaceae	*Oxytropis* DC.	Locoweed
		Hedysarum L.	Sweetvetch
	Polygonaceae	*Polygonum* L.	Knotweed
		Rumex L.	Docks and sorrels
	Saxifragaceae	*Saxifraga* L.	Saxifrages
	Caryophyllaceae	*Stellaria* Seguier	Chickweed
		Silene L.	e.g., Campion, Catchfly
	Equisetaceae	*Equisetum* L.	Horsetail
Grasses	Poaceae	*Agrostis* L.	Bentgrass
		Arctagrostis Griseb.	Polargrass
		Calamagrostis Adans.	Reedgrass
		Deschampsia Beauvois	e.g., Tussock grass
		Festuca L.	Fescue
		Hierochloe R. Br.	Sweetgrass
		Poa L.	e.g., Meadow grass
Sedges	Cyperaceae	*Carex* L.	Sedge
		Eriophorum L.	Cottongrass
		Kobresia Willd.	Bog sedge
	Juncaceae	*Juncus* L.	Rush
Bryophytes and Lycopods	Aulacomniaceae	*Aulacomnium* Schwaegr.	Aulocomnium moss
	Lycopodiaceae	*Lycopodium* L.	Clubmoss
	Polytrichaceae	*Polytrichum* Hedw.	Haircap moss
	Selaginellaceae	*Selaginella* L.	Spikemoss
	Sphagnaceae	*Sphagnum* L.	Peat moss
	Dicranaceae	*Dicranum* Hedw.-type	Dicranum moss
Lichens	Lecanorineae (suborder)	*Alectoria* Ach.	
	Parmeliaceae	*Cetraria* Ach.	
		Dactylina Nyl.	
	Cladoniaceae	*Cladonia* Hill ex P. Browne	Reindeer lichen
	Peltigeraceae	*Peltigera* Willd.	
	Stereocaulaceae	*Stereocaulon* Hoffm.	

between pollen and plant-fragment assemblages has been previously reported in the feces of cattle (Akeret et al., 1999) and extinct mountain goats (Mead et al., 1987) and may be due to differences in plant digestibility, taphonomy, or provenance (i.e., pollen input through pollen rain vs. ingestion; Richard, 1986).

Woodland caribou in northwestern Canada migrate long distances (> 100 km; Weaver, 2008) on a seasonal basis, but direct observations show that daily movements are much smaller ("one hour's travel time"; Oosenbrug and Theberge, 1980:66) as animals move upslope to ice patches during the day and descend in late afternoon. Caribou are ruminants, and food items can take one to three days to pass through their gut (Thomas and Kroeger, 1981). Their diurnal migrations, which probably cover about 100 m change in elevation, define the vegetation area sampled by microhistology and palynology, which includes a variety of plant communities in the Selwyn Mountains. Animal behaviour can concentrate pollen types rarely found in abundance in sediments deposited by water into dung. The presence of pollen in ice patch dung thus permits reconstruction of vegetation that grew in the wide range of habitats used by caribou (e.g., Scott et al., 2003; Bjune et al., 2005; Bowyer, 2011).

Various paleoclimatological reconstructions for the late Holocene of the western NWT and YT suggest that a relatively stable cool and moist modern-type climate has persisted since approximately 6000 cal. yr BP (MacDonald, 1983, 1987; Cwynar and Spear 1995; Vardy et al., 1998). Relative stability in the palynological record of caribou dung also provides evidence for a consistently cool and

TABLE 4. Relative abundances of plant fragments identified in ice patch caribou dung in the Selwyn Mountains, Northwest Territories. Data are graphed in Figure 5. Chronology is from Table 1.

