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A case of early Wisconsinan “over-chill”: New radiocarbon evidence for early extirpation of western camel (*Camelops hesternus*) in eastern Beringia

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ABSTRACT

There are comparatively few fossils that document the presence of the Pleistocene western camel (*Camelops hesternus*) in the unglaciated regions of Alaska and Yukon, northwestern North America (eastern Beringia). It has been previously reported on the basis of stratigraphic and radiocarbon data that this species was present within this region from the Sangamonian interglaciation (Marine Isotope Stage (MIS) 5) through the Last Glacial Maximum (LGM, MIS 2). However, the continued presence of western camel through the LGM is at odds with its ecological preferences as inferred from more southerly parts of the continent. Here we report 43 new radiocarbon dates on 34 western camel fossils from Alaska and Yukon, including specimens that have been dated previously. To minimize exogenous carbon contamination, we utilized either ultrafiltered collagen or single amino acid (hydroxyproline) methodologies in conducting the analyses. All samples, including previously reported specimens with finite ages, yielded ages that were either non-finite or close to the effective limit of radiocarbon dating. These results indicate that dates implying local presence of western camels in Alaska and Yukon during full-glacial conditions of MIS 2 are erroneous by as much as several tens of millennia, probably because of carbon contamination from glue or varnish used in fossil preparation and conservation. The revised radiocarbon chronology, together with other evidence, indicates that western camels were only able to occupy eastern Beringia only during Pleistocene interglaciations such as MIS 5, when forests and shrublands became the dominant regional biomes. The subsequent transition to cold, arid full-glacial conditions during the early Wisconsinan glaciation (MIS 4) around 75 000 years ago created unfavorable environmental conditions, eliminated browse, and led to their local extirpation in eastern Beringia. After their complete population loss in the Arctic and Subarctic, the range of western camels was restricted to the temperate mid-continent, where they eventually went extinct ~13 000 years ago.

1. Introduction

Robust radiocarbon (^{14}C) chronologies for Quaternary vertebrate fossils provide a solid empirical basis for estimating last appearance dates (LADs) and documenting biogeographical fluctuations (MacPhee et al., 2002; Barnosky et al., 2004; Stuart and Lister, 2014; Zazula et al., 2014; Stuart, 2015). In the absence of such chronologies, competing hypotheses concerning the relative influence of factors involved in biological declines or outright losses cannot be adequately tested (Stuart, 2015). However, just as radiocarbon dating methods have improved over the past several decades, concerns have arisen about the precision and accuracy of some previously reported dates on which many such hypotheses rely (e.g. Zazula et al., 2014). Testing and re-dating the fossils

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themselves may be necessary in some cases, in order to ensure that previously published radiocarbon dates on such specimens correctly reflect species chronologies.

Our particular interest concerns the use of radiocarbon records for assessing spatial and temporal patterns of Pleistocene megafaunal occupation in the unglaciated portions of Alaska and Yukon in the extreme northwest of North America (collectively, eastern Beringia; Fig. 1). During the late Quaternary, species living in the Arctic and Subarctic experienced substantial environmental change due to the advance and retreat of continental ice sheets associated with glacial-interglacial cycles (Guthrie, 1990, 2006; Muhs et al., 2001; Zazula et al., 2011). Environmental and paleontological records for eastern Beringia are consistent with the inference that there were times when environmental conditions were favorable for a wide variety of species, as well as other times when only the hardiest taxa would have survived. For widespread but less hardy taxa, records should show a predictable response to climatic oscillations: range reduction or local extirpation at high latitudes as conditions deteriorated, but continued presence elsewhere (such as mid-continental North America). Such generalizations about species adaptability, however, might be overturned if supposedly less hardy taxa could be shown to have persisted at high latitudes through a cold interval. Obviously, assessment of such push-pull responses in the biota requires a thoroughly reliable radiocarbon record (Zazula et al., 2014). Unreliable records may lead to unreliable inferences.

A case in point is the eastern Beringian record for the western camel, *Camelops hesternus* (Leidy, 1873). Western camels are of special interest because *C. hesternus* is one of the few megafaunal species, apart from proboscidean taxa, for which there is any evidence at all of human predation (Waters et al., 2015). This makes its disappearance from its former range particularly relevant to the debate over the cause of North American end-Pleistocene extinctions (Barnosky et al., 2004).

The North American endemic genus *Camelops* first appears in the fossil record of the southwestern USA during the late Blancan (late Pliocene to early Pleistocene) (Thompson and White, 2004). The terminal species *C. hesternus* reached its maximum distribution during the Rancholabrean (late Pleistocene), occupying the western half of the continent south of the continental ice sheets, as far as Honduras, before finally disappearing at the end of the Pleistocene (Webb, 1965; Pinsof, 2002; Lucas, 2008; Baskin and Thomas, 2015; Waters et al., 2015; Jass and Allan, 2016). But fossil records from Alaska and Yukon also establish that *C. hesternus* managed to reach eastern Beringia (Harington, 1977, 1997; Zazula et al., 2011, 2016; Heintzman et al., 2015, Fig. 1), thousands of kilometers from the arid, temperate southwest of the mid-continent. This is not necessarily surprising. *Paracamelus*, the only other camelid currently recognized in the fossil record of extreme northwest North America, entered Eurasia via Beringia during the late Miocene and possibly persisted in the Arctic until the Irvingtonian (early Pleistocene) (Rybczynski et al., 2013).

