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Rapid Communication

Last interglacial western camel (*Camelops hesternus*) from eastern Beringia

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ABSTRACT

Western camel (*C. hesternus*) fossils are rare from Eastern Beringia, thus there is little available information on their chronology, paleoecology, and biogeography in this region. In August of 2010, a partial proximal phalanx of a western camel was recovered from a sedimentary exposure along the White River, in the formerly glaciated terrain of southwest Yukon, northwest Canada. The fossil specimen was recovered *in situ* from sediments that are correlated by stratigraphic, tephra and radiocarbon data to the Marine Isotope Stage (MIS) 5 interglacial period (Sangamonian). Associated paleoenvironmental data indicates that this western camel inhabited a shrub tundra ecosystem that did not include spruce trees or boreal forest during a relatively cold interval between MIS 5e and 5a. This is the oldest reliably dated western camel fossil from Eastern Beringia and supports the model of range expansion for this species to the high latitudes of northwest North America during the last interglacial (*sensu lato*).

1. Introduction

Most Quaternary mammal faunas from the high latitudes of northwest North America, the region known as Eastern Beringia, are recovered from secondary contexts after having been eroded from natural sedimentary exposures or released from frozen ground during placer gold mining activity (Guthrie, 1968, 1990; Harington, 1977, 2003). As such, developing reliable chronologies and reconstructions of mammalian community dynamics are inherently difficult because so few fossils are found from well-defined stratigraphic contexts. This is especially true for faunas that may pre-date the effective limits of radiocarbon (^{14}C) dating (~50000 years BP) as there are few direct dating methods available to assign ages to those fossils. As a result, there are limited chronological data for many of the Pleistocene large mammals in Beringia, especially the rare taxa that are only known from a few localities. Because of the rarity of their fossils, camels are one of the large mammal taxa that have not received much consideration in the overall discussion of Beringian large mammals. However, a greater understanding of their chronology at the northwestern extremity of their geographic range can provide important information on mammalian population dynamics associated with widespread environmental change and extinctions during the late Quaternary.

In this paper we report a new specimen of western camel (*Camelops hesternus* Leidy, 1873) from a stratigraphic locality on the White River, southwest Yukon, Canada (Fig. 1). This is the first reported specimen for this taxon from formerly glaciated terrain in Alaska–Yukon. The specimen was recovered *in situ* from a constrained stratigraphic context which indicates that western camels inhabited this region during a relatively cold interval within the last interglacial (*sensu lato*), Marine Isotope Stage (MIS) 5, making this the oldest verified *C. hesternus* fossil material in Eastern Beringia.

2. Fossil camels in Eastern Beringia

The first discovery of fossil camel remains in northern North America by Copley Armory Jr. in 1912 led to great public and scientific interest. This early collection included a single camel phalanx (United States National Museum. No. 7713) along with

