Rev. bras. paleontol. 19(2):243-258, Maio/Agosto 2016

doi: 10.4072/rbp.2016.2.08

THE RECORD OF CAMELIDS (ARTIODACTYLA, CAMELIDAE) FROM THE VALSEQUILLO BASIN, LATE PLEISTOCENE OF PUEBLA STATE, CENTRAL MEXICO: TAXONOMY, DIET, AND GEOGRAPHIC DISTRIBUTION

VICTOR MANUEL BRAVO-CUEVAS
Museo de Paleontología, Área Académica de Biología, Universidad Autónoma del Estado de Hidalgo, Ciudad del Conocimiento, Carretera Pachuca-Tulancingo km 4.5, CP 42184, Pachuca, Hidalgo, México.
vmbc1@yahoo.com

JOAQUÍN ARROYO-CABRALES
Laboratorio de Arqueozoología M. en C. Ticul Álvarez Solórzano, Subdirección de Laboratorios y Apoyo Académico (SLAA), Instituto Nacional de Antropología e Historia.

JAIME PRIEGO-VARGAS
Museo de Paleontología, Área Académica de Biología, Universidad Autónoma del Estado de Hidalgo, Ciudad del Conocimiento, Carretera Pachuca-Tulancingo km 4.5, CP 42184, Pachuca, Hidalgo, México.

ABSTRACT – Dental and postcranial fossil material referable to camelids, which has been recovered from Quaternary deposits that outcrop in the Valsequillo Basin, Puebla State, central Mexico, is formally described. A comparative study indicates the presence of two species of camelids, including *Hemiauchenia macrocephala* and *Camelops hesternus*. The sample referable to *H. macrocephala* includes maxillary and mandibular fragments, isolated teeth, and several postcranial remains (astragalus, metapodials, and proximal phalanges), which show the following diagnostic features of the species: molariforms covered by a layer of cementum; a mandible increasing in depth from p4 to m3; p4 triangular in outline; long and slender metapodials; and proximal phalanges with a W-shaped suspensory ligament scar. The sample referable to *C. hesternus* is represented by maxillary and mandibular fragments, isolated teeth, and metapodials, sharing with the species its large size; P4 quadrate in outline; p4 triangular in outline and simply folded; and a mandible that is significantly deeper from p4 to m3. A microwear analysis was performed in order to characterize the diet of studied samples, indicating a browser and mixed feeding behavior in *H. macrocephala* and *C. hesternus* respectively. The differences in size and trophic regimes in these species should explained the resource partitioning between them. In the late Pleistocene these camelids were common in Mexican sites between the 19°-25° N, and the record from the Valsequillo Basin is one of the few sites where both species have been reported.

Key words: Camelidae, taxonomy, diet, geographic distribution, Valsequillo Basin, Quaternary.

RESUMO – Material fóssil dentário e pós-craniano atribuído a camelídeos, recuperados de depósitos quaternários aflorantes na Bacia Valsequillo, Estado de Puebla, México central, é descrito formalmente. Um estudo comparativo indica a presença de duas espécies de camelídeos, *Hemiauchenia macrocephala* e *Camelops hesternus*. A amostra atribuída a *H. macrocephala* inclui fragmentos maxilares e mandibulares, dentes isolados, e vários restos pós-cranianos (astrágalos, metapodiais e falanges proximais), que mostram os seguintes caracteres diagnósticos da espécie: molariformes coberto por uma camada de cemento; uma mandíbula aumentando em altura do p4 ao m3; p4 de aspecto triangular; metapodiais longos e finos; e falanges proximais com uma cicatriz no ligamento suspensório em forma de W. A amostra atribuída a *C. hesternus* é representada por fragmentos maxilares e mandibulares, dentes isolados, e metapodiais, compartilhando com a espécie seu grande tamanho; P4 com aspecto quadrangular; p4 de contorno triangular e simplesmente dobrado; e uma mandíbula que é significantemente mais alta de p4 a m3. Uma análise de micro-desgaste foi realizada a fim de caracterizar a dieta de amostras estudadas, indicando hábito ramoneador e a alimentação mista em *H. macrocephala* e *C. hesternus* respectivamente. As diferenças de tamanho e regimes tróficos nestas espécies deve explicar a partilha de recursos entre elas. No final do Pleistoceno, esses camelídeos eram comuns em localidades mexicanas entre 19°-25°N e o registro da Bacia de Valsequillo é um dos poucos locais onde ambas as espécies têm sido relatadas.

Palavras-chave: Camelidae, taxonomia, dieta, distribuição geográfica, Bacia Valsequillo, Quaternário.

INTRODUCTION

Camelids (Artiodactyla, Camelidae) were an important component of Pleistocene mammalian faunas of North America. They were represented by at least five genera, including llamas (Tribe Lamini: *Hemiauchenia* and *Palaeolama*) and camels (Tribe Camelini: *Camelops*, *Titanotylopus*, *Megatylopus*) (Kurtén & Anderson, 1980; Prothero & Schoch, 2002; Heintzman *et al*., 2015). Llamas were generally more common than camels at southern latitudes of North America, including Mexico (Hulbert & Webb, 2001; Bravo-Cuevas *et al*., 2012). Llamas and camels became extinct in North America at the end of the Pleistocene (*ca.* 10,000 years ago), although some relatives of these groups survive in South America and the Old World, respectively (Webb, 1974; Prothero & Schoch, 2002).

Llamas, including representatives of the genera *Palaeolama* and *Hemiauchenia*, dominate the known record of camelids from the Pleistocene of Mexico. The common species is *Hemiauchenia macrocephala*, which have been reported from several localities in northern, central, and southeastern Mexico (Ferrusquía-Villafranca *et al*., 2010). There are other less well-known lamine species, such as *Hemiauchenia gracilis* from the Irvingtonian of Sonora (Croxen *et al*., 2007; White *et al*., 2010) and the Rancholabrean of Hidalgo (Bravo-Cuevas *et al*., 2012), as well as *Palaeolama mirifica* from the Rancholabrean of Puebla (Bravo-Cuevas & Jiménez-Hidalgo, 2015).

The record of camels includes *Camelops hesternus* and several nominal species of *Camelops* from Pleistocene localities in central Mexico (*e.g. C. mexicanus*, *C. traviswhitei*, and *C. conidens*) (Ferrusquía-Villafranca *et al*., 2010). Furthermore, there is a single occurrence referable to *Titanotylopus* (or *Gigantocamelus*) from the Irvingtonian of Sonora (Croxen *et al*., 2007).

Since the second half of the nineteenth century, paleontological and archaeological research has been conducted at the Valsequillo Basin area, Puebla State, central Mexico, resulting in an important collection of mammalian fossil remains (including specimens belonging to humans) (*e.g.* Armenta, 1957, 1959, 1978; Ochoa-Castillo *et al*., 2003). So far as is known, the mammalian record represents a late Pleistocene assemblage represented by armadillos, glyptodonts, ground sloths, saber-tooth cats, wolves, bears, rodents, lagomorphs, horses, tapirs, camelids, antilocaprids, bison, gomphotheres, mastodons, and mammoths (Jiménez-Hidalgo *et al*., 2015). However, formal taxonomic characterization of the majority of those mammalian groups has not been attempted, including the material referable to camelids.

A set of fossil specimens from the Valsequillo Basin is housed at the Laboratorio de Arqueozoología M. en C. Ticul Álvarez Solórzano, Subdirección de Laboratorios y Apoyo Académico (SLAA), Instituto Nacional de Antropología e Historia (INAH), Mexico City, Mexico. A review of that collection revealed an important number of specimens belonging to camelids, including dental and postcranial elements that represent at least two different taxa. The purpose of present study is to formally describe and characterize that material, as well as to provide information regarding the diet of the camelids from the Valsequillo Basin by means of the microscopic evaluation of dental wear patterns (= microwear). Furthermore, some aspects regarding the geographic distribution of these species are discussed.

STUDY AREA

Sites around the Valsequillo dam (named "Manuel Ávila Camacho"), in the State of Puebla, have been studied by several archaeologists (see Gonzalez *et al*., 2007, for an extensive discussion on the site) as one of the most promising areas for finding an association between early human presence and extinct megafauna. It is found at around 18°54'-18°55'20"N, 98°10'10"-98°10'55"W, at 2040-2056 m.a.s.l., 15 km south from city of Puebla (Cruz-Muñoz *et al*., 2009) (Figure 1). Present climate is temperate, and the original vegetation was a shrub associated with pine forest (INEGI, 1987), although currently there are many settlements around the dam.

The stratigraphic context at the site is composed of alluvial and volcanic deposits that are separated by a major erosional unconformity that comprise five major stratigraphic units. The oldest unit has been referred as to the Xalnene Tuff dating in approximately 1.3 million years BP (Renne *et al*., 2005), overlaid by the Hueyatlaco Ash, Tetela Lahar, and Toba Buena Vista, which have dates that soon will be reported (M. Waters, pers. com., 2015). However, different interpretations have been proposed for the stratigraphy at the Valsequillo Basin (see Malde *et al*., 2011), and further analyses is warranted. In fact, it seems that the Hueyatlaco Ash, Tetela Lahar, and Toba Buena Vista layers were part of the channel where alluvial sediments containing fossil bones were found, but materials from that channel have not been dated so far (M. Waters, pers. com., 2015). In any case, Pichardo (1997) identified three faunal zones, mainly based on dates, with zone I dated around 9,500 yr BP, zone II between 20,000 and 26,000 yr BP, and zone III with more than 200,000 yr. Supposedly elements pertaining to camelids were found in all three zones.

MATERIAL AND METHODS

The sample consists of maxillary and mandible fragments, numerous isolated teeth, and several postcranial elements. The fossil elements are cataloged using a provisional identification number. The specimens are housed at the Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano", Subdirección de Laboratorios y Apoyo Académico (**SLAA**), Instituto Nacional de Antropología e Historia (**INAH**), Mexico City, Mexico. The fossil material from the Valsequillo Basin was compared with dental and postcranial remains of selected camelid taxa housed at the vertebrate paleontology collections of both Natural History Museum of Los Angeles County and the George C. Page Museum of La Brea Discoveries (**LACM**), Los Angeles, California; Vertebrate Paleontology Laboratory of the University of Texas at Austin, Texas (**TMM**); Vertebrate

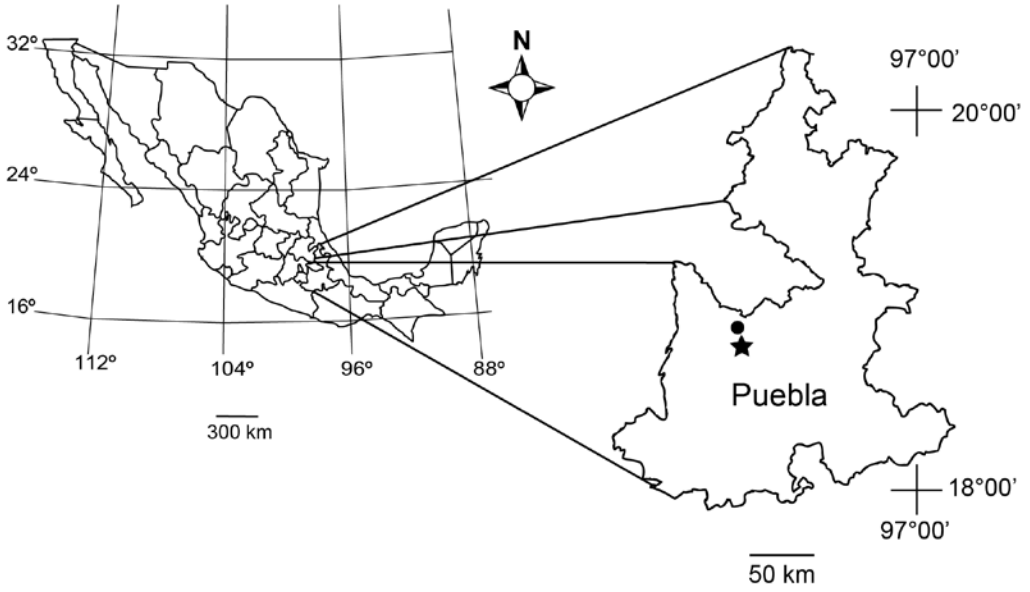

Figure 1. Index map of the study area, State of Puebla, central Mexico. The capital of the State, Puebla of the Zaragoza city (**circle**) and the late Pleistocene Valsequillo Basin area (**star**) are depicted.

Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida (**UF**); and Sección de Macrovertebrados, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, México (**UAHMP**).

The nomenclature of the upper and lower dentition is that of Bärmann & Rössner (2011). The tooth wear stages are those proposed by Breyer (1977: 529) and are related to a particular individual category. The crown height (along the mesostyle) and the anteroposterior length and transverse width at the occlusal surface, were measured with a digital caliper. The greatest length and transverse diameter (across the diaphysis) of postcranial remains were also measured; in some instances, those were taken using a 5 m flexible measurement tape. All measurements are in millimeters.

A low magnification stereoscopic microwear analysis (35 X) was performed using the M1/m1, M2/m2, and M3/m3 tooth positions. A set of 11 molars was considered for the analysis, including three of the upper dentition and eight of the lower dentition. Molds and casts of the occlusal surface of each tooth were made using dental impression material of polyvinyl siloxane and clear epoxy resin respectively (Solounias & Semprebon, 2002). The conventional microwear features, scratches and pits, were counted in a square of 0.4 X 0.4 mm. In the upper molars, microwear features were scored in two representative areas on the second enamel band of the paracone or metacone; in the lower molars, on the second enamel band of the paraconid or hypoconid.

The small pits are distinguished as structures with well-defined rounded borders and high refraction, while the large pits are at least twice the diameter of small pits, deeper, and with low refraction. On the other hand, the fine scratches are shallow structures with a low refractivity, whereas the coarse scratches are deeper and are very refractive (Solounias & Semprebon, 2002).

A single observer performed the quantification and scoring of the microwear features (Jaime Priego Vargas) in order to avoid inter-observer error (Mihlbachler *et al.*, 2012). The nomenclature and score system for scratches and pits are those from Solounias & Semprebon (2002) and Semprebon *et al*. (2004), as follows: large pits (0 = less than four large pits, 1 = more than four large pits); cross scratches (0 = less than four cross scratches; 1 = more than four cross scratches); gouges (0 = no; 1 = yes); texture of scratches (0 = fine; 1 = mixture of fine and coarse; 2 = coarse). In general, the microwear pattern of a typical grazer has a high number of scratches and a low number of pits, whereas a typical browser has a low number of scratches and high number of pits. Mixed feeder shows a microwear signature that switches between browsing and grazing (seasonally and/or regionally) (Solounias & Semprebon, 2002).

The microwear features in the samples of *Hemiauchenia macrocephala* and *Camelops hesternus* from Valsequillo Basin were compared to the extant ungulate dataset sampled by Solounias & Semprebon (2002) by plotting the average number of pits (**AP**) versus the average number of scratches (**AS**). A Discriminant Function Analysis (**DFA**) on the Solounias & Semprebon (2002) dataset was performed, assuming equal prior classification probabilities for all groups, in order to classify the studied sample into one of the following dietary categories: leaf browsers, fruit browsers, meal-by-meal mixed feeders, seasonal/regional mixed feeders, and grazers. The variables expressed in percentage, including cross scratches, fine scratches, coarse scratches, large pits, and gouges, were normalized for the DFA, using the arcsine transformation.

Statistical analyses were run on PAST vr.3.04 (Hammer *et al*., 2001) software package for Mac. The significance level for statistical analyses is a *p*-value of 0.05.

The abbreviations used in preset study are as follows: **CH/ch**, upper/lower teeth crown height; **GL**, greatest length

of the bone element; **L**, left; **LTRL**, lower tooth row length; **M/m**; upper/lower molar; **Mtc**, metacarpal; **Mtt**, metatarsal; **P/p**, upper/lower premolar; **R**, right; **TD**, transverse diameter across the diaphysis; **TW/tw**, upper/lower teeth transverse width; **UTRL**, upper tooth row length.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Family CAMELIDAE Gray, 1821
Subfamily CAMELINAE Gray, 1821
Tribe LAMINI Webb, 1965

Hemiauchenia Gervais & Ameghino, 1880

Type species. *Hemiauchenia paradoxa* Gervais & Ameghino, 1880, Pampean region of Argentina, Lujanian (late Pleistocene).

Hemiauchenia macrocephala Cope, 1893
(Figures 2-6; Tables 1-4)

Referred material. One right maxillary fragment with P4-M1 (66-1-C-5-27), one left maxillary fragment with P3-M3 (66-1-K-4-25), two right mandible fragments with p4-m3 (64-R-12-5-20, 66-1-V-1-190), one right mandible fragment with p4-m2 (66-1-p2-28), one right mandible fragment with m1-m3 (64-1-C3-19), one left mandible fragment with p4-m3 (66-1-1-E-280), 16 isolated molariforms (64-1-D-5-18, M3R; 66-1-W-0-18, M3R; 64-1-Z-15, M3L; 66-1 2X-10, p4L; 64-1-F-6-21, m1R; 64-1-H-6, m1L; 64-1-B-3-8, m1L; 64-1-Z-3-15, m1/2L; 66-1-1-W-1814, m2L; 66-1-L-5-260, m3R, 64-1-Z-3-16, m3R; 64-1-Z-1-15, m3R; 66-1-X-0-16, m3R; 66-1-1-W-1814, m3L; 64-I-Z-Z-1-16, m3L; 64-I-H-6-22, m3L), eight metacarpals (64-1-H-17, R; 66-1-Y-9-25, R; 66-1-U-O-190, R; 66-1-1-K-240, L; 66-1-L-5-28, L; 552, L; 622, L; 66-1-2-W-140, L), nine metatarsals (66-1-U-O-190, R; 66-1-M-8-300, R; 66-1-K-1-30, R; 66-1-V-0-19, R; 66-1-1-R-23, R; 544, L; 66-1-F-4-280, L; 66-1-C-4-27, L; 66-1-D-1-25, L), two astragali (64-11-Z-3-17, L; 66-1-Z-W-16, L), and 13 proximal phalanges (66-1-0-5-2-40, 66-1-1-W-16, 64.1-F4-17, 66-1-K-2-21, 64.1-J-3-19, 66-1-B-2-23, 64-1-Z-Z-2-15, 66-1-1-Q-10, 66-1-U-1-20, 64-1-G-7-S, 64.1-F-H-17, 64.1-D-4-19 , 66-1-B-2-10).

Distribution. *Hemiauchenia macrocephala* has been reported from numerous Pleistocene localities from California to Florida (Kurtén & Anderson, 1980). Furthermore, it is known from localities in northwestern, northcentral, central, and southwestern Mexico (Ferrusquía-Villafranca *et al*., 2010). There is a single occurrence from the early Pleistocene of El Salvador, Central America (Cisneros, 2005).

Description. The P3 to M3 UTRL in the specimen 66-1-K-4-25 is 108.1 mm. In the maxillary fragments (specimens 66-1-C-5-27 and 66-1-K-4-25), the molariforms have late moderate tooth wear stage, which is a condition related to adult individuals (Figure 2). The mean molar CH in the M3 along the mesostyle is of about 25 mm (Table 1). A thin layer of cementum covers the teeth (≈ 1 mm thick). The P3 is small, two-rooted, and rectangular in outline; its occlusal surface is situated below the crown height of P4 and M1-M3, indicating that this tooth was non-functional. In occlusal view, the P4 is trapezoidal in outline with an elongated fossette, and it is significantly larger than the P3. The molars are distinguished by having styles, ribs, parastyle and mesostyle well developed, whereas the metastyle is less developed. The protocones and the metaconules are subequal in size, rounded, and U-shaped. The pre- and postfossettes are unfolded and somewhat sinuous in outline. In occlusal view, the M1 is quadrangular, the M2 is rectangular, and the M3 is triangular. The M2 is the largest

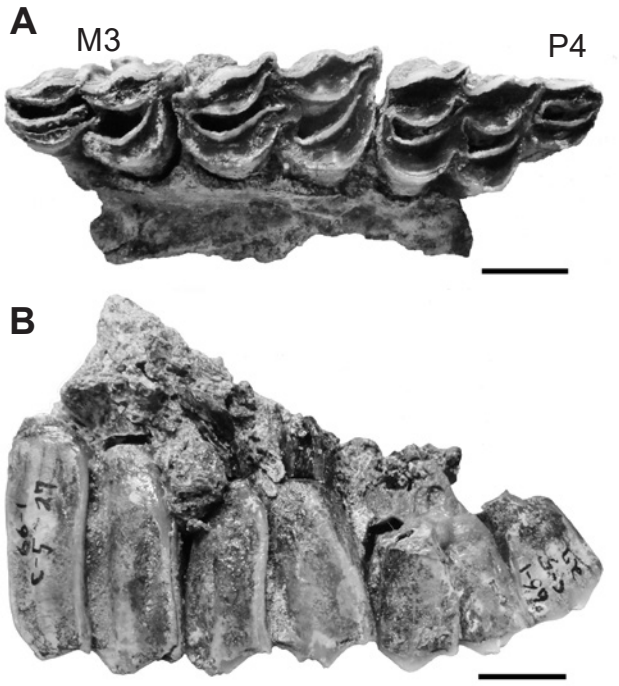

Figure 2. Upper dentition of *Hemiauchenia macrocephala* from the late Pleistocene of Valsequillo Basin, Puebla, central Mexico. **A**, right maxillary fragment with P4-M3 of an adult individual (66-1-C-5-27) in occlusal (**A**) and lateral (**B**) views. Scales bars = 10 mm.

Table 1. Measurements (in mm) of the upper dentition referable to *Hemiauchenia macrocephala* from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations: CH**, crown height; **APL**, anteroposterior length; **TW**, transverse width; **L**, left; **R**, right. *estimate.