However, biogeographical and chronological details concerning *Camelops hesternus* in eastern Beringia are poorly understood. In contrast to abundant and well dated remains of taxa such as steppe bison (*Bison priscus*), woolly mammoth (*Mammuthus primigenius*), and horse (*Equus* sp.) in Alaska and Yukon (Guthrie, 2006), western camel fossils are rare in this region and generally lack stratigraphic or temporal context (Frick, 1930; Geist, 1953, 1956; Guthrie, 1968; Weber et al., 1981; Harington, 1997; Zazula et al., 2011;

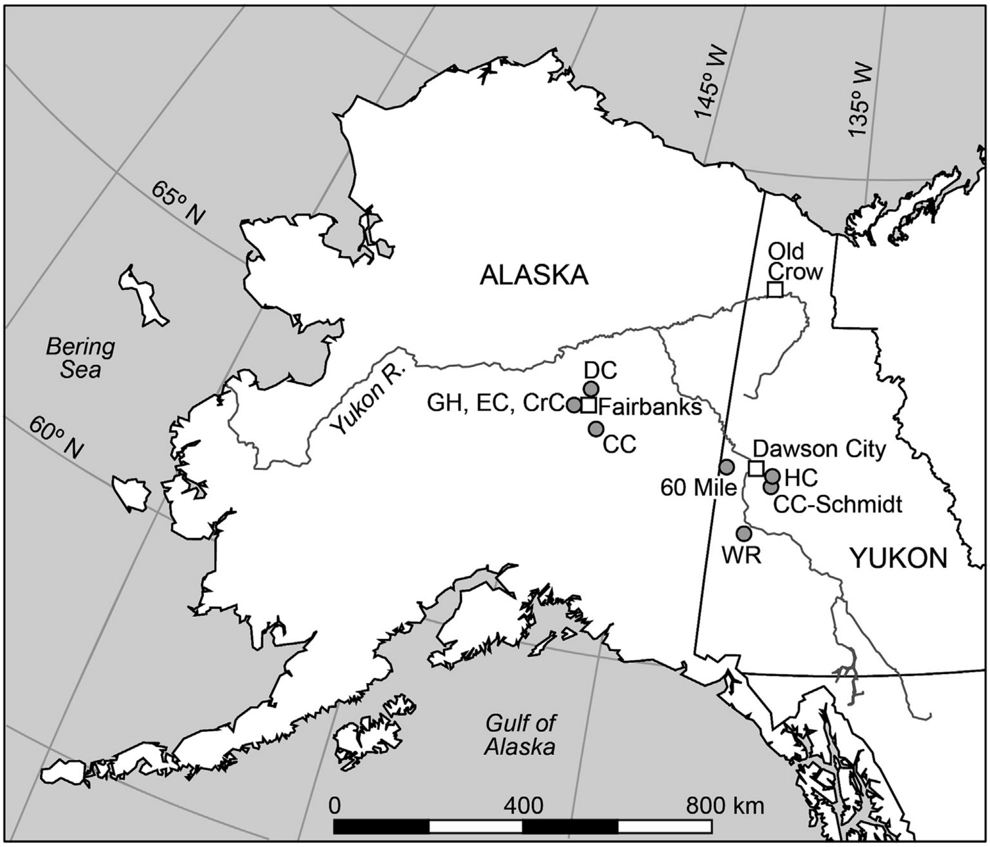

Fig. 1. Map of Alaska and Yukon with sites that have yielded *Camelops hesternus* fossils. 60 Mile = Sixtymile, Yukon; CC = Canyon Creek, Alaska; CC-Schmidt = Canyon Creek, Yukon; DC = Dawson Cut, Alaska; EC = Ester Creek, Alaska; GH = Gold Hill, Alaska; HC = Hunker Creek, Yukon; WR = White River, Yukon.

Heintzman et al., 2015). An exception is the partial proximal phalanx (YG 400.6) that was recovered *in situ* along the White River in southwest Yukon, within sediments dated to MIS 5e to MIS 5b (~115-87 ka (thousand years ago)), with associated paleoecological indicators for regional shrub-tundra vegetation (Zazula et al., 2011). This record demonstrates that western camels had dispersed into eastern Beringia from the mid-continent at least as early as the Sangamonian interglaciation.

However, published ^{14}C dates of 23 320 ± 640 ^{14}C yr BP (NMC 38227) and 19 770 ± 640 ^{14}C yr BP (YG 29.199) on *Camelops hesternus* fossils from Yukon (Table 1) have been interpreted to suggest that, although the taxon might never have been common, it was still regionally present during the late Wisconsinan (MIS 2) full-glacial (Harington, 1997, 2003; Storer, 2001). Harington (1997), trying to account for the presence of a camelid in eastern Beringia during the Last Glacial Maximum (LGM), inferred that it must have been primarily a grazer, able to tolerate the cold, arid, and periodically snow-covered steppe-tundra of eastern Beringia. Given this existing, yet sparse, chronology, it would be reasonable to hypothesize that, if western camels could have survived the LGM in Yukon and Alaska, then they should have been able to persist there into late-glacial times before dying out with the rest of the megafauna at the end of the Pleistocene (cf., Guthrie, 2006). Can such a long and apparently uninterrupted tenure, from MIS 5 though the end of MIS 2, be corroborated?

To address this question we radiocarbon dated, and in several cases, re-dated, as many western camel fossils from eastern Beringia as were available in order to establish a regional LAD (Fig. 2). If western camels had been present in eastern Beringia without interruption before, as well as during, the Wisconsinan full-glacial, then their radiocarbon date distribution ought not to show any particular bias. Conversely, a uniform skew of dates toward, or beyond, the analytical limit of radiocarbon dating (~50 000 ^{14}C yr BP) would imply a much different scenario—that *Camelops hesternus* was actually absent from eastern Beringia during most or all of radiocarbon time. The key problem then becomes how to account for the previously published finite dates that imply the persistence of *Camelops* into MIS 2.

2. Materials and methods

2.1. Fossil localities

The material analyzed for this study includes almost all the eastern Beringian fossils of *Camelops hesternus* in public institutions collected from the 1930s onwards (Fig. 2), as follows: (1) Frick Collections, American Museum of Natural History (AMNH), New York, USA (specimen acronym FAM): specimens from the Gold Hill, Cripple Creek and Engineer Creek placer gold mines near Fairbanks, Alaska, collected between the 1930s and 1950s (Geist, 1953, 1956; Guthrie, 1990). (2) Quaternary Vertebrates Collection, Canadian Museum of Nature (CMN), Ottawa, Canada (specimen acronym NMC): specimens from a gold mine locality at Sixtymile River, west-central Yukon, collected between 1975 and 1986 (Harington, 1997). (3) United States Geological Survey (USGS), Denver, USA (specimen acronym AWR): Three fossils collected along with other typical Rancholabrean taxa between 1974 and 1978 from a naturally occurring outcrop at Canyon Creek in east-central Alaska (Weber et al., 1981). (4) Yukon Government Palaeontology Program, Whitehorse, Canada (specimen acronym YG): Specimens collected since 2008 during annual surveys at placer gold mines at Hunker Creek and Canyon Creek, west-central Yukon. Fossil assemblages from Yukon placer gold mines yielding fossils of *Camelops hesternus* typically include remains of *Bison*, a biostratigraphic marker for the Rancholabrean (Froese et al., 2017). Detailed osteological descriptions of all western camel material reported in this paper, in addition to other specimens which were not radiocarbon dated, are reported in Zazula et al. (2016).

