Osteological assessment of Pleistocene *Camelops hesternus* (Camelidae: Camelinae: Camelini) from Alaska and Yukon

GRANT D. ZAZULA,[1] ROSS D. E. MACPHEE,[2] ELIZABETH HALL,[1]
AND SUSAN HEWITSON[1]

ABSTRACT

During the past century, fossils of Pleistocene camels have been occasionally reported from unglaciated regions of Alaska and Yukon (collectively known as eastern Beringia), yet detailed descriptions of these materials are limited or lacking altogether. The detailed osteological treatment presented here establishes that these fossils are virtually indistinguishable from the species *Camelops hesternus*, a common member of Blancan to Rancholabrean faunas and known best from temperate regions of western North America. Metrically, high-latitude members of *C. hesternus* seem to have been smaller bodied than representatives from more southerly parts of the species range, a finding that is consistent with body-mass differences among populations of other large mammals whose ranges extended into the far north. The presence of *C. hesternus* in Alaska and Yukon was likely episodic, limited to relatively warm intervals such as the Last Interglaciation (Sangamonian).

INTRODUCTION

The unexpected news that camels once inhabited arctic North America was first revealed in a *New York Times* article announcing the discovery of Pleistocene camel fossils in northern Yukon, Canada (Armory, 1913; Gidley, 1913). Although extant camels and llamas are popularly

associated with the hot, arid regions of Africa, Asia, and South America, living camelines are also well suited to relatively cold contexts. From that perspective their previous presence in Pleistocene high-latitude North America is unsurprising, although their record is relatively scanty. Paleontological research for over a century has diligently attempted to clarify which of the two surviving, little-varied tribes of Camelinae these arctic and subarctic camels most likely belong to—the Afroasian Camelini (*Camelus bactrianus, C. ferus,* domesticated and wild Bactrian camels respectively; *C. dromedarius*, dromedary), or the South American Aucheniini (*Lama glama*, llama; *L. guanicoe*, guanaco; *Vicugna vicugna,* vicuña/alpaca).

The Eurasian fossil record reveals that camelids first dispersed from North America across the Bering Isthmus during the Late Miocene (Pickford et al., 1995), indicating that by this point at least some late Neogene taxa were already well adapted to high latitude conditions. Supporting this inference is the fact that fossils of so-called giant camels, mostly lacking temporal contexts, have been occasionally recovered in the highly fossiliferous deposits of Old Crow basin in northern Yukon (67° N). Harington (1977) noted that these fossils are similar to large-bodied camelins such as *Titanotylopus*, known from the Miocene of midwestern North America (Barbour and Schultz, 1939), and *Paracamelus*, the presumed ancestor of extant *Camelus* (Zdansky, 1926) from the Pliocene of Eurasia. Recently, remains of a large-bodied camel were recovered at a site located at 78° N on Ellesmere Island in the Canadian High Arctic, and cosmogenically dated to ~3.8 million years ago (Rybczynski et al., 2013). Morphological and proteomic results indicate that the Ellesmere Island taxon (currently unnamed) is probably related to the large Yukon camelin and/or Eurasian *Paracamelus*, indicating that one or more species of these big-bodied, wide-ranging artiodactyls spanned the Holarctic during the Early Pliocene to Middle Pleistocene (Rybczynski et al., 2013).

There were, however, much smaller camelins in high-latitude northwestern North America that persisted into the Late Pleistocene. Fossils attributable to the genus *Camelops* have been occasionally reported from deposits exposed at placer gold mines and other sites in the subarctic interior of Alaska and Yukon (Frick, 1930; Geist, 1953, 1956; Guthrie, 1968; Weber et al., 1981; Harington, 1997) (fig. 1). In contrast to the abundance of typical Rancholabrean large mammals such as steppe bison (*Bison priscus*), woolly mammoths (*Mammuthus primigenius*), and horse (*Equus* spp.) frequently recovered at these localities (Harington, 1977), *Camelops* remains from Alaska and Yukon are exceptionally rare. Perhaps for this reason these fossils have received very limited study and their systematic status remains obscure. Although usually referred in the literature to *Camelops*, how they relate systematically to much better-known members of this genus from midcontinental North America, such as *Camelops hesternus*, or to other aucheniins such as *Hemiauchenia,* is poorly understood. The same applies to their affinities—if any—with the "giant" lineages known from the same region.

Taxonomy, Nomenclature, and Phylogeny of Camelops

Morphological convergence is pervasive among cameline lineages (Dalquest, 1992). Indeed, the scale of parallelism is so egregious in both camelins and aucheniins that virtually every diagnostic character that has been proposed in the past to diagnose one or another natural

FIG. 1. Map of Alaska and Yukon with sites mentioned in this paper. 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; 60 Mile = Sixtymile, Yukon.

grouping at low taxonomic levels is encountered in other, unrelated lineages (Churcher, 1965; Harrison, 1979). A direct function of this is the large amount of species-level synonymy due to oversplitting (Savage, 1951; Pinsof, 1998). These problems are particularly well demonstrated in the genus *Camelops*.

The type species *Camelops kansanus* was first described by Leidy (1854) on the basis of a partial left premaxilla/maxilla with associated canine, discovered in "gravel drift" in Kansas. The generic name "*Camelops*" was largely ignored in subsequent publications. Leidy (1873) himself referred Pleistocene camelines from California now recognized as *Camelops* to "*Auchenia hesterna.*" The name *Camelops* was revived by Wortman (1898) as part of his generic revision of this taxon. He synonymized three nominal species that he considered indistinguishable from one another—*Camelops hesternus* (= *Auchenia hesterna*) (Leidy, 1873), *Camelops huerfanensis* (Cragin, 1892), and *Camelops sulcatus* (Cope, 1893)—with the type species *Camelops kansanus*. However, Savage (1951) demonstrated that the *C. kansanus* type actually lacks diagnostic characteristics to distinguish it from other named species in the genus (see also Webb, 1965). In the interests of practicality as well as nomenclatural stability, Webb (1965) included *C. kansanus* within *Camelops hesternus*, both because the former could not be distinguished from the latter, and because *Camelops hesternus* was in any case far better known osteologically, thanks to the extensive recovery of material of this species at Rancho La Brea.

The comprehensive treatment of Camelidae by Honey et al. (1998) further reduced the number of species within *Camelops* from 17 to six. More recently still, Baskin and

Thomas (2015) trimmed the *Camelops* tree even further, to only two branches: one for the small-bodied, largely Irvingtonian *Camelops minidokae,* best known from the southernmost United States (and retained only tentatively), and the other for the more widespread and somewhat larger-bodied *Camelops hesternus* of Irvingtonian to Rancholabrean age. In their revision, Baskin and Thomas (2015) reconfirmed Wortman's (1898) revision and concluded that all other available names, such as *Camelops sulcatus, C. huerfanensis*, and *C. traviswhitei* should be considered junior synonyms of highly variable *Camelops hesternus.*

The higher-level phylogeny of *Camelops* was also significantly reinterpreted recently. Mitochondrial and nuclear-sequence information (Heintzman et al., 2015) obtained from well-preserved fossils recovered at Hunker Creek, Yukon, suggests that *Camelops* is actually sister to the extant Afroasian camelins represented by extant *Camelus* rather than to the South American aucheniins represented by *Lama* and *Vicugna*. These results contradict earlier morphology-based hypotheses that placed *Camelops* within Aucheniini (Harrison, 1985; Honey et al., 1998), suggesting heretofore unrecognized convergence at the tribal level. Calibration of these new molecular data also suggests that the split between the lineages that terminated in *Camelops* and the Old World camelins occurred during the Late Miocene (Heintzman et al., 2015).

These new data underscore the need for a meaningful assessment of intrataxon variability within camelines. This paper, which focuses on *Camelops*, presents a comprehensive osteological and mensurational treatment of all material from high-latitude northwestern North America (Alaska and Yukon) that were at least tentatively assigned to this taxon and are available for study in public repositories, including fossils recently collected under the auspices of the Yukon Palaeontology Program, Government of Yukon. We hope that the detailed descriptions, measurements, and abundant imagery presented here will provide a useful source of information for additional systematic and comparative work on *C. hesternus* and its relatives.

Materials and Methods

Material examined in this study was collected by various workers at sites in interior Alaska and Yukon from the 1930s onward. At these localities, camel fossils are usually present as relatively rare, isolated elements within larger accumulations of bones and other organic materials recovered in frozen deposits of Rancholabrean age (Frick, 1930; Geist, 1953, 1956; Guthrie, 1968; Froese et al., 2009). As articulated skeletons are almost never encountered in these deposits, we hypothesize that each specimen described below most likely represents an individual animal. Most of these specimens were initially assigned to (and sometimes published as) *Camelops* by previous workers (fig. 2), although usually without much mensurational or descriptive data. A total of 65 fossils are described in this study, including mandibles ($n = 4$), mandibular teeth ($n = 5$), maxillary teeth ($n = 2$), axis vertebra ($n = 1$), cervical vertebra ($n = 1$), thoracic vertebra ($n = 1$), humeri ($n = 2$), radioulnae ($n = 10$), tibiae ($n = 1$), astragali ($n = 6$), calcanea ($n = 5$), metacarpals ($n = 7$), metatarsals ($n = 5$), and proximal phalanges ($n = 15$).

FIG. 2. Photo of Richard Harington of the Canadian Museum of Nature holding a cervical vertebra of *Camelops hesternus* (NMC 38228) collected in 1982 at a placer gold mine along the Sixtymile River, Yukon.

Materials for this study are deposited in the following repositories:

74-AWR-14	Specimens with these accession numbers are from Canyon Creek, Alaska, and are stored at the U.S. Geological Survey in Denver, Colorado
F:AM	Frick Collection, Department of Vertebrate Paleontology, American Museum of Natural History, New York
NMC	Canadian Museum of Nature, Ottawa, Ontario, Canada
UAMES	University of Alaska Museum, Earth Sciences Collection, Fairbanks, Alaska
YG	Yukon Government Palaeontology Program, Whitehorse, Yukon, Canada

Published descriptions, mensurational data, and associated imagery were used as aids in the identification and description of material. The paper by Webb (1965), which provides extensive documentation of *Camelops hesternus* remains from Rancho La Brea, California, was particularly useful for this project. Other important references are noted in the bibliography (Zdansky, 1926; Savage, 1951; Lundelius, 1972; Breyer, 1974; Mooser and Dalquist, 1975; Wilson and Churcher, 1978; Harrison, 1979, 1985; Voorhies and Corner, 1986; Olsen, 1988; Dalquest, 1992; Thompson, 2002; Meachen, 2003, 2005; Hilton et al., 2000; Jiménez-Hidalgo and Carranza-Castañeda, 2010; Rybczynski et al., 2013; Jass and Allan, 2016).

All measurements of newly described specimens from Alaska and Yukon were taken using Mitotuyo digital callipers to the nearest 0.01 mm following those reported in Webb (1965) and other relevant literature (see individual tables). Many of the specimens described in this study are rather incomplete; descriptions are accordingly based on the most complete specimens available, in order to allow detailed comparisons with previously published descriptions. However, some fragmentary specimens preserved sufficient morphological and mensurational features for evaluation and taxonomic allocation.

Isolated cameline elements, especially if incomplete or otherwise damaged, can be difficult to distinguish from those of other large artiodactyls that lived in the Pleistocene of northern North America. For convenience we refer to these taxa as the noncamelin BARCs, an acronym based on the four largest genera (*Bison*, *Alces*, *Rangifer*, and *Cervus*). This grouping should be understood to include smaller artiodactyls as well, such as muskox (*Ovibos*), sheep (*Ovis*), and saiga (*Saiga*), although for most elements from these taxa there is little chance of their being confused with those of camels. Comparison of the fossil cameline material with these other large artiodactyls was aided by the extensive collection of Quaternary fossil and modern comparative vertebrates at the Yukon Palaeontology Program, which includes representatives of all the above named taxa. Detailed examination of the proximal phalanges for extant camelids was aided by comparative material in the Department of Mammalogy, American Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla

Family Camelidae

Subfamily Camelinae

Tribe Camelini

Camelops hesternus Leidy, 1854

Mandible and Lower Dentition

Referred specimens: F:AM 35172 (Gold Hill, Alaska), mandible fragment, juvenile, with unworn, partially erupted p4–m1 (fig. 3A–C); F:AM 34631 (Cripple Creek, Alaska), right mandible fragment, with heavily worn m1–m3 (fig. 3D–F); F:AM 35168 (Fairbanks Creek, Alaska), anterior mandible fragment with symphysis, diastema, and roots of right p4 (fig. 3, G, H); NMC 42549 (Sixtymile Loc. 3, Yukon), left, juvenile, mandible with dp3–dp4, m1, lacking symphysis and coronoid process (fig. 3I–L); F:AM 144676 (Cripple Creek, Alaska), heavily worn left m3, roots broken off (fig. 4A–C); F:AM 35154 (Cripple Creek, Alaska), heavily worn, right m3, roots broken off (fig. 4D–F); F:AM 35169 (Gold Hill, Alaska), right, moderately worn m2?, root of posterior lobe sampled, anterior root broken off (fig. 4G–I); F:AM 35170 (Dawson Cut, Alaska), relatively unworn, left m1 or m2, roots and anterior margin broken off (fig. 4J–L); F:AM 35173 (Gold Hill, Alaska), left m2, anterior cusp and root missing (fig. 4M–O).
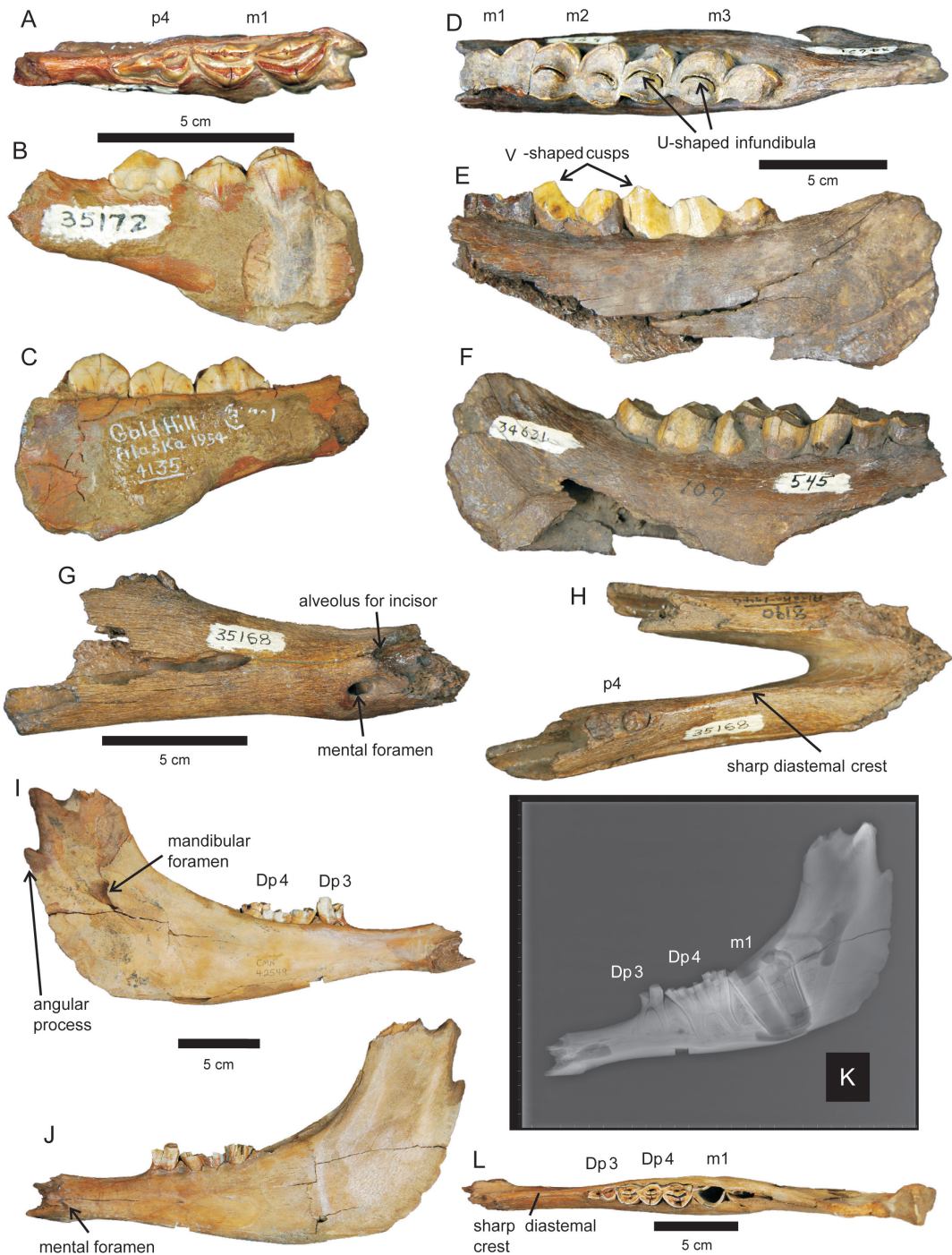
FIG. 3. *Camelops hesternus* mandibles from Alaska and Yukon. F:AM 35172: **A,** occlusal, **B,** labial, and **C,** lingual views. F:AM 34631: **D,** occlusal, **E,** labial, and **F,** lingual views. F:AM 35168: **G,** labial (right side) and **H,** occlusal views. NMC 42549: **I,** lingual, **J,** labial, **K,** radiograph of labial side (showing m1 within alveolus), and **L,** occlusal views.