Specimen	Position	CH	APL	TW
66-1-K-4-25	P3L	---	7.8	5.4
66-1-K-4-25	P4L	---	15.8	11.6
66-1-K-4-25	M1L	---	29.1	21.0
66-1-K-4-25	M2L	---	38.5	20.4
66-1-K-4-25	M3L	---	28.8	14.3
66-1-C-5-27	P4R	17.5	14.1*	9.8*
66-1-C-5-27	M1R	12.1	20.3	16.9
66-1-C-5-27	M2R	19.1	26.7	15.3
66-1-C-5-27	M3R	26.2	20.8	12.0
64-1 D-5 18	M3R	---	22.9	18.3
66-1 W-0 18	M3R	22.6	25.6	19.0
64-1-Z-15	M3L	24.3	25.4	15.2

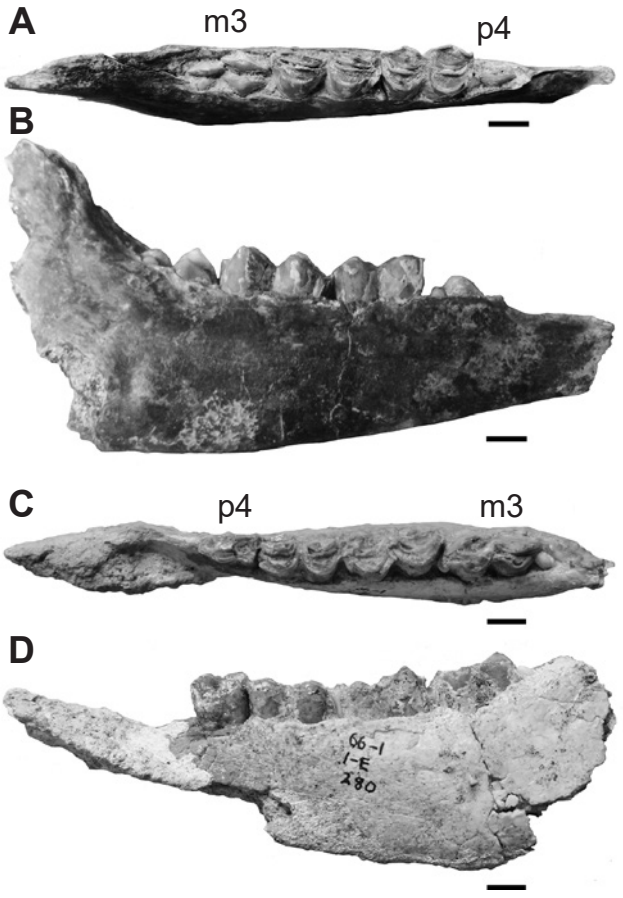

Figure 3. *Hemiauchenia macrocephala* from the late Pleistocene of Valsequillo Basin, Puebla, central Mexico. **A-D**, mandible fragments of a young individual (66-1-V-1-190) and of a young adult individual (66-1-1-E-280) in occlusal (**A**, **C**) and lateral (**B**, **D**) views respectively. Scale bars = 10 mm.

Table 2. Measurements (in mm) of the lower dentition referable to *Hemiauchenia macrocephala* from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations: ch**, crown height; **apl**, anteroposterior length; **tw**, transverse width; **L**, left; **R**, right. *estimate.

Specimen	Position	ch	apl	Tw
64-R-12-5-20	p4R	12.1	12.6	7.03
66-1-P-228	p4R	11	12.5	10.2
66-1-V-1-190	p4R	---	14.2*	6.9*
66-1-1-E-280	p4L	14.5*	24.1	7.3
66-1 2X 10	p4L	---	12.2	7.10
64-R-12-5-20	m1R	18.7	18.8	11.7
66-1-P-228	m1R	11.4	20.6	12.7
66-1-V-1-190	m1R	---	23.4	11.5
64-1-C3-19	m1R	10.5	16.3*	12.7
64-1 F-6 21	m1R	---	19.7	12.2
66-1-1-E-280	m1L	---	21.8	7.6*
64-1 -H-6	m1L	8.6	17.9	13.4
64-1 B-3 18	m1L	10.9	18.5	13.2
64-1 Z-3 15	m1/2L	14.6	23.1	13.7
64-R-12-5-20	m2R	24.2	27.2	10.9
66-1-P-228	m2R	25.3	27.3	12
66-1-V-1-190	m2R	---	27.3*	---
64-1-C3-19	m2R	20.6	24.4	13.3
66-1-1-E-280	m2L	---	27.4	11.9
66-1-1-W-1814	m2L	20.6*	24.7	
66-1-L-5-260	m3R	---	33.5	14.7
66-1-V-1-190	m3R	---	---	---
64-1-C3-19	m3R	32.6	30.4	10.3
64-R-12-5-20	m3R	32.1	31.1	8.9
64-1-Z-3 -16	m3R	14.1	32.5	12.9
64-1 Z-1 15	m3R	23.3	28.8	11.9
66-1 X-0 16	m3R	19.0	30.0	12.7
66-1-1-E-280	m3L	---	30.3	9.8
66-1-1-W-1814	m3L	24.7	30.2	11.2
64-I Z Z-1 16	m3L	21.7	29.6	12.1
64-I H-6 22	m3L	24.9	33.4	13.4

molar. The anterior loph is wider than the posterior loph in the M3 (Figure 2A).

In the majority of the mandible fragments (specimens 64-R-12-5-20, 66-1-p2-28, 64-1-C3-19, and 66-1-1-E-280), the p4 and m1 are at early moderate wear stage, the m2 at a moderate wear stage, and the m3 at an early wear stage. The observed wear on the molariform series (p4-m3) corresponds to the wear stage two of Breyer (1977), which in turn is indicative of young adult individuals. In one of the mandible fragments (specimen 66-1-V-1-190), the p4 and m3 are in the beginning of eruption, whereas the m2 and m3 are at early tooth wear stage; the observed wear in the molariform series (p4-m3) corresponds to the wear stage one of Breyer (1977) and it is indicative of a young individual (Figure 3). The mandibular depth increases anteroposteriorly from p4 to m3 (mean depth below anterior p4 = 25.51 mm; mean depth below posterior m3 = 45.43 mm). The mean molar ch in unworn m3 is of about 32 mm (Table 2). The p4 is triangular in outline, shows a well-developed enamel protuberance in its anteriormost region, the anterolingual groove is strong, and there is a single fossettid at the posterior end of the occlusal surface. As in the upper molariforms, a thin layer of cementum covers the lower teeth. The molars show a distinct antero external stylid ("llama buttresses"); this structure disappears at moderate tooth wear stage in the m1, whereas is persistent in the m2 and m3. The protoconid and hypoconid are subequal in size and U-shaped. The fossettids are simple, elongated anteroposteriorly, and become narrower in their middle portion. A well-differentiated hypoconulid is present on the m3 (Figures 3A,C).

The metacarpals are long and slender with a mean length/width ratio (GL:TD hereafter) of 12.3, although are less gracile than the metatarsals (Table 3, Figure 4). The proximal articular surface consists of three facets (Figure 4): a large medial anterior facet for the magnum, which is oval-elongate in shape; a small and rounded medial facet for the trapezoid is postero-medially located; and the lateral and largest facet for the cuneiform (Figure 4A). The dorsal surface is slightly convex, while the lateral and medial sides are flattened. The diaphysis bears a faint narrow channel extending on to the

Table 3. Measurements (in mm) of the metapodials referable to *Hemiauchenia macrocephala* and *Camelops hesternus* from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations: L**, left; **Mtc**, metacarpal; **Mtt**, metatarsal; **GL**, greatest length; **TD**, transverse diameter across the diaphysis; **R**, right.

Specimen	Element	GL	TD
Hemiauchenia macrocephala			
64-1-H-17	MtcR	300	22.07
66-1-Y-9-25	MtcR	310	25.29
66-1-U-O-190	MtcR	346	26.58
66-1-1-K-240	MtcL	330	25.38
66-1-L-5-28	MtcL	270	24.70
552	MtcL	245	21.46
622	MtcL	315	26.69
66-1-2-W-140	MtcL	312	24.07
66-1-U-O-190	MttR	335	24.05
66-1-M-8-300	MttR	287	22.07
66-1-K-1-30	MttR	333	21.74
66-1-V-0-19	MttR	341	22.79
66-1-1-R-23	MttR	317	21.78
544	MttL	317	21.59
66-1-F-4-280	MttL	305	24.91
66-1-C-4-27	MttL	329	21.10
66-1-D-1-25	MttL	210	17.71
Camelops hesternus			
66-1-1-X-C-19-N-1-29-5	MtcR	384	51.96
66-1-M-1-230	MtcL	385	50.62
IV-23-63	MttR	405	39.19

Figure 4. *Hemiauchenia macrocephala* from the late Pleistocene of Valsequillo Basin, Puebla, central Mexico. **A-F**, right metacarpal and left metatarsal (66-1-V-0-190) in proximal (**A**, **D**), anterior (**B**, **E**), and posterior (**C**, **F**) views, respectively. **Labels: a**, 4th metacarpal facet; **b**, trapezoid facet; **c**, magnum facet; **d**, entocuneiform facet; **e**, ectomesocuneiform facet; **f**, cuboid facet. Scale bars: A, D = 10 mm; B, C, E-F = 50 mm.

proximal quarter of its dorsal side. The ventral side shows a broad and deep channel, extending near the distal end of the diaphysis. The distal end is formed by the unfused portion of metacarpals III and IV. The distal condyles are large and slightly divergent. The sagittal ridge of the condyles is prominent and extends dorsoventrally on to the distal portion of the shaft (Figures 4B-C).

The astragalus is distinguished by having a lateral crest that is relatively higher than the medial crest. A wide valley separates the medial and the lateral crests. The medial trochlear crest is prominent. The navicular condyle is smaller than the cuboid condyle. There are three facets in lateral view: (i) the fibular facet that is situated on the border of the lateral crest; (ii) an elongated parasustentacular facet that is curved in the opposite direction to the fibular facet; and (iii) a kidney-shape distal astragalar facet. The fibular salient is well differentiated from the fibular and parasustentacular facets. There is a broad and moderate deep horizontal sulcus that separates the fibular facet from the distal astragalar facet. In medial view, the surface for the tibial ligament is large and it is parallel to that of the medial articular facets. The sustentacular facet occupies a greatest part of the posterior surface. The subsustentacular fossa is moderate deep and well developed (Figure 5).

The metatarsals are long and slender with a mean GL:TD ratio of 13.9 (Table 3). Their proximal articular surface is trapezoidal, with a central moderate deep cavity, and it bears three articular facets: the cuboid (lateral) and the entocuneiform (medial) facets are bean-shaped and subequal in size; and the ectomesocuneiform that is the smallest facet, oval-elongate in shape, and situated behind the entocuneiform facet (Figure 4D). The diaphysis shows a similar configuration to that observed in the metacarpals. As in the metacarpals, the distal condyles are large and slightly divergent, and the sagittal ridge of the condyles is well developed (Figures 4E-5F).

The proximal phalanges are slender with a mean GL:TD ratio of 6.3 (Table 4). The diaphysis is convex on its dorsal surface and flat on its ventral side. At the proximal posterior surface, the scar for the suspensory ligament is W-shaped, it is short and occupies the first fourth of the bone. The distal end is formed by two crests, with the lateral crest being larger than the medial one (Figure 6).

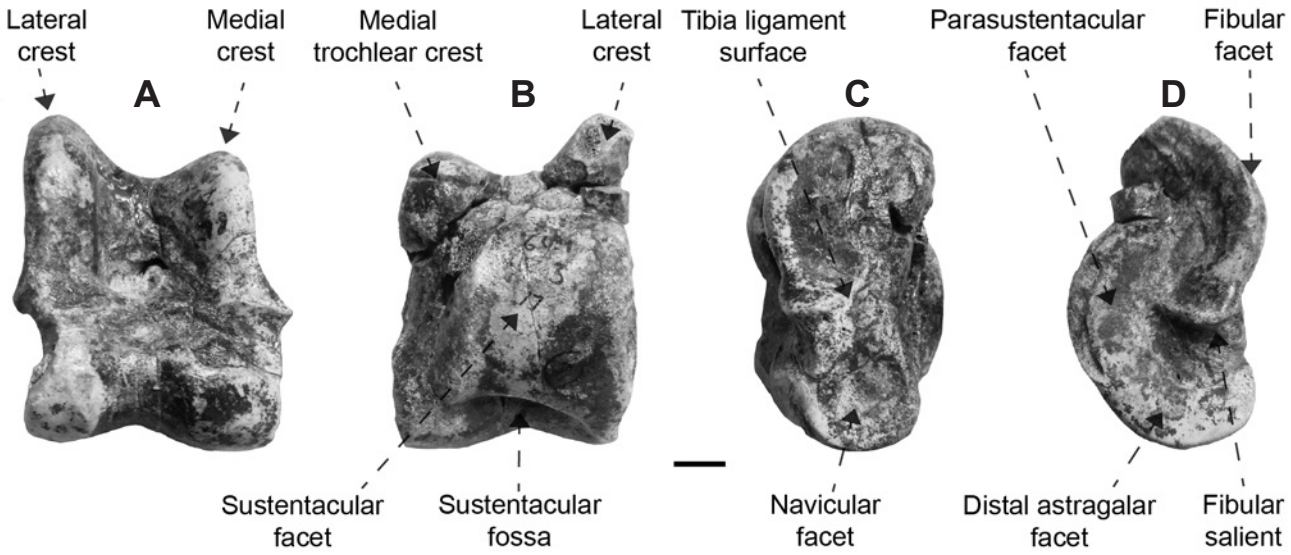

Figure 5. *Hemiauchenia macrocephala* from the late Pleistocene of Valsequillo Basin, Puebla, central Mexico. **A-D**, right astragalus (64-11-Z-3-17) in anterior (**A**), posterior (**B**), medial (**C**), and lateral (**D**) views. Scale bar = 10 mm.

