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Late Pleistocene age, size, and paleoenvironment of a caribou antler from Haida Gwaii, British Columbia

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Abstract: The basal portion of a fossil caribou antler from Graham Island is the only evidence of large terrestrial vertebrates older than the Fraser (late-Wisconsin) glaciation on Haida Gwaii. This antler has been radiocarbon dated three times by different laboratories and all ages fall within the mid-Wisconsin Olympia Interglaciation (Marine Isotope Stage 3, MIS 3). We suggest that the latest date, using ultrafiltration of bone collagen, is closest to the true age at 43 200 ± 650 years BP (48 200 – 45 200 cal BP). Previous paleoecological analysis from Graham Island reconstructed a vegetation cover during MIS 3 consisting of mixed coniferous forest with nonforested openings, similar to cool subalpine forests of today. These conditions are consistent with environments that support woodland caribou and the related extinct Dawson caribou. Morphometric comparison of antlers from woodland and Dawson caribou suggest that they are more similar than previously interpreted and raise questions about the inferred differences between the mainland and island subspecies.

Key words: Haida Gwaii, caribou, fossil antler, accelerator mass spectrometry dating, paleoecology, MIS 3.

Résumé : La portion basale de bois de caribou fossiles de l'île Graham est le seul indice de la présence de grands vertébrés terrestres plus ancienne que la glaciation de Fraser (Wisconsinien tardif) dans l'archipel Haida Gwaii. Le panache a été daté au carbone radioactif à trois reprises par différents laboratoires, et tous les âges tombent dans la période de l'interglaciaire d'Olympia du Wisconsinien moyen (stade isotopique marin 3, MIS 3). Nous suggérons que l'âge le plus récent, obtenu par la méthode d'ultrafiltration sur collagène osseux, est celui qui se rapproche le plus de l'âge réel, à 43 200 ± 650 ans BP (48 200 – 45 200 étal. BP). Une analyse paléoécologique antérieure de l'île Graham a reconstitué une couverture végétale durant le MIS 3 consistant en une forêt de conifères mixte avec des ouvertures non boisées, semblable aux forêts subalpines de régions fraîches actuelles. Ces conditions concordent avec des milieux qui supportent le caribou des bois et l'espèce apparentée aujourd'hui disparue du caribou de Dawson. La comparaison morphométrique de panaches de caribous des bois et de Dawson indiquerait une plus grande similitude des deux espèces qu'interprétée auparavant et soulève des questions quant aux différences inférées entre les sous-espèces continentales et insulaires. [Traduit par la Rédaction]

Mots-clés : Haida Gwaii, caribou, panache fossile, datation spectrométrie de masse par accélérateur, paléoécologie, MIS 3.

Introduction

Haida Gwaii (formerly Queen Charlotte Islands) is a large archipelago of two main islands and many smaller ones located about 80 km west of mainland British Columbia on the edge of the North American continental shelf. These islands have been called the "Canadian Galapagos" and have been the subject of much research on the biogeography and endemism of their fauna and flora as well as their glacial history (Foster 1965; review papers in Scudder and Gessler 1989; Fedje and Mathewes 2005).

Wigen (2005), in her review of the vertebrate fauna of Haida Gwaii, noted that the history of caribou deserves special consideration, likely due to the fact that the endemic form called Dawson caribou (*Rangifer tarandus dawsoni*) has long attracted attention and speculation regarding details of its origin, physical characteristics, and extinction (Seton-Thompson 1900; Foster 1965; Banfield 1963; Byun et al. 2002).