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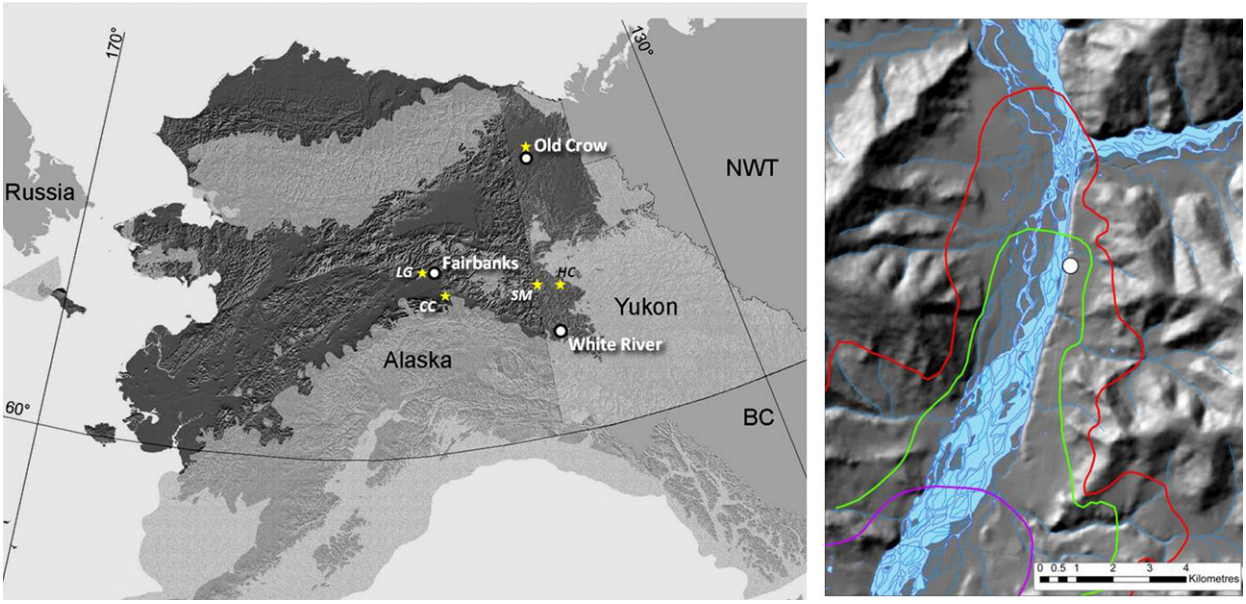

Fig. 1. Map showing location of the White River fossil locality relative to other *Camelops* localities recorded in Eastern Beringia. LG = Livengood, Alaska; CC = Canyon Creek, Alaska; SM = Sixtymile River, Yukon; HC = Hunker Creek, Yukon (left). The aerial photograph shows the fossil locality represented by the white dot on the eastern bank of the White River (right). The MIS 6 (Reid) glacial limit is in red (most extensive), the MIS 4 (Gladstone) limit is in green; whereas the MIS 2 (McConnell) glacial limit is shown in purple (least extensive).

a variety of other bones that were recovered about 80 km up the Old Crow River in northern Yukon and later reported by Gidley (1913); however, no generic or specific designation was provided for the specimen. Further examination of the specimen by Hay (1921) suggested this proximal phalanx represented a new species named *Camelus arctoamericanus* which he considered to be more closely related to extant camels (*Camelus*), rather than fossil *Camelops* which was known from the mid-continent.

Subsequent work on the Plio-Pleistocene vertebrate fauna from Eastern Beringia revealed that two species of camelids inhabited this region (Harington, 1977). Fossils of a larger bodied camelid, similar in size and morphology to members of the genus *Titanotylopus* Barbour and Schultz, 1934 (tribe Camelini) are best known from localities on the Old Crow River (Harington, 1977). Further examination of the specimen collected by Copley Jr. indicates it belongs to this group of large bodied fossil camels (Harington, 1977). These specimens may belong to the lineage of the late Pliocene-early Pleistocene true camels that crossed the Bering Land Bridge westward and eventually giving rise to extant Eurasian camels (Harington, 1977; Kurtén and Anderson, 1980). The second Pleistocene camelid taxon recorded in Eastern Beringia is *C. hesternus* (tribe Camelopini) which was confined to North America and best known from Late Pleistocene Rancholabrean faunas in the western half of the continent (Harington, 1977; Kurtén and Anderson, 1980). Systematic analysis of Cenozoic camels by Honey et al. (1998) suggests *Camelops* is more closely related to the clade which includes llamas (*Lama*) and vicugna (*Vicugna*), rather than the true camels. Specimens of *C. hesternus* have been reported from the Fairbanks region in central Alaska (Guthrie, 1968; Harington, 1977, 1997b; Weber et al., 1981), Old Crow River in northern Yukon (Harington, 1977) and near Sixtymile River (Harington, 1989, 1997a,b) and Hunker Creek (Zazula, unpublished) in the mining districts of west-central Yukon.