Table 4. Measurements (in mm) of the proximal phalanges referable to *Hemiauchenia macrocephala* from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations: GL**, greatest length; **TD**, transverse diameter across the diaphysis.

Specimen	GL	TD
66-1 0-5 2-40	84.9	13.2
66-1 1-W 16	---	11.7
64.1 F4 17	65.6	11.7
66-1 K-2 21	75.3	11.9
64.1 J-3 19	77.9	12.2
66-1 B-2 23	84.4	12.3
64-1 Z Z-2 15	75.8	12.3
66-1 1-Q 10	87.4	13.4
66-1 U-1 20	77.1	13.0
64-1 G-7 S	83.1	13.2
64.1 F-H 17	69.5	11.1
64.1 D-4 19	81.8	10.9
66-1 B-2 10	76.9	12.1

Taxonomic assessment. The specimens from Puebla share with *Hemiauchenia* the following diagnostic features: high crowned cheek teeth; molariforms with U-shaped crescents; teeth covered by a layer of cementum; p4 triangular in outline; a mandible increasing in depth from p4 to m3; long and slender metapodials; and proximal phalanges with a W-shaped suspensory ligament scar (Webb, 1974; Honey *et al*., 1998; Hulbert & Webb, 2001). The genus *Palaeolama* differs in having low crowned cheek teeth (crown height ≤ 20 mm); molariforms with V-shaped crescents; teeth lacking cementum and with crenulated enamel; p4 with complex infolding; mandible robust and consistently deeper below p4; and stout legs. *Camelops* is distinguished by having very hypsodont cheek teeth (crown height *ca.* 50 mm); upper molars with reduced external styles; mandible very deep and robust; shortened and robust metapodials; proximal phalanges with

Figure 6. *Hemiauchenia macrocephala* from the late Pleistocene of Valsequillo Basin, Puebla, central Mexico. **A-B**, right proximal phalange (66-1-0-5-2-40) in anterior (**A**) and posterior (**B**) views. Scale bar = 10 mm.

the scar for the suspensory ligament extending almost to the center of diaphysis; and a significantly larger size (Webb, 1965; Kurtén and Anderson, 1980; Honey *et al*., 1998). The South American genera *Lama* and *Vicugna* are distinguished by its smaller sizes (Prothero & Schoch, 2002). Particularly, the genus *Lama* differs from the specimens of Puebla by having stronger anteroexternal stylids on the lower molars (Webb, 1965, 1974; Meachen, 2003). The UTRL (P3-M3) in the specimen 66-1-K-4-25 is 108.1 mm and is suggestive of a medium-sized individual. In the Pleistocene species of *Hemiauchenia*, *H. gracilis* is a small-sized form (Meachen, 2003, 2005; Bravo-Cuevas *et al*., 2012) and *H. macrocephala* is a medium-sized form (Webb 1974; Breyer 1977; Kurtén & Anderson 1980). The UTRL in the specimen from Puebla is similar to that observed in specimens of *Hemiauchenia macrocephala*, including LACM 138-5 (UTRL = 116.77; partial skull with RP3-M3 and LP4-M3) and TMM 40685-832 (UTRL = 100.37 mm; right maxillary fragment with P3-M3) from the late Pleistocene of California and Zesch Cave, Mason County, Texas respectively; and it is somewhat larger (of about 15%) to that observed in the dental series of a partial skull of *H. gracilis* (UAHMP-1142, UTRL = 91.08) from the late Pleistocene of Hidalgo, central Mexico. The morphology of the upper dentition in the specimens from Puebla is comparable to that of *Hemiauchenia macrocephala* and *H. gracilis* in the presence of a two-rooted P3, U-shaped molar selenes, and well-developed styles and ribs (Meachen, 2003, 2005; Bravo-Cuevas *et al*., 2012). Furthermore, the study teeth resemble those of *H. macrocephala* in the configuration and size of the P4 and in the presence of large and robust molars (Webb, 1974); the latter condition is remarkable in the M2 (Table 1).

The mean LTRL (p4-m3) in the specimens from Puebla (= 82 mm) is comparable to that of *Hemiauchenia gracilis*, including UAHMP-1144 (left mandible fragment with p4-m3; LTRL = 82 mm) from the late Pleistocene of Hidalgo, central Mexico (Bravo-Cuevas *et al*., 2012). However, it is shorter (of about 20%) than that of *H. macrocephala*, such as the specimens TMM 40685-676 (a left mandible fragment with p4-m3; LTRL = 101.6 mm) from the late Pleistocene of Texas; LACM 138-7 (a left mandible fragment with p4-m3 and a right mandible fragment with the incisive and p4-m3; mean LTRL = 105.12) from McKittrick Tar Seeps, late Pleistocene of California; and UF 11420 (a left mandible fragment with p3-m3; LTRL = 96.5 mm) from Coleman IIA, late Irvingtonian of Florida (Webb, 1974). The difference in size may be explained by intraspecific variation related to age, given that the specimens from Puebla belong to young adult individuals, whereas those from California, Texas, and Florida belong to adult individuals (the m3 in these specimens are completely erupted and at early moderate wear stage). The configuration of the mandible fragments from Puebla resembles that of *H. macrocephala* in being deep and robust (depth at p4 ≥ 25 mm; depth at m3 ≥ 40 mm), whereas the mandible of *H. gracilis* is shallow and slender (depth at p4 ≤ 25 mm; depth at m3 ≤ 35 mm) (Meachen, 2003; Bravo-Cuevas *et al*., 2012). The lower dentition of the specimens from Puebla is comparable to that of *Hemiauchenia macrocephala* in having high-crowned cheek teeth (crown height in unworn m3 of about 32 mm), strong anteroexternal stylids, p4 that is wide and labially convex with a strong anterolingual groove (Webb, 1974; Kurtén & Anderson, 1980). The m3s from Puebla show a well-differentiated hypoconulid, resembling teeth referable to *H. gracilis* in this regard (Meachen, 2003, 2005).

The postcranial morphology of the lamines is relatively homogeneous. However, there is some taxonomic variation in size and proportion of the limb elements (see Breyer, 1974; Webb, 1974; Honey *et al*., 1998). The metapodial length of some specimens from Puebla (66-1-U-O-190 (MttR), 66-1-K-1-30, 66-1-C-4-27) have a similar length to that of *Hemiauchenia gracilis* (UAHMP-962: GL = 330 mm, left metatarsal from the Rancholabrean of Hidalgo, Hidalgo, central Mexico) (Bravo-Cuevas *et al*., 2012: 505, table 3), other specimens (66-1-U-O-190 (MtcR), 66-1-V-0-19) have a length that is comparable to that of *H. macrocephala* (UF 133908: GL = 343 mm, right metatarsal from Leisey Shell Pit, early Irvingtonian of Florida) (Hulbert & Webb, 2001: 264, fig. 13.29D), and there are several specimens whose metapodial length is even smaller (GL ≤ 300 mm) than that observed in metapodials referable to *H. gracilis* and *H. macrocephala*. However, the metapodials from Puebla exhibit a greater transverse diameter (mean TD = 24.5 mm) than metapodials of *H. gracilis* (mean TD = 16.7 mm) and comparable to that of metapodials of *H. macrocephala* (mean TD = 24.8) (Meachen, 2005). The mean length/width ratio of the specimens from Puebla (GL:TD, 12.5) is indicative of long and slender metapodials. The metapodials of *H. macrocephala* are long and slender (GL:TD, 12.2) whereas those of *H. gracilis* are even longer and slenderer (GL:TD, 16.7) (Meachen, 2005; Bravo-Cuevas *et al*., 2012). The comparisons indicate that metapodials of *H. gracilis* and *H. macrocephala* could exhibit a similar length; although, those of *H. macrocephala* are commonly wider than those of *H. gracilis*, indicating that *H. macrocephala* was a less gracile-legged form. The latter condition could be related to the metapodials from Puebla.

The length/width ratio of the proximal phalanges from Puebla (GL:TD, 6.3) is intermediate between that of *Hemiauchenia gracilis* (*ca.* 7.1) and that of *H. macrocephala* (5.4) (Meachen, 2003, 2005). The comparison indicates that proximal phalanges of the specimens from Puebla and those of *H. macrocephala* developed a less-gracile appearance than those belonging to *H. gracilis*.

The configuration of the astragali from Puebla is typically lamine (see Webb, 1965). The elements considered here are larger and more robust (length = 44.6 mm, width = 32.9 mm) in comparison to those of *Hemiauchenia gracilis* (length = 39.0 mm, width = 24.6 mm) (Meachen, 2003). Furthermore, the length/width ratio in the specimens from Puebla (1.35) is comparable to that of *H. macrocephala* (1.39) (Meachen, 2005).

Overall, the comparison of dental and postcranial remains of the specimens from Puebla with the Pleistocene species *Hemiauchenia macrocephala* and *H. gracilis* indicates that they share several dental features, size, and limb proportions with *H. macrocephala*, thus it is assigned to this species.

Tribe CAMELINI Webb, 1965

Camelops Leidy, 1854

Type species. *Camelops kansanus* Leidy, 1854.

Camelops hesternus Leidy, 1873
(Figures 7-8; Tables 3,5-6)

Referred material. One right maxillary fragment with P4-M3 (64-R-1-5-21), one left hemimandible with broken teeth (uncatalogued), one right mandible fragment with p4-m3 (66-1 B-2 240), 25 isolated molariforms (64-R-1-5-21, P4R; 64-R-1-5-21, M1R; 64-R-1-5-21, M2R; 64-R-1-5-21, M3R; 64-R-3 5-19, P4R; 66-R-8-33, P4R; 66-1-W-0-19, M1R; 66-1-3V-12 , M1R; 66-1-V-0-18, M1L; 66-1-W-0-19, M2; 66-R-20-12, M2L; 64-1 D-2 17, M3L; 5556A, M3L; 66-1 4-V 14, M3L; 66-1 B-1 30, M3L; 66-1-T-1-28, p4R; I-YY 12 1, p4R; 66-1-V-17, p4L; 66-1 2-Y 19, p4L; 66-1 W-0 19, m1R; 66-1B-7 24, m1/2R; 66-1 98, m2R; 64.1. Y-7 5, m2R; 66-1-O-20, m2L; 5556a, m3R; 5556b, m3R; 5556c, m3L; 64.1 X.1 23, m3L), two metacarpals (66-1-1-X-C-19-N-1-29-5, MtcR; 66-1-M-1-230, MtcL), and one metatarsal (IV-23-63, MttR).