The geologist G.M. Dawson brought the existence of Haida Gwaii caribou to the attention of Ernest Seton-Thompson in 1899, who provided a preliminary description and named the new species *Rangifer dawsoni* (Seton-Thompson 1900) in honour of Dawson. It was later reduced to subspecies status (*Rangifer tarandus dawsoni*) of mountain caribou (woodland caribou) (*Rangifer tarandus caribou*), its likely ancestor. Three ecotypes of mountain caribou are currently recognized in British Columbia with different distributions (southern mountain, northern mountain, and boreal), but all are classified as the same subspecies (Ministry of Environment 2000). Mitochondrial DNA analysis (Byun et al. 2002) revealed that Dawson caribou are not genetically distinct from mountain caribou on the mainland of British Columbia, although the attributed physical characteristics of smaller size, reduced antlers, and pale pelage have long been recognized as distinctive and different when compared to mainland caribou. These characteristics are, however, based on few observations and a very small sample of antlers and skulls (including the holotype) and a skin of the last shot specimen (Banfield 1963).

It is not known if Dawson caribou is a postglacial neoendemic island form (Reimchen and Byun 2005), an older relict taxon, or even an immigrant from an unknown glacial refuge on the northwest coast. It is now widely accepted that glaciation of Haida

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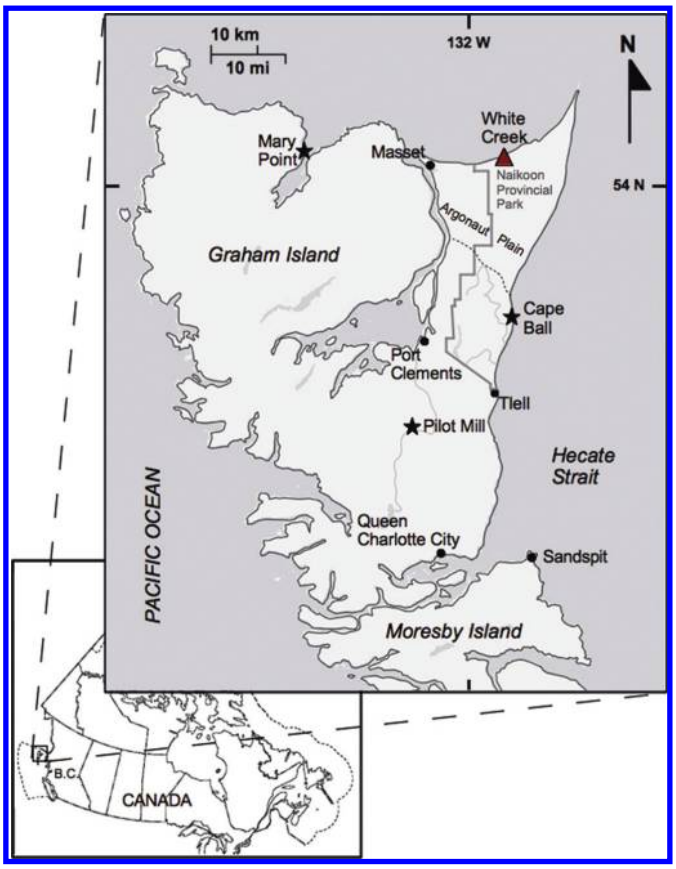
Fig. 1. Map of Graham Island showing the location of the White Creek antler collection site and other names mentioned in the text. [Colour online.]



Gwaii was less extensive than on the adjacent mainland, with a thin local ice cap that receded earlier here than elsewhere on the coast (Clague et al. 1982; Warner et al. 1982; Mathewes and Clague 2017). There is increasing evidence that ice-free biotic refugia existed along the northwest coast during the last (Fraser) glaciation on both geological and biological grounds (Heusser 1989; Heaton et al. 1996; Barrie et al. 2005; Carrara et al. 2007; Shafer et al. 2010; Mathewes et al. 2015; Mathewes and Clague 2017). Details of the extent of local ice cover and biological responses to it are still uncertain, although we know that lowered sea levels during late and postglacial periods exposed much of vegetated land that was not drowned until postglacial sea levels rose again (Fedje and Josenhans 2000; Lacourse et al. 2003), thereby reducing the isolation of Haida Gwaii from the mainland during glacial periods, which would facilitate migration by cold-adapted animals like caribou.