Description: The most complete mandible in this collection represents a juvenile (NMC 42549), described below. This and others specimens described here exhibit several features consistent with their allocation to *Camelops hesternus* (Webb, 1965), including: (1) sharp, labially concave diastemal crest (fig. 3H, L); (2) deep horizontal ramus featuring slight concavity below diastema and relatively straighter ventral border in lateral view compared to other BARCs (fig. 3I–K); (3) large mental foramen situated low on the mandible, below posterior end of canine root (fig. 3G, J); (4) distinct angular "spur-shaped" process present on posterior margin of ascending ramus, below condyle but above level of horizontal ramus (fig. 3I–K), and lacking inflection seen in other camelines (Harrison, 1985). The mandibular fragments representing mature adult individuals (F:AM 34631 and F:AM 35168) exhibit horizontal rami that are much broader transversely and more robust than in other BARCs (table 1).

Individual mandibular dental loci can be readily differentiated from those of other BARCs. Key features consistent with descriptions and illustrations of *Camelops hesternus* (Webb, 1965; Dalquest, 1992) include: (1) lower molars large, highly hypsodont (fig. 4G, H), and relatively long mesiodistally compared to their transverse widths (fig. 4A–F); (2) molar lophs separated by deep, narrow valleys on the labial side (fig. 4D, F), relatively flat on the lingual side (fig. 4E, F); (3) loph crests higher and sharper lingually than labially, and more strongly developed on anterior cusps than posterior (fig. 4B); (4) typical wedge shape when viewed in lateral profile, with the occlusal surface much wider than the base, best exemplified by the unworn m2 F:AM 35169 (fig. 4G, H); (5) long, thin, weakly U-shaped infundibula (lakes) on occlusal surfaces, opening lingually, with thicker enamel on lingual side than labial and lacking internal cementum (fig. 4C, F, I ,L). Only one specimen, F:AM 35173 (partial left m2; fig. 4O) exhibits infundibular cementum; (6) F:AM 35169, an unworn m2, presents a weakly developed mesiolabial enamel fold or "llama buttress" (fig. 4I), a typical feature of *Camelops hesternus* lower molars (Webb, 1965, Dalquest, 1992). However, "llama buttresses" are missing from most of our sample of mandibular molars, presumably as a consequence of wear.

The juvenile NMC 42549 possesses deciduous premolars dp3 and dp4 and an unerupted m1. Both premolars are notably molariform, though splayed roots can be detected radiographically (fig. 3K). The dp4 is strongly trilobate, resembling an m3, while dp3 is weakly bilobate, resembling a deformed m2 (fig. 3L). Due to marked interproximal wear (a common feature of cameline lower dentitions; see Meachen, 2003), the dentition of F:AM 34631 appears very compressed (fig. 3D). Enamel has been almost completely removed from the mesial and distal surfaces of m1 and m2, with the result that the mesial margin of the latter is inset into the distal margin of the former. The degree of mandibular molar wear on this individual suggests that it was an old, but not yet senile, individual (see Dalquest, 1992).

Maxillary Dentition

Referred specimens: F:AM 35153 (Cripple Creek, Alaska), moderately worn, right M3 (fig. 4P–R); F:AM 35171 (Gold Hill, Alaska) highly worn, right M1 or M2 (fig. 4S–U).

Description: There are fewer referable upper teeth in collections, perhaps because camel skulls are rarely recovered. The two specimens described here have well-developed labial styles that

TABLE 1. Mandibles and mandibular dentition of *Camelops hesternus* material from Alaska and Yukon.

Mandibles and mandibular dentition	Measurements (mm)							
	F:AM 34631	F:AM 35172	NMC 42549	F:AM 35154	F:AM 144676	F:AM 35169	F:AM 35170	F:AM 35173
	Mandible (m1–m3)	Mandible (p4–m1)	Mandible (Dp3–m1)	m3	m3	m2	m1 or m2	m1 or m2
Length of mandible at alveolar level			252.60					
Depth below posterior part of Dp3			40.67					
Depth below posterior part of Dp4		21.04	55.5					
Minimum depth of diastema		19.17	24.92					
Minimum width of diastema		8.66	13.2					
Length of dental row: alveoloar/occlusal	120.87/ 119.55		96.87 (alveolar)					
Dp3: anteropoterior length/transverse width			17.26/ 8.93					
Dp4: anteropoterior length/transverse width			45.76/ 14.82					
p4: anteropoterior length/transverse width		19.83/8.3						
m1: max. ateroposterior length, alveolar/occlusal	28.77/ 28.09	19.17 (occlusal)					34.19 (occlusal)	18.68 (occlusal)
m1: max. transverse width, alveolar/occlusal	18.36/ 22.33	8.66 (occlusal)					15.43 (occlusal)	
m1: min. transverse width	12.42						10.25	
m1: max. crown height, labial/lingual	11.45/ 13.32						34.21 (labial)	30.09/ 30.74
m2: max. ateroposterior length, alveolar/occlusal	31.5/ 34.81					36.53/ 44.95		
m2: max. transverse width, alveolar/occlusal	23.27/ 24.95					19.50/ 15.72		
m2: min. transverse width	14.09					8.37		
m2: max. crown height, labial/lingual	16.42/ 20.23					70.50/ 80.76		
m3: max. anteroposterior length, alveolar/occlusal	57.49/ 57.99			51.28/ 56.26	51.55/ 51.5			
m3: max. transverse width, alveolar/occlusal	22.94/ 22.67			21.48/ 18.83	17.29/ 15.08			
m3: min. transverse width	10.95			9.2	6.24			
m3: max. crown height, labial/lingual	17/22.12			37.63/ 41.71	28.16/ 40.80			

V-shaped cusps

2 cm

Deep narrow valleys

2 cm

2 cm

U-shaped infundibula

weak
llama
buttress

2 cm

2 cm

2 cm

labial
style

labial
rib

2 cm
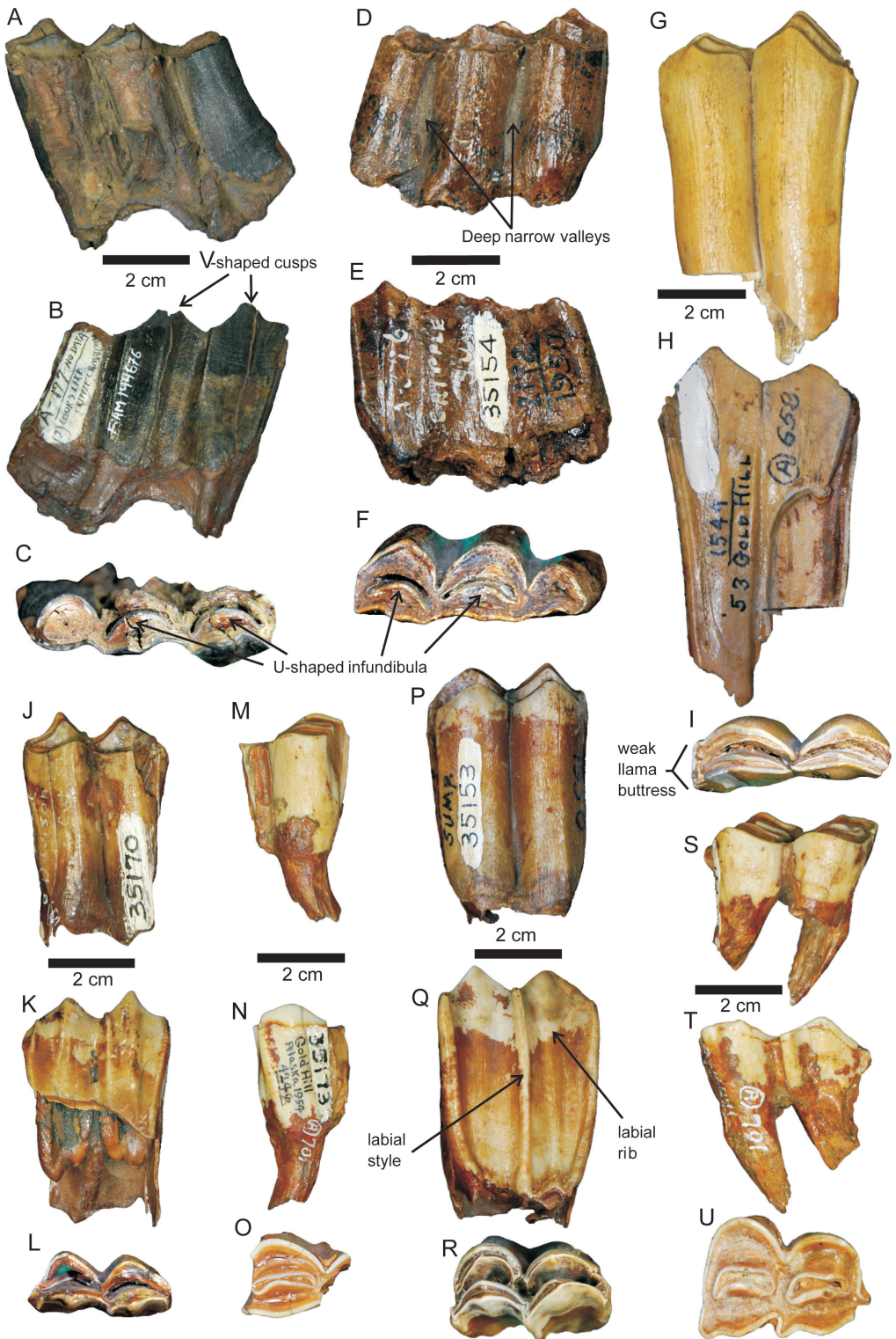
TABLE 2. Maxillary dentition of *Camelops hesternus* material from Alaska.

Maxillary dentition		Measurements (mm)				
		Anteroposterior length: alveolar/ occlusal	Transverse width, occlusal: anterior/ posterior	Transverse width, alveolar: anterior/ posterior	Minimum transverse width	Maximum crown height: labial/lingual
F:AM 35153	M3	32.34/36.56	20.29/17.14	24.93/22.98	8.43	47.87/51.54
F:AM 35171	M1 or M2	30.41/40.83	26.64/21.16	24.17/20.22	17.74	13.75/16.47

extend upward to the valleys between the cusps and ribs that extend to the V-shaped crests of the cusps (fig. 4P–T). Cusps are higher labially. The large infundibula on F:AM 35153 are somewhat U-shaped (opening labially), with thicker enamel on the labial margin than the lingual, and lacking internal cementum (fig. 4R). F:AM 35171 is complete but heavily worn, and the infundibula are filled with cementum (fig. 4U). The enamel margins of the lakes are thicker labially.

The identified teeth are consistent in size (table 1, 2) and morphology with those from Rancho La Brea identified by Webb (1965) as *Camelops hesternus*. They are much larger than those reported for *Hemiauchenia* (Meachen, 2003, 2005; Morgan et al., 2008a; Bravo-Cuevas et al., 2012) but smaller than those representing larger-bodied *Paracamelus* from Asia (Zdansky, 1926) or Old Crow, Yukon (Harington, 1977; Rybczynski et al., 2013).

Cervical Vertebrae

Axis

Referred specimen: F:AM 35167 (Cripple Creek, Alaska), dorsal portions missing, transverse processes broken, and lacking posterior zygapophyses (fig. 5).

Description: Although this specimen is incomplete, the great length of this axis readily distinguishes it from that of other BARCs. The morphology is consistent with published descriptions of axis vertebrae assigned to *Camelops hesternus* from Rancho La Brea (Webb, 1965). Relevant features include: (1) short, broad odontoid process is spoutlike, and tip lacks both medial notch (fig. 5A) as in *Camelus* (Lundelius, 1972; Olsen, 1988; Webb, 1965;) and lateral notches as in *Hemiauchenia* (Lundelius, 1972); (2) stumps of transverse processes are thin, horizontal, extending most of length of vertebral body (fig. 5A); (3) hypapophysis on ventral surface of centrum is large, posteriorly deepening (fig. 5B), although not as pronounced or deep as in *Camelus* (Olsen, 1988); (4) rostral articular surface faces slightly upward (fig. 4C);

FIG. 4. *Camelops hesternus* teeth from Alaska and Yukon. F:AM 144676, m3: **A,** labial, **B,** lingual, and **C,** occlusal views. F:AM 35154, m3: **D,** labial, **E,** lingual, and **F,** occlusal views. F:AM 35169, ?m2: **G,** labial, **H,** lingual, and **I,** occlusal views. F:AM 35170, m1 or m2: **J,** labial, **K,** lingual, and **L,** occlusal views. F:AM 35173, m2: **M,** labial, **N,** lingual, and **O,** occlusal views. F:AM 35153, M3: **P,** lingual, **Q,** labial, and **R,** occlusal views. F:AM 35171, M1 or M2: **S,** lingual, **T,** labial, and **U,** occlusal views.
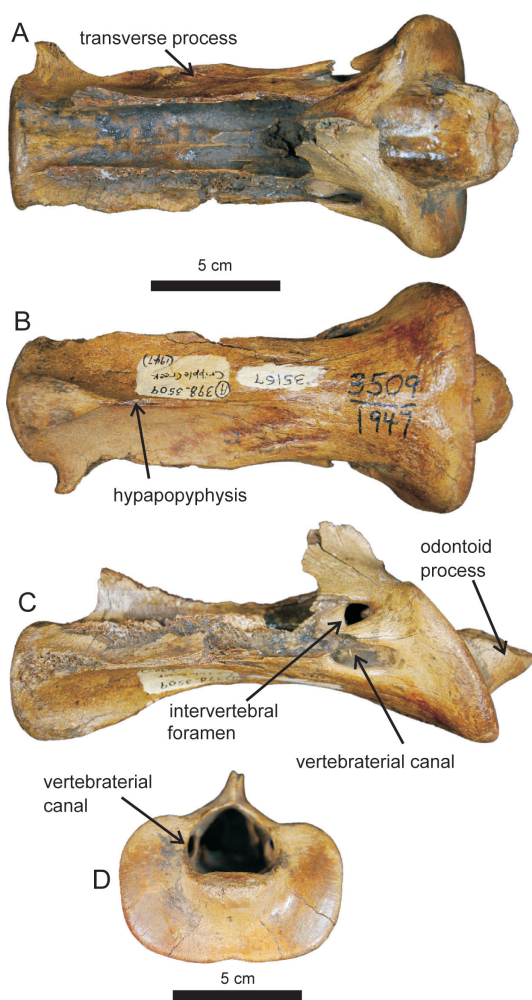
FIG. 5. *Camelops hesternus* axis from Alaska. F:AM 35167: **A,** dorsal, **B,** ventral, **C,** lateral, and **D,** proximal views.

(5) rostral opening of vertebrarterial canal opens dorsolaterally, near anterior end of element, below intervertebral foramen and separated from it externally by anterior portion of transverse process (fig. 5C), as in *Lama* and *Camelops hesternus* (Webb, 1965).

The position for the rostral opening of the vertebrarterial canal in F:AM 35167 also differs substantially from that of *Camelus*, where it lies posterior to the intervertebral foramen and above the anterior crest of the transverse process (Olsen, 1988). As in other *Camelops hesternus*, the caudal opening of the canal in F:AM 35167 lies inside the neural arch halfway along its length (fig. 5D). F:AM 35167 is larger and more robust than axis vertebrae of aucheniin taxa such as *Alforjas* (Harrison, 1979) or *Hemiauchenia* (see Lundelius, 1972), but smaller than the large camelin *Megatylopus* (Thompson, 2002). The Alaskan specimen F:AM 35167 is slightly smaller than the range reported by Webb (1965) for *Camelops hesternus* from Rancho La Brea (table 3).

?Fifth Cervical Vertebrae

Referred specimen: NMC 38228 (Sixtymile Loc. 3., Yukon), ?5th cervical, lacking neural spine and both anteroventral costellar processes. The original fossil is now lost and is here represented by a cast, YG 572.39 (fig. 6).

Description: The length and morphology of this cervical vertebra is consistent with published descriptions of cervicals of *Camelops hesternus* from Rancho La Brea (Webb, 1965). Comparison with cervical vertebrae of an extant *Lama* skeleton and overall size suggests that this specimen represents an element from the caudal part of the series, probably the 5th cervical vertebra.

Distinguishing features of NMC 38228 include: (1) neural spine, although broken, clearly extended along length of dorsal surface (fig. 6A); (2) relatively broad, flat platform posterior to spine extends onto dorsal surface and posterior zygapophyses overhang centrum (fig. 6A); (3) the hypapophysis on ventral surface of centrum is extensive, posteriorly deepening (fig. 6B); (4) long, wing-shaped transverse processes extend outward at a 45° angle from the long axis of the vertebra at the posterior end (fig. 6C); (5) pedicles of incomplete anteroventral costellar processes are oriented nearly vertically (fig. 6C).

TABLE 3. Vertebrae of *Camelops hesternus* from Alaska and Yukon and comparison with some other camelines. M = mean; OR = observed range; N = number of specimens.