Five published radiocarbon dates obtained from *C. hesternus* fossils recovered near the Sixtymile River place them in the unglaciated region of west-central Yukon between ~44 000 and 23 000 ^{14}C yr BP (Harington, 2003). In addition, a metapodial recovered at Livengood near Fairbanks, Alaska yielded a radiocarbon date of 27 900 (+1000/-1100; Harington, 2002). However, considering that several of these ages are near the effective limits of radiocarbon dating (~50 ^{14}C kyr BP) and/or with large margins of error, we suggest that interpretations about *C. hesternus* chronology based on these dates should be considered tentative. At Canyon Creek, in interior Alaska, a radio-ulna, proximal phalanx and thoracic vertebra (Fig. 2) were recovered in sediments stratigraphically above MIS 6 Delta glaciation drift and below MIS 2 Donnelly glaciation colluvium. Based on the collective evidence from the site, Weber et al. (1981) suggest that the western camel remains at Canyon Creek are correlative to the MIS 3 Middle Wisconsinan interstadial. However, the chronological uncertainty on the Canyon Creek fossils, and tentative radiocarbon ages on other specimens recovered in the region, indicates that further work needs to be done to verify the MIS 3 interstadial presence of *C. hesternus* in Eastern Beringia.

3. Systematic paleontology and referred specimen

Class: Mammalia
Order: Artiodactyla
Family: Camelidae
genus: *Camelops* Leidy, 1854
C. hesternus (Leidy), 1873; western camel

The specimen Yukon Government (YG) 400.6 recovered along from the White River locality is a distal portion of a proximal phalanx (Fig. 3). This specimen closely matches other fossil material (Fig. 2c) and detailed lined drawings of *C. hesternus* proximal phalanges (Tables 10, 12 in Webb, 1965). Furthermore, measurements on the midshaft and distal portion of YG 400.6 (Table 1) more closely match the size of proximal phalanges of *C. hesternus* reported from California (Tables 10,12 in Webb, 1965), rather than those of the large bodied cf. *Titanotylopus* from Old Crow (Table 73 in Harington, 1977). Up to six species of Plio-Pleistocene *Camelops* have been described in North America, though the validity of some of these species has been questioned (Dalquest, 1992). A major problem in the precise identification of *Camelops* fossils is the reliance on molar teeth for specific characters, and most non-

Fig. 2. Fossil remains of *Camelops hesternus* from Canyon Creek, Alaska (Weber et al., 1981). Specimens from United States Geological Survey 74-AWR-14 B, identified by Charles Reppenning. Photographs of these specimens, including the proximal phalanx we used for comparison in our study, were not provided in the original publication by Weber et al. (1981), but are presented here (scale bar in centimeters): A) radio-ulna; B) thoracic vertebra; C) proximal phalanx.

cranial elements recovered from local faunas without holotypes are best referred to as *Camelops* sp. (Dalquest, 1992). However, we follow Harington's (1997a) view suggesting that Late Pleistocene smaller bodied camelid fossil material from Alaska–Yukon can be reliably referred to as *C. hesternus*.

4. White River locality

4.1. Stratigraphy, paleoenvironment and chronology

The western camel phalanx YG 400.6 was recovered in August 2010 by D. Turner and B. Ward *in situ* from the top of an 8 m high sedimentary exposure composed of five units, 7 km beyond the MIS 2 glacial limit (62° 34′ 41" N; 139° 59′ 47" W; Figs. 1 and 4). The complete description and analyses of the stratigraphic, chronological and paleoenvironmental data are presented in Turner et al. (in submission). The contextual data relevant to the western camel fossil are presented here.

Unit 1 is 3 m of till, likely deposited during the MIS 6 Reid glaciation (~190–130 ka) (Westgate et al., 2001). Above this, Unit 2 is 1 m of extensively weathered gravel with disintegrated clasts, ventifacts and other evidence of prolonged subaerial exposure. Unit 3 is 1.5 m of mostly inorganic loess, with Donjek tephra present discontinuously above the lower contact. Unit 4 is 1.5–4 m of organic-rich silt and sand. Snag tephra was identified in this unit. The top unit (Unit 5) is 1.5 m of till deposited during the MIS 4 Gladstone glaciation (~75–60 ka) (Ward et al., 2007). The two tills were interpreted as such because of their regional extensiveness, strong clast fabric orientations parallel to the valley, and the presence of keeled and striated clasts with lee-end fractures. Specimen YG 400.6 was located 50 cm below the contact between Units 4 and 5.