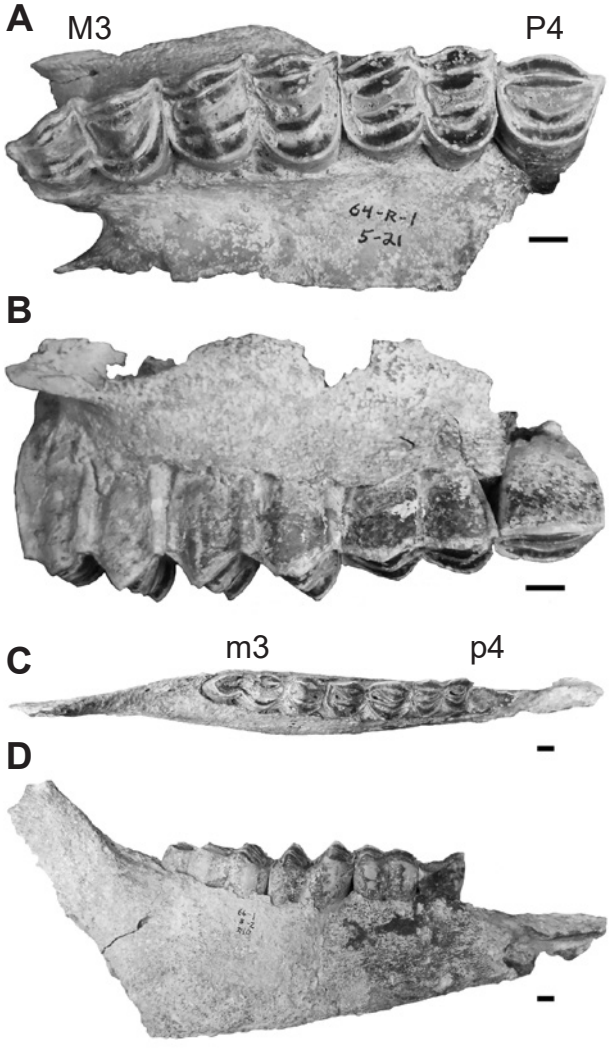

Figure 7. *Camelops hesternus* from the late Pleistocene of Valsequillo Basin, Puebla, central Mexico. **A-D**, right maxillary (64-R-1-5-21) and mandibular (66-1 B-2 240) fragments of adult individuals in occlusal (**A**, **C**) and lateral (**B**, **D**) views, respectively. Scale bars = 10 mm.

Distribution. This late Pleistocene camel was widely distributed across western North America and north to the Yukon and Alaska (Kurtén & Anderson, 1980; Zazula *et al*., 2011). It reached areas of northwestern, north central, and central Mexico (Ferrusquía-Villafranca *et al*., 2010).

Description. In the maxillary fragment, the molariforms are at moderate to late moderate wear stages, indicating an adult individual (Figures 7A-B). The P4 to M3 UTRL in 64-R-1-5-21 is of 159.50 mm. A thin layer of cementum covers the teeth. In occlusal view, the P4s are subrectangular in outline; the lingual cone is wide and U-shaped; the anterior style is well developed and the posterior style is less developed; there is a single fossa that is anteroposteriorly elongated. The molars show well developed styles and ribs. The mean molar CH in the M3 is of about 50 mm (Table 5). In the M1 and M2 the parastyle and mesostyle are well developed and the metastyle is less developed. The parastyle, mesostyle and metastyle are well developed in the M3. The molars are distinguished by having an anterior loph that is wider than the posterior loph. The protocones and metaconules are U-shaped; however, the protocone is somewhat narrower than the metaconule. The M1 and M2 have fossae with simple and shallow internal plications that are persistent at moderate wear stages. A single and moderately deep fold in the posterior border of the anterior fossa is sometimes present in the M3 (Figures 7A-B).

The mandible fragment with teeth shows the p4 in a late wear stage, the m1 and m2 are at moderate wear stages, and the m3 is at an early wear stage (66-1 B-2 240); these teeth wear stages correspond to wear stage three of Breyer (1977), suggesting an adult individual (Figures 7C-D). The hemimandible is long and slender, the diastema is long, there is an oval mental

Table 5. Measurements (in mm) of the upper dentition referable to *Camelops hesternus* from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations:** as in Table 1.

Specimen	Position	CH	APL	TW
64-R-1-5-21	P4R	---	28.2	24.2
64-R-1-5-21	M1R	---	41.1	24.4
64-R-1-5-21	M2R	---	49.3	29.2
64-R-1-5-21	M3R	---	43.6	26.2
64-R-3 5-19	P4R	23.6	25.4	24.9
66-R-8-33	P4R	20.9	26.2	23.0
66-1-W-0-19	M1R	36.3	38.7	30.7
66-1-3V-12	M1R	39.0	48.3	33.3
66-1-V-0-18	M1L	---	---	30.6
66-1-W-0-19	M2	39.9	48.8	30.1
66-R-20-12	M2L	56.8	49.6	26.8
64-1 Y-2 16	M3R	30.2	44.3	28.6
64-1 D-2 17	M3L	---	45.6	28.3
5556A	M3L	41.9	44.9	26.8
66-1 4-V 14	M3L	26.3	54.0	30.3
66-1 B-1 30	M3L	49.7	51.9	31.0

foramen situated in the anterior most part of the element, the ramus is broad, and the coronoid process is relatively higher than the posterior condyle. The mandibular depth increases significantly from p4 to m3 (mean depth below anterior to p4 = 48.05 mm; mean depth below posterior m3 = 91.02 mm) in both mandible fragments (Figure 7D). The lower molariforms are covered by cementum. The mean molar ch in the m3 is of about 50 mm; an extraordinary crown height of about 70 mm is observed in the specimen 5556c (m3L) (Table 6). The p4 is triangular, with one elongated fossettid at the posterior region of the occlusal surface. The anteroexternal stylid is absent. The protoconid and hypoconid are subequal in size and U-shaped. The mesostylid and entostylid are well developed. The anterior and posterior fossettids are anteroposteriorly elongated and constricted in their middle section. The hypoconulid is large and it is well differentiated from the hypoconid and protoconid on m3 (Figure 7C)**.**

Both, metacarpals and metatarsals are robust and relatively short (GL:TD, 8.5) (Table 3). The distal articular surfaces are large, robust, and diverge considerably (Figure 8). Otherwise, they show a similar configuration to that observed in the llama-like metapodials (Webb, 1965; Breyer, 1974).

Taxonomic assessment. The sample from Puebla shows several diagnostic features of *Camelops*, including large size; very hypsodont cheek teeth; upper molars with reduced external styles; mandible very deep due to increased hypsodonty; lacking of p3; weak anteroexternal stylids on the lower molars; and robust metapodials (Kurtén & Anderson, 1980; Honey *et al*., 1998). The specimens from Puebla differs from *Hemiauchenia*, *Palaeolama*, and *Lama* by the larger size, very hypsodont teeth, and poorly developed "llama buttresses" on the lower molars (Honey *et al*., 1998).

The nominal species in the genus *Camelops* are in need of taxonomic revision (Dalquest, 1992). A recent review of this camel has shown that there are two valid previously named species, including *C. hesternus* (*C. hesternus*, *C. sulcatus*, *C. huerfanensis*, and *C. traviswhitei* are junior synonyms) and *C. minidokae*. The former species includes the large size forms from the Pleistocene (mainly late Pleistocene), whereas the latter species it has been considered for the smaller forms from the early Pleistocene (Baskin & Thomas, 2016).

The dental morphology of *Camelops* lacks significant taxonomic variation for species determination (Dalquest, 1992; Baskin & Thomas, 2016). Nevertheless, the dental specimens from Puebla share with *Camelops hesternus* a P4 that is quadrate and submolarifom, whereas the p4 is triangular and with a posterior enamel fold (Kurtén & Anderson, 1980). The P4-M3 UTRL of 64-R-1-5-21 = 159.50 mm is indicative of a larger individual relative to *Hemiauchenia*. The dimension of the specimen from Puebla is comparable to that of LACM HC 6347 (UTRL = 160.74 mm) a left maxillary fragment with P4-M3 of *Camelops hesternus* from Rancho La Brea, Late Pleistocene of California.

The mandibles from Puebla are similar to *Camelops hesternus* in being significantly deeper from p4 to m3. In this regard, the specimens from Puebla show similar depths

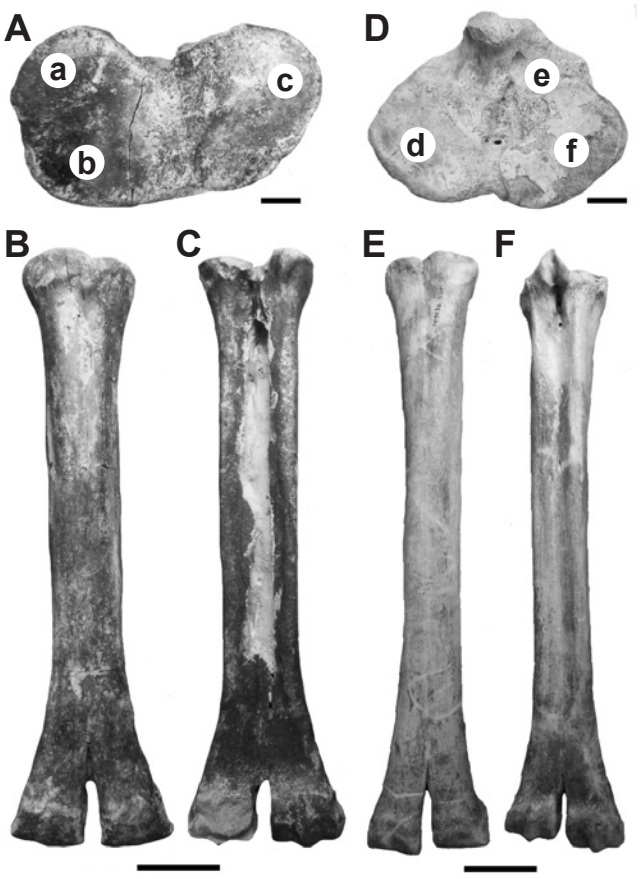

Figure 8. *Camelops hesternus* from the late Pleistocene of Valsequillo Basin, Puebla, central Mexico. **A-F**, left metacarpal (66-1-M-1-230) and right metatarsal (IV-23-63) in proximal (**A**, **D**), anterior (**B**, **E**), and posterior (**C**, **F**) views, respectively. **Labels: a**, trapezoid facet; **b**, magnum facet; **c**, 4th metacarpal facet; **d**, cuboid facet; **e**, ectomesocuneiform facet; **f**, entocuneiform facet. Scale bars: A, D = 10 mm; B-C, E-F = 50 mm.

Table 6. Measurements (in mm) of the lower dentition referable to *Camelops hesternus* from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations**: as in Table 2.

Specimen	Position	ch	apl	tw
66-1 B-2 240	p4R	---	28.6	15.2
66-1 B-2 240	m1R	---	35.6	21.4
66-1 B-2 240	m2R	---	49.0	22.3
66-1 B-2 240	m3R	---	65.7	20.2
66-1-T-1-28	p4R	10.9	24.9	13.0
I-YY 12 1	p4R	13.7	23.8	14.6
66-1-V-17	p4L	12.5	25.0	14.5
66-1 2-Y 19	p4L	31.5	32.7	16.7
66-1 W-0 19	m1R	24.6	34.5	16.7
66-1B-7 24	m1/2R	42.4	---	20.6
66-1 98	m2R	28.4	39.6	21.4
64.1. Y-7 5	m2R	42.0	39.5	18.8
66-1-O-20	m2L	25.6	42.4	29.9
5556[a]	m3R	56.4	59.8	20.6
5556b	m3R	23.8	58.6	21.1
5556c	m3L	71.5	55.8	16.1
64.1 X.1 23	m3L	42.2	---	20.0

at p4 (48.05 mm) and at m3 (91.02 mm) to those of LACM HC 700 (depth at p4 = 56.32 mm and depth at m3 = 81.25 mm) a right mandible fragment with p4, m1, and m3 from Rancho La Brea, late Pleistocene of California. Furthermore, the lower tooth row length (LTRL) of p4-m3 in the specimen 66-1 B-2 240 (LTRL = 173.68 mm) is comparable to that of LACM HC 700 (LTRL = 188.10 mm).