2.2. Sample selection and the problem of glues, varnishes and consolidants

A total of 34 specimens of *Camelops hesternus* were selected for ^{14}C dating and sampled using handheld, rotating/cutting tools. Visual inspection revealed that several of the western camel specimens from the AMNH, CMN and USGS collections selected for analysis were heavily treated with unknown museum conservation substances such as glues, varnishes and consolidants. In contrast, the fossils recovered by the Yukon Government Palaeontology Program since 2008 were not treated with any conservation substances. Analyses of the radiocarbon content of common museum conservation substances have conclusively established that these substances will affect radiocarbon dating if methodological precautions to remove them are not taken (Crann and Grant, 2016). For example, substances like shellac and fish-based glue that were typically used by museums decades ago contain “young” carbon and can make radiocarbon ages on bone “too young” if not adequately removed during sample pretreatment. Inversely, many of the petroleum based substances commonly used in present-day conservation treatments contain “old” carbon that make radiocarbon ages on bone “too old” if not removed (Crann and Grant, 2016). As we have noted in previous work on American mastodon fossils (Zazula et al., 2014), such substances may stabilize the fossils, but they substantially increase the likelihood that dated specimens will yield erroneous radiocarbon ages (Nalawade-Chavan et al., 2014; Zazula et al., 2014). Ultrafiltration (UF) pretreatment can effectively remove low molecular weight exogenous contaminants from collagen samples (Zazula et al., 2014). This is especially pertinent for samples suspected to near the effective limit of radiocarbon dating, because of the limited amount of endogenous ^{14}C left within the sample (Higham et al., 2006; Stuart and Lister, 2014).

Since many of the western camel fossils showed clear evidence of the use of varnish or glues, we were particularly concerned that

Table 1
Previously published radiocarbon dates on western camel fossils from Alaska and Yukon. STD = standard collagen treatment (Longin, 1971).

Specimen #	Element	Locality	^{14}C yr BP	±	Lab #	Collagen treatment	Reference
Yukon							
YG 29.199	metacarpal	Hunker Creek	19770	640	TO-7740	STD	Storer, 2001
NMC 38227	humerus	Sixtymile River	23320	640	Beta-8864	STD	Harington, 1997
NMC 42549	mandible	Sixtymile River	38980	350	Beta-115207	STD	Harington, 1997
NMC 46728	radius	Sixtymile River	43230	500	Beta-115205	STD	Harington, 1997
NMC 29194	astragalus	Sixtymile River	43580	1100	Beta-89985	STD	Harington, 1997
Alaska							
	metapodial	Fairbanks area	27900	1100	I-2117	STD	Harington, 2003

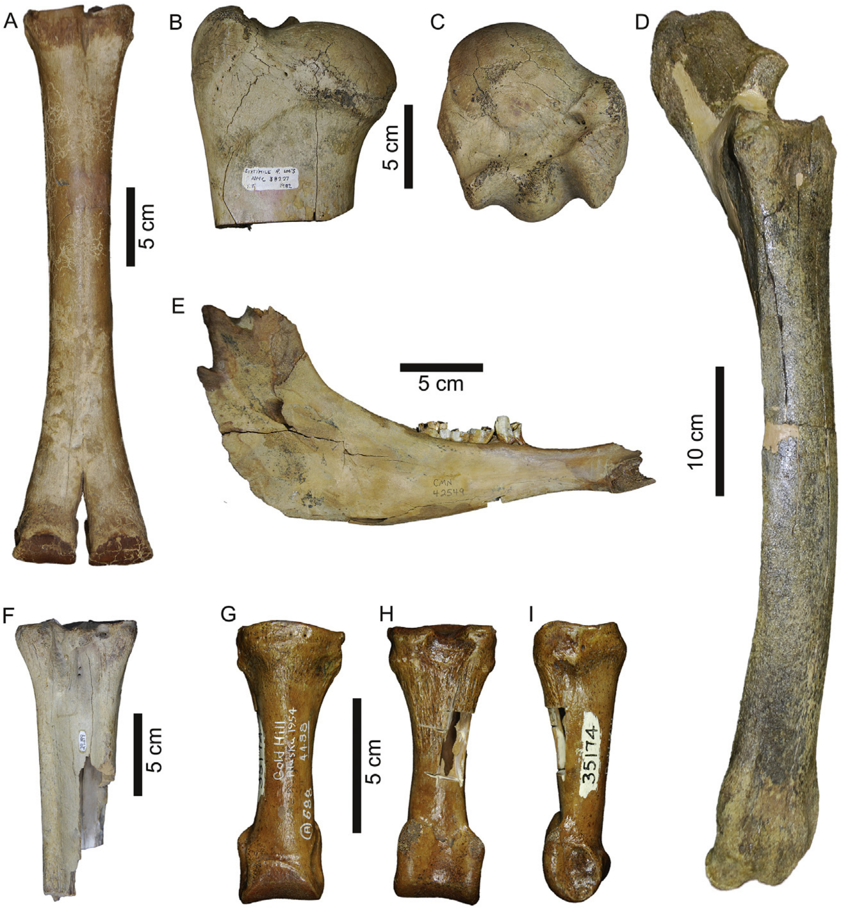

Fig. 2. Some of the fossils of *Camelops hesternus* that were radiocarbon dated as part of this study. A) Anterior view of metatarsal YG 328.23; B) medial view of humerus NMC 38227; C) proximal view of humerus NMC 38227; D) lateral view of radioulna 74-AWR-14; E) lingual view of mandible NMC 42549; F) Posterior view of metacarpal YG 29.199; G) anterior view of proximal phalanx FAM:35174; H) posterior view of proximal phalanx FAM:35174; I) medial view of proximal phalanx FAM:35174.

exogenous carbon contamination could affect our radiocarbon dates. First, we re-analyzed all samples that previously yielded finite radiocarbon dates, even if collagen extracted from them had undergone UF pretreatments. Re-extraction and rigorous UF revealed that initial pretreatments had not been adequate to remove all the exogenous carbon. For samples that were dated multiple times, each subsequent collagen preparation involved more rigorous attempts to remove exogenous carbon.