Sample	KfTe-1 Core 1 224.5–228.5 cm	KfTe-1 Core 1 254–256 cm	KfTe-1 Core 2 189–191 cm	KfTe-1 Core 2 256–258 cm	KfTe-1 Core 2 bottom	KhTe-2 Core 1 bottom	KhTe-2 Core 2 107–110 cm	KhTe-2 Core 2 136–142 cm	KhTe-2 Core 3 bottom	KhTe-2 Core 5 bottom	Mean (± SD)
Dry weight (g)	3.53	2.92	4.6	4.62	9.58	2.6	7.22	4.66	2.38	5.1	
Age (^{14}C)[1]	1150 ± 40	2840 ± 40	1630 ± 40	3280 ± 40	3780 ± 40	2420 ± 40	1700 ± 40	3270 ± 40	1160 ± 40	1160 ± 40	
Age (Cal.)[1]	1070 ± 100	2960 ± 110	1550 ± 140	3510 ± 110	4140 ± 110	2520 ±180	1620 ± 140	3500 ± 110	1070 ± 100	1070 ± 100	
Forbs:											
Antennaria	–	–	0.5	–	–	–	–	–	–	–	0.5
Artemisia	–	–	0.2	–	–	–	–	–	–	–	0.2
Equisetum	–	–	1.8	0.8	1.0	1.2	–	–	–	–	1.2 (0.4)
Hedysarum	0.2	–	0.9	0.2	–	0.2	0.2	–	–	–	0.3 (0.3)
Oxytropis	–	–	–	0.4	–	0.2	–	0.2	–	–	0.3 (0.1)
Polemonium	–	–	–	0.4	–	–	–	–	–	–	0.3
Polygonum	0.7	–	–	–	–	0.7	–	1.6	–	1.0	1 (0.4)
Rumex	0.5	–	0.9	–	–	–	–	–	1.0	0.2	0.7 (0.4)
Saxifraga	1.3	0.9	0.2	0.6	–	1.8	–	–	–	–	1 (0.6)
Stellaria	–	0.7	0.3	–	–	0.7	0.5	–	–	–	0.6 (0.2)
Silene	0.4	–	–	–	–	0.4	–	–	–	–	0.4 (0)
Composite forb	–	–	–	–	–	0.2	–	–	–	–	0.2
Unknown forb	2.0	–	1.4	0.8	2.0	1.3	–	1.1	1.5	1.3	1.4 (0.4)
Total	**5.1**	**1.6**	**6.2**	**3.2**	**3.0**	**6.7**	**0.7**	**2.9**	**2.5**	**2.5**	**3.4 (1.9)**
Grasses:											
Agrostis	–	–	–	0.4	–	–	–	–	–	–	0.4
Arctagrostis	2.0	2.2	1.9	0.4	1.3	0.9	3.0	1.6	0.8	1.4	1.6 (0.8)
Calamagrostis	1.5	0.4	0.9	1.1	–	–	1.4	0.7	–	–	1 (0.4)
Deschampsia	–	–	–	–	–	–	–	1.6	–	2.6	2.1 (0.7)
Festuca	–	1.1	1.8	1.1	–	1.6	2.8	0.9	1.7	1.8	1.6 (0.6)
Hierochloe	1.5	0.4	1.4	–	–	2.0	1.1	–	1.1	–	1.3 (0.5)
Poa	1.5	2.7	9.1	2.6	2.3	5.2	6.5	7.2	2.7	8.6	4.8 (2.8)
Unknown grass	–	1.1	0.9	1.1	0.6	1.3	1.9	0.7	1.0	1.1	1.1 (0.4)
Total	**6.5**	**7.9**	**16.0**	**6.7**	**4.2**	**11.0**	**16.7**	**12.7**	**7.3**	**15.5**	**10.5 (4.5)**
Sedges:											
Carex	4.3	4.0	7.7	6.2	3.1	3.9	6.5	10.7	3.4	7.2	5.7 (2.4)
Eriophorum	0.5	0.4	2.3	0.6	–	0.5	1.2	1.9	0.8	–	1 (0.7)
Kobresia	–	–	0.3	0.6	–	–	0.5	–	–	–	0.5 (0.2)
Total Cyperaceae	4.8	4.4	10.3	7.4	3.1	4.4	8.2	12.6	4.2	7.2	6.7 (3.1)
Juncus	–	0.5	2.5	–	0.6	–	1.1	2.3	–	4.1	1.9 (1.4)
Total	**4.8**	**4.9**	**12.8**	**7.4**	**3.7**	**4.4**	**9.3**	**14.9**	**4.2**	**11.3**	**7.8 (4.1)**
Shrubs:											
Betula leaf	–	–	–	–	–	–	–	0.9	–	–	0.9
Betula stem	0.9	1.1	2.3	–	0.8	2.1	1.2	–	0.2	–	1.2 (0.7)
Total *Betula*											1 (0.8)
Salix leaf	4.3	0.7	3.3	6.4	2.3	5.0	5.5	4.2	6.9	4.0	4.3 (1.9)
Salix stem	4.3	5.3	5.8	8.1	6.4	10.6	5.3	5.6	13.4	8.8	7.4 (2.9)
Total *Salix*											11.6 (4.2)
Dryas leaf	0.5	–	1.1	2.1	1.2	3.6	1.8	0.7	0.4	0.3	1.3 (1.1)
Dryas stem	4.2	4.6	1.4	1.1	2.5	1.8	1.4	–	3.8	3.4	2.7 (1.3)
Total *Dryas*											3.6 (1.3)
Empetrum leaf	0.2	0.7	–	–	–	1.2	1.9	0.7	1.0	–	1 (0.6)

TABLE 4. Relative abundances of plant fragments identified in ice patch caribou dung in the Selwyn Mountains, Northwest Territories. Data are graphed in Figure 5. Chronology is from Table 1. – *continued:*

Sample	KfTe-1 Core 1 224.5–228.5 cm	KfTe-1 Core 1 254–256 cm	KfTe-1 Core 2 189–191 cm	KfTe-1 Core 2 256–258 cm	KfTe-1 Core 2 bottom	KhTe-2 Core 1 bottom	KhTe-2 Core 2 107–110 cm	KhTe-2 Core 2 136–142 cm	KhTe-2 Core 3 bottom	KhTe-2 Core 5 bottom	Mean (± SD)
Dry weight (g)	3.53	2.92	4.6	4.62	9.58	2.6	7.22	4.66	2.38	5.1	
Age (^{14}C)[1]	1150 ± 40	2840 ± 40	1630 ± 40	3280 ± 40	3780 ± 40	2420 ± 40	1700 ± 40	3270 ± 40	1160 ± 40	1160 ± 40	
Age (Cal.)[1]	1070 ± 100	2960 ± 110	1550 ± 140	3510 ± 110	4140 ± 110	2520 ±180	1620 ± 140	3500 ± 110	1070 ± 100	1070 ± 100	
Shrubs – *continued:*											
Empetrum stem	0.5	0.4	–	–	0.4	–	–	–	–	–	0.4 (0.1)
Total *Empetrum*											0.7 (0.6)
Kalmia/*Ledum* leaf	–	–	–	–	–	0.7	1.9		1.7	6.1	2.6 (2.4)
Ledum stem	0.7	–	–	–	–	–	–	–	–	–	0.7
Cassiope	3.1	0.4	–	0.4	1.0	0.4	4.8	0.3	1.1	1.3	1.4 (1.5)
Vaccinium leaf	0.5	–	–	0.4	–	1.6	0.7	0.3	–	–	0.7 (0.5)
Vaccinium stem	2.2	–	–	–	1.7	0.7	–	–	0.6	–	1.3 (0.8)
Total *Vaccinium*											0.9 (1)
Ericaceous stem	–	–	–	–	–	1.8	–	–	–	–	1.8
Unknown leaf	–	0.9	–	0.4	–	0.9	1.1	1.0	0.6	0.5	0.8 (0.3)
Unknown stem	1.4	–	1.2	1.1	2.3	0.7	–	0.3	0.9	–	1.1 (0.6)
Total	**22.8**	**14.1**	**15.1**	**20.0**	**18.6**	**31.1**	**25.6**	**14.0**	**30.6**	**24.4**	**21.6 (6.4)**
Bryophytes and Lycopods:											
Aulacomnium	2.7	6.7	5.6	6.0	1.1	6.6	3.5	3.9	8.8	1.8	4.7 (2.5)
Lycopodium	–	0.2	1.1	0.6	2.3	0.9	0.5	–	0.6	1.1	0.9 (0.6)
Polytrichum	4.5	2.7	2.6	1.9	1.0	0.9	0.4	1.8	1.1	4.6	2.2 (1.5)
Selaginella	0.5	1.1	0.9	1.5	1.5	0.5	2.1	–	–	–	1.2 (0.6)
Sphagnum	3.3	4.0	2.5	2.6	1.5	3.4	2.3	3.3	2.9	3.7	3 (0.7)
Dicranum–type	18.4	13.3	15.3	19.0	17.3	16.1	8.3	18.2	20.1	8.0	15.4 (4.3)
Total	**29.4**	**28.0**	**28.0**	**31.6**	**24.7**	**28.4**	**17.1**	**27.2**	**33.5**	**19.2**	**26.7 (5.1)**
Lichens:											
Alectoria	6.3	10.2	4.6	6.8	4.3	1.2	2.6	4.2	1.1	3.7	4.5 (2.7)
Cetraria/*Dactylina*	6.1	5.3	7.6	6.4	11.2	3.6	10.8	7.7	12.0	7.3	7.8 (2.7)
Cladonia/*Cladina*	14.6	24.6	7.2	13.2	26.8	11.1	12.4	14.2	6.3	11.5	14.2 (6.7)
Peltigera	4.0	2.9	1.4	4.3	3.5	2.5	3.7	1.9	2.5	3.2	3 (0.9)
Stereocaulon	0.4	0.5	0.9	–	–	–	1.1	0.3	–	1.4	0.8 (0.4)
Unknown lichen	–	–	0.2	0.4	–	–	–	–	–	–	0.3 (0.1)
Total	**31.4**	**43.5**	**21.9**	**31.1**	**45.8**	**18.4**	**30.6**	**28.3**	**21.9**	**27.1**	**30 (8.9)**