Fossil pollen and macrofossil data recovered in Unit 4 sediments associated with the *Camelops* specimen provide important paleoenvironmental information and refine the stratigraphic setting (Turner et al., in submission). Most of these data, including macrofossils of *Chara* and *Potamogeton* (pondweed) and *Pediastrum* (algae), suggest the western camel fossil was deposited in a pond. Other forb plant taxa, such as *Chenopodium* (goosefoot) and *Androsace septentrionalis* (fairy-candelabra), which typically inhabit dry, disturbed settings, suggest that the water levels in the pond fluctuated. However, abundant *Betula* (shrub type) and sedge (*Carex* spp.) pollen and macrofossils indicate the pond was situated in a region characterized by shrub birch tundra. A conspicuous lack of spruce pollen or macrofossil indicates that boreal forest was absent locally and regionally. Together, these data suggest that the *Camelops* from the White River locality inhabited a shrub-tundra ecosystem during a relatively cold interval within the MIS 5 interglacial. This camel did not inhabit, or at least this fossil was not deposited in, a boreal forest environment typical of true interglacial conditions that have been reconstructed for MIS 5e in the interior of Alaska–Yukon (Péwé et al., 1997; Muhs et al., 2001). Furthermore,

Fig. 3. Fossil partial proximal phalanx YG 400.6 *Camelops hesternus* from White River, Yukon (scale bar in centimeters): A) dorsal view; B) ventral view.

this ecosystem was not as cold and arid as those reconstructed for full-glacial conditions which were characterized by widespread herbaceous steppe-tundra communities, such as during MIS 2 and 4 (Zazula et al., 2007, in press).

Further constraint on the MIS 5 age for the western camel specimen YG 400.6 is provided by tephrochronology and stratigraphic relationships (Snag, Donjek and Woodchopper Creek tephras), and paleoenvironmental reconstructions at additional localities. Woodchopper Creek tephra (124–77 ka; Jensen et al., 2008), was identified ~12 m below a white spruce-rich fossil peat at a site along the White River ~500 m to the south. In the Klondike, ~175 km to the north, Woodchopper creek tephra lies in close association with Donjek tephra (B. Jensen, unpublished data) indicating a similar age for Unit 3. While this overlying peat bed could be either MIS 5c or 5a, a boreal forest unit described by Schweger (2003) at Ash Bend was assigned an MIS 5a age by Westgate et al. (2008), and confirms that boreal forest conditions existed in Yukon during MIS 5a. Snag tephra, sampled from Unit 4, was also identified above a different, likely MIS 5e aged white spruce (*Picea glauca*) peat bed 1 km to the south (Turner et al., in submission). These tephras and two peat beds therefore constrain the age of YG 400.6 to a relatively cold interval

Table 1
Measurements of proximal phalanges of *C. hesternus* from White River Canyon Creek, and California compared with those of large Camelini (cf. *Titanotylopus*) from Old Crow, Yukon. M = mean, OR = Observed Range, N = number of specimens.

Specimens		Measurements (mm)						
		Total Length	Proximal Width	Proximal Depth	Midshaft Width	Midshaft Depth	Distal Width	Distal Depth
First (proximal) phalanx								
Camelops hesternus								
White River, Yukon								
YG 400.6					22.9	25.9	31.5	24.8
Canyon Creek, Alaska								
74AWR14		105.4	46.4	40.7	22.2	28.4	36.3	29.2
Pleistocene, California								
Webb 1965, Table 10,11								
Forelimb	M	122.3 ± 1.62	47.3 ± 0.97	38.9 ± 1.20			39.9 ± 0.71	33.9 ± 0.71
	OR	117.0–127.0	44.0–52.0	36.0–45.0			38.0–42.0	32.0–37.0
	N	7	7	7			7	7
Hindlimb	M	108.4 ± 1.19	65.2 ± 1.04	38.7 ± 0.83			36.6 ± 0.85	31.1 ± 0.48
	OR	103.0–114.0	42.0–51.0	36.0–43.0			34.0–42.0	29.0–34.0
	N	9	9	9			9	9
large Camelini cf. *Titanotylopus*								
Old Crow, Yukon								
Harington, 1977, Table 73								
NMC 27266		134.3	56.1	46.9	34.9	29.1	50.9	40.0
NMC 26957		124.5	56.7	45.4	33.7	27.1	49.1	36.3
NMC 14775		121.0	62.0		33.0		50.0	
NMC8623 (USNM 7713)		115.2	52.5	40.7	34.1	25.2	44.8	34.4