2.3. *Radiocarbon dating methods*

Collagen extraction was conducted at the Keck Carbon Cycle AMS facility at the University of California, Irvine (UCIAMS) using a modified version of the Longin (1971) method with ultrafilteration (UF) pretreatment (Beaumont et al., 2010). Briefly, specimens were manually cleaned with a handheld grinding tool, and samples of ~150 mg of crushed bone were decalcified for 24–36 h at room temperature in 0.5 M HCl, rinsed with Milli-Q water, hydrolyzed overnight at 60 °C with 0.01 M HCl, and filtered. The high molecular weight fraction (>30 kDa) of the resulting gelatin solution was freeze-dried, and aliquots were used for AMS radiocarbon dating (Beverly et al., 2010) and for stable isotope and elemental (C and N) analyses. For samples in which the presence of consolidants or varnishes was known or suspected, decalcification was preceded by sonication for 30 min each in acetone, methanol and water at ~45 °C; the solvent sonication was repeated if the initial treatment produced obvious flocculent material or solvent coloration. Aliquots of radiocarbon-dead mammoth and whale bone were prepared and measured with the fossil western camel samples to provide process blanks.

Collagen from two fossils (FAM:35152 and FAM:35174) showing physical evidence of varnish or consolidant (probably shellac) proved particularly recalcitrant during the initial pretreatment process. A second solvent approach was employed to remove the contaminant, based on the observation that aged/polymerized shellac can be depolymerized through treatment with slightly acidic alcohols (NIIR Board, 2002). These samples (and process blanks) were sonicated in ca. 5 ml of methanol acidified with 3 drops of 0.1 N HCl (1 hr), then MQ water (1 hr). Two variations on this procedure were attempted: first, sonication prior to decalcification, gelatinization at 75 °C and selection of an intermediate molecular weight fraction (3–30 kDa) by ultrafiltration; second, sonication after decalcification, followed by the standard UF protocol of 60 °C gelatinization and selection of the high molecular weight (>30 kDa) fraction.

A different approach was employed at the Oxford Radiocarbon Accelerator Unit (ORAU) for another problematic specimen (74-AWR-14) that was heavily coated with varnish or consolidant. Here the objective was to separate the amino acid hydroxyproline from hydrolyzed bone collagen using mixed-mode preparative chromatography (Stafford et al., 1991; McCullagh et al., 2010). The recovered hydroxyproline (Hyp) fractions were evaporated to dryness using a vacuum evaporator and reconstituted in pH 3 water so as to facilitate their application onto Chromosorb™ tin capsules on the day of combustion. ORAU's routine procedures were followed for combustion, graphitization and AMS dating of the hydroxyproline (Nalawade-Chavan et al., 2014). As a control, hydroxyproline fractions, using the same procedures, were separated from a laboratory background age standard, an Alaskan bison bone considered to be 70 000–60 000 yr BP (Brock et al., 2010).

3. Results and discussion

3.1. Radiocarbon dating results and problematic specimens

The pool of ^{14}C dates developed for this study is one of the most comprehensive LAD datasets currently available for *Camelops hesternus*. A total of 43 new radiocarbon dates were obtained from 34 specimens (Tables 2 and 3). Our dataset includes new dates (Table 2) on specimens from Yukon that were previously reported as having finite radiocarbon ages (Table 1). UF collagen from five of these (YG 29.199, NMC 29194, NMC 38227, NMC 42549, NMC 46728) yielded non-finite radiocarbon dates that are several tens of millennia older than previously published age determinations (Table 2; Fig. 3). Some of the newly dated museum specimens initially yielded finite ages, but as they had clearly been treated with conservation substances and their ages were strong outliers in the pattern of other radiocarbon dates, we suspected that remnant contamination was still present (Zazula et al., 2014; Stuart and Lister, 2014). Modified methods, including solvent sonication and dating the single amino acid hydroxyproline, were employed on these specimens to more effectively remove suspected contaminants; except in one case, subsequent re-analyses resulted in non-finite ages consistent with the rest of our dataset (Table 3). The exception is FAM:35161, which yielded a date of 47 400 ± 3400 ^{14}C yr BP, very close to, but still within, the effective limit of ^{14}C dating. Given that all other specimens returned non-finite ages after appropriate levels of pretreatment, we feel justified in regarding this date as an anomaly and strongly suspect it is actually non-finite in radiocarbon age.

The initial analysis of UF collagen from the radioulna 74-AWR-1, from Canyon Creek (Alaska), yielded a date of 34 590 ± 810 ^{14}C yr BP (UCIAMS 124938). This date seemingly indicates that *Camelops hesternus* was present in central Alaska during the MIS 3 interstadial. However, Weber et al. (1981) remarked that this specimen was recovered *in situ* from sediments that hosted reworked pods of Dome Ash Bed, a tephra that post-dates the peak warmth of MIS 5e and likely dates to one of the later sub-stages of MIS 5 or early MIS 4 (Muhs et al., 2008; Jensen et al., 2016). A subsequent radiocarbon date on the hydroxyproline fraction of this specimen produced a non-finite age of >48 100 ^{14}C yr BP (OxA-28664), which places it beyond the effective limit of radiocarbon time and is consistent with the site tephrostratigraphy (Weber et al., 1981) and the rest of our dataset (Table 3; Fig. 3). 74-AWR-1 is a specimen that had been broken in half, glued back together, and heavily coated with an unknown consolidant or varnish prior to our sampling. Thus, we infer that the initial, younger date was the result of incomplete removal of contaminating "young" carbon, even after ultrafiltration, while the SAA analysis provided a more reliable radiocarbon age assessment.