Fossil remains of caribou are known on Graham Island, Haida Gwaii, from several postglacial (~6000–1500 ^{14}C years BP) archeological sites such as Bluejackets Creek near Masset and Cohoe Creek near Port Clements (Fig. 1). Fossil caribou bones have also been dated to ca. 13 300 cal BP (Fedje and Smith 2010) at K-1 cave on northwestern Moresby Island along with grizzly and black bear remains and other vertebrates. This unpublished report confirms that caribou were once present on both Graham and Moresby islands.

Regarding the Graham Island skeletal elements, Wigen (2005) pointed out that none of these show evidence of the dwarfing attributed to Dawson caribou, suggesting that it may be a recent development. However, morphometric data are not presented in support of the contention that the archeological specimens are larger than those of Dawson caribou. Since the number of specimens of Dawson caribou available for study is very limited (several antlers and skulls and one skin, without other skeletal elements), it is possible that the range of body and antler sizes for Dawson caribou may have been larger than currently accepted. Dawson caribou is the only member of the deer family in which females supposedly do not possess antlers (Cowan and Guiget 1956), which complicates any generalizations due to the very small sample size of specimens and field observations.

The donation by Mr. Art Lightburn of a fossil caribou antler fragment to the Queen Charlotte Islands Museum (now Haida Gwaii Museum at *Kay Llnagaay*) in 1981 was a significant event, since it was the first find in a nonarcheological setting and listed by Wigen (2005) as the only definite preglacial vertebrate from Haida Gwaii. The fossil was found in sediments at the mouth of White Creek (Fig. 1), also known by its Haida name of *SGidlii Gandl*. Mr. Lightburn recalls only that he found the antler in 1978 "in one of the washouts at the mouth of White Creek" based on a telephone conversation with Mr. Lightburn by Nathalie MacFarlane on December 3, 2018. White Creek (54.0526°N, 131.88904°W) flows north on the Argonaut Plain (Fig. 1) and empties into the waters of South Beach along Dixon Entrance, where tidal influences and stream discharges create shifting conditions of erosion and deposition in the sand and gravel at the stream mouth.

This paper outlines the history of radiocarbon dating and paleoenvironmental interpretation of this antler fragment. Its age, based on the first radiocarbon date, has been variously cited (as personal communication with R.W. Mathewes) at around 40 000 years or older (Byun et al. 2002; Wigen 2005) but the actual ages have not been previously published and interpreted.

Materials and methods

The fossil caribou antler from White Creek represents the basal portion (burr) where it is attached to the skull and the main beam with two broken tines (brow and bez) (Fig. 2). It was originally made available to R.W. Mathewes for study and radiocarbon dating by the Queen Charlotte Islands Museum in 1994 and recently again for study and redating by the Haida Gwaii Museum at *Kay Llnagaay* at Skidegate, Graham Island, where it is housed under accession number NH 17001.

The first radiocarbon sample was prepared by Erle Nelson at Simon Fraser University, who extracted collagen and sent the sample for dating by accelerator mass spectrometry (AMS) to Lawrence Livermore National Laboratory in 1994. A second sample of tissue drilled from the interior of the antler was analyzed for DNA at the University of Victoria by Reimchen but no DNA was recovered. The remainder of this sample was later sent for AMS radiocarbon dating to Beta Analytic Inc. in Florida, who also determined a finite, but younger age than the original date. The most recent third sample using ultrafiltration dating of solid bone collagen was collected by M. Richards at Simon Fraser University and sent to the A.E. Lalonde AMS Laboratory at the University of Ottawa for analysis.

To evaluate morphometrics, we measured width and thickness at each of two positions on the fossil antler fragment (Fig. 2). Equivalent measurements were also obtained from antlers taken from three Dawson caribou killed in the late 1800s and early 1900s and from five woodland caribou from mainland British Columbia. All specimens are curated at the Royal British Columbia Museum, formerly known as the British Columbia Provincial Museum, Victoria. The four highly correlated metrics were reduced with principal components analysis before plotting.