[1] Age (^{14}C) is ^{14}C yr BP ± 90% CI and Age (Cal.) is the median cal. yr BP ± 95% CI.

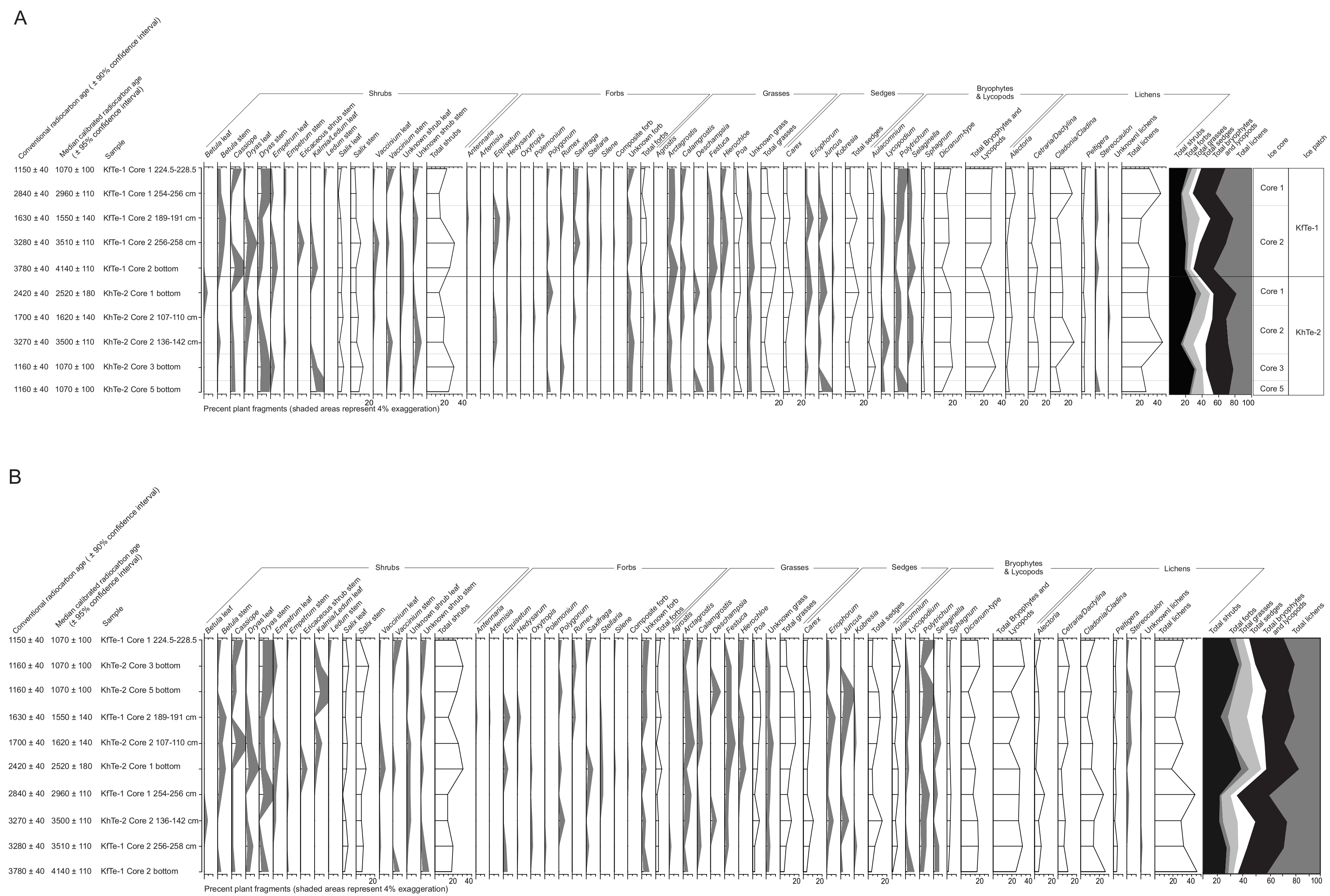


FIG. 5. Relative abundances of plant remains preserved in ice patch caribou dung in the Selwyn Mountains, Northwest Territories. Samples are arranged by ice core and ice patch (A). A composite diagram including samples from all ice cores from all ice patches is arranged in chronological order (B). Area graph of plant types whose fragments are identified is also shown. Data are from Table 4 and chronology is from Table 1.