Measurements (mm)					
Axis Vertebra		**Length centrum**	**Maximum breadth of anterior articular surface of axis body**	**Width of odontoid process**	**Breadth/height of centrum at posterior margin**
F:AM 35167		196.43	91.02	41.41	51.58/45.17
Camelops hesternus	M	233.9±2.72			
Webb, 1965: table 7	OR	205–247			
	N	12			
Megatylopus gigas		216			
Thompson, 2002					
Alforjas taylori	OR	174.1–180.2	62.2–65.7		
Harrison, 1979: table 5	N	2	3		

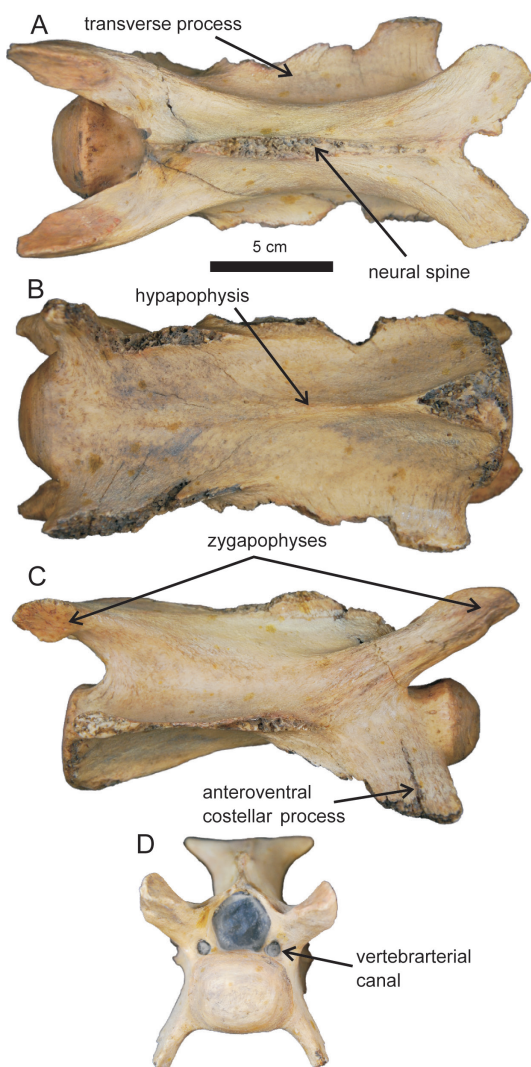| **Cervical vertebra**		**Length centrum**	**Height of centrum to base of spine**	**Width/height of centrum at anterior margin**	**Breadth/height of centrum at posterior margin**	**Breadth across anterior/ posterior zygophyses**
YG 572.29 (cast of NMC 38228)		162.93	76.15	44.21/34/18	55.18/42.66	78.74/73.82
Camelops hesternus	M	198.5±2.99	96±2.03			
Webb, 1965: table 7; C-5	OR	186–218	87–107			
	N	10	9			
Megatylopus gigas		185				
Thompson, 2002. C-5						
Thoracic vertebra		**Length centrum**				
74-AWR-14		66.14				
Camelops hesternus	M	73.9±0.35				
Webb, 1965: table 8; late thoracics	OR	72–75				
	N	8				

FIG. 6. *Camelops hesternus* cervical from Yukon. YG 572.39 (cast of NMC 38228): **A,** dorsal, **B,** ventral, **C,** lateral, and **D,** proximal views.

The rostral opening of the vertebrarterial canal is nearly flush with the pedicle notch on the neural arch (fig. 6D), a feature seen in *Paracamelus* (Zdansky, 1926) and *Camelus* but not *Camelops hesternus* according to Webb (1965). The anteroposterior length of the centrum for the Yukon specimen NMC 38228 is smaller (table 3) than the ranges reported for *Camelops* from Texas (Slaughter, 1966) and *Camelops hesternus* from Rancho La Brea (Webb, 1965).

Thoracic Vertebra

Referred specimen: 74-AWR-14 (Canyon Creek, Alaska), 7th or 8th thoracic (fig. 7).

Description: The neural spine was attached to the centrum by means of poorly applied plaster, obscuring several parts of the element. As reconstructed, the neural spine is broad in lateral view and tilts sharply caudally from the centrum (fig. 7A), unlike thoracic elements in other BARCs but consistent with descriptions of *Camelops hesternus* from Rancho La Brea (Webb, 1965). Judging from specimens described from known position at Rancho La Brea (Webb, 1965), it seems that the specimen 74-AWR-14 is a 7th or 8th thoracic. The right transverse process, prezygapophysis, and anterior capitular facet are broken off; parts of the left transverse process, prezygapophysis, and anterior capitular facet are present (fig. 7B). The large, oval postzygapophyseal facets are narrowly separated and face posteriorly. The centrum's articular epiphyses are lacking. The unfused epiphyses, coupled with the element's relatively small size (table 3) in comparison with those reported by Webb (1965) from Rancho La Brea, indicates a juvenile.

Forelimb

Humerus

Referred specimen: NMC 38227 (Sixtymile Loc. 3, Yukon), left, proximal fragment (shaft sampled previously for conventional radiocarbon dating according to Harington, 1997) (fig.

8A–D); NMC 38277 (Sixtymile Loc. 3, Yukon), left, distal fragment (fig. 8E–H).

Description: These two large and robust humeri fragments closely match illustrations and descriptions of *Camelops hesternus* from Rancho La Brea (Webb, 1965) and Alberta (Wilson and Churcher, 1978; Jass and Allan, 2016) and exhibit morphological features that differentiate them from other large Quaternary BARCs. Distinguishing features consistent with allocation to *Camelops* include: (1) head separated from tuberosities by broad, shallow fossa (fig. 8D); (2) head not overhanging anterior and posterior surfaces of shaft to degree seen in other BARCs (fig. 8A, B); (3) medial tuberosity notably bulbous (fig. 8C); (4) medial segment of deep bicipital groove wider and shallower than lateral segment (fig. 8C); (5) medial epicondyle curves laterally into olecranon fossa (fig. 8H); (6) medial condyle slightly thicker than lateral condyle (fig. 8E), but difference not as pronounced as in *Bison* or other BARCs; (7) distal end of lateral epicondyle wider than medial epicondyle. (8) distal surface of lateral epicondyle roughened and relatively flattened compared to the medial epicondyle (fig. 8H); (9) angle between distal end of the shaft and proximal part of lateral epicondyle very pronounced (~130°) (fig. 8E); (10) sulci separating condyles from epicondyles more marked laterally than medially (fig. 8H); (11) deep sagittal groove on trochlear surface of medial condyle centered between medial and lateral condyles and appearing concave in distal view (fig. 8H); (12) demarcation between trochlear surface and olecranon fossa well defined in posterior view, without abrupt ledge seen in *Bison* (fig. 8F); (13) olecranon fossa maximum depth larger than maximum width (fig. 8F); (14) large, ovoid coronoid fossa centered over sagittal groove, shallower than in *Bison* (fig. 8E).

FIG. 7. *Camelops hesternus* thoracic from Alaska. 74-AWR-14: **A,** lateral and **B,** anterior views.
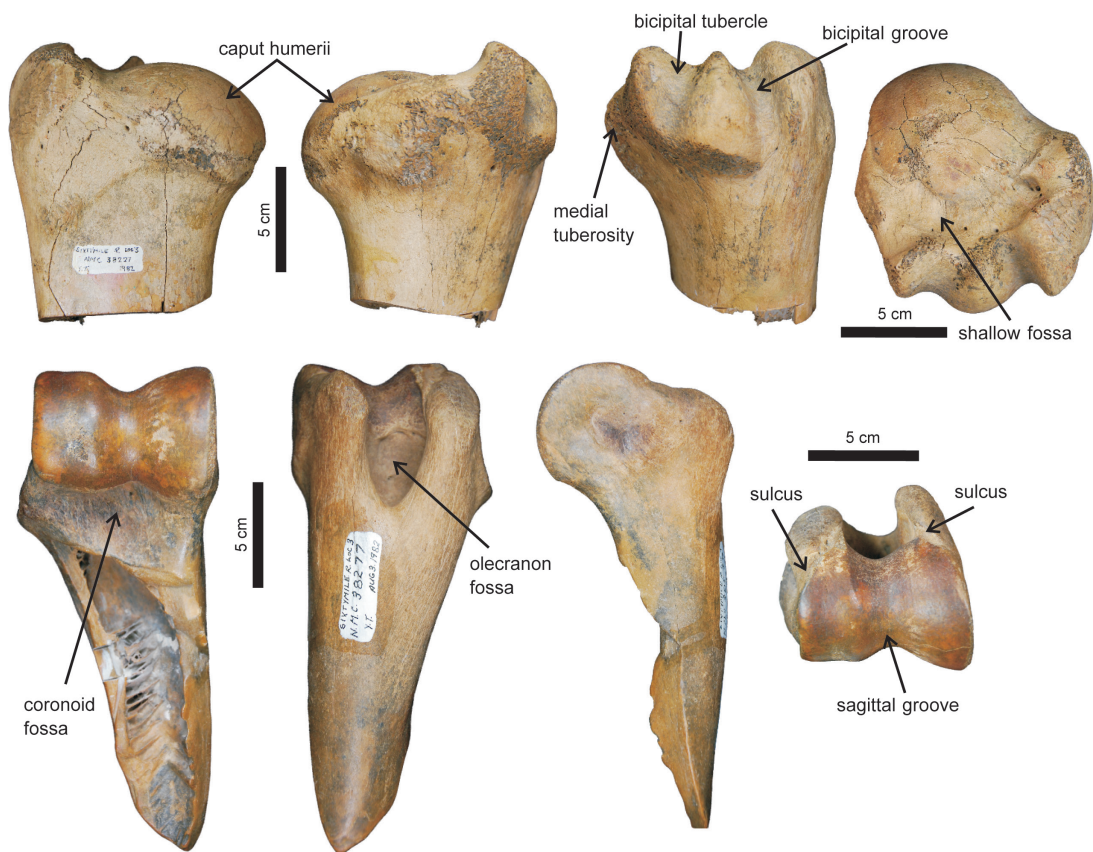
FIG. 8. *Camelops hesternus* humeri from Yukon. NMC 38227: **A,** medial, **B,** lateral, **C,** anterior, and **D,** proximal views. NMC 38277: **E,** anterior, **F,** posterior, **G,** medial, and **H,** distal views.

Metric data from the two Yukon humeri (table 4) demonstrate they are more robust than those from the relatively gracile aucheniins *Alforjas* (Harrison, 1979) and *Hemiauchenia* (Meachen, 2003; Morgan et al., 2008b), but less so than those from the large camelins *Megatylopus* (Thompson, 2002), *Megacamelus* (Harrison, 1985), and *Titanotylopus* (Barbour and Schultz, 1939; Meade, 1945). The Yukon fossil humeri are smaller than those reported for *Camelops hesternus* from Rancho La Brea (Webb, 1965) and are similar to those reported for *Camelops* cf. *hesternus* from Alberta (Jass and Allan, 2016).

RADIOULNA

Referred specimens: F:AM 35155 (Cripple Creek, Alaska) left radioulna, lacking tip of olecranon and proximal posterior margin of ulna (fig. 9A–F); 74-AWR-14 (Canyon Creek, Alaska) right radioulna, lacking proximal posterior margin of ulna; F:AM 35165 (Cripple Creek, Alaska) left radioulna, proximal fragment lacking tip of olecranon and most of radial shaft (fig. 9G); YG 504.64 (Hunker Creek, Yukon) left radioulna, distal fragment lacking most of shaft (fig. 9H, I); YG 474.285 (Hunker Creek, Yukon) right radius, proximal fragment lacking most of olecranon and lateral tuberosity; YG 474.52 (Hunker Creek, Yukon) right

TABLE 4. Humeri of *Camelops hesternus* from Alaska and Yukon and comparison with some other camelines. M = mean; OR = observed range; N = number of specimens. UF = University of Florida vertebrate paleontology collections; NMMNH = New Mexico Museum of Natural History Museum.

| Humeri		Measurements (mm)						
		Maximum length	Width across tuberosities	Maximum transverse width of camput humeri	Maximum anteroposterior diameter in lateral face	Maximum anteroposterior diameter of caput humeri	Trochlear width	Depth below medial epicondyle
NMC 38277							76.21	90.97
NMC 38227			114.04	71.93	131.47	80.97		
Camelops hesternus	M	456.1± 4.51	136.7± 2.04				97.1± 1.03	105.3± 1.4
Rancholabrean, California	OR	441– 465	129– 136				94–105	100–114
Webb, 1965: table 12	N	5	6				10	9
Camelops cf. *hesternus* Wilson and Churcher, 1978			135	79	139.8	90.4		
Camelops cf. *hesternus* Jass and Allan, 2016: table 3								
P98.2.122							82.95	
P98.8.32							71.86	
Alforjas taylori	M						63±4.7	
Harrison, 1979: table 5	OR						57.0–72.7	
	N						16	
Hemiauchenia Morgan, Sealey, and Lucas, 2008a: table 5								
NMMNH 31463							58.5	56.2
NMMNH 31516							68.3	65.8
NMMNH 26642							66.6	65.9
Hemiauchenia gracilis Meachen, 2003, 2005								
UF 176915							36.8	
UF 210702							40.9	
Megatylopus gigas Thompson, 2002		522	167				109.8	
Megacamelus merriami	M						111.4	
Harrison, 1985: table 4	OR	532.7					106–117	
	N	1					5	
Titanotylopus spp.	OR	427– 550	160– 200				93–112	
Barbour and Schultz, 1939; Meade, 1945	N	4	3				3	
Camelus dromedarius	OR	441– 465	129– 136				94–105	100–114
Wilson and Churcher, 1978: table 1	N	5	6				10	9
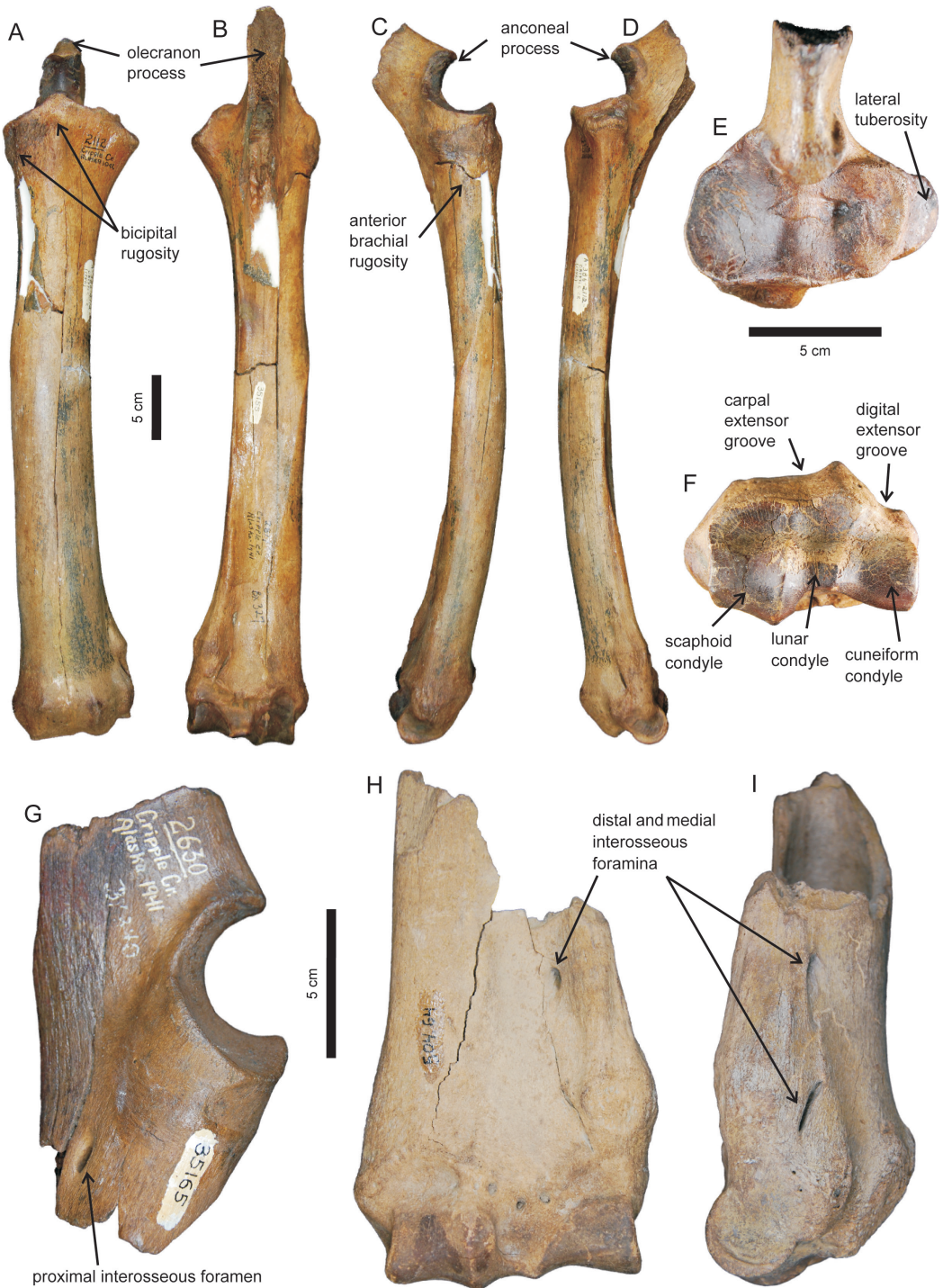
FIG. 9. *Camelops hesternus* radioulnae from Alaska and Yukon. F:AM 35155: **A,** anterior, **B,** posterior, **C,** medial, **D,** lateral, **E,** proximal, and **F,** distal views. F:AM 35165: **G,** medial view. YG 504.64: **H,** posterior and **I,** lateral views.
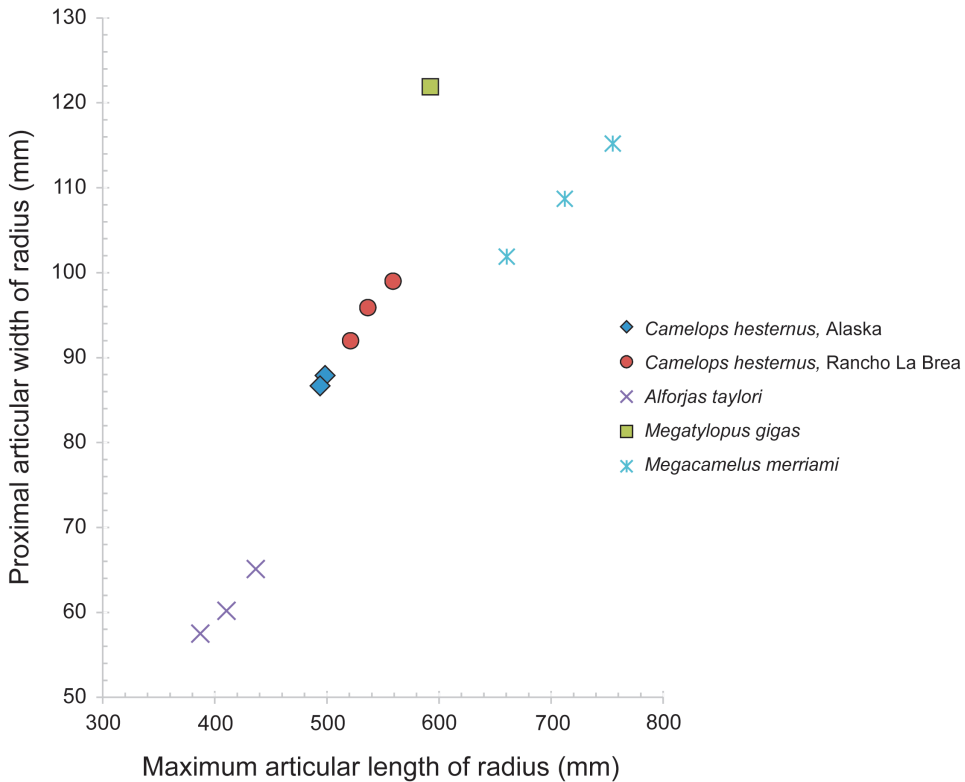
FIG. 10. Comparison of radioulnae from Alaska with various North American fossil camelines. Data for *Camelops hesternus* from Rancho La Brea (Webb, 1965), *Alforjas taylori* (Harrison, 1979) and *Megacamelus merriami* (Harrison, 1985) represent the respective minimum, mean, and maximum measurements reported. Data for *Megatylopus gigas* from Thompson (2002).

radius, proximal fragment lacking most of lateral articular surface; NMC 46728 (Sixtymile Loc. 3, Yukon) right radioulna, distal fragment; F:AM 35157 (Cripple Creek, Alaska) left radioulna, proximal fragment lacking most of medial side of proximal shaft; YG 587.2 (Canyon Creek, Yukon) left radioulna, proximal fragment lacking posterior portion of olecranon and shaft; YG 587.4 (Canyon Creek, Yukon) right radioulna, proximal fragment lacking olecranon and lateral tuberosity.