Ensuring date credibility where "young" carbon contamination is suspected can be both difficult and expensive. Two specimens from near Fairbanks, Alaska that originally yielded finite

Table 2
Previously reported and new studied western camel specimens from Alaska and Yukon with single new radiocarbon dates. UF = ultrafiltration.

Specimen #	Element	Locality	^{14}C yr BP	±	Lab #	>30kD collagen yield %	δ^{13}C (‰VPDB)	δ^{15}N (‰ air)	%N	%C	C/N (atomic)	Collagen treatment
New radiocarbon dates on previously published specimens												
Yukon												
YG 29.199	metacarpal	Hunker Creek	>49900		UCIAMS 72416	7.7	−20	4.4	13.9	39	3.27	UF
NMC 29194	astragalus	Sixtymile River	>48500		UCIAMS 175349	3.8	−19.6	3.8	14.9	41.4	3.23	UF
NMC 38227	humerus	Sixtymile River	>49900		UCIAMS 123843	6	−19.6	4.8	15.1	42	3.22	UF
			>45000		UCIAMS 124944	5.7	−19.6	4.5	16.1	44	3.21	UF
NMC 42549	mandible	Sixtymile River	>51200		UCIAMS 175351	5.5	−18.9	5.3	14.7	40.5	3.23	UF
NMC 46728	radius	Sixtymile River	>46900		UCIAMS 123844	3.9	−19.4	4.5	14.5	40	3.26	UF
New specimens with single radiocarbon dates												
Yukon												
YG 328.21	first phalanx	Hunker Creek	>51700		UCIAMS 117244	8.4	−19.7	7.6	15.9	44	3.22	UF
YG 328.22	first phalanx	Hunker Creek	>51700		UCIAMS 117245	7	−19.7	4.2	15.9	45	3.30	UF
YG 328.23	metatarsal	Hunker Creek	>51700		UCIAMS 117246	9.8	−19.3	4.9	15.6	43	3.23	UF
YG 328.259	metacarpal	Hunker Creek	>49900		UCIAMS 72418	7.2	−19.6	6.9	15.3	43	3.28	UF
YG 328.281	first phalanx	Hunker Creek	>50300		UCIAMS 117247	9.4	−19.3	4.6	15.9	44	3.23	UF
YG 328.287	metatarsal	Hunker Creek	>49900		UCIAMS 72417	8.1	−19.4	4.7	14.5	41	3.27	UF
YG 474.52	radius	Hunker Creek	>49200		UCIAMS 151377	5	−19.4	4.3	16.3	44	3.15	UF
YG 474.89	metacarpal	Hunker Creek	>46400		UCIAMS 151378	1.6	−19.7	5	14.2	40	3.29	UF
YG 474.262	tibia	Hunker Creek	>49200		UCIAMS 151380	2.7	−19.9	5.8	15.2	43	3.33	UF
YG 474.285	radioulna	Hunker Creek	>49200		UCIAMS 151379	4.6	−19.8	4.8	15.9	43	3.19	UF
YG 504.32	first phalanx	Hunker Creek	>48500		UCIAMS 156798	1.6	−20.8	7.4	13	42	3.79	UF
YG 504.64	radius	Hunker Creek	>51700		UCIAMS 156797	3.9	−19.5	4.1	14.9	43	3.35	UF
YG 587.1	first phalanx	Canyon Creek	>49200		UCIAMS 175354	3.6	−19.6	4.2	14.8	43	3.35	UF
YG 587.2	radioulna	Canyon Creek	>51700		UCIAMS 171261	5.1	−19.6	5	15.4	43	3.22	UF
YG 587.3	metatarsal	Canyon Creek	>51700		UCIAMS 171262	7.9	−19.5	4.1	15.3	42	3.17	UF
YG 587.4	radioulna	Canyon Creek	>51700		UCIAMS 171263	2.1	−21.7	8.8	12.2	34	3.21	UF
NMC 38226	astragalus	Sixtymile River	>41200		UCIAMS 175352	8.3	−19.7	4.5	15.4	42.3	3.20	UF
NMC 38277	humerus	Sixtymile River	>54000		UCIAMS 175350	6	−19.6	4.5	15.0	41.1	3.19	UF
NMC 42104	metapodial	Sixtymile River	>48800		UCIAMS 123845	2.4	−19.8	4.3	15.1	43	3.33	UF
NMC 42390	metacarpal	Sixtymile River	>49900		UCIAMS 123846	5	−19.6	6.2	15.1	42	3.27	UF
NMC 42515	calcaneum	Sixtymile River	>54000		UCIAMS 175348	9.4	−19.7	4.5	15.7	43	3.21	UF
Alaska												
FAM:35161	first phalanx	Cripple Creek	47400	3400	UCIAMS 124942	6.4	−20.7	7.2	15.7	43	3.22	UF
FAM:35175	calcaneum	Gold Hill	>48300		UCIAMS 124941	4.4	−19.6	6.3	15.3	42	3.20	UF
FAM:35150	first phalanx	Engineer Creek	>48100		UCIAMS 124945	6.2	−19.8	5.9	15.8	43	3.20	UF
FAM:35159	first phalanx	Cripple Creek	>45600		UCIAMS 124940	5.9	−20.4	7.9	14.5	40	3.20	UF

Table 3
Newly studied western camel specimens from Yukon and Alaska with multiple radiocarbon dates. UF = ultrafiltered; UFSS = ultrafiltration with acidified solvent sonication; HYP = hydroxyproline amino acid.