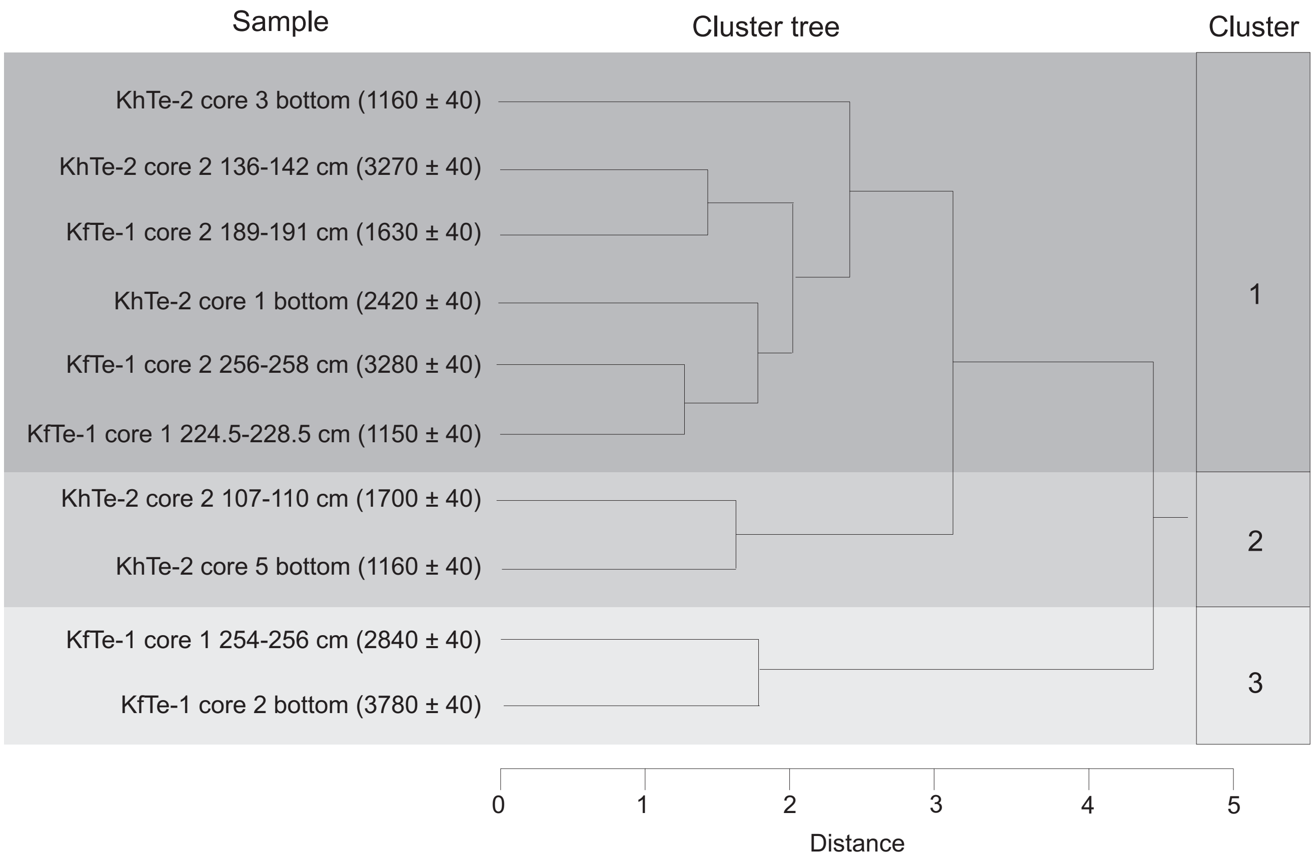


FIG. 6. Hierarchical Q-mode cluster analysis (Ward's dissimilarity measure and Euclidean distance) of relative abundance of plant fragments in ice patch caribou dung in the Selwyn Mountains, Northwest Territories, shows that samples do not cluster by ice patch or radiocarbon age.

TABLE 5. Comparison of the mean relative abundances of plant types identified as pollen and spores or plant fragments in ice patch caribou dung in the Selwyn Mountains, Northwest Territories.

Plant type	Mean pollen/spores (± SD)		Mean plant fragments (± SD)	
Coniferous trees and shrubs	29.2	(14.1)	0.0	–
Deciduous trees and shrubs	9.7	(8.5)	21.6	(6.4)
Forbs	34.1	(16.3)	3.4	(1.9)
Grasses	2.7	(2.2)	10.5	(4.5)
Sedges	0.3	(0.8)	7.8	(4.1)
Ferns	3.3	(2.7)	0.0	–
Bryophytes and Lycopods	2.0	(2.2)	26.7	(5.1)
Lichens	0.0	–	30.0	(8.9)

moist late Holocene climate in the study region because climate is the main driver of vegetation change on millennial time scales (Miller et al., 2008).

The dung palynological record suggests that mixed coniferous and deciduous communities consisting of *Pinus* L., *Picea*, *Abies*, and *Populus* L. grew downslope of ice patches in lowlands and valley bottoms. The relatively low occurrence of *Betula*, *Salix*, and *Alnus* pollen in caribou dung suggests that deciduous shrub communities existed in riparian habitats and shrub communities below 1600 m, in a pattern similar to present-day distributions in the study area. Relatively high proportions of *Artemisia* pollen and a diversity of pollen from forbs, as well as grasses and sedges, suggest that floristically rich herbaceous communities, probably a mosaic of lichen-grass, lichen-heath, and sedge meadow tundra, grew in high-altitude habitats. Fern and bryophyte/lycopod spores present in dung samples suggest that moist habitats were also present, probably on north-facing slopes where drainage was impeded by summer permafrost.