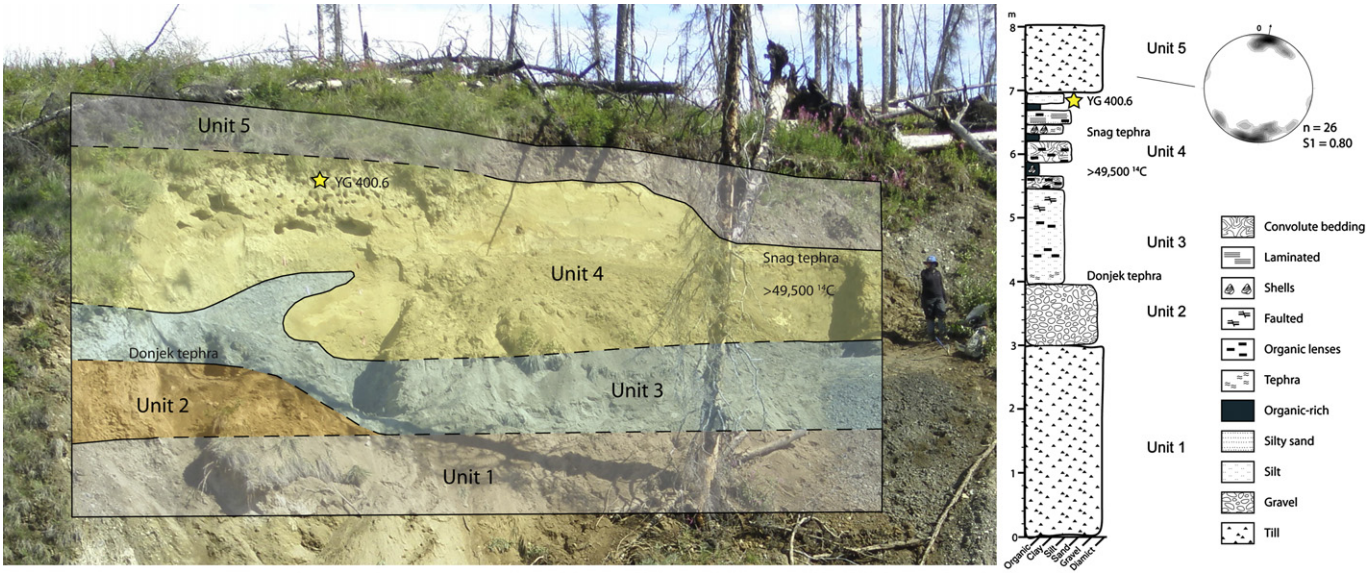

Fig. 4. Stratigraphy of the White River locality after Turner et al.'s, (in submission) Site D. Western camel specimen YG 400.6 was recovered from near the top of Unit 4.

between MIS 5e and 5a (~115–87 ka). This age range is allowed by a non-finite radiocarbon date of >49500 ^{14}C yrs (UCIAMS-40355) on a seed from Unit 4, 75 cm below the western camel specimen YG 400.6.