Description: The overall length and relative dimensions of the two nearly complete radioulnae (F:AM 25155 and 74-AWR-14) far exceed those of other Pleistocene artiodactyls known from the region. Articular ends (proximal and distal radioulnae) usually preserve features sufficient to differentiate them from other BARCs. Important features include: (1) robust, crescentic olecranon process that arches back at a sharp angle (fig. 9C); (2) complete radioulnar fusion (fig. 9A–D), the line of which is marked by three large interosseous foramina: medial foramen penetrating from anterior to posterior (fig. 9H, I); proximal foramen not complete and penetrating deeply only on posterior side, with shallow penetration anteriorly (fig. 9G); and distal foramen not complete and penetrating deeply only on posterior side, with shallow penetration anteriorly (fig. 9I); (3) broad, massive anconeal process completely fused with

TABLE 5. Radioulnae of *Camelops hesternus* from Alaska and Yukon and comparison with some other camelines. M = mean; OR = Observed Range; N = Number of Specimens. UF = University of Florida vertebrate paleontology collections.

Radioulnae		Measurements (mm)						
		Maximum Length	Articular length of radius	Minimum depth of olecranon process	Width of proximal articular process	Midshaft width	Midshaft depth	Distal articular width
YG 474.285					77.56			
YG 587.2					77.9			
YG 587.4					78.3			
YG 504.64								78.71
NMC 46728								81.51
F:AM 35155			498.3		87.9	58.5	39.5	
74-AWR-14		593.02	493.82	76.46	86.67	64.41	39.36	80.51
Camelops hesternus	M	624± 0.39	536.5± 0.37	80.5±1.13	95.9±0.69	78.9±1.19	43.1±0.94	87.3±0.91
Webb, 1965: table 9	OR	614–642	521–559	77–84	92–99	74–87	40–50	79–93
	N	7	10	8	10	12	12	16
Camelops cf. *hesternus*								
Jass and Allan, 2016: table 4								
P94.12.24		557.02	475.65	87.28	86.1			84.53
Hemiauchenia gracilis								
Meachen, 2003, 2005								
UF 8917		472		40.3				
Hemiauchenia blancoensis								
Jiménez-Hidalgo and Carranza-Castañeda, 2010		470			68.4			73
Alforjas taylori	M		410.4± 18.1		60.2±2.3			66.5±3.4
Harrison, 1979: table 5	OR		387.0– 436.4		57.7–65.1			61.0–71.3
	N		5		8			6
Paracamelus gigas								
Zdansky, 1926				82		67	51	100

Radioulnae		Measurements (mm)						
		Maximum Length	Articular length of radius	Minimum depth of olecranon process	Width of proximal articular process	Midshaft width	Midshaft depth	Distal articular width
Megacamelus merriami	M	803.3	712.2		108.7±4.3			113.9
Harrison, 1985: table 4	OR	726.5–857.0	660.3–755.0		101.9–115.2			104.0–126.2
	N	4	4		6			5
Megatylopus gigas Thompson, 2002								
Right		682	592		121.9			118.4
Left		680			121.4			

proximal radius, no suture line in adult (fig. 9C–E); (4) well-marked origin of M. extensor digitalis lateralis from lateral tuberosity (fig. 9E); (5) rugose insertion for M. brachalis anterior (fig. 9A); (6) distal articular surface divided by three sharp crests into areas for cylindrically shaped medial scaphoid condyle (largest, most extensive distally), lunar articular surface (narrowest), and lateral cuneiform condyle (least extensive distally) (fig. 9F); (7) on anterodistal surface of radius, marked grooves for carpal extensor medially and common digital extensor laterally (fig. 9F).

The specimens from Alaska and Yukon are morphologically consistent with fossils of *Camelops hesternus* from Rancho La Brea (Webb, 1965), though are smaller in size (table 5; fig. 10) to the single specimen of *Camelops* cf. *hesternus* reported from Alberta (Jass and Allan, 2016). They are also smaller and much less robust than elements ascribed to large extinct camelins such as *Paracamelus* (Zdansky, 1926), *Megacamelus* (Harrison, 1985), and *Megatylopus* (Thompson, 2002). By contrast, in overall proportions the radioulnae from Alaska and Yukon are markedly more robust than those of gracile aucheniin taxa such as *Hemiauchenia* (Breyer, 1974; Jiménez-Hidalgo and Carranza-Castañeda, 2010) and *Alforjas* (Harrison, 1979).

Hind limb

Tibia

Referred specimen: YG 474.262 (Hunker Creek, Yukon) left, fragment lacking most of medial shaft and completely lacking the proximal end (fig. 11).

Description: Although this specimen is problematic because of its condition, preserved features are consistent with descriptions, illustrations, and metric data for *Camelops hesternus* from Rancho La Brea (Webb, 1965). Significant features differentiating tibiae of *Camelops* from those of other BARCs include: (1) distal shaft anteroposteriorly flattened (fig. 11A–C), with
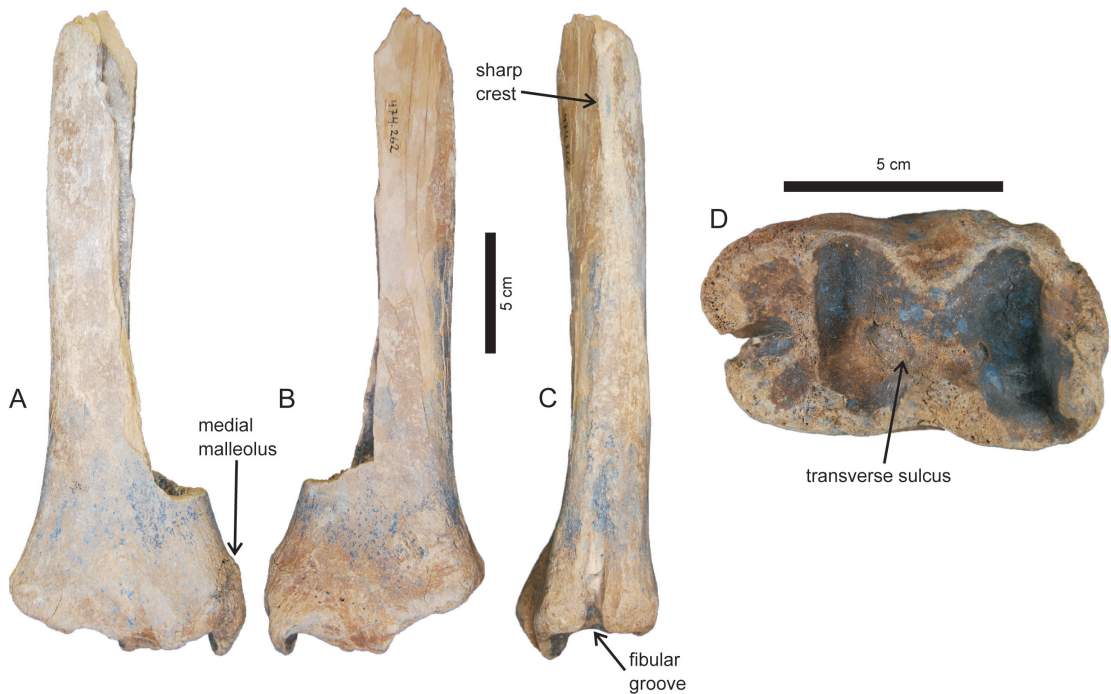
FIG. 11. *Camelops hesternus* tibia from Yukon. YG 447.262: **A,** anterior, **B,** posterior, **C,** lateral, and **D,** distal views.

broad and relatively shallow distal articular surface (fig. 11D); (2) sharp longitudinal crest on lateral surface of shaft (fig. 11C); (3) prominent medial malleolus closing notch for astragalus (fig. 11A); (4) posterior portion of fibular facet much larger than anterior, portions separated by a long, deep fibular groove (fig. 11C); (5) articular surface for lateral trochlea wider than medial, with prominent tongue separating them (fig. 11D); (6) irregularly shaped, shallow, transverse sulcus that cuts across trochlear articular surface (fig. 11D). The distal tibia YG 474.262 differs from that of *Camelus* in that in extant camels the lateral and medial trochlear surfaces are similar in width (Webb, 1965; Olsen, 1988).

Metric data from YG 474.262 are within the range for *Camelops hesternus* from Rancho La Brea reported by Webb (1965). As in the case of other elements, tibiae of *Camelops hesternus* (table 6) are smaller than those of other extinct camelins such as *Megatylopus* (Thompson, 2002), *Megacamelus* (Harrison, 1985), and *Paracamelus* (Zdansky, 1926), but larger and more robust than those of the gracile aucheniins *Paleolama* (Meachen, 2003), *Hemiauchenia* (Morgan et al., 2008b), and *Alforjas* (Harrison, 1979).

Astragalus

Referred specimens: F:AM 144557 (Dawson Cut, Alaska) left (fig. 12); F:AM 35175A (Gold Hill, Alaska) left; F:AM 35177 (Gold Hill, Alaska) left; F:AM 144556 (Cripple Creek, AK) right; NMC 38226 (Sixtymile Loc. 3, Yukon) right; NMC 29194 (Sixtymile Loc. 5, YT) left.

TABLE 6. Tibiae of *Camelops hesternus* from Alaska and Yukon and comparison with some other came-lines. M = mean; OR = observed range; N = number of specimens.

Tibiae	Measurements (mm)				
		Maximum length	Proximal width	Distal width	Distal depth
YG 474.262				93.33	53.96
Camelops hesternus	M	525.5±6.06	149.3±4.02	86.3±4.11	51.3±0.62
Webb, 1965: table 10, 11	OR	506–545	144–156	78–100	49–53
	N	6	6	6	6
Camelops Jiménez-Hidalgo and Carranza-Castañeda, 2010		447		92	55.4
Hemiauchenia Morgan, Sealey, and Lucas, 2008b: table 11		475	88.9	64.3	46.5
Paleolama mirifica Meachen, 2003	M	359.75±17.44		39.39±2.25	
Alforjas taylori Harrison, 1979: table 5				74.8	
Paracamelus gigas Zdansky, 1926				102	60
Megacamelus merriami	M	670		112	
Harrison, 1985: table 4	OR	670		109.5–114.5	
	N	1		2	
Megatylopus gigas Thompson, 2002 (right)				104.4	

Description: The robust fossil astragali from large artiodactyls, such as *Camelops*, are usually found complete, as is the case with the specimens evaluated here. They are also relatively easy to distinguish from their homologs among BARCs. In overall features and dimensions, the material from Alaska and Yukon closely corresponds to descriptions and illustrations of *Camelops* from Nebraska (Breyer, 1974) and central Mexico (Jiménez-Hidalgo and Carranza-Castañeda, 2010), as well as *Camelops hesternus* from Rancho La Brea (Webb, 1965). Diagnostic features include: (1) on proximal trochlea, lateral condyle narrower and higher than medial condyle (fig. 12A, B); (2) medial condyle surface distinctly lower than articular surface of sustentaculum; (3) three distinct facets present on lateral surface, with parasustentacular facet curving in direction opposite to fibular facet, and small paracuboid facet separated from other lateral facets by a horizontal sulcus (fig. 12C); (4) proximal medial condyle much deeper than distal navicular process (fig. 12D); (5) fibular facet culminating distally in a prominent, pointed fibular salient (fig. 12B, C); (6) parasustentacular facet sometimes separated from sustentacular surface by a slight longitudinal sulcus (fig. 12C); (7) tibial ligament surface situated at oblique angle to long axis of astragalus (fig. 12A, D); (8) deep, horizontal subsustencular fossa separat-
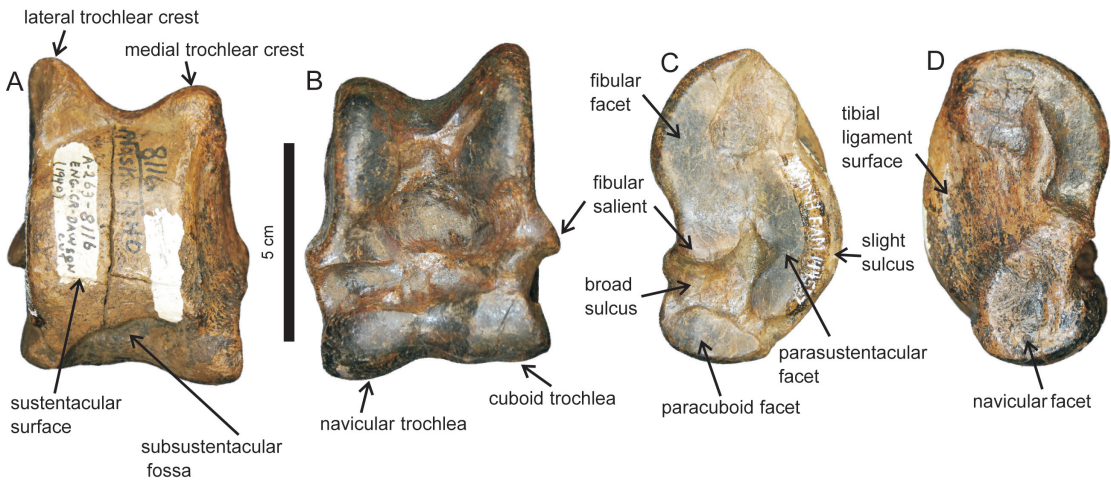
FIG. 12. *Camelops hesternus* astragalus from Alaska. F:AM 144557: **A,** posterior, **B,** anterior, **C,** lateral, and **D,** medial views.

ing sustentacular surface from posterior processes of cuboid and navicular (fig. 12A); (9) medial edge of sustentacular facet arises from posterior surface of navicular trochlea (fig. 12A).

In comparison to those of extant *Camelus*, the astragali described here differ in that the groove on the proximal trochlea is relatively wider; the medial side of the medial condyle lacks a prominent tubercle; the width and breadth of the navicular trochlea are greater than those of the cuboid trochlea (in *Camelus* they are subequal); the tibial ligament surface is broad and flat, rather than narrow and convex; and the subsustentacular fossa is much deeper and well developed (Webb, 1965; Breyer, 1974; Olsen, 1988).

Astragali of *Camelops* (table 7; fig. 13) are larger and more robust than those of the relatively gracile aucheniins *Hemiauchenia* (Breyer, 1974; Meachen, 2003, 2005, Jiménez-Hidalgo and Carranza-Castañeda, 2010) and *Alforjas* (Harrison, 1979), but less robust and smaller than those of the large camelins *Megatylopus* (Thompson, 2002), *Megacamelus* (Harrison, 1985) and *Paracamelus* (Zdansky, 1926; Harington, 1977). Metric data from the Alaskan and Yukon astragali are below or at the lower end of the sizes reported from *Camelops hesternus* at Rancho La Brea (Webb, 1965).

Calcaneum

Referred specimens: F:AM 35175 (Gold Hill, Alaska) left, complete (fig. 14A–D); F:AM 35176 (Cripple Creek, Alaska) left, complete; F:AM 35158 (Ester Creek, Alaska) right, complete; YG 504.22 (Hunker Creek, Yukon) right, posterior margin and proximal tuber calcis highly eroded (fig. 12E–H); NMC 42512 (Sixtymile Loc. 3, Yukon) left, complete.

Description: Calcanea survive well in paleontological contexts, and there are several features that differentiate this element in *Camelops* from those of large Pleistocene artiodactyls. The overall size and proportions of calcanea from Alaska and Yukon correspond well to calcanea of *Camelops* from localities in more southerly latitudes (Webb, 1965; Breyer, 1974; Hilton

TABLE 7: Astragali of *Camelops hesternus* from Alaska and Yukon and comparison with some other cam-
elines. M = mean; OR = observed range; N = number of specimens.