The composition of plant fragments in dung samples suggests that the summer diet of ancestral Redstone caribou in the Selwyn Mountains has remained stable over the past ~5000 years. Food habits of ancestral Redstone caribou are similar to the summer diet inferred for late Holocene (past ~4500 years) woodland caribou populations in the YT (Kuzyk et al., 1999; Farnell et al., 2004) and to that of woodland and barren-ground caribou in northwestern Canada today, which typically consists of a variety of deciduous shrubs, grasses, sedges, lichens, and mosses (Boertje,

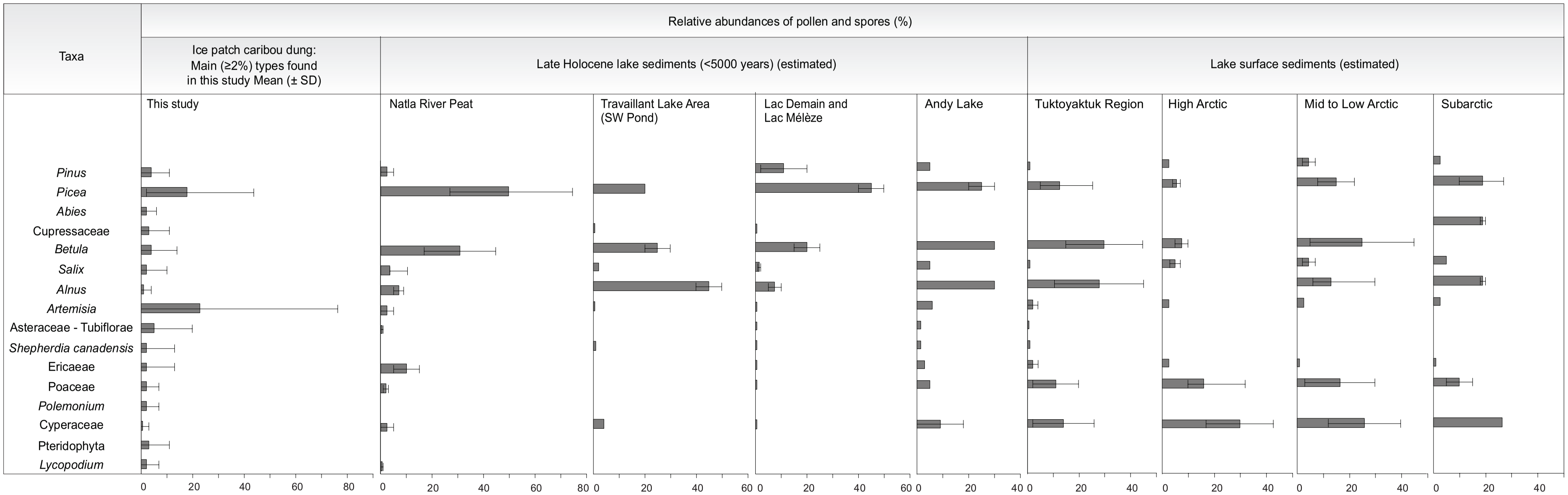


FIG. 7. Bar chart showing comparison of the mean relative abundances (± SD) of main (≥ 2%) pollen and spore types identified in ice patch caribou dung in the Selwyn Mountains, Northwest Territories, and estimated percentages of pollen and spores in late Holocene-aged sediments (from the past 5000 years) of lakes in the western Northwest Territories and sediment-water interface samples from lakes in the Northwest Territories. If relative abundance of palynomorph type is variable during the late Holocene, the approximate range of variability is shown. References: Natla River (MacDonald, 1983); Travaillant Lake (Ritchie, 1984); Lac Demain and Lac Mélèze (MacDonald, 1987); Andy Lake (Szeicz et al., 1995); Tuktoyaktuk region (MacDonald and Ritchie, 1986); High Arctic, mid to Low Arctic, Subarctic (Ritchie et al., 1987).

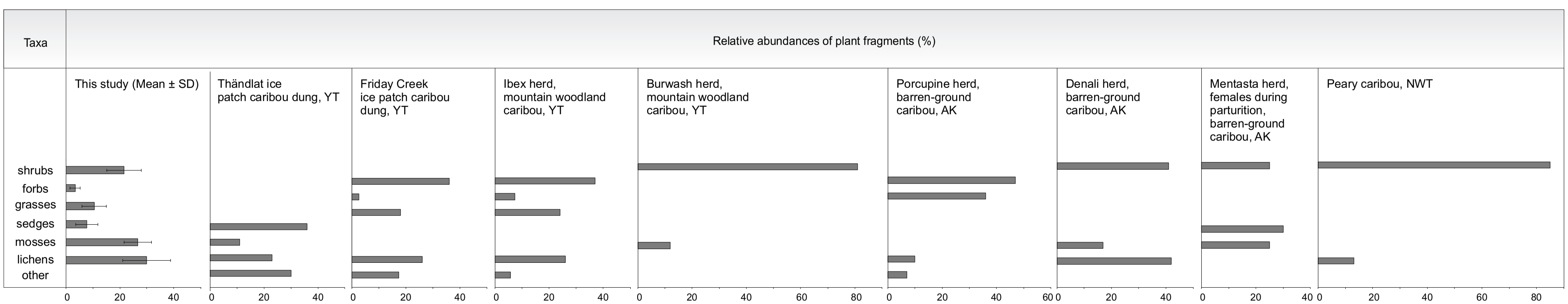


FIG. 8. Bar chart showing comparison of the mean relative abundances (± SD) of main plant fragment types identified in ice patch caribou dung in the Selwyn Mountains, Northwest Territories, and relative abundances of plant remains in the dung of other caribou in northwestern North America. References: Thändlat caribou dung (Kuzyk et al., 1999); Friday Creek and Ibex herd (Farnell et al., 2004); Burwash herd (Gauthier and Theberge, 1986); Porcupine herd (Russell et al., 1993); Denali herd (Boertje, 1984); Mentasta herd (Barten et al., 2001); Peary caribou (Shank et al., 1978; Larter and Nagy, 2004).