Results and discussion

The three AMS radiocarbon ages from antler fragment NH 7001 are summarized in Table 1, showing the original and calibrated ages. Although the three finite AMS ages are different, they all fall within Marine Isotope Stage 3 (MIS 3), the mid-Wisconsin substage

Fig. 2. (A) Distal and (B) proximal views of the fossil caribou antler (NH 17001) from White Creek. The two measurement points for width and thickness are indicated by the double-headed arrows on Fig. 2A. The attachment point to the skull (burr) is at the base of both images. Scale bar = 5 cm. [Colour online.]

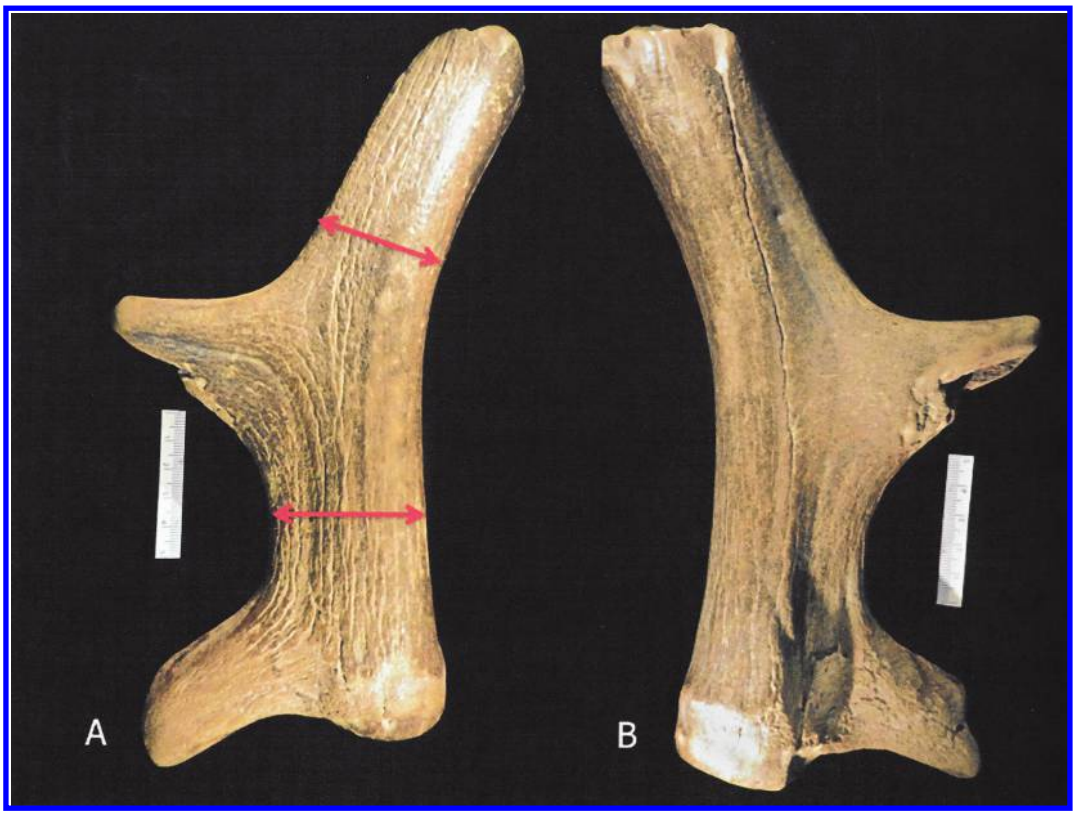


Table 1. Radiocarbon ages determined from the White Creek fossil caribou antler (Graham Island) from Haida Gwaii.