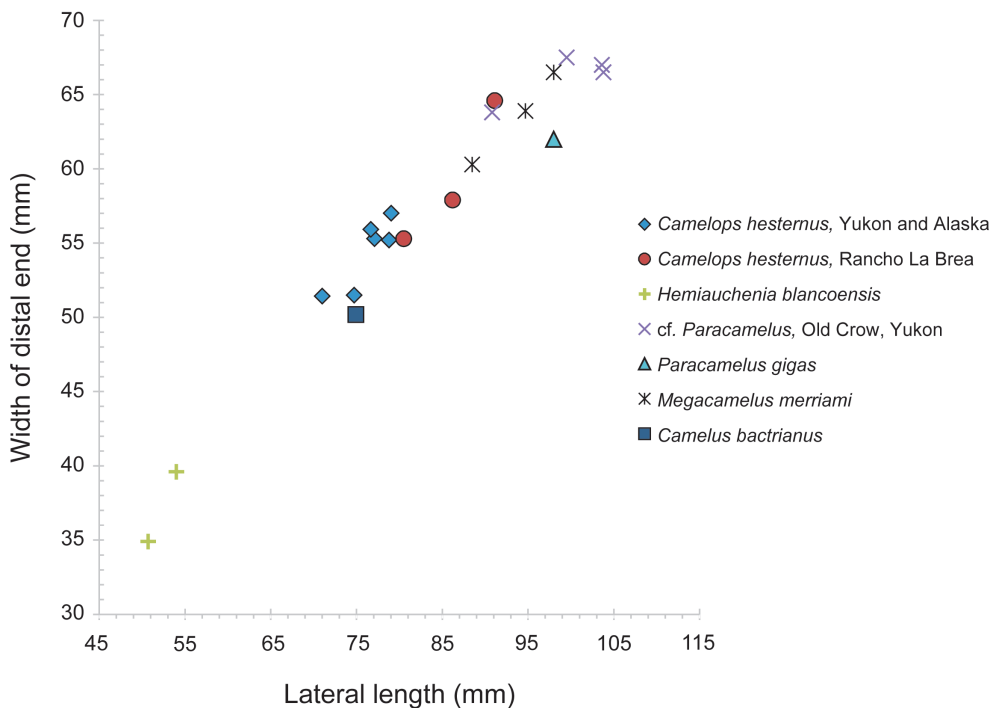| Astragali		Measurements (mm)						
		Medial length	Lateral length	Minimum length	Depth of medial condyle	Depth of lateral condyle	Width of distal end	Maxi-mum width
NMC 38226		72.9	78.8	61	35.34	46.2	55.21	58.6
NMC 29194		71.5	77.1	58.2	36.84	45.8	55.3	57.8
F:AM 35175A		67.66	70.98	57.82	40.87	44.06	51.44	56.41
F:AM 144557		73.9	76.67	62.92	43.29	45.92	55.93	60.62
F:AM 35177		71.48	74.73	57.87	40.48	44.11	51.5	54.26
F:AM 144556		74.25	79.04	61.28	46.61	48.44	57.01	60.91
Camelops hesternus	M	80.2±0.74	86.2±0.50	67.3±0.73			57.9±0.59	
Webb, 1965: table 12	OR	75.2–85.3	80.5–91.1	62.4–72.5			55.3–64.6	
	N	18	18	18			18	
Hemiauchenia cf. *macrocephala*								
Breyer, 1974: table 1								
Broadwater A Locality	M		59±0.66	46±0.51				
	N		32	32				
Gordon, Hay Springs, Rushville Localities	M		64±0.9	50±1.65				
	N		6	6				
cf. *Paracamelus*								
Harington, 1977: table 71								
NMC 13590		88.1	99.5	77.3			67.5	
NMC 14100		95.1	103.6	79.9			67	
NMC 19082		95.2	103.8	82.2			66.5	
NMC 22951		94.4	99.2	78.7				
NMC 23568		93	90.8	82.4			63.8	
NMC 20208			92					
Paracamelus gigas								
Zdansky, 1926		88.5	98	75.5			62	
Gigantocamelus spatula								
Breyer, 1974: table 4								
Broadwater A Locality	M		97±2.99	77±0.99				
	N		2	2				
Lisco B Locality	M		88±1.29	70±0.96				
	N		18	18				
Lisco C Locality	M		90±0.88	72±0.70				
	N		36	36				
Megacamelus merriami	M	85.7±3.4	94.7±3				63.9±2.1	
Harrison, 1985: table 4	OR	81.9–89.8	88.5–98.0				60.3–66.5	
	N	7	7				7	
Camelus bactrianus								
Harington, 1977: table 71		68.8	74.9	56			50.2	

FIG. 13. Comparison of astragali from Yukon and Alaska with various camelines. Data for *Camelops hesternus* from Rancho La Brea represent the minimum, mean, and maximum measurements reported by Webb (1965); *Hemiauchenia blancoensis* from Jiménez-Hidalgo and Carranza-Castañeda (2010); cf. *Paracamelus*, Old Crow, Yukon, from Harington (1977); *Paracamelus gigas* from Zdansky (1926); *Megacamelus merriami* from Harrison (1985); and *Camelus bactrianus* from Harington (1977).

et al. 2000). Diagnostic features include: (1) tuber calcis terminating in a blunt, pyramidal proximal facet (fig. 14A–C); (2) anterior border of tuber calcis slightly concave, terminating proximally in a bulbous peak; posterior border relatively straight to convex distally (fig. 14A); (3) posterior margin of distal region of tuber calcis with strongly developed rugosity (fig. 14C); (4) maximum anteroposterior measurement of corpus calcanei greater than proximodistal measurement; (5) corpus calcanei posteriorly convex, anterior process relatively short with limited distal projection (fig. 14B, C); (6) large sustentacular surface subdivided into small subtriangular facet anteriorly (fig. 14D) and weakly separated triangular facet laterally (fig. 14B); (7) cuboid articular facet relatively much wider than in BARCs such as *Bison* (fig. 14C); (8) distal astragalar surface divided into medially facing distal part and anteriorly facing proximal part (fig. 14A); (9) fibular articular surface convex proximally, concave distally; proximally positioned groove much shallower than in *Bison* (fig. 14B).

The calcanea from Yukon and Alaska are more robust than those of extant *Camelus* (Webb, 1965; Breyer, 1974; Olsen, 1988), especially in the region of the tuber calcis. The tubers on the calcanea from Yukon and Alaska terminate in blunt, pyramidally shaped facets, while in *Camelus*, the proximal facet is divided by a curved transverse crest that is concave toward the plantar side. The corpus calcanei in *Camelops hesternus* and the Yukon and Alaska calcanea are
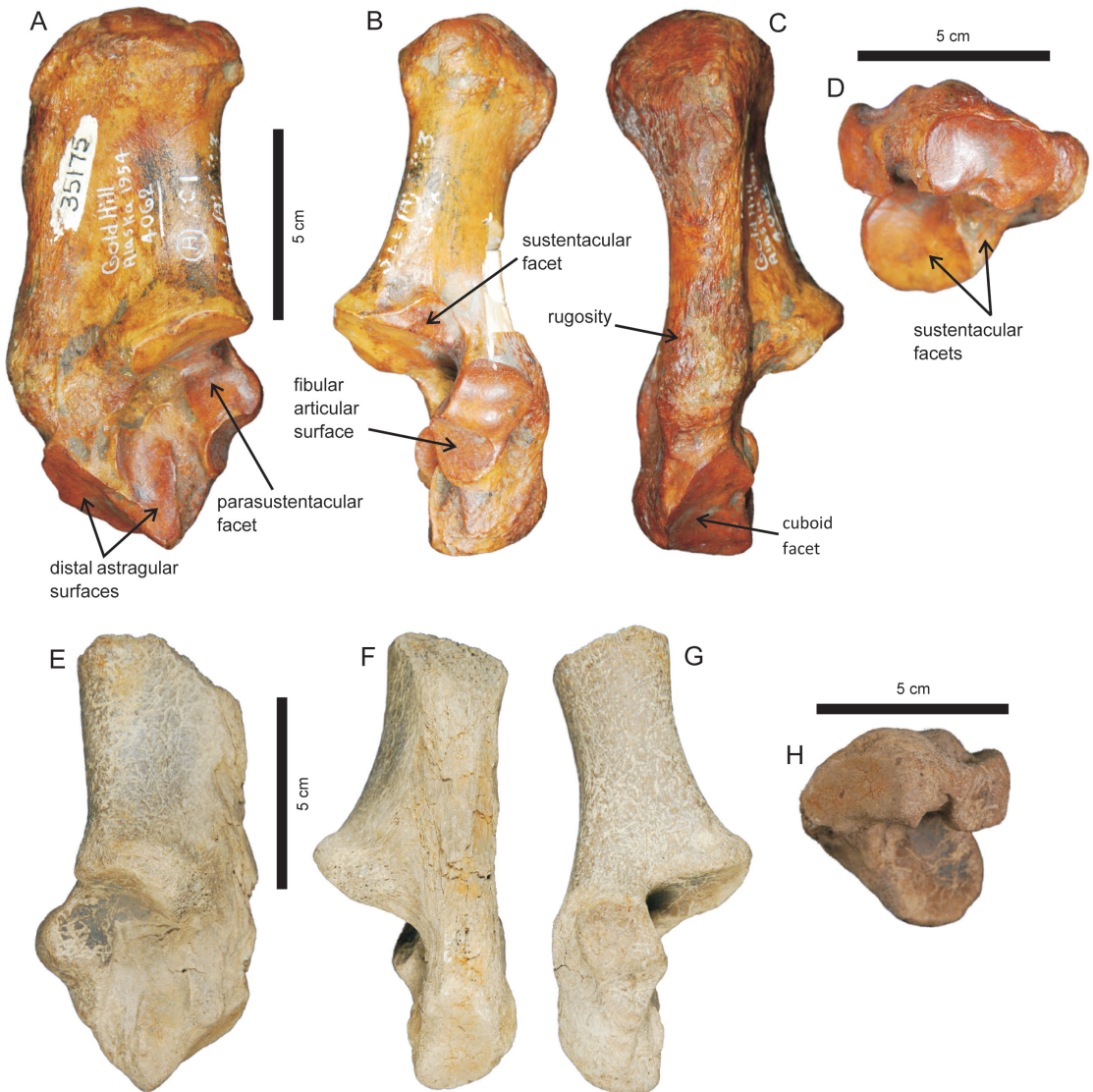
FIG. 14. *Camelops hesternus* calcanea from Alaska and Yukon. F:AM 35175: **A,** medial, **B,** anterior, **C,** posterior, and **D,** proximal views. YG 504.22: **E,** medial, **F,** posterior, **G,** anterior, and **H,** proximal views.

shorter than in *Camelus* and exhibit a convex rather than concave posterior border (see Breyer, 1974: fig. 8).

Metric data demonstrate the Yukon and Alaska calcanea (table 8; fig. 15) are near or below the reported ranges for *Camelops hesternus* from Rancho La Brea (Webb, 1965) and elsewhere (Breyer, 1974; Corner, 1977; Hilton et al., 2000). These calcanea are larger and more robust than those ascribed to *Hemiauchenia* (Breyer, 1974; Meachen, 2003, 2005) and *Alforjas* (Harrison, 1979), but smaller and less robust than those of the large extinct camelins, including *Megatylopus* (Thompson, 2002), *Megacamelus* (Harrison, 1985), *Gigantocamelus* (Breyer, 1974), and *Paracamelus* (Zdansky, 1926).

TABLE 8. Calcanea of *Camelops hesternus* from Alaska and Yukon and comparison with some other camelines. M = mean; OR = observed range; N = number of specimens.

| Calcanea		Measurements (mm)			
		Maximum length	**Maximum anteroposterior**	**Tuber: traverse**	**Tuber: anteroposterior**
YG 504.22		116.78 (min)	56.59 (min)	39.51	44.52
NMC 42512		141.8	67.5	40.1	49.1
F:AM 35175		137.55	66.26	39.21	54.17
F:AM 35176		129.23	63.34	37.53	47.57
F:AM 35158		138.97	72.79	39.11	51.18
Camelops hesternus	M	161.9±1.14	70.7±1.39	48.1±0.92	59.8±0.79
Webb, 1965: table 12	OR	157–170	65–76.7	40.5–53.2	56.4–65.3
	N	13	13	13	13
Camelops					
Breyer, 1974: table 2					
Lisco B Locality	M	147±0.99	61±0.49		
	N	2	2		
Gordon, Hay Springs, Rushville Localities	M	146±0.73	62±0.31		
	N	37	37		
Alforjas taylori	M	128.4±7	55.7±3.3		
Harrison, 1979	OR	120–137.1	52.1–61.7		
	N	9	11		
Hemiauchenia cf. *macrocephala*					
Breyer, 1974: table 1					
Broadwater A Locality	M	124±1.59	53±0.69		
	N	12	12		
Gordon, Hay Springs, Rushville Localities	M	130±7.22	57±2.89		
	N	5	5		
Harington, 1977: table 71					
NMC 13589		207.1	102.6	60.8	70
Paracamelus gigas					
Zdansky, 1926		181	90	52.5	57
Megacamelus merriami	M	186.4	79		
Harrison, 1985: table 4	OR	176.8–195.6	72.1–83.0		
	N	4	4		
Gigantocamelus spatula					
Breyer, 1974: table 4					
Broadwater A Locality		189	84		
Lisco B Locality	M	194	81		
	N	12	12		
Lisco C Locality	M	188±1.77	79±0.76		
	N	28	28		
Camelus bactrianus					
Harington, 1977: table 72		139.9	71.4	52.5	57
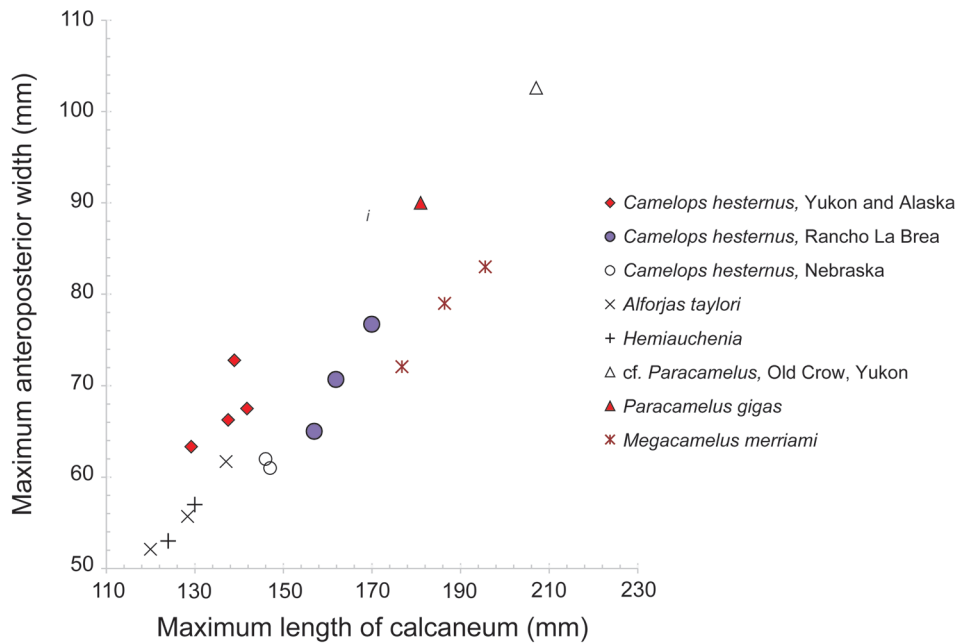
FIG. 15. Comparison of calcanea from Alaska and Yukon with various camelines. Data from *Camelops hesternus* from Rancho La Brea (Webb, 1965), *Alforjas taylori* (Harrison, 1979), and *Megacamelus merriami* (Harrison, 1985) represent minimum, mean, and maximum measurements reported. Data for *Camelops* from Nebraska is from Breyer (1974); *Hemiauchenia* from Breyer (1974) and Meachen (2003); cf. *Paracamelus*, Old Crow, Yukon, from Harington (1977) and *Paracamelus gigas* from Zdansky (1926).

Metapodials

Metacarpal (Mc)

Referred specimens: F:AM 35163 (Gold Hill, Alaska), right, distal fragment (fig. 16A, B); F:AM 35156 (Cripple Creek, Alaska), ?right, lacking proximal end, most of shaft; distal end gnawed; F:AM 35152 (Cripple Creek, Alaska), right, lacking distal condyles (juvenile) (fig. 16C–F); YG 328.259 (Hunker Creek, Yukon) ?metacarpal, distal fragment lacking right condyle; YG 29.199 (Hunker Creek, Yukon) right, proximal fragment (fig. 16F, G, H); YG 474.89 (Hunker Creek, Yukon), right condyle fragment; NMC 38172 (Sixtymile, Loc. 3, Yukon) right, fragment lacking distal condyles and the posterolateral process for branch of long plantar ligament (due to postmortem carnivore gnawing).