Specimen #	Element	Locality	^{14}C yr BP	±	Lab #	>30kD collagen yield %	δ^{13}C (‰ VPDB)	δ^{15}N (‰ air)	%N	%C	C/N (atomic)	Collagen treatment
Yukon												
YG 474.237	metatarsal	Hunker Creek	46700	2200	UCIAMS 156941	1.2						UF
			>52200		UCIAMS 175353	2.8	−19.2	4.9	14.8	42.4	3.34	UF
Alaska												
FAM:35174	first phalanx	Gold Hill	39300	1200	UCIAMS 124939	3.6	−19.5	3.4	13.9	39.9	3.34	UF
			48100	2000	UCIAMS 175972							UFSS
			48600	2100	UCIAMS 175357	3.5	−19.2	3.5	14.8	40.8	3.21	UF
			>46700		UCIAMS 176688							UFSS
FAM:35152	metatarsal	Cripple Creek	44200	2000	UCIAMS 124943	4.9	−19.6	5	16	44.6	3.27	UF
			51300	3000	UCIAMS 175356	5.8	−20	6.3	15.1	41.8	3.22	UF
			>52200		UCIAMS 175971							UFSS
			>51200		UCIAMS 176687							UFSS
74-AWR-14	radioulna	Canyon Creek	34590	810	UCIAMS 124938	2.2	−20.3	5.7	14.8	41.4	3.28	UF
			>48100		OxA-28664		−24.23					HYP

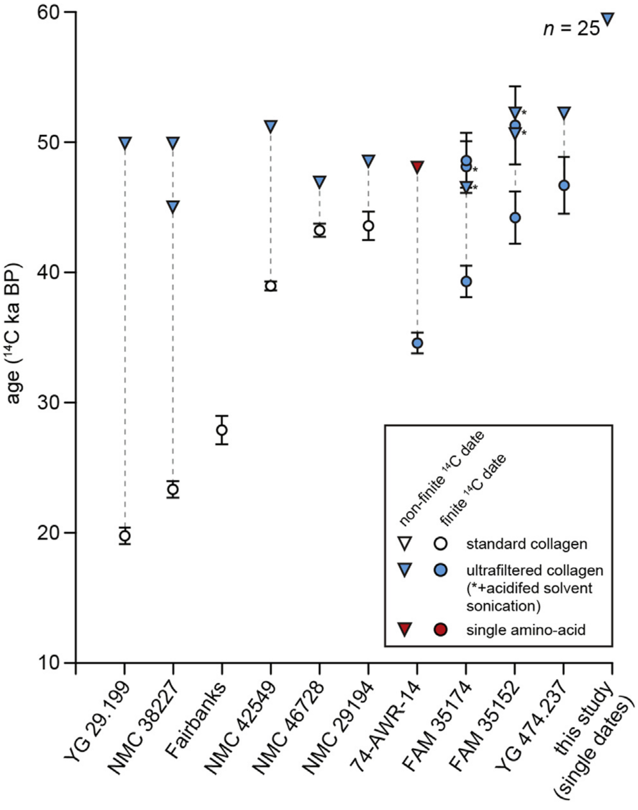

Fig. 3. Summary of the effects of different western camel bone collagen pretreatments on ^{14}C dates. Age (ka) = 10^3 ^{14}C years BP. White, blue and red symbols denote, respectively, standard collagen, ultrafiltered collagen, and single amino acid hydroxyproline. Finite ^{14}C ages (circles) have 1σ laboratory uncertainty bars. Non-finite ^{14}C dates (triangles) should be interpreted as "greater than" the indicated age.

radiocarbon dates on UF collagen were subsequently retested using modified collagen preparation methods (Table 3; Fig. 3). The original sample cut from the metatarsal FAM:35152 was treated with collagen UF methods and yielded a date of 44 200 ± 2000 ^{14}C yr BP (UCIAMS 124943). However, it was observed that the varnish had penetrated rather deeply into the bone and we suspected it may have affected the radiocarbon date. A second sample was subsequently cut from the fossil and its outermost portion discarded. Analysis of this second sample resulted in another, but older, finite date of 51 300 ± 3000 ^{14}C yr BP (UCIAMS 175356). Investigation could have ended here, with the conclusion that, as both results were finite, western camels were evidently able to survive in Alaska during MIS 3. Although the conclusion was certainly reasonable at one level, the two dates were still considerable outliers in the overall dataset. As a further test of accuracy, we employed a modified collagen UF treatment (acidified solvent sonication) on the remaining material from the second sample of FAM:35152, which yielded two non-finite ages, >52 200 and > 51 200 ^{14}C yr BP (UCIAMS 175971 and 176687).

This experience prompted us to use the acidified solvent sonication method on another problematic specimen of doubtful age, the phalanx FAM:35174 (Table 3). This specimen had originally yielded finite ages of 39 300 ± 1200 ^{14}C yr BP (UCIAMS 124939) which was suspected to be problematic since the specimen was heavily varnished. After more rigorous physical removal of varnish on the specimen surface, and collagen treatment prior to decalcification the high temperature gelatinization gave a very low yield of 3–30 kDa collagen (<1%) and resulted in a radiocarbon age of 48 600 ± 2100 ^{14}C yr BP (UCIAMS 175357). However, a third sample was subjected to post-decalcification acidified solvent treatment plus the standard gelatinization/UF protocol and returned a non-finite age on the >30 kDa UF collagen fraction of >46 700 ^{14}C yr BP (UCIAMS 176688), possibly because the treatment was more effective in removing exogenous contaminants. The efforts to radiocarbon date this specimen demonstrates that UF collagen pretreatments can yield age assemblages spanning ~10 000 years for highly contaminated specimens.

3.2. Dating outliers

Obviously, there has to be a limit—financial, if nothing else—imposed on how many re-analyses should be undertaken on any given sample. The integrity and long-term interests of the fossil specimen must also be considered, especially if species are rare in a particular region such as *Camelops hesternus* in eastern Beringia. Removal of multiple subsamples may cause substantial physical damage to the fossil and compromise the value of the specimen for subsequent research. Our objective in this particular case was to establish whether there really was consistency in our data set: although the date trend was clearly in favor of concluding that *Camelops hesternus* had not occupied northwestern North America during the last ~50 000 years, the number of dates we originally obtained that hovered around the limit of radiocarbon time could not be ignored. The only way of proceeding was therefore to date or re-date as much of the western camel material that was available to us.

Even so, we were not able to resolve all cases, such as the date of 47 400 ± 3400 (UCIAMS 124942) obtained from a heavily varnished proximal phalanx FAM:35161 from Alaska (Table 2). This date is at the effective limit of radiocarbon dating but still remains as the only analytically finite result in our new dataset and stands as an outlier. In view of the problems encountered with exogenous carbon contamination in other specimens, this result must be considered suspect, and therefore rejected (Stuart and Lister, 2014).