1984; Russell et al., 1993; Fischer and Gates, 2005; Fig. 8). However, the frequency of lichens is higher in ice patch dung samples in the Selwyn Mountains (~30%) and the southwest YT (~25%; D. Russell, pers. comm. 2011) than in summer feces of other caribou in northwestern Canada. For example, in the diets of the Burwash woodland caribou herd in the southwestern YT, lichen constitutes 12% during calving season (June–July), 25% during the fall rut season, and 39% during the winter (Gauthier and Theberge, 1986). Similarly, diets of Alaskan Denali caribou, a mountain caribou herd, have an average of 25% lichen and 41% *Salix* during spring months (late May to July), but lichens become less important during summer (mid-July to mid-August), when they represent only 17% of the diet (Boertje, 1984). Lichens are an important food item for woodland caribou during winter, but their consumption is often reduced during summer when woodland caribou migrate upslope from low-elevation winter habitat and shift to foraging among forbs, deciduous shrubs, and grasses to maintain a diet with high contents of protein and digestible carbohydrates (Gauthier and Theberge, 1986; Russell et al., 1993). Woodland caribou in the Selwyn Mountains that frequented high-elevation (> 1600 m) habitats such as ridge tops and ice patches to avoid insect harassment may have sacrificed forage opportunities to do so. In addition, lichens may have become an increasingly important food source near ice patches as other plants began senescence in the late summer (D. Russell, pers. comm. 2011).

CONCLUSIONS

Pollen and plant-fragment analyses of layers of caribou dung preserved in alpine ice patches contribute to the understanding of regional late Holocene paleoenvironments in the Selwyn Mountains and provide insight into the behaviour and diet of ancestral Redstone caribou. The presence of pollen from a variety of forbs, conifers, and deciduous shrubs demonstrate that a diversity of habitats and plant communities has existed in the Selwyn Mountains for at least the past five millennia. Food habits of ancestral Redstone caribou in the Selwyn Mountains, inferred from plant fragments in dung, also displayed continuity over the past 5000 years; the fragments suggest that this population has maintained a summer diet consisting of a variety of lichens, mosses, shrubs, grasses, and sedges throughout the late Holocene. Food habits reconstructed for ancestral Redstone caribou are broadly similar to modern diets of ecologically similar caribou, although lichens remained an important food source at the high-elevation (> 1600 m) habitats that caribou in the Selwyn Mountains exploited to avoid insect harassment.

ACKNOWLEDGEMENTS

Funding for this project was provided by International Polar Year (IPY) 2007–08 (CC018 to T.D. Andrews), the Government of the Northwest Territories, and the Tulita Dene Band, and by in-kind contributions and support from Golder Associates Ltd. (Yellowknife) and IMG Golder Corporation (Inuvik). Parasite DNA work was supported through IPY 2007–08 award #162 for the CircumArctic Rangifer Monitoring and Assessment (CARMA) Network (S.J. Kutz and co-principal investigators), and through a University of Calgary Veterinary Medicine Postdoctoral Research Fellowship to D.M. Schock. We thank Leon Andrew of the Tulita Dene Band and Haley Peterson of the University of Calgary for field assistance. We are grateful to the Taiga Environmental Laboratory for use of laboratory space, equipment, and chemicals, and to Linda Dancey (Geological Survey of Canada, Calgary) for additional pollen preparations. Figure 1 was provided by Amy Barker. Secure storage of biological samples recovered from ice patches is provided by Collections at the Prince of Wales Northern Heritage Centre in Yellowknife, NWT. We are grateful for the constructive suggestions and comments made by Arthur Sweet, James White, Grant Zazula, and two anonymous reviewers, which have greatly improved the manuscript. This paper represents Natural Resources Canada/Ressources naturelles Canada Earth Science Sector (Geological Survey of Canada/Commission géologique du Canada) Contribution Number 20110122.

REFERENCES

Akeret, Ö., Haas, J.N., Leuzinger, U., and Jacomet, S. 1999. Plant macrofossils and pollen in goat/sheep faeces from the Neolithic lake-shore settlement Arbon Bleiche 3, Switzerland. The Holocene 9:175–182.

Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E., and Halvorsen, O. 2002. The role of parasites in the dynamics of a reindeer population. Proceedings of the Royal Society of London Series B 269:1625–1632.

Andrews, T.D., MacKay, G., and Andrew, L. 2012. Archaeological investigations of alpine ice patches in the Selwyn Mountains, Northwest Territories, Canada. Arctic 65(Suppl. 1):1–21.

Aptroot, A., and van Geel, B. 2006. Fungi of the colon of the Yukagir mammoth and from stratigraphically related permafrost samples. Review of Palaeobotany and Palynology 141:225–230.

Barten, N.L., Bowyer, R.T., and Jenkins, K.J. 2001. Habitat use by female caribou: Tradeoffs associated with parturition. Journal of Wildlife Management 65:77–92.

Bjune, A.E., Mangerud, J., and Moe, D. 2005. Past grazing habitats for Svalbard reindeer indicated by the pollen content of 3300-year-old faeces from Edgeøya, Svalbard. Grana 44:45–50.

Boertje, R.D. 1984. Seasonal diets of the Denali caribou herd, Alaska. Arctic 37:161–165.

Bowyer, V. 2011. Seasonal hunting at ice patches: Seasonal mobility and long-term land-use in the southwest Yukon. PhD thesis, Department of Anthropology, University of Alberta.

Bowyer, V., Kuzyk, G.W., Russell, D.E., Farnell, R.S., Gotthardt, R.M., Hare, P.G., and Blake, E. 1999. Caribou remains at Thandlät: Archaeology and paleoecology of some well-preserved sites on ice patches in the southerwestern Yukon.

32nd Annual Conference of the Canadian Archaeological Association, Yellowknife, Northwest Territories.

Carrión, J.S. 2002. A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. Review of Palaeobotany and Palynology 120:217 – 232.

Carrión, J.S., Riquelme, J.A., Navarro, C., and Munuera, M. 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 176:193 – 205.

Carrión, J.S., Gil, G., Rodríquez, E., Fuentes, N., García-Antón, and Arribas, A. 2005. Palynology of badger coprolites from central Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 226:259 – 271.

Carrión, J.S., Scott, L., Arribas, A., Fuentes, N., Gil-Romera, G., and Montoya, E. 2007. Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites. Journal of Quaternary Science 22:191 – 202.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2002. COSEWIC assessment and update status report on the woodland caribou *Rangifer tarandus caribou* in Canada. Gatineau, Québec: COSEWIC.