Metatarsal (Mt)

Referred specimens: YG 328.23 (Hunker Creek, Yukon) left, complete (fig. 17A–D); YG 328.287 (Hunker Creek, Yukon) fragment, shaft lacking proximal articular surfaces and distal condyles; NMC 42104 (Sixtymile, Loc. 3, Yukon) right, distal fragment (fig. 17E, F); NMC 42390 (Sixtymile, Loc. 3, Yukon) left, fragment lacking distal condyles, fusion of Mt III and Mt IV incomplete at proximal end (juvenile); YG 587.3 (Canyon Creek, Yukon) right, distal fragment.
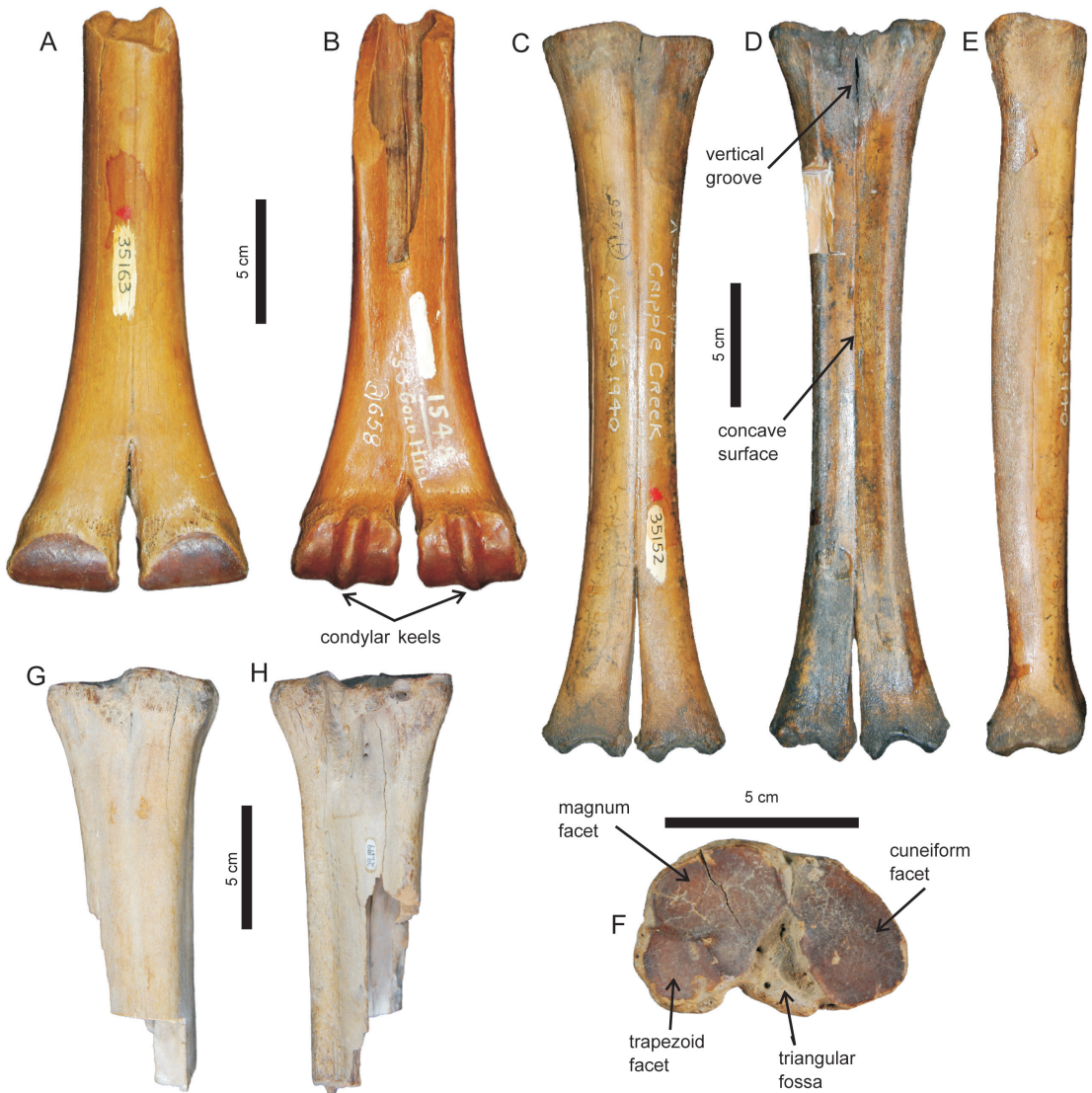
FIG. 16. *Camelops hesternus* metacarpals from Alaska and Yukon. F:AM 35163: **A,** anterior view, **B,** posterior view. F:AM 35152: **C,** anterior, **D,** posterior, and **E,** lateral view. YG 29.199: **F,** proximal. **G,** anterior, and **H,** posterior view.

Description: It is characteristic of camelids that the functional metapodial rays (III and IV in both limbs) are fully fused except at their distal ends, which diverge abaxially to form separate articular surfaces (condyles) for the proximal phalanges (fig. 17; tables 9, 10). For our assessment of distal metapodial fragments from Alaska and Yukon, we followed the descriptions of Webb (1965) that demonstrates the distal ends and diaphysis of the metacarpus are wider and more robust than those of the metatarsus.

The metapodial material from Alaska and Yukon closely matches features of metapodials described for *Camelops hesternus* from Rancho La Brea (Webb, 1965), including: (1) condylar
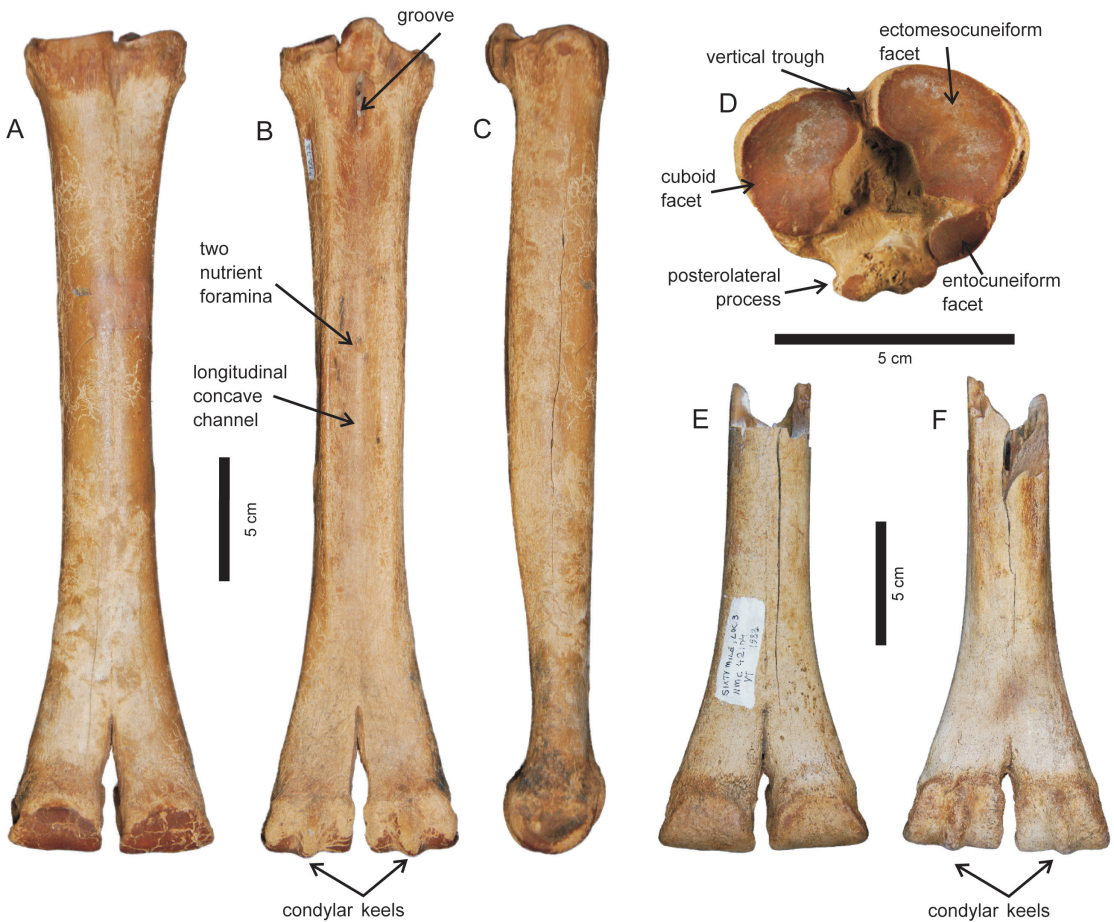
FIG. 17. *Camelops hesternus* metatarsals from Yukon. YG 328.23: **A,** anterior, **B,** posterior, **C,** medial, and **D,** proximal views. NMC 42104: **E,** anterior and **F,** posterior views.

keels (splines) of both the Mc and Mt confined to posterior surfaces (fig. 16B; fig. 17B, F); (2) lateral and medial margins of the Mc and Mt shaft convex anteroposteriorly (fig. 16E; 17C); (3) shaft of both the Mc and Mt deeply grooved posteriorly by wide longitudinal concave channel (fig. 16B, D; fig. 17B); (4) slight difference in height between contributions of Mc III and IV to proximal articular surface (fig. 16F); (5) proximal articular surface of Mc III separated from that of Mc IV by triangular fossa on posterior side (fig. 17I, F); proximal articular surface of the Mc III with a large anterior facet for the magnum and a small facet for the trapezoid while the entire proximal surface of the Mc IV articulates with the cuneiform (fig. 16F); (6) two small, closely positioned nutrient foramina approximately halfway down middle of palmar surface of Mt shaft (fig. 17B); (7) prominent posterolateral process, for long plantar ligament, found on proximal articular surface of Mt and bordered below by long, open ventral groove (fig. 17C, D); (8) proximal articular surface of the Mt with a large cuboid facet that is separated from ectomesocuneiform facet by a vertical trough (fig. 17D); (9) evidence of Mt III–IV fusion in form of narrow vertical groove near the proximal end (fig. 17D).

TABLE 9. Metacarpals of *Camelops hesternus* from Alaska and Yukon and comparison with some other camelines. M = mean; OR = observed range; N = number of specimens.

Metacarpals		Measurements (mm)							
		Maximum length	Proximal width	Proximl depth	Mid-shaft width	Midshaft depth	Length of free ends	Maximum distal depth	Maximum distal articular width
YG 29.199			68.97	42.59					
YG 474.89								41.11	
NMC 38172			65.22	45.11	39.37	39.86			
F:AM 35163					40.42	35.08	58.02	45.01	92.73
F:AM 35152		285.67 (min)	68.46	40.27	34.03	30.18			
F:AM 35156							66.7		92.99
Camelops hesternus	M	376.3	87.7	52.1	54.7	43	59	47.7	
Webb, 1965: table 10, 11	OR	374–380	82–92	50–54	51–57	41–46	55–61	46–51	
	N	3	3	3	3	3	3	3	
Camelops	M	361±2.50	72±1.10						91±1
Breyer, 1974: table 4	N	4	4						4
Camelops cf. *hesternus* Jass and Allan, 2016									
P05.10.52									68.34
P98.8.34		337	77						
Alforjas taylori	M	313.4±17.8	53.3±3.6						69.1±4.1
Harrison, 1979	OR	279.6–335.5	47.4–64.2						62.8–74.5
	N	10	21						9
Hemiauchenia cf. *macrocephala* Breyer, 1974: table 4		385	51						55
Hemiauchenia sp. Morgan, Sealey, and Lucas, 2008b: table 11		~385	44.1	31.8	25.6				
Paracamelus gigas Zdansky, 1926		462	90	58.5	53	49	98.5	55	
Gigantocamelus spatula Breyer, 1974: table 4									
Lisco B Locality	M	456±5.82	90±2.46						119±4.03
	N	5	5						5
Lisco C Locality	M	460±6.70	98±1.77						131±2.41
	N	8	8						5
Megacamelus merriami	M	510.8±20.7	91.2±11.0						118.8±3.3
Harrison, 1985: table 4	OR	483.9–542.9	81.1–116.4						113.8–123.0
	N	7	8						7
Megatylopus gigas Thompson, 2002									
Right		431	95.4						119.5
Left		432	94.2						116.9

TABLE 10, Metatarsals of *Camelops hesternus* from Alaska and Yukon and comparison with some other camelines, M = mean; OR = observed range; N = number of specimens.

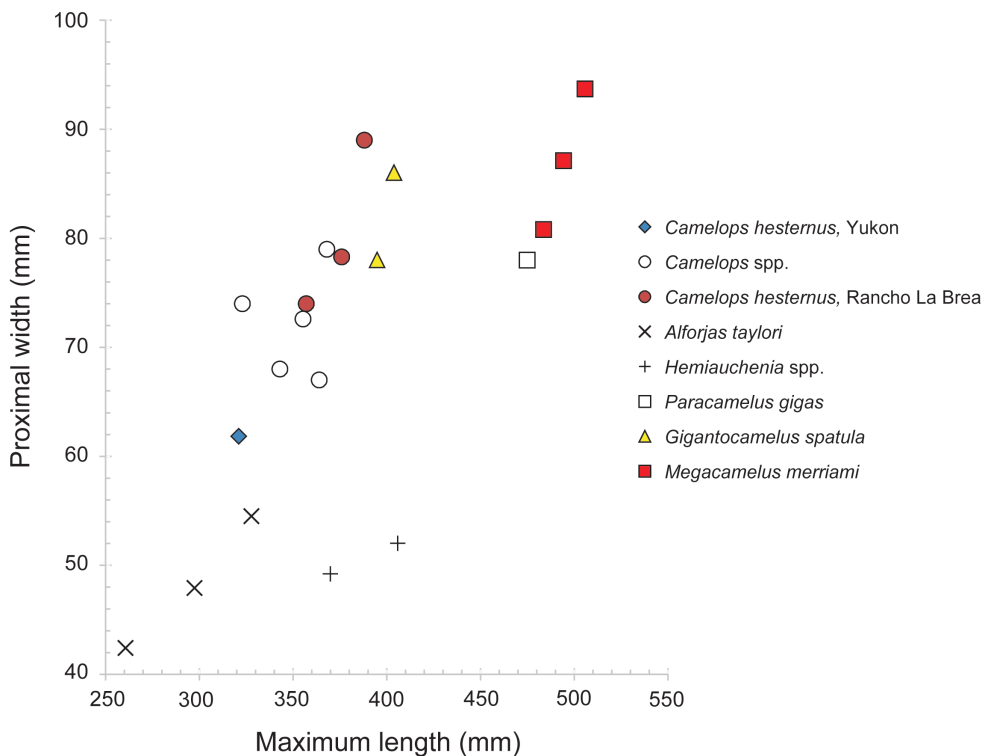| Metatarsals		Measurements (mm)							
		Maximum length	Proximal width	Proximal depth	Midshaft width	Midshaft depth	Length of free ends	Maximum distal depth	Maximum distal articular width
YG 328.23		321.12	61.82	46.64	34.07	35.9	53.19	38.25	77.17
YG 328.287					32.17	29.89			
YG 587.3							61.42	39.27	78.45
NMC 42104					32.42	36	54.35	40.84	81.54
NMC 42390		312 (min)	60.73	45.75	33.22	29.75			
Webb, 1965: table 10, 11	OR	357–388	74–89	53–59	40–49	39–51	51–65	42–50	
	N	5	6	6	6	6	7	7	
Camelops Breyer, 1974: table 4	M	364±3.49	67±0.84						82±0.69
	N	11	11						11
Camelops Mooser and Dalquist, 1975		323	74	54	46.1	39.5		41	87.1
Camelops Corner, 1977	M	355.3	72.6						86.3
	OR	343–368	68–79						82–93
	N	3	3						3
Alforjas taylori	M	297.5± 22.2	47.9±3.6						63.9±3.7
Harrison, 1979: table 5	OR	260.7–327.9	43.3–54.5						56.5–69.2
	N	12	15						15
Hemiauchenia cf. *macrocephala*	M	406±9.95	52±0.5						58±1.5
Breyer, 1974: table 4	N	4	4						4
Hemiauchenia gracilis Meachen, 2003, 2005		320	33		19.1				39.4
Bravo-Cuevas et al., 2012		330	39.7		25.3				
Paracamelus gigas Zdansky, 1926		475	78	61.5	46	51	79	48.5	
Camelus knoblochi Havesson, 1954								43	108
Gigantocamelus spatula Breyer, 1974: table 4 Lisco B Locality	M	395±4.08	78±1.58						102±1.77
	N	10	10						10
Lisco C Locality	M	404±4.60	86±2.13						112±2.43
	N	10	10						10
Megacamelus merriami	M	494.4	87.1						103.5
Harrison, 1985: table 4	OR	483.7–505.8	80.6–93.7						100.1–107.5
	N	5	2						4

FIG. 18. Comparison of metatarsals from Alaska and Yukon with various camelines. Data from *Camelops hesternus* from Rancho La Brea (Webb, 1965); *Alforjas taylori* (Harrison, 1979); and *Megacamelus merriami* (Harrison, 1985) represent minimum, mean, and maximum measurements reported. Data from *Camelops* spp. from Mooser and Dalquist (1975) and Corner (1977); *Hemiauchenia* spp. from Breyer (1974) and Morgan et al. (2008b); *Paracamelus gigas* from Zdansky (1926); and *Gigantocamelus spatula* from Breyer (1974).

In morphological characters and relative dimensions, the metapodials described and measured here (tables 9, 10; fig. 18) are similar to their equivalents in *Camelops* sp. from the late Blancan/Irvingtonian of Mexico (Mooser and Dalquist, 1975), Irvingtonian of Nebraska (Breyer, 1974), and *Camelops hesternus* from the Rancholabrean of California (Webb, 1965) and Alberta (Jass and Allan, 2016). As with other elements, metapodials from Alaska and Yukon are much smaller and less robust than those of the large extinct camelins, including *Paracamelus* (Zdansky, 1926), *Gigantocamelus* (Breyer, 1974), *Megacamelus* (Harrison, 1985), and *Megatylopus* (Thompson, 2002) (table 8, 9), but much more robust than those of gracile aucheniins including *Hemiauchenia* (Breyer, 1974; Meachen, 2003), *Alforjas* (Harrison, 1979), *Blancocamelus*, and *Lama* (Voories and Corner, 1986; Jiménez-Hidalgo and Carranza-Castañeda, 2012).