Radiocarbon age (^{14}C years BP)[a]	Calibrated age (cal years BP)[b]	Laboratory No.	Isotopic signature ^{13}C/^{12}C
32 980±180	38 500 to 37 000	BETA-317984	None
43 209±649*	48 200 to 45 200	UOC-5713	Measured: 14.6‰
47 600±2600*	57 600 to 43 300	CAMS-12921	None

Note: BETA, Beta Analytic Inc., Miami, Florida; UOC, A.E. Lalonde AMS Laboratory, University of Ottawa, Ottawa, Ontario, Canada; CAMS, Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, University of California, Berkeley, California.

*Material dated is collagen extracted from solid bone, except for BETA, which is collagen extracted from the interior cavity tissue.

[a]Error term ±1σ.

[b]Age range at ±2σ using the OxCAL4.2 Online calibration program (Bronk Ramsey 2009) with the IntCal 13 data set (Reimer et al. 2013) rounded to the nearest 100.

also known as the Olympia Interglaciation or Olympia Interstadial on the west coast (Hebda et al. 2016). Based on the latest ultrafiltration date on bone collagen, we consider the 43 200 BP age to be closest to the true age. It also overlaps the age range of the oldest age of 47 600 BP (Table 1). The youngest age (32 980 BP) falls outside the ranges of both older finite ages for undetermined reasons, but it was determined on tissue collected originally for DNA analysis from the inside (marrow region) of the antler, rather than on collagen extracted from solid bone.

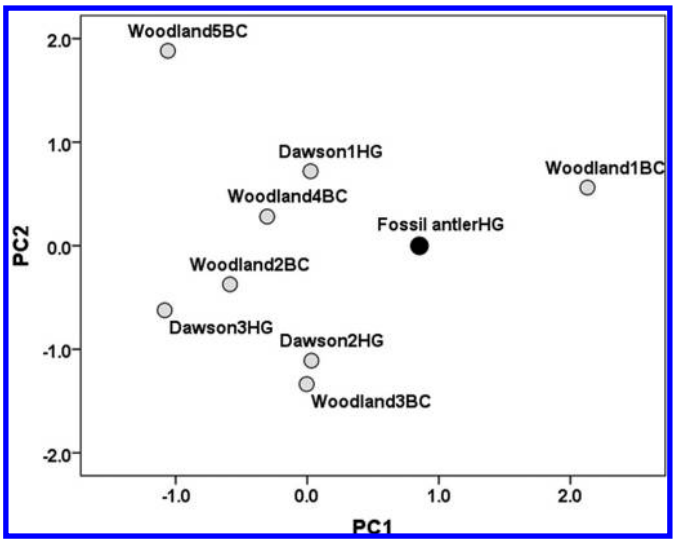
Relative to isotopic signatures for modern caribou from coastal Alaska and Svaalbard (Zwolicki et al. 2016; Pacyna et al. 2018), our signatures for the Haida Gwaii fossil caribou antler (δ^{13}C = –14.6‰, δ^{15}N = 9.9‰) are enriched. Such elevated isotopic values could be associated with consumption of terrestrial vegetation growing in the vicinity of seabird colonies (Zwolicki et al. 2016) or alternatively with consumption of intertidal algae, which are highly enriched in both isotopes (Fox et al. 2018). We are currently undertaking additional isotope studies of caribou (including sulphur isotope measurements and compound-specific amino acid isotope measurements) to better understand this surprising isotope result.

Paleoenvironment during MIS 3

The presence of caribou during the mid-Wisconsin is consistent with a local environment interpreted as being cooler than present, which supported coniferous forest with subalpine elements such as mountain hemlock (*Tsuga mertensiana*) and parkland- like openings with wet herbaceous meadows and peatland vegetation. This interpretation is based on the only MIS 3 pollen and plant macrofossil record from Haida Gwaii (Warner et al. 1984) recorded at the Pilot Mill site on Graham Island (Fig. 1). A photograph and ecological summary of the Pilot Mill peat bed are published in Mathewes (1989). The Pilot Mill peat study concluded that annual temperatures were lowered by 2 °C compared to modern and treelines were depressed by ~400 m. A review of mid-Wisconsin environments in other localities in western Canada and Alaska generally confirms cooler climatic conditions during MIS 3 (Clague et al. 2004; Hebda et al. 2016) with the most open and largely treeless conditions at the base of the Pilot Mill peat and also at the base of Lynn Valley peat at Vancouver at >48 ^{14}C ka BP (Hebda et al. 2016).