Coyne, M.J., and Smith, G. 1994. Trichostrongylid parasites of domestic ruminants. In: Scott, M.E., and Smith, G., eds. Parasitic and infectious diseases: Epidemiology and ecology. San Diego: Academic Press. 235 – 247.

Cronin, M., Shideler, R., Hechtel, J., Strobeck, C., and Paetkau, D. 1999. Genetic relationships of grizzly bears (*Ursus arctos*) in the Prudhoe Bay region of Alaska: Inference from microsatellite DNA, mitochondrial DNA, and field observations. Journal of Heredity 90:622 – 628.

Cwynar, L.C., and Spear, R.W. 1995. Paleovegetation and paleoclimatic changes in the Yukon at 6 ka BP. Géographie physique et Quaternaire 49:29 – 35.

Environment Canada. 2011. Management plan for the northern mountain population of woodland caribou (*Rangifer tarandus caribou*) in Canada [proposed]. Species at Risk Act Management Plan Series. Ottawa: Environment Canada.

Fægri, K., Iversen, J., Kaland, P.E., and Krzywinski, K. 1989. Textbook of pollen analysis, 4th ed. New Jersey: The Blackburn Press.

Farnell, R., Hare, G.P., Blake, E., Bowyer, V., Schweger, C., Greer, S., and Gotthardt, R. 2004. Multidisciplinary investigations of alpine ice patches in southwest Yukon, Canada: Paleoenvironmental and paleobiological investigations. Arctic 57:247 – 259.

Fischer, L.A., and Gates, C.C. 2005. Competition potential between sympatric woodland caribou and wood bison in southwestern Yukon, Canada. Canadian Journal of Zoology 83:1162 – 1173.

Gardener, C.J., McIvor, J.G., and Jansen, A. 1993. Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. Journal of Applied Ecology 30:63 – 74.

Gauthier, D.A., and Theberge, J.B. 1986. Wolf predation in the Burwash caribou herd, southwest Yukon. Rangifer Special Issue 1:137 – 144.

Grimm, E.C. 1993. TILIA v2.0 (computer software). Springfield: Illinois State Museum Research and Collections Center.

Hoste, H., Chilton, N.B., Gasser, R.B., and Beveridge, I. 1995. Differences in the second internal transcribed spacer (ribosomal DNA) between five species of *Trichostrongylus* (Nematoda: Trichostrongylidae). International Journal for Parasitology 25:75 – 80.

Hughes, J., Albon, S.D., Irvine, R.J., and Woodin, S. 2009. Is there a cost of parasites to caribou? Parasitology 136:253 – 265.

Ion, P.G., and Kershaw, G.P. 1989. The selection of snowpatches as relief habitat by woodland caribou (*Rangifer tarandus caribou*), Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T., Canada. Arctic and Alpine Research 21:203 – 211.

Kapp, R.O., Davis, O.K., and King, J.E. 2000. Guide to pollen and spores, 2nd ed. College Station: The American Association of Stratigraphic Palynologists.

Kershaw, G.P. 1984. Tundra plant communities of the Mackenzie Mountains, Northwest Territories: Floristic characteristics of long-term surface disturbances. In: Olson, R., Hastings, R., and Geddes, J., eds. Northern ecology and resource management: Memorial essays honouring Don Gill. Edmonton: The University of Alberta Press. 239 – 309.

Kropf, M., Mead, J.I., and Anderson, R.S. 2007. Dung, diet, and the paleoenvironment of the extinct shrub-ox (*Euceratherium collinum*) on the Colorado Plateau, USA. Quaternary Research 67:143 – 151.

Kuzyk, G.W., Russell, D.E., Farnell, R.S., Gotthardt, R.M., Hare, G.P., and Blake, E. 1999. In pursuit of prehistoric caribou on Thandlät, southern Yukon. Arctic 52:214 – 219.

Larter, N.C., and Nagy, J.A. 2004. Seasonal changes in the composition of diets of Peary caribou and muskoxen on Banks Island. Polar Research 23(2):131 – 140.

Letts, B., Fulton, T.L., Stiller, M., Andrews, T.D., MacKay, G., Popko, R., and Shapiro, B. 2012. Ancient DNA reveals genetic continuity in mountain woodland caribou of the Mackenzie and Selwyn Mountains, Northwest Territories, Canada. Arctic 65(Suppl. 1):80 – 94.

MacDonald, G.M. 1983. Holocene vegetation history of the Upper Natla River Area, Northwest Territories, Canada. Arctic and Alpine Research 15:169 – 180.

———. 1987. Postglacial vegetation history of the Mackenzie River Basin. Quaternary Research 28:245 – 262.

MacDonald, G.M., and Ritchie, J.C. 1986. Modern pollen spectra from the Western Interior of Canada and the interpretation of Late Quaternary vegetation development. New Phytologist 103:245 – 268.

Mead, J.I., Agenbroad, L.D., Phillips, A.M., III, and Middleton, L.T. 1987. Extinct mountain goat (*Oreamnos harringtoni*) in southeastern Utah. Quaternary Research 27:323 – 331.

Meulendyk, T., Moorman, B.J., Andrews, T.D., and MacKay, G. 2012. Morphology and development of ice patches in Northwest Territories, Canada. Arctic 65(Suppl. 1):43 – 58.

McAndrews, J.H., Berti, A.A., and Norris, G. 1973. Key to the Quaternary pollen and spores of the Great Lakes region. Toronto: Royal Ontario Museum Life Sciences Miscellaneous Publication.

McLoughlin, P.D., Dzus, E., Wynes, B., and Boutin, S. 2003. Declines in populations of woodland caribou. Journal of Wildlife Management 67:755–761.

Miller, P.A., Giesecke, T., Hickler, T., Bradshaw, R.H.W., Smith, B., Seppä, H., Valdes, P.J., and Sykes, M.T. 2008. Exploring climatic and biotic controls on Holocene vegetation change in Fennoscandia. Journal of Ecology 96:247–259.