PROXIMAL PHALANX

Referred specimens: YG 328.21 (Hunker Creek, Yukon) complete, well preserved (fig. 19A–D); UAMES 35061 (Ester Creek, Alaska), complete, well preserved (fig. 19E–H); F:AM 35174 (Gold
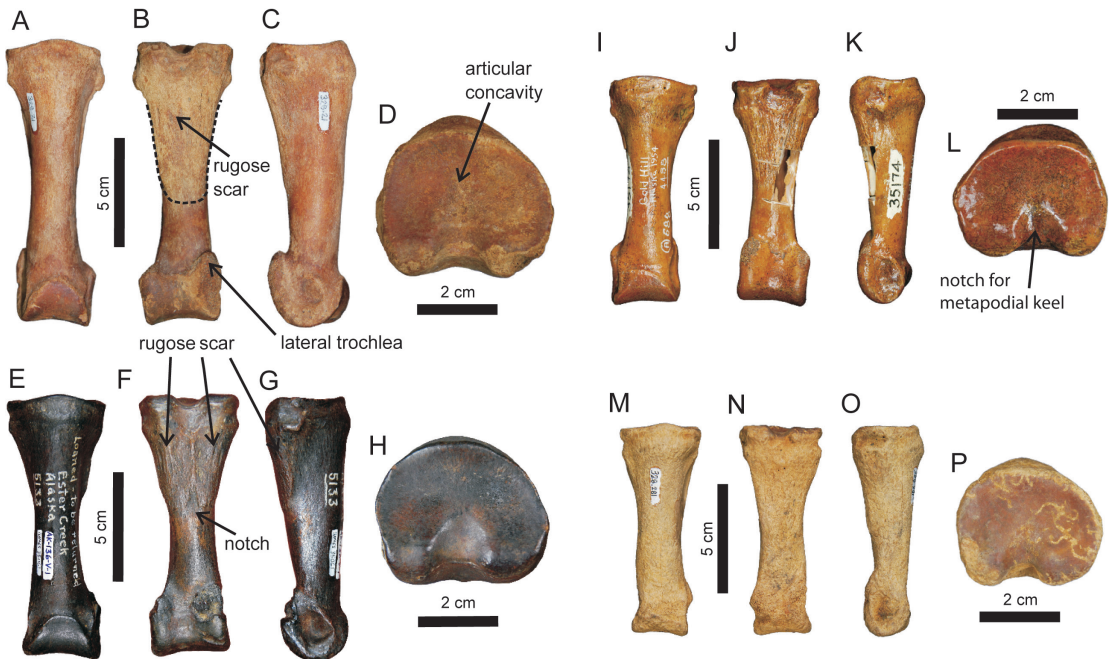
FIG. 19. *Camelops hesternus* proximal phalanges. Forefoot examples: YG 328.21: **A,** posterior, **B,** anterior, **C,** lateral, and **D,** proximal views; UAMES 35061: **E,** posterior, **F,** anterior, **G,** medial view. Hindfoot examples: F:AM 35174: **I,** anterior, **J,** posterior, **K,** medial, and **L,** proximal views; YG 328.281: **M,** anterior, **N,** posterior, **O,** medial, and **P,** proximal views.

Hill, Alaska) well preserved, complete (fig. 19I–L); YG 328.281 (Hunker Creek, Yukon) complete, abraded (fig. 19M–P); YG 587.1 (Canyon Creek, Yukon); YG 328.22 complete, heavily abraded; YG 400.6 (White River, Yukon) fragment, lacking proximal articular surface; YG 504.32 (Hunker Creek, Yukon) fragment, distal articular surface is lacking and proximal end is heavily eroded, possibly carnivore gnawed; 74-AWR-14 (Canyon Creek, Alaska) complete, well preserved but broken midshaft (repaired); F:AM 35151 (Cripple Creek, Alaska) complete but distal end heavily eroded; F:AM 35159 (Cripple Creek, Alaska) complete; F:AM 35150 (Engineer Creek, Alaska) complete; F:AM 35160 (Cripple Creek, Alaska) complete; F:AM 13161 (Cripple Creek, Alaska) fragment, proximal articular surface not fused and lacking (juvenile); F:AM 35162 (Dawson Cut, Alaska) complete, distal and proximal ends heavily abraded.

Description: Several well-preserved proximal phalanges (especially YG 328.21 and UAMES 35061) from northwestern North America have features resembling those found in *Camelops hesternus* according to detailed descriptions provided by Webb (1965), Breyer (1974), and Voorhies and Corner (1986). These features include: (1) proximal articular surface dorsoventrally concave, with groove or notch on the posterior margin for reception of metapodial keel (fig. 19D, L, H, P); (2) large rugose scar on proximopalmar surface (for ligamentous attachment) extending distally approximately half to two-thirds across center of shaft (fig. 19B, C, F, G), exhibiting only a slight, minimally recessed notch in middle of distal margin (fig. 19F); and (3) lateral (abaxial) side of ventral trochlea larger than medial (fig. 19B). Proximal phalanges of

the forelimb are larger than those of the hindlimb (Webb, 1965). Likely forelimb specimens include YG 328.21, 74; YG 587.1; UAMES 35061; 74-AWR-14, F:AM 144555, F:AM 35151, and F:AM 35150; smaller hindlimb versions are represented by YG 328.281, YG 328.22, YG 400.6, YG 504.32, F:AM 35159, F:AM 35160, F:AM 35174, and F:AM 35162.

As camelid proximal phalanges are distinctive and tend to fossilize well, it is unsurprising that they have played a prominent part in higher-level systematics (Webb, 1965). A good example is the great emphasis placed on the taxonomic and phylogenetic significance of the proximopalmar ligament scar ("proximal scar"; Breyer, 1974; Harrison, 1979; Voorhies and Corner, 1986; Honey et al., 1998; Rybczynski et al., 2013). Although this feature is usually described as an attachment point for the suspensory ligament, this statement is incomplete. In the extant dromedary *C. dromedarius* (Smuts and Bezuidenhout, 1987) the suspensory ligament (actually a highly modified interosseous muscle; Lesbre, 1903) originates from the palmar aspect of the carpus/tarsus and associated metapodials and inserts into the distal sesamoids of the metapodials. However, what anchors the sesamoids firmly to the subjacent bone are the straight sesamoid ligaments (ligg. sesamoideum rectum), the fibers of which fan out to insert into the phalangeal palmar surface. Also contributing fibers, especially to the margins of this area, are the collateral ligaments, palmar annular ligament, and the metacarpophalangeal (fetlock) joint capsule (Smuts and Bezuidenhout, 1987: fig. 2.7).

The principal osteological result of these arrangements is a substantial rugose zone ("proximal scar") occupying one-quarter to one-half of the palmar proximal end of the proximal phalanx (fig. 19B, F). Camelines vary in the definition, length, and certain characteristic features of the proximal scar. In both extant *Camelus* species, the scar is trapezoidal and distinctly raised. It occupies approximately one-third of the bone's length, surrounded by considerable numbers of small vascular foramina, especially peripherally (see Breyer, 1974: fig. 8). There is some within-species (and even within-individual) variation in the form of the scar's distal margin: it may be described as straight or moderately wavy, occasionally with a slight notch in the midline. In extant aucheniins the scar has a different appearance. Typically, it is sharply divided into two inverted triangles separated by a V-shaped notch. In *Lama* especially the notch between triangle apices is smooth and deep, indicating that few or no fibers insert therein. The result is that the aucheniin proximal scar characteristically exhibits a W-shaped distal margin, in contrast to extant camelins in which the margin is apparently always fairly straight. In *Vicugna* the scar is sometimes quite indistinct, without raised sides, although it has the same form as in *Lama* and exhibits a central notch.

Fossil camels also characteristically differ. In cf. *Paracamelus* from Old Crow, Yukon, the caudal margin bears a very pronounced V-shaped notch in the distal margin, and extends for a distance less than half the length of the phalangeal shaft (Harington, 1977; Rybczynski et al., 2013). A deeply recessed V-shaped notch is also seen in other large extinct camelins such as *Gigantocamelus* and *Megatylopus* (Voorhies and Corner, 1986), though it is not always as pronounced as it is in *Paracamelus* (Harrison, 1979). In *Hemiauchenia,* the notch is even more pronounced than in this last group, and the essentially separate triangular scars are unequal in length and extend for only a short distance distally (Breyer, 1974; Meachen, 2003). Scar mor-

phology in *Alforjas* is described as most closely resembling that of extinct *Hemiauchenia* and extant *Lama* (Breyer, 1974), although in the former the scar extends further down the length of the shaft (Harrison, 1979).

The proximal scar in *Camelops* differs to a greater or lesser degree from all the aforementioned taxa (Webb, 1965; Breyer, 1974). In particular, the scar complex in *Camelops* roughens more than half to two-thirds of the length of the palmar surface of the phalanx, and the V-shaped notch is either absent or very indistinct (Harrison, 1979). This complex in *Camelops* is much more developed than in extant *Camelus*, in which the scar is confined to the proximal one-third of the shaft (see Breyer, 1974: fig. 8). In combination, these features presumably indicate that the ligamentous attachment area in *Camelops* was relatively continuous, without a smooth zone intervening. This difference, together with the greater distal extension of the scar complex, may imply the existence of some biomechanical constraint in this taxon, perhaps connected with the need to assume or resist certain foot postures.

Proximal scar shape in proximal phalanges from Alaska and Yukon, especially as seen in complete specimens (e.g., YG 328.21), closely resembles conditions described for *Camelops hesternus* (Webb, 1965; Breyer, 1974; Voorhies and Corner, 1986). UAMES 35061 exhibits a very slight dimple in the distal margin, conforming to the position of the V-shaped notch described for some other taxa (fig. 19F). This last feature is not mentioned in the literature on *Camelops*; our conclusion is that it is probably frequently present but is so small as to escape notice.

Mensurational data from the proximal phalanges in our set (table 11) reveal they are relatively narrow compared to the more robust versions seen in cf. *Paracamelus* material from Old Crow, Yukon (Harington, 1977; Rybczynski et al., 2013), or other large extinct camelins such as *Paracamelus* (Zdansky, 1926), *Gigantocamelus* (Breyer, 1974), *Megacamelus* (Harrison, 1985), and *Megatylopus* (Thompson, 2002). As elsewhere in the skeleton, proximal phalanges of *Camelops* are much more robust than those of *Hemiauchenia* (Breyer, 1974; Meachen, 2003, 2005; Morgan et al., 2008b; Jiménez-Hidalgo and Carranza-Castañeda, 2010; Bravo-Cuevas et al., 2012;), *Alforjas* (Harrison, 1979), *Blancocamelus*, *Lama* (Voorhies and Corner, 1986; Jiménez-Hidalgo and Carranza-Castañeda, 2012), and other gracile aucheniins. Metrically, the Yukon and Alaska material is in good agreement with *Camelops hesternus* from Rancho La Brea (fig. 20; Webb, 1965).

DISCUSSION

The osteological descriptions and mensurational data presented here demonstrate that a camelin, morphologically closely resembling *Camelops hesternus* as recently revised by Baskin and Thomas (2015), lived in interior Alaska and Yukon during the late Pleistocene. As we also show, fossils of *C. hesternus* can be reliably distinguished from those of the larger-bodied "Yukon giant camel" cf. *Paracamelus* that is well represented in the Old Crow basin faunas of northern Yukon (Harington, 1977; Rybczynski et al., 2013).

Although our dataset is limited, most of the metric data for Alaskan and Yukon *Camelops hesternus* falls below or near the lower end of size ranges reported from temperate localities,

TABLE 11. Proximal phalanges of *Camelops hesternus* from Alaska and Yukon and comparison with some other camelines. M = mean; OR = observed range; N = number of specimens.

Proximal phalanges	Measurements (mm)						
	Maximum length	Proximal width	Proximal depth	Midshaft width	Minimum midshaft depth	Distal width	Distal depth
YG 328.21	126.61	45.44	40.81	21.74	21.03	36.96	31.56
YG 587.1		43.88	37.25	22.19	20.24		
YG 328.281	95.24	37.22	33.24	19.75	15.72	29.29	21.52
YG 328.22	106.61	37.77	32.25	19.35	17.39	30.83	25.52
YG 400.6				22.69	17.64	31.81	25.92
YG 540.32	107.17 (min)	38.68 (min)		21.13	19.3		
74-AWR-14	129.11	47.34	40.48	22.93	20.69	36.13	30.17
UAMES 35061	120.35	44.87	39.8	22.23	20.98	36.26	30.82
F:AM 35151	123.16	42.17	36.37	23.47	19.99	33.38 (min)	19.41 (min)
F:AM 35159	111.85	39.51	40.69	19.61	19.58	33.67	29.78
F:AM 35150	120.31	43.31	38.09	21.48	20.52	33.06 (min)	28.73
F:AM 35160	107.94	39.07	33.28	21.93	18.52	30.18	25.92
F:AM 35174	103.22	39.66	34.26	19.56	17.22	31.58	27
F:AM 13161	102.69 (min)	39.78	36.07	19.69	19.66	34.53	31.02
F:AM 35162	103.64			19.09	17.92	28.02	24.94
Camelops hesternus							
Webb, 1965: tables 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	9	9	9			9	9
Hindlimb	M	108.4±1.19	45.2±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	7	7	7			7	7
Alforjas taylori							
Harrison, 1979: table 5	OR	88.2–88.3	26.8–30.4					
	N	2	2					
Hemiauchenia cf. *macrocephala*							
Breyer, 1974: table 1							

Proximal phalanges		Measurements (mm)						
		Maximum length	**Proximal width**	**Proximal depth**	**Midshaft width**	**Minimum midshaft depth**	**Distal width**	**Distal depth**
Broadwater A Locality	M	96±3.52	28±0.25					
	N	4	4					
Gordon, Hay Springs, Rush-ville Localities	M	110±1.96	34±0.83					
	N	10	10					
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		33.1		50.0	
NMC 8623 (USNM 7713)		115.2	52.5	40.7	34.1	25.2	44.8	34.4
Camelus bactrianus								
Harington, 1977: table 73								
Forelimb		100.3	41.6	34	20.8	20.6	38.9	29.8
Hindlimb		91.3	37.8	29.7	18.6	17.7	34.3	26.5

including Rancho La Brea and sites in the midcontinent of North America (Breyer, 1974; Webb, 1965). The smaller size of many elements was also noted for *Camelops* cf. *hesternus* from Alberta, Canada (Jass and Allan, 2016). Like many studies of *Camelops* in the literature, our interpretation of relative body size should be reviewed with some caution as the relative rarity of fossils from eastern Beringia prohibits a strict statistical morphometric analysis. However, our general observation that most *Camelops hesternus* material from Alaska and Yukon is relatively small sized is consistent with the interpretation that it represents a smaller-bodied population of Rancholabrean *C. hesternus*, rather than a geographic and temporal range extension of *C. minidokae*. Regarded in older literature as the smallest member of the *Camelops* genus, *C. minidokae* is generally thought to have been confined to the Irvingtonian of the midcontinental United States (Baskin and Thomas, 2015). Although in their revision Baskin and Thomas (2015) retained this taxon, they did so tentatively, in light of Miller's (1980) view that *C. minidokae* may only be a junior synonym of *C. hesternus*. This may well be correct, but we hesitate to formally endorse this synonymy since we have not studied the original material of *Camelops minidokae*.

The fossil record from eastern Beringia demonstrates there were at least two separate dispersals of camelins from midcontinental North America to the high latitudes. The earlier event occurred during the Late Miocene and culminated in the appearance of Holarctic *Paracamelus*, which possibly persisted in arctic Yukon until the Early to Middle Pleistocene (Rybczynski et al., 2013). *Paracamelus* is also the putative ancestor of extant *Camelus*, which appeared in the
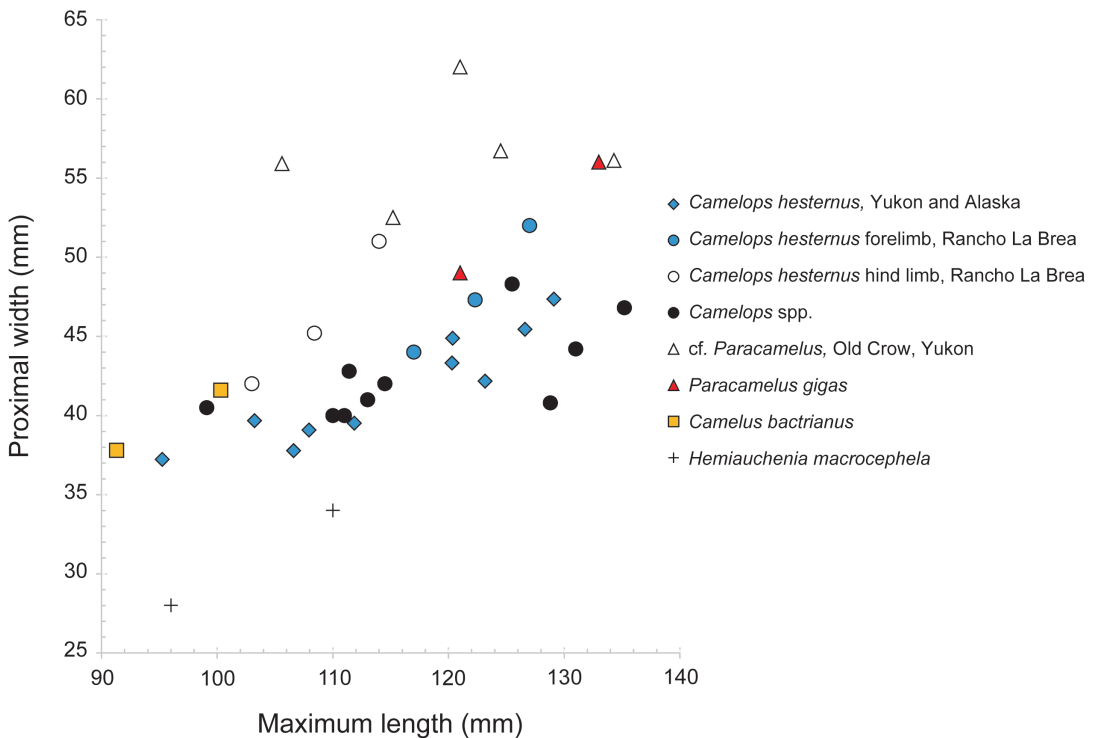
FIG. 20. Comparison of proximal phalanges from various camelines. Data for *Camelops hesternus* from Rancho La Brea (Webb, 1965) represents the minimum, mean, and maximum measurements reported. Data for *Camelops* spp. from Breyer (1974) and Morgan et al. (2008a). Data for cf. *Paracamelus*, Old Crow, from Harington (1977) and this study; *Paracamelus gigas* from Zdansky (1926); *Camelus bactrianus* from Harington (1977); and *Hemiauchenia macrocephala* from Breyer (1974).

early Middle Pleistocene in central Asia (Titov, 2008). The second northward dispersal was that undertaken by separately evolved *Camelops hesternus* during the Late Pleistocene. Stratigraphic and biostratigraphic data from Yukon provide no indication that *Paracamelus* and *Camelops hesternus* were ever coeval in the subarctic or arctic of North America.