The mean length of the metacarpals (GL = 385 mm) and that of the metatarsal (GL = 405 mm; specimen IV-23-63) from the Valsequillo Basin is about to the upper limit of the observed range in metacarpals (GL = 374-380 mm; Webb, 1965) and metatarsals (GL = 357– 388 mm; Webb, 1965) of *Camelops hesternus* from Rancho La Brea, late Pleistocene of California. However, they are larger (of about 10%) than metapodials (both metacarpals and metatarsals) of *C. minidokae* (mean GL = 360 mm) from Irvington, early Pleistocene of California (Baskin & Thomas, 2016).

The configuration of P4/p4, the upper tooth row length (that is related to large-sized individuals), the mandible configuration, and the metapodial length of the specimens from Puebla are similar to those of *Camelops hesternus*, thus the sample considered here has been assigned to this species.

DISCUSSION

Diet characterization

The microwear pattern of *Hemiauchenia macrocephala* from Valsequillo is distinguished by having a higher number of pits than of scratches (Figure 9A). The large pits are common, whereas gouges and cross scratches are uncommon (Tables 7-8). The AP/AS ratio (3.9) of the sample falls within the morphospace of extant browsers, between those observed in the common eland (*Taurotragus oryx*) and the sable antelope (*Hippotragus niger*) (Figure 10).

The microwear pattern of *Camelops hesternus* is characterized by an important number of pits and a relatively low number of scratches (Figure 9B). The large pits and cross scratches are common, whereas gouges are uncommon (Tables 7,9). The AP/AS ratio (2.0) falls in the area between the morphospaces considered for the extant browsers and grazers, close to that observed in the extant South American vicuña (*Vicugna vicugna*) (Figure 10).

A pairwise comparison by a two-sample t-test revealed significant differences in the average number of pits and in the average number of scratches ($p < 0.05$) between the samples referable to *Hemiauchenia macrocephala* and *Camelops hesternus* from Valsequillo Basin, indicating that study samples have distinctive microwear signatures.

The DFA correctly classifies 76.1% of the extant species in its dietary category, 81.8% for the browsers, 100% for fruit browsers, 75.0% for meal-by-meal mixed feeders, 53.8% for seasonal-regional mixed feeders, and 77.7% for grazers. The sample of *Hemiauchenia macrocephala* is classified with the browsers at a posterior probability of 96.3%, whereas the sample of *Camelops hesternus* is classified with the seasonal-regional mixed feeders at a posterior probability of 69.2%.

The distinctive microwear dental patterns of *Hemiauchenia macrocephala* and *Camelops hesternus* from the Valsequillo Basin can be related to different trophic strategies. The significant representation of pits in comparison to scratches in the sample of *H. macrocephala* (AP/AS = 3.9) is related to a tooth enamel damage where the attrition (tooth-on-tooth contact) dominates over abrasion (food-on-tooth contact), suggesting a browsing behavior (Solounias & Semprebon, 2002). In *C. hesternus*, the ratio in the average number of pits and the average number of scratches (AP/AS = 2.0) should be related to a differential effect of attrition and abrasion, considering that it is similar to that observed in some extant seasonal/regional mixed feeders (Solounias & Semprebon, 2002), such as the Sumatran serow (*Capricornis sumatraensis*) and the vicuña (*Vicugna vicugna*). This interpretation is in agreement with the results obtained from the DFA. The presence of mixed scratches in the samples of *Hemiauchenia macrocephala* and *Camelops hesternus*

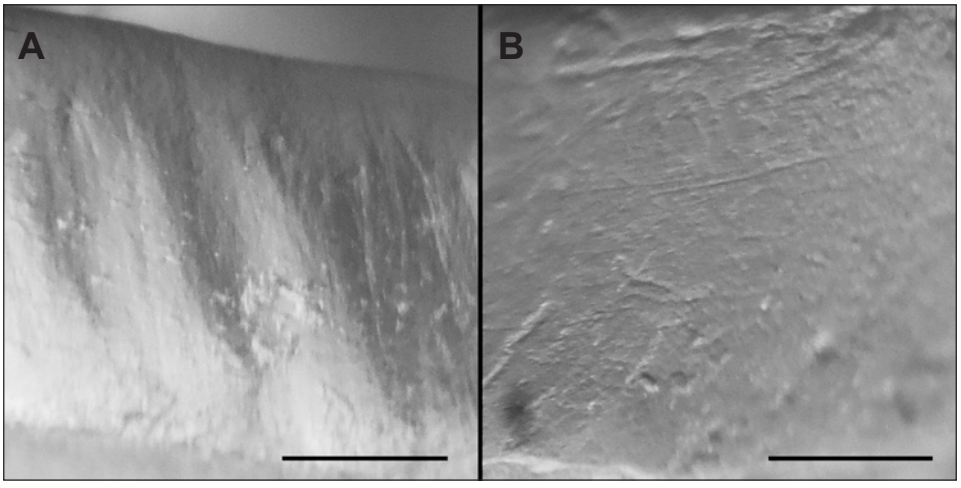

Figure 9. Microwear in molars of *Hemiauchenia macrocephala* (**A**) and *Camelops hesternus* (**B**) from Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **A**, 66-1-1-W-1814 (m2L) showing small pits and fine scratches; **B**, 66-1-3V-12 (M1R) showing small and large pits, as well as a mixture of fine and coarse scratches. Scale bars = 0.4 mm.

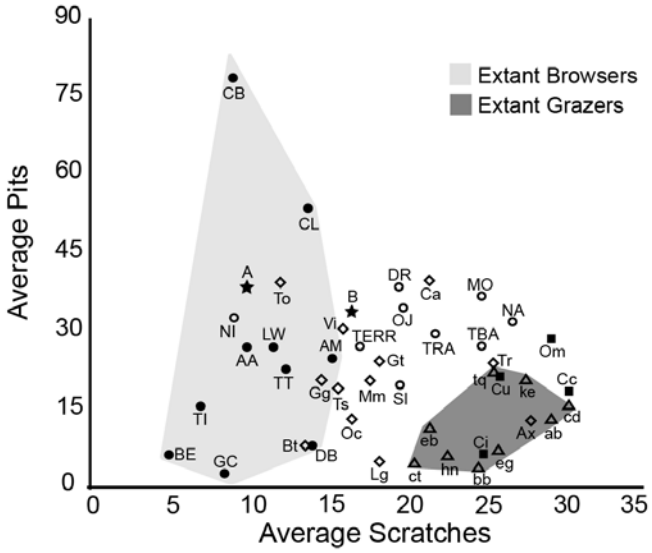

Figure 10. Bivariate plot of the average number of scratches and the average number of pits in extant ungulates (data from Solounias & Semprebon, 2002) and fossil samples of *Hemiauchenia macrocephala* (**A**) and *Camelops hesternus* (**B**) from Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations:** Leaf Browsers (**close circle**): **BE**, *Boocercus eurycerus*; **TI**, *Tragelaphus imberbis*; **GC**, *Giraffa camelopardalis*; **CB**, *Camelus bactrianus*; **AA**, *Alces alces*; **LW**, *Litocranius walleri*; **TT**, *Tragelaphus strepsiceros*; **CL**, *Camelus dromedarius*; **DB**, *Diceros bicornis*; **AM**, *Antilocapra americana*. Fruit Browsers (**open circle**): **NI**, *Cephalophus niger*; **TERR**, *Tapirus terrestris*; **DR**, *Cephalophus dorsalis*; **SL**, *Cephalophus silvicultor*; **OJ**, *Okapia johnstoni*; **TRA**, *Tragulus* spp.; **MO**, *Moschus moschiferus*; **TBA**, *Tapirus bairdii*; **NA**, *Cephalophus natalensis*. Seasonal/regional mixed feeders (**open rhombus**): **To**, *Taurotragus oryx*; **Ca**, *Capricornis sumatraensis*; **Bt**, *Budorcas taxicolor*; **Gg**, *Gazella granti*; **Ts**, *Tragelaphus scriptus*; **Vi**, *Lama vicugna*; **Oc**, *Ovis canadensis*; **Lg**, *Lama glama*; **Gt**, *Gazella thomsoni*; **Tr**, *Boselaphus tragocamelus*; **Ax**, *Axis axis*; **Mm**, *Muntiacus muntjak*. Meal by meal mixed feeders (**close square**): **Cu**, *Cervus unicolor*; **Om**, *Ovibos moschatus*; **Cc**, *Cervus canadensis*; **Ci**, *Capra ibex*. Grazers (**open triangle**): **ct**, *Connochaetes taurinus*; **eb**, *Equus burchellii*; **hn**, *Hippotragus niger*; **bb**, *Bison bison*; **tq**, *Tetracerus quadricornis*; **eg**, *Equus grevyi*; **ke**, *Kobus ellipsiprymnus*; **ab**, *Alcelaphus buselaphus*; **cd**, *Cervus duvaucelii*.

from Valsequillo Basin is somewhat common (*ca*. 50%) (Table 7). A microwear dental pattern distinguished by the common presence of mixed scratches has been observed in seasonal/regional mixed feeders that inhabited forested areas and/or alpine grasslands, such as the elk or wapiti (*Cervus canadensis*) and the llama (*Lama glama*) respectively. By contrast, the microwear pattern observed in extant frugivore browsers (fruit- and seedeaters) is distinguished by having a high frequency of coarse scratches (Solounias & Semprebon, 2002). The information suggests that the camelids from Puebla were able to include soft (*e.g.* leaves, shoots, and/or twigs) and abrasive (*e.g*. grasses and/or external grit) resources into their diets, although, the sample of *Hemiauchenia macrocephala* emphasized less abrasive resources.

Given the above, the dental microwear pattern in the samples of *Hemiauchenia macrocephala* from Puebla is indicative of a browsing diet and that of *Camelops hesternus* is related to a mixed feeding. These two proposed dietary behaviors indirectly indicates the presence of forested and opened vegetation areas at the Valsequillo Basin during the late Pleistocene. Perez-Crespo *et al*. (2014) have considered a similar scenario at the Valsequillo Basin, based on data derived from the analysis of stable carbon isotopes in the teeth of ground sloths, capybaras, horses, mammoths, and gomphotheres. Semprebon & Rivals (2010) found that the microwear pattern in samples of *Hemiauchenia macrocephala* from the Irvingtonian of Nebraska is comparable to that of extant mixed feeders, whereas the microwear pattern in samples of *Camelops nevadus* from the Rancholabrean of Nevada and *Camelops* sp. from the Rancholabrean of New Mexico and Baja California had been related to that of extant browsers. In the present study, we observe different microwear patterns and trophic regimes in samples of *Hemiauchenia macrocephala* (browser) and *Camelops hesternus* (mixed feeder) from the Valsequillo Basin. The observed differences could be explained by the differential use of local resources, dietary flexibility of these taxa, or both, reflecting particular properties of the habitat and a wide spectrum on their trophic regimes respectively.