Mountain caribou require old-growth forests as winter habitat and for arboreal and terrestrial lichens as winter food, and the pollen record at Pilot Mill indicates a forest composed of spruce (*Picea*) and true fir (*Abies*) in addition to mountain hemlock, likely providing the needed forest cover for mountain caribou to thrive during winters.

Fig. 3. Principal components analysis of morphometrics of Dawson and woodland caribou antler beams from Haida Gwaii and mainland British Columbia. Dawson1HG is the type specimen (British Columbia Provincial Museum (BCPM) label 1483), Dawson2HG was shot in 1909 (BCPM label 1486), Dawson3HG is a museum mount (BCPM label 1484), Woodland1BC (BCPM label 1469), Woodland2BC (BCPM label 6933), Woodland3BC (BCPM label 1498), Woodland4BC (BCPM label 1837), and Woodland5BC (BCPM label 10225). All individuals are male except for Woodland5BC, which is female. The sex of the fossil antler is unknown.



The base of the Pilot Mill pollen record (zone P-1) dated at 45 700 ± 700 ^{14}C BP marks a change from basal sandy silt sediment with high Cyperaceae, grass, and diverse herbs of alpine to subalpine affinity to silty peat with increasing tree pollen and macrofossils of wetland and bog herbs in the upper part of the record. This herb-dominated basal unit is similar to the tundra environment recorded by pollen at Cape Ball during the preceding cold Marine Isotope Stage 4 (MIS 4) at around 57 000 years ago (Mathewes et al. 2015). The peat bed at Cape Ball contains fruitifactions and very abundant spores of several coprophilous (dung-loving) fungi, notably *Sporormiella* and *Sordaria* type, indicating the presence of unknown but likely large grazing mammals. Whether or not caribou were present on Graham Island at this time is not known, but the cold tundra-like environment of MIS 4 preceding the Olympia Interglaciation suggests the possibility that caribou have a longer history on Haida Gwaii than currently known.

Comparison of the fossil antler with woodland and Dawson caribou antlers

Of the four metrics measured on the fossil fragment and antlers from hunted caribou, the first principal component (PC1) accounted for 91% of the variation and was characterized by a size vector with all metrics loading very high (all >0.89). PC2 (7% of the variation) showed the highest loading (0.46) for maximum width at the base. A plot of the PCs (Fig. 3) shows a wide scatter with the fossil fragment exhibiting marginally higher PC1 values than all of the Dawson caribou as well as higher than four of the five woodland caribou. Dawson3HG, which is the smallest (<PC1) of all the samples, is similar in size to a female Woodland caribou (Woodland5BC). This is consistent with specimens found at the mid-Holocene Blue Jackets Creek site near Massett in which fossil caribou bones are inferred to be larger than those of the Dawson caribou and resemble in size those of the woodland caribou from mainland British Columbia (Wigen 2005).

Although our study was not designed to evaluate the morphological uniqueness of Dawson caribou, the metrics that we identified on the antlers allow comment on this issue. Seton-Thompson (1900) and subsequently Cowan and Guiget (1956) characterized the antlers of Dawson as "poorly developed", which accurately describes the antler (Dawson3HG) on the reconstructed mount widely used in descriptions of this caribou. Yet our data on the two additional antlers from this taxon as well as the fossil fragment show these to be similar or larger than three of the four male woodland caribou. Consequently, we suspect that the original characterization of Dawson caribou as a small-bodied form placed too much emphasis on the museum mount, which was the smallest of the three specimens. Accordingly, the evidence for the description of Dawson caribou as a "dwarf" subspecies of mountain caribou should be reexamined.

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