Genomic data demonstrate that *Camelops* was a camelin (and not an aucheniin, as previously thought; Heintzman et al., 2015) that probably evolved in the western portion of midcontinental North America, sharing a last common ancestor with the *Paracamelus-Camelus* lineage in the late Miocene. Molecular reinterpretation of late Neogene camelin phylogeny strongly indicates that the earlier placement of *Camelops* within Aucheniini was a consequence of underappreciated morphological parallelisms. To make further progress, it will be important in future to reassess Late Miocene taxa in order to address and potentially resolve the largely enigmatic ancestry of *Camelops* within primitive camelins.

If the smaller body sizes suggested by our data represents high morphological variability within a single, wide-ranging Rancholabrean taxon, then this contradicts Bergmann's rule, which predicts that many wide-ranging mammals tend to exhibit larger body sizes in colder climates and/or higher latitudes as an adaptation for enhanced thermoregulation (Clauss et

al., 2013). McDonald et al. (2000) also arrived at a similar conclusion for Jefferson's ground sloth (*Megalonyx jeffersonii*) of Rancholabrean age in Yukon, which exhibited relatively smaller body sizes compared to conspecifics from more southerly localities. However, Geist (1987) has criticized the application of Bergmann's rule to large herbivores in the subarctic and Arctic, pointing out that body size of animals in the north are often smaller due to the limited nutrient and energy pulses available to them during their short growth periods. For example, present-day Peary caribou in the Canadian High Arctic are much smaller than caribou living further south due to limited available vegetation and overall productivity at extreme polar latitudes (Banfield, 1961; see also Huston and Wolverton (2011) for further challenges to Bergmann's rule and discussion of body size and geographic variability in net productivity). On the basis of our fossil data we speculate that competition for scarce food resources in generally harsher, northern climatic conditions might have been significant, resulting in smaller body sizes among high-latitude western camels.

Camelops hesternus was a highly successful species, having achieved during its tenure a vast distribution from the subtropics of Honduras (Lucas, 2008) to the high latitudes of central Alaska and Yukon. Fossils from Arizona place the earliest *Camelops* in the southwestern United States during the middle Blancan (~3.2–4.0 million years ago; Thompson and White, 2004), with the terminal species *C. hesternus* suffering complete extinction at the end of the Rancholabrean ~13,000 years ago (Waters et al., 2015). Its apparently remarkable environmental adaptability is reflected in metric and morphological data gathered from across its range (e.g., substantial variation in dental characteristics, body size). However, several caveats need to be applied. First, *Camelops* fossils are extremely rare in the high-latitude faunas of northwestern North America. This may imply that western camel populations were continuously present during the Late Pleistocene but always very rare. Alternatively, western camels may have dispersed northward into and occupied the eastern Beringia only during the relatively warm Last Interglaciation (Sangamonian), a hypothesis supported by emerging radiocarbon and stratigraphic data (Zazula et al., 2011; Heintzman et al., 2015). This interpretation correlates well with interpretation of the similar, but more extensive, radiocarbon dataset for arctic and subarctic American mastodons (*Mammut americanum*) (Zazula et al., 2014). Other taxa known to be very rare in high-latitude faunas, such as Jefferson's ground sloth (*Megalonyx jeffersonii*) (McDonald et al., 2000) and giant beavers (*Castoroides ohioensis*) (Harington, 1990), may have been similarly constrained ecologically to interglacial forests and shrublands (Muhs et al.2001), although this would need to be tested with appropriately large radiocarbon and stratigraphic datasets.

SUMMARY

Rare fossils attributed to *Camelops hesternus* have been recovered from several localities across the interior of Alaska and Yukon during the past century. These fossils are virtually indistinguishable in morphology from those described from the rich deposits at Rancho La Brea and elsewhere across the temperate parts of western North America. Metric data, however,

suggests these high-latitude populations may have been composed of smaller-bodied individuals. Limited radiocarbon and stratigraphic data suggests that *Camelops hesternus* was a member of the diverse community of large herbivores that occupied the interglacial forests and shrublands during the Sangamonian Interglaciation in eastern Beringia.

ACKNOWLEDGMENTS

REFERENCES

Armory, C., Jr. 1913. Camel fossil found in Arctic circle. New York Times, July 20, 1913: 7.

Banfield, A.W.F., 1961. A revision of the reindeer and caribou genus *Rangifer*. National Museums of Canada Bulletin 177. Biological Series 66: 137 pp.

Barbour, E.H., and C.B. Schultz. 1939. A new giant camel, *Titanotylopus nebraskensis*, gen. et sp. nov. Bulletin of the Nebraska State Museum 1: 291–294.

Baskin, J., and R. Thomas. 2015. A review of *Camelops* (Mammalia, Artiodactyla, Camelidae), a giant llama from the Middle and Late Pleistocene (Irvingtonian and Rancholabrean) of North America. Historical Biology 28: 120–127.

Bravo-Cuevas, V.M., E. Jiménez-Hidalgo, G.E. Cuevas-Ruiz, and M.A. Cabral-Perdomo. 2012. A small camelid *Hemiauchenia* from the late Pleistocene of Hidalgo, central Mexico. Acta Palaeontologica Polonica 57: 497–508.

Breyer, J. 1974. Examination of selected postcranial elements in Pleistocene camelids. University of Wyoming Contributions to Geology 13: 75–85.

Churcher, C.S. 1965 Camelid material of the genus *Palaeolama* Gervais from the Talara tar-seeps, Peru, with a description of a new subgenus, *Astylolama*. Proceedings of the Zoological Society of London 145: 161–205.

Clauss, M., M.T. Dittmann, D.W.H. Muller, C. Meloro, and D. Codron. 2013. Bergmann's rule in mammals: a cross-species interspecific pattern. Oikos 122: 1465–1472.

Cope, E.D. 1893. A preliminary report on the vertebrate paleontology of the Llano Estacado. Geological Survey of Texas, Fourth Annual Report, 1–136.

Corner, R.G. 1977. A Late Pleistocene–Holocene vertebrate fauna from Red Willow County, Nebraska. Transactions of the Nebraska Academy of Sciences and Affiliated Societies. Paper 423: 77–93.

Cragin, F.W. 1892. Observations on llama remains from Colorado and Kansas. American Geologist 9: 257–260.

Dalquest, W.W. 1992. Problems in the nomenclature of North American Pleistocene camelids. Annales Zoologici Fennici 28: 291–299.

Frick, C. 1930. Alaska's frozen fauna. Natural History 30: 71–80.

Froese, D.G., et al. 2009. The Klondike goldfields and Pleistocene environments of Beringia. GSA Today 19 (8): 4–10.

Geist, O.W. 1953. Collecting Pleistocene fossils in Alaska. Proceedings of the Second Alaska Science Conference, Science in Alaska: 171–172.

Geist, O.W. 1956. Biogeography – the fossil record. Proceedings of the Fourth Alaska Science Conference: 200–201.

Geist, V. 1987. Bergmann's rule is invalid. Canadian Journal of Zoology 65: 1035–1038.

Gidley, J.W. 1913. Notice of the occurrence of Pleistocene camel north of the Arctic Circle. Smithsonian Miscellaneous Collections 60 (26): 1–2.

Guthrie, R.D. 1968. Paleoecology of the large-mammal community in interior Alaska during the Late Pleistocene. American Midland Naturalist 79: 346–363.

Harington, C.R. 1977. Pleistocene mammals of the Yukon Territory. Ph.D. dissertation, Department of Zoology, University of Alberta, Edmonton. 1060 pp.

Harington, C.R. 1990. Vertebrates of the Last Interglaciation in Canada–a review, with new data. Géographie Physique Quaternaire 44: 375–387.

Harington, C.R. 1997. Pleistocene vertebrates of Sixtymile, Yukon Territory: a preliminary discussion. *In* M.E. Edwards, A.V. Sher, R.D. Guthrie (editors), Terrestrial paleoenvironmental studies in Beringia: 83–90. Fairbanks: Alaska Quaternary Center, University of Alaska.

Harrison, J.A. 1979. Revision of the Camelinae (Artiodactyla, Tylopoda) and description of the new genus *Alforjas*. University of Kansas Paleontological Contributions 95:1–27.

Harrison, J.A. 1985. Giant camels from the Cenozoic of North America. Smithsonian Contributions to Paleobiology 57: 1–29.

Havesson, J.I. 1954. Tertiary camels of the Eastern Hemisphere (genus *Paracamelus*). Proceedings of the Paleontological Institute, Moscow 67: 100–161.

Heintzman, P.D., et al. 2015. Genomic data from extinct North American revise camel evolutionary history. Molecular Biology and Evolution 32 (9): 2433–2440.

Hilton, R.P., D.C. Dailey, and H.G. McDonald. 2000. A late Pleistocene biota from the Arco Arena site, Sacramento, California. PaleoBios 20 (1): 7–12.

Honey, J.G., J.A. Harrison, D.R. Prothero, and M.S. Stevens. 1998. Camelidae. *In* C.M. Janis, K.M. Scott, and L.L. Jacobs (editors), Evolution of Tertiary mammals of North America, vol. 1.: terrestrial carnivores, ungulates, and ungulatelike mammals: 439–462. Cambridge: Cambridge University Press.

Huston, M.A., and S. Wolverton. 2011. Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. Ecological Monographs 81: 349–405.

Jass, C.N., and T.E. Allan. 2016. Camel fossils from gravel pits near Edmonton and Vauxhall, and a review of the Quaternary camelid record of Alberta. Canadian Journal of Earth Sciences 53: 485–493.

Jiménez-Hidalgo, E., and O. Carranza-Castañeda. 2010. Blancan camelids from San Miguel de Allende, Guanajuato, Central México. Journal of Paleontology 84 (1): 51–65.

Leidy, J. 1854. Description of a fossil apparently indicating an extinct species of the camel tribe. Proceedings of the Academy of Natural Sciences of Philadelphia 68: 131–150.

Leidy, J. 1873. Contributions to the extinct vertebrate fauna of the Western Territories. U.S. Geological Survey of the Territories, Report 1: 14–358.

Lesbre, F.X. 1903. Recherches anatomiques sur les camélidés. Archives du Muséum d'Histoire Naturelle de Lyon 8: 1–195.

Lucas, S.G. 2008. Pleistocene mammals from Yeroconte, Honduras. *In* S.G. Lucas, G.S. Morgan, J.A. Spielmann, and D.R. Prothero (editors), Neogene mammals. New Mexico Museum of Natural History and Science Bulletin 44: 403–408.

Lundelius, E.L., Jr. 1972. Fossil vertebrates from the Late Pleistocene Ingleside Fauna, San Patricio County, Texas. Austin: University of Texas at Austin Bureau of Economic Geology, Report of Investigations 77: 1–74.

McDonald, H.G., C.R. Harington, and G. De Iuliis. 2000. The ground sloth *Megalonyx* from Pleistocene deposits of the Old Crow Basin, Yukon, Canada. Arctic 53: 213–220.

Meachen, J.A. 2003. A new species of *Hemiauchenia* (Camelidae; Lamini) from the Plio-Pleistocene of Florida. Master of Science thesis, University of Florida, Gainesville, 58 pp.

Meachen, J.A. 2005. A new species of *Hemiauchenia* (Artiodactyla, Camelidae) from the Late Blancan of Florida. Bulletin of the Florida Museum of Natural History 45: 435–447.

Meade, G.E. 1945. The Blanco fauna. University of Texas Publication 4401: 509–556.

Miller, W.E. 1980. The Late Pliocene Las Tunas local fauna from southernmost Baja California. Journal of Paleontology 54: 762–805.

Mooser, O., and W.W. Dalquist. 1975. A new species of camel (Genus *Camelops*) from the Pleistocene of Aguascalientes, Mexico. Southwest Naturalist 19: 341–345.

Morgan, G.S., P.L. Sealey, and S.G. Lucas. 2008a. Pliocene (Blancan) vertebrates from Arroyo de la Parida, Palomas Formation, Socorro County, Central New Mexico. *In* S.G. Lucas, G.S. Morgan, J.A. Spielmann, and D.R. Prothero (editors), Neogene mammals. New Mexico Museum of Natural History and Science Bulletin 44: 189–206.

Morgan, G.S., P.L. Sealey, and S.G. Lucas. 2008b. Late Pliocene (Late Blancan) vertebrate faunas from Pearson Mesa, Duncan Basin, southwestern New Mexico and southeastern Arizona. *In* S.G. Lucas, G.S. Morgan, J.A. Spielmann, and D.R. Prothero (editors), Neogene mammals. New Mexico Museum of Natural History and Science Bulletin 44: 141–188.

Muhs, D.R., T.A. Ager, and J.E. Begét. 2001. Vegetation and paleoclimate of the last interglacial period, central Alaska. Quaternary Science Reviews 20: 41–61.

Olsen, S.J. 1988. The camel in ancient China and osteology of the camel. Proceedings of the Academy of Natural Sciences of Philadelphia 140: 18–58.

Pickford, M., J. Morales, and D. Soria. 1995. Fossil camels from the Upper Miocene of Europe: implications for biogeography and faunal change. Geobios 28: 641–650.

Pinsof, J.D. 1998. The American Falls local fauna: late Pleistocene (Sangamonian) vertebrates from southeastern Idaho. *In* W.A. Akersten, H.G. McDonald, D.J. Meldrum, and M.E.T. Flint (editors), And whereas... Papers on the vertebrate paleontology of Idaho honoring John A. White, vol. 1: 121–145. Idaho Museum of Natural History Occasional Paper 36.

Rybczynski, N., et al. 2013. Mid-Pliocene warm-period deposits in the High Arctic yield insight into camel evolution. Nature Communications 4: 1–9.

Savage, D.E. 1951. Late Cenozoic vertebrates of the San Francisco Bay region. University of California Publications, Department of Geological Sciences Bulletin 28: 215–314.

Slaughter, B.H. 1966. *Platygonus compressus* and associated fauna from the Laubuch Cave of Texas. American Midland Naturalist 752: 475–494.

Smuts, M.M.S., and A.J. Bezuidenhout. 1987. Anatomy of the dromedary. Oxford: Oxford Science Publications.

Thompson, M.E. 2002. Osteology of a giant camel from Elmore County, Idaho. *In* W.A. Akersten, H.G. McDonald, D.J. Meldrum, and M.E.T. Flint (editors), And whereas...Papers on the vertebrate paleontology of Idaho honoring John A. White, vol. 2: 35–51. Idaho Museum of Natural History Occasional Paper 37.

Thompson, M.E., and R.S.J. White. 2004. Getting over the hump: Blancan records of *Camelops* from North America, with special reference to Hagerman, Idaho and the 111 Ranch, Arizona. Denver, Colorado: Geological Society of America. Abstracts with Programs 36: 54.

Titov, V.V. 2008. Habitat conditions for *Camelus knoblochi* and factors in its extinction. Quaternary International. 179: 120–125.

Voorhies, M.R., and R.G. Corner. 1986. *Megatylopus* (?) *cochrani* (Mammalia: Camelidae): a re-evaluation. Journal of Vertebrate Paleontology 6: 65–75.

Waters, M.R., T.W. Stafford, Jr., B. Kooyman, and L.V. Hills. 2015. Late Pleistocene horse and camel hunting at the southern margin of the ice-free corridor: reassessing the age of Wally's Beach, Canada. Proceedings of the National Academy of Natural Sciences of the United States of America 112: 4263–4267.

Webb, S.D. 1965. The osteology of *Camelops*. Bulletin of the Los Angeles County Museum 1: 1–54.

Weber, F.R., T.D. Hamilton, D.M. Hopkins, C.A. Repenning, and H. Haas. 1981. Canyon Creek: a late Pleistocene vertebrate locality in interior Alaska. Quaternary Research 16: 167–180.

Wilson, M., C.S. Churcher. 1978. Late Pleistocene *Camelops* from the Gallelli Pit, Calgary, Alberta: morphology and geologic setting. Canadian Journal of Earth Sciences 15: 729–740.

Wortman, J.L. 1898. The extinct Camelidae of North America and some associated forms. Bulletin of the American Museum of Natural History 10 (7): 93–142.

Zazula, G.D., et al. 2014. American mastodon extirpation in the Arctic and Subarctic predates human colonization and terminal Pleistocene climate change. Proceedings of the National Academy of Sciences of the United States of America 111: 18460–18465.

Zazula, G.D., D.G. Turner, B.C. Ward, and J. Bond. 2011. Last interglacial western camel (*Camelops hesternus*) from eastern Beringia. Quaternary Science Reviews 30: 2355–2360.

Zdansky, O. 1926. *Paracamelus gigas*, Schlosser. Palaeontological Sinica C, vol. 2, part 4: 1–44.