Hemiauchenia macrocephala is a medium-sized llama with a mean body mass of about 96 kg, whereas the species *Camelops hesternus* is a camel with a mean body mass of about 437 kg (Mendoza *et al*., 2006). Hence, the differences in size and trophic regimes could explain their coexistence at the Valsequillo Basin, allowing them to partition food resources. Large mammals tend to have large home ranges (McNab, 1963) and are more migratory than small mammals (Eisenberg, 1981). Thus, the potential differences in home range and vagility between these species, suggest that probably *Hemiauchenia macrocephala* has been a local inhabitant at the area and *Camelops hesternus* has been more migratory. This contention could also have explained the greater abundance of material belonging to *H. macrocephala* in comparison to that of *C. hesternus*.

Geographic distribution

In Mexico, *Hemiauchenia macrocephala* and *Camelops hesternus* have been reported from a small number of localities within the following morphotectonic provinces (Ferrusquía-Villafranca, 1993): Baja California Peninsula [El Carrizal,

Table 7. Dental microwear variables in the samples of *Hemiauchenia macrocephala* and *Camelops hesternus* from Valsequillo Basin, Rancholabrean of Puebla, central Mexico. **Abbreviations: AS**, average of scratches; **AP**, average of pits; **%CS**, percentage of cross scratches; **%LP**, percentage of large pits; **%G**, percentage of gouges; **%fs**, percentage of fine scratches; **%cs**, percentage of coarse scratches; **%ms**, percentage of mixed scratches.

	AS	AP	%CS	%LP	%G	%fs	%cs	%ms
Hemiauchenia macrocephala	10.00	39.86	26.66	60.00	33.33	53.33	0.00	46.66
Camelops hesternus	16.33	32.66	50.00	66.66	33.33	50.00	0.00	50.00

Baja California Sur (Ferrusquía-Villafranca & Roldán, 1980); Central Plateau [El Cedazo, Aguascalientes (Mooser & Dalquest, 1975; Ferrusquía-Villafranca *et al*., 2010)]; Sierra Madre Oriental [Laguna de la Media Luna, San Luis Potosí (Hernandez-Junquera, 1977)]; and Trans-Mexican Volcanic Belt [Valsequillo Basin, Puebla (Ferrusquía-Villafranca *et al*., 2010 and present study)]. Likewise, these two camelids typically occurred in areas between the 19°-25°N, within the Baja California Peninsula (southern Baja California Sur), Central Plateau and Sierra Madre Oriental (northcentral Mexico), Trans-Mexican Volcanic Belt (central Mexico), and Yucatan Platform (northwestern Yucatan) morphotectonic provinces (Figure 11).

In Mexico, during the late Pleistocene, *Camelops hesternus* was more widespread in comparison to the medium-sized *Hemiauchenia macrocephala* (Figure 11). The known

Table 8. Dental microwear data in the sample of *Hemiauchenia macrocephala* from Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations: LP**, large pits (0 = less than four pits, 1 = more than four pits); **CS**, cross scratches (0 = less than four scratches; 1 = more than four scratches); **G**, gouges (0 = no; 1 = yes); **TS**, texture of scratches (0 = fine; 1 = mixture of fine and coarse; 2 = coarse).

Specimen	Position	Scratches	Pits	CS	LP	G	TS
66-1-P-228	m2R	7	47	0	1	0	1
66-1-P-228	m2R	10	45	1	1	0	1
66-1-P-228	m1R	10	34	1	1	0	1
66-1-P-228	m1R	8	38	0	1	1	0
64-1-C3-19	m1R	10	33	0	0	0	0
64-1-C3-19	m2R	13	42	0	0	1	0
64-1-C3-19	m2R	15	38	0	1	1	0
64-1 Z-3 15	m1/2L	10	41	0	0	1	1
64-1 Z-3 15	m1/2L	9	34	0	1	1	0
66-1-1-W-1814	m2L	13	46	0	0	0	0
66-1-1-W-1814	m2L	10	42	0	0	0	1
66-1-C-5-27	M1R	7	39	0	1	0	1
66-1-C-5-27	M1R	7	40	0	0	0	0
66-1-C-5-27	M2R	10	37	1	1	0	0
66-1-C-5-27	M2R	11	42	1	1	0	1

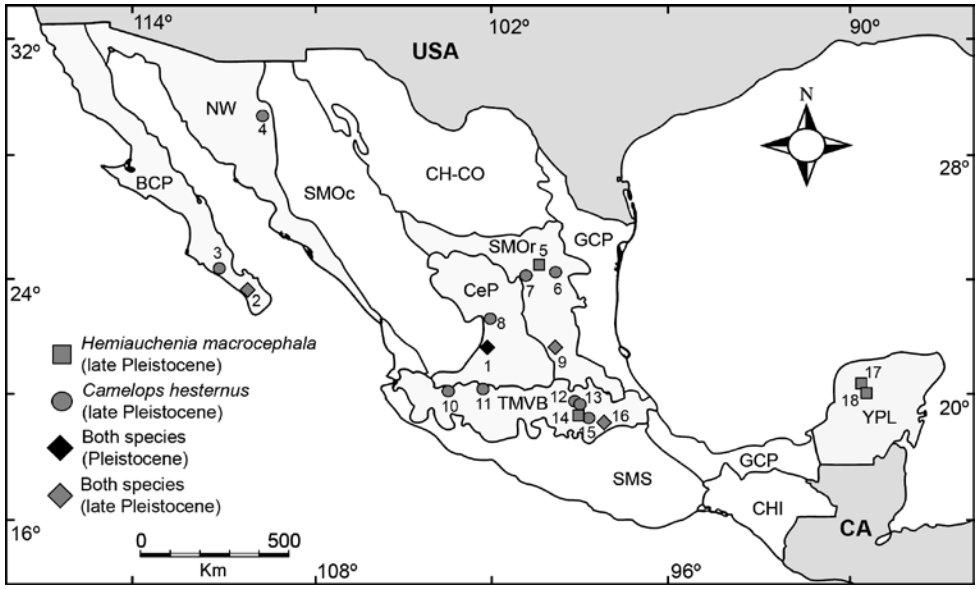

Figure 11. Pleistocene localities where *Hemiauchenia macrocephala* and *Camelops hesternus* have been reported set on the Mexican morphotectonic provinces (Ferrusquía-Villafranca, 1993). **Localities: 1**, El Cedazo, Aguascalientes; **2**, El Carrizal, Baja California Sur; **3**, Santa Rita, Baja California Sur; **4**, Térapa, Sonora; **5**, Minas, Nuevo León; **6**, San Josecito, Nuevo León; **7**, El Cedral, San Luis Potosí; **8**, Laguna de las Cruces, San Luis Potosí; **9**, Laguna de la Media Luna, San Luis Potosí; **10**, Chapala-Zacoalco, Jalisco; **11**, La Piedad, Michoacán; **12**, Tequixquiac, Estado de México; **13**, Santa Lucia, Estado de México; **14**, Tláhuac, Distrito Federal; **15**, Tlapacoya, Estado de México; **16**, Valsequillo, Puebla; **17**, Cueva de Loltún, Yucatán; **18**, La Chimenea, Yucatán. **Morphotectonic provinces: BCP**, Baja California Peninsula; **NW**, Northwestern Plains and Sierras; **SMOc**, Sierra Madre Occidental; **CH-CO**, Chihuahua-Coahuila Plateaus and Ranges; **SMOr**, Sierra Madre Oriental; **GCP**, Gulf Coastal Plain; **CeP**, Central Plateau; **TMVB**, Trans-Mexican Volcanic Belt; **SMS**, Sierra Madre del Sur; **CHI**, Sierra Madre de Chiapas; **YPL**, Yucatan Platform (modified from Ferrusquía-Villafranca *et al*., 2010).

Table 9. Dental microwear data in the sample of *Camelops hesternus* from Valsequillo Basin, late Pleistocene of Puebla, central Mexico. **Abbreviations:** as in Table 7.

Specimen	Position	Scratches	Pits	CS	LP	G	TS
66-1-W-0-19	M1R	16	34	0	0	0	0
66-1-W-0-19	M1R	17	31	0	1	0	1
66-1-3V-12	M1R	17	32	1	1	0	1
66-1-3V-12	M1R	18	37	1	0	0	0
66-1-W-0-19	M2	14	32	0	1	1	0
66-1-W-0-19	M2	16	30	1	1	1	1

geographic distribution of *Hemiauchenia macrocephala* indicates that it was widespread across a great part of the North American subcontinent during the Pleistocene, from California to Florida (Kurtén & Anderson, 1980) and from southern Canada [Medicine Hat locality Unit VII, Alberta (Churcher, 1984)] to southeastern Mexico [La Chimenea and Loltún localities, Yucatan State (González-González *et al*., 2008; Arroyo-Cabrales & Polaco, 2003)]; in addition, there is an occurrence from the early Pleistocene Río Tomaye locality, El Salvador, Central America (Cisneros, 2005). The late Pleistocene *Camelops hesternus* was distributed from California to Texas (Kurtén & Anderson, 1980) and from Alaska (Zazula *et al*., 2011) to its southernmost occurrences in temperate areas of central Mexico (Ferrusquía-Villafranca *et al*., 2010), including the Valsequillo Basin Area, Puebla State.

Comment on the occurrence of *Hemiauchenia* and *Camelops* at the Valsequillo Basin

In previous studies *Hemiauchenia macrocephala*, *Camelops hesternus*, and *C. minidokae* have been considered as part of the faunal assemblages from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico (Guenther & Bunde, 1973; Pichardo, 1997; Ferrusquía-Villafranca *et al*., 2010). To extent of our knowledge, the information regarding the characterization and kind of materials that support the taxonomic identity of those records is unavailable. In this study, the occurrence of *H. macrocephala* and *C. hesternus* at the study area is formally provided. It should be stated that the sample considered here includes specimens assigned to the large-sized species *Camelops hesternus*, although, we do not have evidence on the presence of the smallest species *C. minidokae*.

CONCLUSIONS

A collection of dental and postcranial remains of camelids from the Valsequillo Basin, late Pleistocene of Puebla, central Mexico is formally described. A comparative study indicates that the studied sample represents two species of camelids, including *Hemiauchenia macrocephala* and *Camelops hesternus*.

The dental microwear pattern of the camelids from Puebla is distinguished by having a higher number of pits than scratches. The microwear signature in the sample of *Hemiauchenia macrocephala* implied processing of soft resources and should be related to a browsing diet, whereas that of *Camelops hesternus* is indicative of an intake of soft and/or abrasive resources associated to a mixed feeder. At the Valsequillo Basin, the resource partitioning between these species is explained by their differences in size and trophic regimes.

The Mexican record of *Hemiauchenia macrocephala* and *Camelops hesternus* indicates that were common in areas between the 19°-25°N, within the Baja California Peninsula, Central Plateau, Sierra Madre Oriental, Trans-Mexican Volcanic Belt, and Yucatan Platform morphotectonic provinces. The record from the Valsequillo Basin constitutes one of the few Mexican areas of Pleistocene age where both species have been reported.

ACKNOWLEDGEMENTS

We thank to J. Baskin and to C.S. Scherer for their comments and suggestions that greatly improved the final version of the manuscript. The first author thanks S.A. McLeod, V.R. Rhue and A. Farrell, for their kind support during his visit to the Vertebrate Paleontology and the Page Museum, La Brea Tar Pits collections at the Natural History Museum of Los Angeles County. In the same way, thanks to C. Sagebiel, collection manager of the Vertebrate Paleontology collection at the Texas Memorial Museum.

REFERENCES

Armenta, C.J. 1957. *Hallazgos prehistóricos en el valle de Puebla*. Puebla, Centro de Estudios Históricos de Puebla. (Report 2).

Armenta, C.J. 1959. Hallazgo de un artefacto asociado con un mamut en el valle de Puebla, México. *Instituto Nacional de Antropología e Historia, Dirección Prehistoria*, **7**:7-25.