Another specimen previously reported as yielding a finite radiocarbon date remains untested, though we consider it problematic (Table 1; Fig. 3). A metapodial specimen from Livengood, near Fairbanks, Alaska, lacking both accession number and named repository, has a reported age of 27 900 + 1100/-1000 yr BP (Table 1; I-2117; Harington, 2003). In an earlier paper Harington (1977) reported the date on this specimen as 24 900 + 1100/-1000 yr BP. We cannot resolve the discrepancy, but both versions are consistent with the conclusion that western camels lived in the area during the middle Wisconsinan interstadial of MIS 3 (Harington, 1997, 2003). Searches were unsuccessful in the likeliest potential repositories (University of Alaska Museum of the North, American Museum of Natural History, Canadian Museum of Nature). Published date lists (e.g. Trautman and Willis, 1966) for ISOTOPES Inc. (later Teledyne Isotopes, Inc.), the laboratory that produced the date in question, indicate that “suitable bones” were routinely prepared for combustion and ^{14}C measurement by proportional gas counting using an early collagen extraction technique (Berger et al., 1964). Since the specimen was analyzed in 1968 or earlier, prior to the application of accelerator mass spectrometry to radiocarbon dating, in all likelihood the specimen was completely consumed for a conventional date. Our conclusion is that I-2117 must be considered a low-quality date given the great methodological and analytical advances in collagen preparation techniques and radiocarbon dating since the early 1970s. It is also important that it is unsupported by any other relevant evidence, such as complementary dates on other *Camelops hesternus* specimens. On these grounds we reject it as either erroneous or unverifiable.

4. Interpretations

4.1. Revised radiocarbon chronology for Camelops hesternus in eastern Beringia

In this paper we present a new radiocarbon dataset for *Camelops hesternus* and critically re-evaluate a series of finite dates that were previously interpreted to mean that western camels were continuously present in eastern Beringia during the MIS 3 interstadial and the Last Glacial Maximum (Harington, 1997, 2003; Storer, 2001). Our dataset is consistent with the conclusion that western camels had been locally extirpated in eastern Beringia tens of millennia before MIS 2, and thus well before the arrival of humans (Goebel et al., 2008) or the onset of any of the dynamic environmental changes of the terminal Pleistocene (Guthrie, 2006). We posit that western camels were eliminated from eastern Beringia prior to ~50 000 years ago, a temporal pattern of extirpation not experienced by megafaunal populations in southerly areas of North America as far as is now known. Further, the camel dates mirror results obtained for Alaskan and Yukon mastodon (*Mammut americanum*) fossils (Zazula et al., 2014), and represent another clear demonstration that fossils contaminated by conservation substances will yield erroneous radiocarbon dates when inadequate sample preparation methods are applied (Nalawade-Chavan et al., 2014).

4.2. Western camels of eastern Beringia during the last interglaciation

Data on habitat and forage preferences of western camels aid in the interpretation of their population history in eastern Beringia. Analyses of premaxilliary shape (Dompierre and Churcher (1996), meso/microwear (Jones and Desantis, 2015), hypsodonty indices (Semprebon and Rivals, 2010) and stable isotopes (Yann et al., 2016) collectively demonstrate that western camels were primarily leaf browsers living in habitats that included substantial trees and shrubs, rather than grazers that occupied open, herbaceous landscapes. Given this ecological constraint, western camels were probably able to disperse northwards into eastern Beringia only during times when warm climates permitted the growth of sufficient browse within boreal forest and shrubby habitats, such as during the Sangamonian interglaciation of MIS 5 (Muhs et al., 2001) or, possibly, earlier interglaciations.

The fossil phalanx (YG 400.6) from White River, Yukon, with a tephra date of 115–87 ka (Zazula et al., 2011), provides evidence for the earliest known occupation by western camels in eastern Beringia, within a habitat dominated by birch (*Betula*) shrub-tundra. However, interglacial occupation of eastern Beringia by western camels was likely terminated abruptly by the transition to the full-glacial conditions of the early Wisconsinan (MIS 4). Stratigraphic and paleoecological data from interior Yukon and Alaska demonstrate that severe cooling and aridification during the MIS 5-4 transition ~75 000 years ago eliminated widespread interglacial forests and shrub habitats and replaced them with cryo-xeric steppe-tundra (Muhs et al., 2001; Zazula et al., 2011). Climatic deterioration would have progressively limited browsing opportunities for small populations of *Camelops hesternus*, leading to their elimination or withdrawal southwards (Fig. 4). In short, this was a case of local extirpation by “over-chill”, caused by the apparent inability of the camels to adapt to full-glacial conditions at high latitudes. The result was a major reduction in the geographic range of western camels, which were thereafter restricted to more temperate areas south of the continental ice sheets.

4.3. Interglacial browsers in eastern Beringia

The advance of continental ice sheets, climatic cooling, and aridification during the MIS 5-4 transition ~75 000 years ago resulted in dramatic restructuring of the regional large mammal fauna in arctic and subarctic North America. Wisconsinan glaciation created climatic and physiographic conditions, such as arid, open steppe-tundra, that might well have been beyond the physiological limits of western camels and other interglacial browsers, especially