Moe, D. 1983. Palynology of sheep's faeces: Relationship between pollen content, diet, and local pollen rain. Grana 22:105–113.

Olsen, B., MacDonald, M., and Zimmer, A. 2001. Co-management of woodland caribou in the Sahtu Settlement Area: Workshop on research, traditional knowledge, conservation and cumulative impacts. Special Publication 1. Tulita, Northwest Territories: Sahtu Renewable Resources Board.

Oosenbrug, S.M., and Theberge, J.B. 1980. Altitudinal movements and summer habitat preferences of woodland caribou in the Kluane Ranges, Yukon Territory. Arctic 33:59–72.

Putman, R.J. 1984. Facts from faeces. Mammal Review 14:79–97.

Quayle, J.F., and Kershaw, G.P. 1996. Use of summer habitat by caribou on the north slope of a mountain near the Macmillan Pass, N.W.T. Rangifer Special Issue 9:311–318.

Rasmussen, P. 1993. Analysis of goat/sheep faeces from Egolzwil 3, Switzerland: Evidence for branch and twig foddering of livestock in the Neolithic. Journal of Archaeological Science 20:479–502.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., and Bronk Ramsey, C., et al. 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. Radiocarbon 51:1111–1150.

Richard, H. 1986. Analyse pollinique des niveaux archéologiques et des coprolithes. In: Pétrequin, P., ed. Les sites littoraux néolithiques de Clairvaux-les-Lacs, Jura. I : Problematique générale. L'example de la station III. Paris: Edition de la Maison des Sciences de l'Homme.

Ritchie, J.C. 1984. A Holocene pollen record of boreal forest history from the Travaillant Lake area, Lower Mackenzie River Basin. Canadian Journal of Botany 62:1385–1392.

Ritchie, J.C., Hadden, K.A., and Gajewski, K. 1987. Modern pollen spectra from lakes in Arctic western Canada. Canadian Journal of Botany 65:1605–1613.

Rowe, J.S. 1972. Forest regions of Canada. Ottawa: Canadian Forest Service.

Russell, D.E., Martell, A.M., and Nixon, W.A.C. 1993. Range ecology of the Porcupine caribou herd in Canada. Rangifer Special Issue 8. Harstad, Norway: Nordic Council for Reindeer Research. 167 p.

Scott, L., and Cooremans, B. 1992. Pollen in recent *Procavia* (hyrax), *Petromus* (dassie rat) and bird dung in South Africa. Journal of Biogeography 19:205–215.

Scott, L., and Woodborne, S. 2006. Pollen analysis and dating of Late Quaternary faecal deposits (hyraceum) in the Cederberg, Western Cape, South Africa. Review of Palaeobotany and Palynology 144:123–134.

———. 2007. Vegetation history inferred from pollen in Late Quaternary faecal deposits (hyraceum) in the Cape winter-rain region, and its bearing on past climates in South Africa. Quaternary Science Reviews 26:941–953.

Scott, L., Fernández Jalvo, Y., Carrión, J.S., and Brink, J. 2003. Preservation and interpretation of pollen in hyaena coprolites: Taphonomic observations from Spain and southern Africa. Paleontologia Africana 39:83–91.

Shank, C.C., Wilkinson, P.F., and Penner, D.F. 1978. Diet of Peary caribou, Banks Island, N.W.T. Arctic 31:125–132.

Slater, D.S. 1985. Pollen analysis of postglacial sediments from Eildun Lake, District of Mackenzie, N.W.T., Canada. Canadian Journal of Earth Sciences 22:663–674.

Sparks, D.R., and Malechek, J.C. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21:264–265.

Stien, A., Irvine, R.J., Ropstad, E., Halvorsen, O., Langvatn, R., and Albon, S.D. 2002. The impact of gastrointestinal nematodes on wild reindeer: Experimental and cross-sectional studies. Journal of Animal Ecology 71:937–945.

Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. Pollen et Spores 13:615–621.

Stuiver, M., Reimer, P.J., and Reimer, R. 2005. CALIB 6.0. http://calib.qub.ac.uk/calib/manual.

Szeicz, J.M., MacDonald, G.M., and Duk-Rodkin, A. 1995. Late Quaternary vegetation history of the central Mackenzie Mountains, Northwest Territories, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 113:351–371.

Thomas, D.C., and Kroeger, P. 1981. Digestibility of plants in ruminal fluids of barren-ground caribou. Arctic 34:321–324.

Thompson, R.S., Van Devender, T.R., Martin, P.S., Foppe, T., and Long, A. 1980. Shasta ground sloth (*Nothrotheriops shastensis* Hoffstetter) at Shelter Cave, New Mexico: Environment, diet, and extinction. Quaternary Research 14:360–376.

Todd, J.W., and Hansen, R.M. 1973. Plant fragments in the feces of bighorns as indicators of food habits. Journal of Wildlife Management 37:363–366.

van der Knapp, W.O. 1989. Past vegetation and reindeer of Edgeøya (Spitsbergen) between c. 7900 and c. 3800 BP, studied by means of peat layers and reindeer faecal pellets. Journal of Biogeography 16:379–394.

Vardy, S.R., Warner, B.G., and Aravena, R. 1998. Holocene climate and the development of subarctic peatland near Inuvik, Northwest Territories, Canada. Climatic Change 40:285–313.

Weaver, J.L. 2008. Conserving caribou landscapes in the Nahanni trans-border region: Using fidelity to seasonal ranges and migration routes. Wildlife Canada Conservation Report 4. Toronto: Wildlife Conservation Society.

Wiken, E.B., Compiler. 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series 19. Hull, Quebec: Environment Canada.

Wilmshurst, J.M., and McGlone, M.S. 2005. Origin of pollen and spores in surface lake sediments: Comparison of modern palynomorph assemblages in moss cushions, surface soils and surface lake sediments. Review of Palaeobotany and Palynology 136:1–15.

Yll, R., Carrión, J.S., Marra, A.C., and Bonfliglio, L. 2006. Vegetation reconstruction on the basis of pollen in Late Pleistocene hyena coprolites from San Teodoro Cave (Sicily, Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 237:32–39.