Armenta, C.J. 1978. *Vestigios de labor humana en huesos de animales extintos de Valsequillo*. Puebla, Consejo Editorial del Gobierno del Estado de Puebla, 128 p.

Arroyo-Cabrales, J. & Polaco, O.J. 2003. Caves and the Pleistocene vertebrate paleontology of Mexico. *In*: B.W. Schubert; J.I. Mead & R.W. Graham (eds.) *Ice age cave faunas of North America*, Indiana University Press, p. 273-291.

Bärmann, E.V. & Rössner, G.E. 2011. Dental nomenclature in Ruminantia: Towards a standard terminological framework. *Mammalian Biology*, **76**:762-768. *doi:10.1016/j.mambio.2011.07.002*

Baskin, J. & Thomas, R. 2016. 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. *doi:10.1080/08912963.2015.1020800*

Bravo-Cuevas, V.M. & Jiménez-Hidalgo, E. 2015. First reported occurrence of *Palaeolama mirifica* (Camelidae, Lamini) from the Late Pleistocene (Rancholabrean) of Puebla, central Mexico. *Boletín de la Sociedad Geológica Mexicana*, **67**:13-20.

Bravo-Cuevas, V.M.; Jiménez-Hidalgo, E., Cuevas-Ruiz, G.E. & Cabral-Perdomo, M.A. 2012. A small camelid *Hemiauchenia* from the Late Pleistocene of Hidalgo, central Mexico. *Acta Palaeontologica Polonica*, **57**:497-508. *doi:10.4202/app.2011.0005*

Breyer, J.A. 1974. Examination of selected postcranial elements in Pleistocene camelids. *Contributions to Geology*, **13**:75-85.

Breyer, J.A. 1977. Intra- and interspecific variation in the lower jaw of *Hemiauchenia*. *Journal of Paleontology*, **51**:527-535.

Churcher, C.S. 1984. Faunal correlations of Pleistocene deposits in western Canada. *In*: W.C. Mahaney (ed.) *Correlation of Quaternary Chronologies, Symposium on Correlation of Quaternary Chronologies*, Atkinson College, York University, p. 145-158.

Cisneros, J.C. 2005. New Pleistocene vertebrate fauna from El Salvador. *Revista Brasileira de Paleontologia*, **8**:239-255.

Cope, E.D. 1893. *A preliminary report on the vertebrate paleontology of the Llano Estacado: 4th Annual Repository.* Austin, Geological Survey Texas, 137 p.

Croxen, F.W. III.; Shaw, C.A. & Sussman, D.R. 2007. Pleistocene Geology and Paleontology of the Colorado River Delta at Golfo de Santa Clara, Sonora, Mexico. *In*: R.E. Reynolds (ed.) *Wild, Scenic and Rapid: A Trip Down the Colorado River Trough: The 2007 Desert Symposium Field Guide and Abstracts from Proceedings*, California State University, p. 84-89.

Cruz-Muñoz, V.J.; Arroyo-Cabrales, J. & Graham, R.W. 2009. Rodents and lagomorphs (Mammalia) from the Late-Pleistocene deposits at Valsequillo, Puebla, México. *Current Research in the Pleistocene*, **26**:147-149.

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

Eisenberg, J.F. 1981. *The Mammalian radiations: An analysis of trends in evolution, adaptation, and behavior*. Chicago, University of Chicago Press, 610 p.

Ferrusquía-Villafranca, I. 1993. *Geology of Mexico: a synopsis*. New York, Oxford University Press, 792 p.

Ferrusquía-Villafranca, I. & Roldán, V.T. 1980. El registro de mamíferos terrestres del Mesozoico y Cenozoico de Baja California. *Revista Mexicana de Ciencias Geológicas*, **4**:56-62.

Ferrusquía-Villafranca, I.; Arroyo-Cabrales, J.; Martínez-Hernández, E.; Gama-Castro, J.; Ruíz-González, J.; Polaco, O.J. & Johnson, E. 2010. Pleistocene mammals of Mexico: A critical review of regional chronofaunas, climate change response and biogeographic provinciality. *Quaternary International*, **217**:53-104. *doi:10.1016/j.quaint.2009.11.036*

Gervais, H. & Ameghino, F. 1880. *Les mammifères fossiles del'Amérique du Sud*. Paris, Library F. Savy, 225 p.

González-González, A.; Sandoval, C.R.; Mata, A.T.; Sanvicente, M.B.; Stinnesbeck, W.; Jerónimo-Avilés, O.; De los Ríos, M. & Acevez, E. 2008. The arrival of humans on the Yucatan Peninsula: Evidence from submerged caves in the state of Quintana Roo, Mexico. *Current Research in the Pleistocene*, **25**:1-24.

Gonzalez, S.; Huddart, D. & Bennett, M. 2007. Valsequillo Pleistocene archaeology and dating: ingoing controversy in Central Mexico. *World Archaeology*, **38**:611-627. *doi:10.1080/00438240600963155*

Gray, J.E. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository*, **15**:296-310.

Guenther, E.W. & Bunde, H. 1973. Investigaciones geológicas y paleontológicas en México durante los años de 1965 a 1969. *Comunicaciones Proyecto Puebla–Tlaxcala*, **7**:19-20.

Hammer, Ø.; Harper, D.A.T. & Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, **4**:1-9. Available at http://palaeoelectronica.org/2001_1/past/issue1_01.htm; accessed in 31/07/2016.

Heintzman, P.D.; Zazula, G.D.; Cahill, J.A.; Reyes, A.V.; MacPhee, R.D.E. & Shapiro, B. 2015. Genomic data from extinct North American *Camelops* revise camel evolutionary History. *Molecular Biology and Evolution*, **32**:2433-2440. *doi:10.1093/molbev/msv128*

Hernández-Junquera, A. 1977. *Fauna local Laguna de la Media Luna, Pleistoceno Tardío, Municipio de Río Verde, San Luis Potosí, México*. Facultad de Ciencias, Universidad Nacional Autónoma de México, Undergraduate monography, 102 p.

Honey, J.G.; Harrison, A.J.; Prothero, D.R. & Stevens, M.S. 1998. Camelidae. *In*: C.M. Janis; K.M. Scott & L.L. Jacobs (eds.) *Evolution of Tertiary Mammals of North America: Carnivores, ungulates and ungulate-like mammals*, Cambridge University Press, p. 439-462.

Hulbert, R.C. Jr. & Webb, S.D. 2001. Mammalia 5: Artiodactyls. *In*: R.C. Hulbert (ed.) *The fossil vertebrates of Florida*, University Press of Florida, p. 242-279.

INEGI. 1987. *Síntesis Geográfica, Nomenclator y Anexo Cartográfico del Estado de Puebla*. Ciudad de México, Secretaría de Programación y Presupuesto, 18 p.

Jiménez-Hidalgo, E.; Carbot-Chanona, G.F. & Castañeda-Posadas, C. 2015. El registro de mamíferos fósiles de Puebla. *In*: C. Castañeda-Posadas (ed.) *El registro paleobiológico del estado de Puebla*, Benemérita Universidad Autónoma de Puebla, p. 173-186.

Kurtén, B. & Anderson, E. 1980. *Pleistocene mammals of North America*. New York, Columbia University Press, 442 p.

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*, **7**:172-173.

Leidy, J. 1873. Contributions to the extinct vertebrate fauna of the western territories. *United States Geological Survey Territories Repository*, **1**:14-358.

Malde, H.E.; Steen-McIntyre, V.; Naeser, C.W. & VanLandingham, S.L. 2011. The stratigraphic debate at Hueyatlaco, Valsequillo, Mexico. *Palaeontologia electronica*, **3**:44A.

McNab, B. 1963. Bioenergetics and the determination of home range size. *American Naturalist*, **97**:133-140. *doi:10.1086/282264*

Meachen, J. 2003. A new species of *Hemiauchenia* (Camelidae: Lamini) from the Plio-Pleistocene of Florida. University of Florida, M.Sc. thesis, 57 p.

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

Mendoza, M.; Janis, C.M. & Palmqvist, P. 2006. Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *Journal of Zoology*, **270**:90-101. *doi:10.1111/j.1469-7998.2006.00094.x*

Mihlbachler, M.C.; Beatty, B.L.; Caldera-Siu, A.; Chan, D. & Lee, R. 2012. Error rates and observer bias in dental microwear analysis using light microscopy. *Palaeontologia Electronica*, **15**:1-22.

Mooser, O. & Dalquest, W.W. 1975. Pleistocene mammals from Aguascalientes, Central Mexico. *Journal of Mammalogy*, **56**:781-820. *doi:10.2307/1379653*

Ochoa-Castillo, P.; Pérez-Campa, M.; Martín del Pozzo, A.L. & Arroyo-Cabrales, J. 2003. New excavations in Valsequillo, Puebla, México. *Current Research in the Pleistocene*, **20**:61-63.

Owen, R. 1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamys vectianus* and *Hyopotamys bovinus*) discovered by the Marchioness of Hasting in the Eocene deposits on the N.W. coast of the Island of Wight: with an attempt to develope Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, **4**:103-141.

Perez-Crespo, V.A.; Arroyo-Cabrales, J.; Alva-Valdivia, L.M.; Morales-Puente, P.; Cienfuegos-Alvarado, E.; Otero, F.J. & Ochoa-Castillo, P. 2014. La Paleodieta de Cinco Especies de Mamíferos Herbívoros Rancholabreanos de Valsequillo (Puebla, México). *Revista Chilena de Antropología*, **30**:76-82.

Pichardo, M. 1997. Valsequillo Biostratigraphy: New evidence for Pre-Clovis date. *Anthropologischer Anzeiger*, **55**:233-246.

Prothero, D.R. & Schoch, R.M. 2002. *Horns tusks, & flippers. The evolution of hoofed mammals*. Baltimore, The Johns Hopkins University Press, 311 p.

Renne, P.R.; Feinberg, J.M.; Waters, M.R.; Arroyo-Cabrales, J.; Ochoa-Castillo, P.; Perez-Campa, M. & Knight, K.B. 2005. Age of Mexican ash with alleged "footprints". *Nature*, **438**:E7-E8. *doi:10.1038/nature04425*

Semprebon, G.M. & Rivals, F. 2010. Trends in the paleodietary habits of fossil camels from the Tertiary and Quaternary of North America. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **295**:131-145. *doi:10.1016/j.palaeo.2010.05.033*

Semprebon, G.M.; Godfrey, L.R.; Solounias, N.; Sutherland, M.R. & Jungers, W.L. 2004. Can low-magnification stereomicroscopy reveal diet? *Journal of Human Evolution*, **47**:115-144. *doi:10.1016/j.jhevol.2004.06.004*

Solounias, N. & Semprebon, G. 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *American Museum Novitates*, **3366**:1-49.

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

Webb, S.D. 1974. Pleistocene llamas of Florida, with a brief review of the Lamini. *In*: S. Webb (ed.) *Pleistocene Mammals of Florida*, The University Press of Florida, p. 170-213.

White, R.S.; Mead, J.I.; Baez, A. & Swift, S.L. 2010. Localidades de vertebrados fósiles del Neógeno (Mioceno, Plioceno y Pleistoceno): una evaluación preliminar de la biodiversidad del pasado. *In*: F.E. Molina-Freaner & T.R. Van Devender (eds.) *Diversidad biológica de Sonora*, Universidad Nacional Autónoma de México, p. 51-72.

Zazula, G.D.; Turner, D.G.; Ward, B.C. & Bond, J. 2011. Last interglacial western camel (*Camelops hesternus*) from eastern Beringia. *Quaternary Science Reviews*, **30**:2355-2360. *doi:10.1016/j.quascirev.2011.06.010*

Received in February, 2016; accepted in July, 2016.