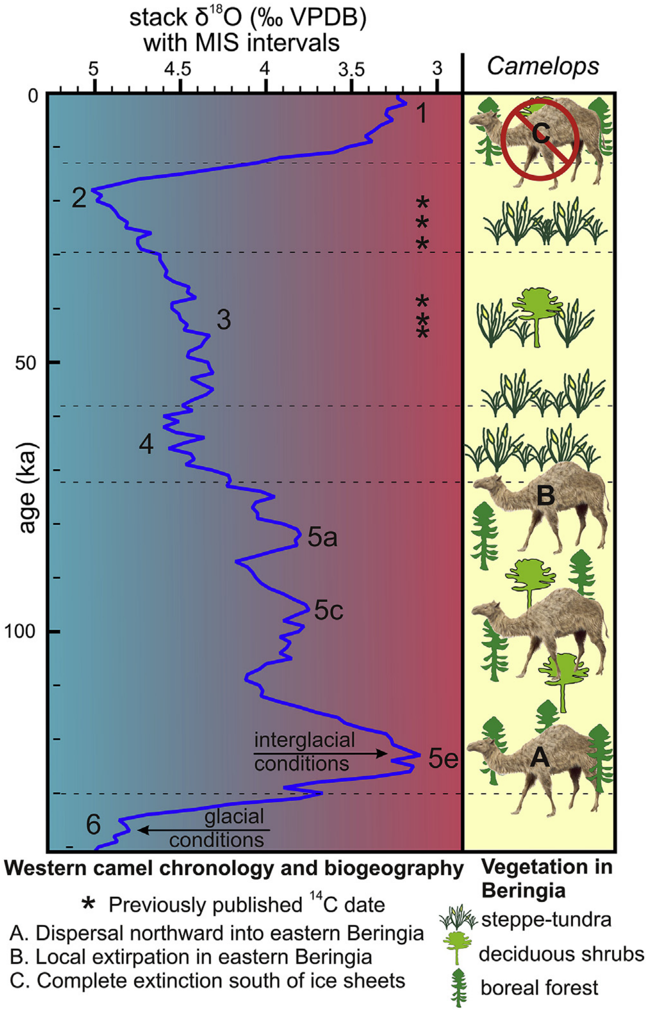

Fig. 4. Summary of late Pleistocene climate changes, Marine Isotope Stages and vegetation in eastern Beringia, and inferred biogeographic history of western camels. Age (ka) - 10^3 calendar years ago. The benthic foraminifera $\delta^{18}O$ stack data is from Lisiecki and Raymo (2005) and vegetation are from Muhs et al. (2001) and Zazula et al., 2014. Previously published radiocarbon dates on western camels are from Storer (2001), Harington, 1997, 2003.

during the winter season. This would have put western camels at a competitive disadvantage relative to better-adapted mammoths, horses, and bison in the comparatively nutrient-poor far north (Guthrie, 2006). Interglacial browsers that were adapted to the temperate south may have experienced great difficulty coping with the physiological and nutritional stresses associated with high-latitude seasonality, such as short, intense growth periods and marked nutrient deficits during long, cold winters. In effect, these species were occupying what must have been for them very marginal rangeland in the north. As a result, they may have suffered nutritional deficiencies that prevented them from achieving and maintaining body sizes similar to their southerly conspecifics. Precisely this kind of impact is reflected in morphometric analyses of both western camel (Zazula et al., 2016) and Jefferson's ground sloth (McDonald et al., 2000) from eastern Beringia. Even with smaller body sizes, seasonal challenges may have been further exacerbated as climates cooled and arid steppe-tundra replaced boreal forest. With the establishment of full-glacial conditions of the early Wisconsinan, local extirpation in eastern Beringia was seemingly inevitable.

The new data and interpretations presented here conform closely to those previously published for arctic and subarctic American mastodons (*Mammut americanum*) (Zazula et al., 2014). Other megabrowsers known to be rare in high-latitude faunas, such as Jefferson's ground sloth (*Megalonyx jeffersonii*) (McDonald et al., 2000) and giant beaver (*Castoroides ohioensis*) (Harington, 1990), are thought to have been similarly constrained; these taxa were likely only able to disperse northward and survive in Alaska and Yukon within the forest and shrubland habitats that characterized relatively warm interglacial climatic conditions. Interestingly, none of these species managed to disperse further west into Asia, which is consistent with the elimination of intercontinental migration routes due to submergence of the Bering Isthmus by high interglacial sea levels (e.g., Hu et al., 2010).

4.4. *High latitude versus temperate North American extinctions of the Pleistocene*

Finally, our new radiocarbon records for western camels in Alaska and Yukon underscore the point that the loss of North American megafauna was by no means a synchronous, cross-continental event during the terminal Pleistocene (Guthrie, 2006; Zazula et al., 2014). Some Holarctic species, especially those well adapted to open steppe-tundra habitats such as woolly mammoths (Guthrie, 2004) and horses (Haile et al., 2009), survived much later compared to their southerly counterparts. Others, particularly the endemic North American megabrowsers (*Camelops, Megalonyx, Mammut, Castoroides*), were apparently extirpated within eastern Beringia as a result of climatic cooling and habitat loss sometime shortly after the Sangamonian (MIS 5) interglaciation, though they persisted south of the continental ice sheets until the terminal Pleistocene. These data demonstrate that the problem of North American megafaunal extinctions should be examined both from a regional as well as a deep temporal perspective in order to examine population changes through successive periods of climatic oscillation in the late Pleistocene. Whether their final disappearance was driven by human overhunting, the Younger Dryas/Holocene transition, or both (or indeed neither), these opportunistic but ultimately poorly adapted species of megafauna suffered dramatic population losses in eastern Beringia and severe range reduction long before their last members succumbed to extinction.

5. Conclusions

New radiocarbon dates on fossils of western camels from Alaska and Yukon refute previous suggestions that they survived in the high latitudes of North America during the Last Glacial Maximum. Rather, our new high quality radiocarbon dataset, based on stringent pretreatment protocols to remove exogenous carbon contamination, reveals western camels suffered regional extirpation sometime before the ~50 000 year limit of radiocarbon dating. Western camels were browsers that seemingly were only able to disperse northward and occupy Alaska and Yukon during the relatively warm interglaciations, such as the Sangamonian of MIS 5, when widespread boreal forest and shrublands provided adequate forage. They subsequently became locally extirpated in eastern Beringia due to the dynamic effects of “over-chill” – the climatic cooling and loss of forested habitats at the onset of the Wisconsinan glaciation ~75 000 years ago during MIS 4. Thereafter, western camels continued to prosper in more southerly parts of North America until the terminal Pleistocene, when they were preyed upon by human hunters. Our data further establish that species losses in eastern Beringia were not synchronous with subsequent extinctions in areas south of the continental ice sheets (Guthrie, 2006). Large mammal communities living at high latitudes were actually in constant flux as a result of dispersal events and local extirpations in response to environmental change. Finally, our data also pose another cautionary tale regarding how regional vertebrate radiocarbon chronologies based on fossil specimens may be seriously compromised by the very conservation substances used to stabilize them.

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