5. Discussion

The Late Pleistocene *C. hesternus* underwent its evolution in the southern latitudes of North America, being ancestrally derived from the Pliocene to early Pleistocene *Megatylopus* (Webb, 1965; Kurtén and Anderson, 1980). The genus *Camelops* first appears in the fossil record in the middle Blancan faunas (~3.2–4.0 Ma) from central Mexico (Jiménez-Hidalgo and Carranza-Castañeda, 2010) and the southern Plains (Morgan and Lucas, 2003; Thompson and White, 2004; Morgan and White, 2005). *Camelops* evolved into possibly as many as six distinct species through the Plio-Pleistocene, however, some camelid specialists recognize the need for a thorough reexamination of the genus (Webb, 1965; Dalquest, 1992; Jiménez-Hidalgo and Carranza-Castañeda, 2010). The species *C. hesternus* is best known from Sangamonian interglacial (MIS 5) and later Rancholabrean faunas from across western North America (Kurtén and Anderson, 1980; Pinsof, 1996; Harington, 1997b). Western camels survived in the North American mid-continent until ~10 300 ^{14}C yr BP with some fossil remains having been recovered from early Paleoindian archaeological sites (Haynes, 2009;Haynes, in press).

Various lines of evidence, including plant remains preserved in teeth (Akersten et al., 1988) and premaxillary morphology (Dompierre and Churcher, 1996) suggest *C. hesternus* was an "intermediate feeder", with a diet that included a mix of grasses and shrubs. Tooth wear analysis conducted on fossils of Late Pleistocene *Camelops* from the mid-continent further suggests that leaf browse was an important component of their diet (Semprebon and Rivals, 2010), with stable isotope data indicating an abundance of the halophytic C_4 shrub *Atriplex* (Vetter et al., 2007). This general trend of mixed feeding strategies in Late Pleistocene *Camelops* may have been an important factor in enabling the western camel to spread across a wide range of environments, from temperate to arctic latitudes, and persist through periods of climatically-induced changes in vegetation.

5.1. Western camel chronology in eastern Beringia

Evidence presented here from the White River localities suggests that western camels first entered the high latitudes of Eastern Beringia during a period of range expansion across western North America during the MIS 5 interglacial. The western camel specimen from White River was recovered in sediments that predate the MIS 4 Gladstone glaciation (~75–60 ka) and the MIS 5a warm substage, pushing back the timing of their appearance in Yukon to at least MIS 5b (>87 ka). Paleoenvironmental data from White River indicate that western camels inhabited a shrub tundra ecosystem during a relatively cold interval between MIS 5e and 5a, with climates seemingly colder than those typical for southwest Yukon at present. The breadth of dietary strategies exemplified in fossil *Camelops* (Dompierre and Churcher, 1996; Semprebon and Rivals, 2010) suggests western camels were capable of meeting their foraging needs in the subarctic shrub birch tundra. Data are inconclusive to whether western camel survived in Eastern Beringia beyond the last glacial maximum (MIS 2) because all previously obtained specimens seemingly correlate with the MIS 3 interstadial. However, as we suggest, some caution must be taken regarding interpretations of those data because of potential uncertainties with their radiocarbon ages and stratigraphic correlations. Although data concerning the timing and mode of western camel extinction in this region are inconclusive, the available evidence suggests they were locally extirpated from Alaska and Yukon several millennia before their last appearance dates on the mid-continent (Guthrie, 2006). The rarity of western camel fossils from Eastern Beringia indicates their populations remained low during the Late Pleistocene, putting them at substantial risk of local extirpation.

6. Conclusions

Western camel fossils are rare components of Late Pleistocene faunas of Eastern Beringia. A new fossil partial phalanx recovered *in situ* from a locality on the White River in southwestern Yukon reported here provides evidence for *C. hesternus* in Yukon during a relatively cold interval within the MIS 5 interglacial (~115–87 ka). Associated paleoenvironmental data indicate that this western

camel inhabited a regional shrub-tundra ecosystem within a climate that was too cold to support spruce forests, yet not as cold and arid as the steppe-tundra of full-glacial periods. As a mixed feeder, the western camel was certainly capable of meeting its dietary requirements across a range of Late Pleistocene ecosystems, a factor which likely facilitated its range expansion across western North America and northward into Eastern Beringia during the last interglacial period.

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