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A small camelid *Hemiauchenia* from the Late Pleistocene of Hidalgo, central Mexico

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Pleistocene camels from Mexico include representatives of llamas and camels. Their record spans from the Early Blancan to the Late Pleistocene, based on several localities in the northern, northwestern and central parts of the country, with members of the genus *Hemiauchenia* being particularly well represented. New specimens of a small llama, collected in the state of Hidalgo, central Mexico, are assigned to *Hemiauchenia gracilis* owing to a combination of cranial and postcranial characters, including a short upper premolar-molar series, the presence of a two-rooted P3, molars covered by a thin layer of cementum, U-shaped molar crescents, well-developed styles and ribs, a small degree of crenulation, a relatively short lower tooth row, the lack of p1 and p3, weakly developed anteroexternal stylids, a shallow and slender mandible, and long and slender metatarsals and phalanges. The material described here extends the Pleistocene geographic distribution of *H. gracilis* from northern to central Mexico, and its biochronological range from the Early Blancan to the Late Pleistocene (Rancholabrean), thus making it the southernmost record and the geochronologically youngest occurrence of this species in North America. The mesowear pattern of the material from Hidalgo suggests that these animals were mainly browsers. Their estimated body mass resembles that of Blancan specimens from Guanajuato, implying that this species maintained approximately the same body mass throughout its biochronological range in central Mexico.

Key words: Camelidae, *Hemiauchenia*, llamas, late Pleistocene, Hidalgo, central Mexico.

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Introduction

Recent members of the family Camelidae include the camels (dromedary and Bactrian camels), llamas, vicuñas, guanacos, and alpacas (Wilson and Reeder 2005). Camelids originated in North America during the Middle Eocene (ca. 45 Ma) and remained restricted to this continent for most of the Cenozoic, before spreading to Eurasia and probably Africa during the latest Miocene (6 Ma), and to South America during the Early Pleistocene (1.8 Ma) (Carroll 1988; Honey et al. 1998; Prothero and Schoch 2002). The modern groups of camels, the lamines (Tribe Lamini) and camelines (Tribe Camelini), radiated during the Early to Middle Miocene and became extinct in North America at the end of the Pleistocene, but survived in South America and the Old World, respectively (Carroll 1988; Honey et al. 1998; Prothero and Schoch 2002).

The known record of Camelidae from the Pleistocene of Mexico includes representatives of both modern groups of camels. Lamines are represented by *Hemiauchenia*, *Camelops*, and *Palaeolama*, with a record spanning from the Irvingtonian of Sonora and Aguascalientes to the Rancholabrean of Baja California Sur, Nuevo León, the Mexican Basin, Puebla and Jalisco (Arroyo-Cabrales et al. 2002; Croxen et al. 2007; Lucas 2008; Ferrusquía-Villafranca et al. 2010). By contrast, the presence of camelines was established based on a single occurrence referable to *Titanotylopus* (or *Gigantocamelus*) from the Irvingtonian of Sonora (Croxen et al. 2007).

Hemiauchenia in particular seems to have been one of the most abundant North American lamines, and has been recovered from numerous Plio-Pleistocene localities (Honey et al. 1998; Prothero and Schoch 2002). Species within this genus include: *H. edensis* from the latest Hemphillian (4.9–4.6 Ma) of the California Coastal Ranges (California), the Gulf Coast

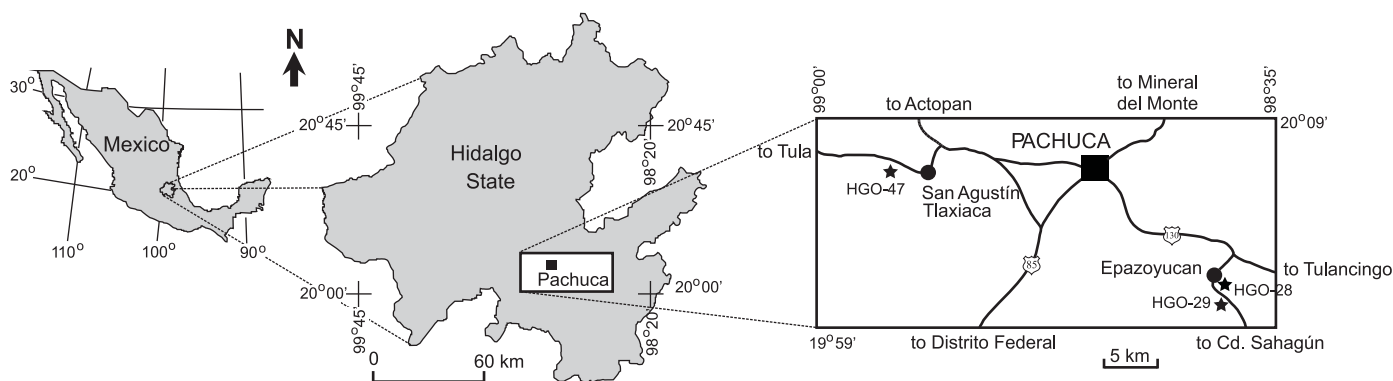


Fig. 1. Index map showing the study area in the southeastern sector of Hidalgo, central Mexico. The Pleistocene localities Barranca del Berrendo (HGO-28), Barranca San Agustín (HGO-29), and El Barrio (HGO-47) are shown.

(Florida) and the Great Basin (Chihuahua, northern Mexico) (Honey et al. 1998; Webb et al. 2008); *H. blancoensis* (= *H. seymourensis* junior synonym, following Breyer [1977]) from the Early Blancan of central Mexico, Guanajuato, the Late Blancan (2.5–2.0 Ma) of the Gulf Coast (Florida), the Southern Great Basin (Arizona, New Mexico, Texas Big Bend Area), the Great Plains (Texas Panhandle, Colorado, Nebraska, Kansas), and the Pacific Northwest (Idaho and Washington) (Morgan and Hulbert 1995; Honey et al. 1998; Ruez 2009; Jiménez-Hidalgo and Carranza-Castañeda 2010), as well as probably from the Pleistocene of El Salvador (Cisneros 2005); *H. gracilis* from the Early Blancan of central Mexico (Guanajuato) and the Pacific Northwest (Idaho), the Late Blancan (2.5–1.8 Ma) of the Gulf Coast (Florida) and the Great Basin (Arizona and New Mexico) (Meachen 2005; White and Morgan 2005; Ruez 2009; Jiménez-Hidalgo and Carranza-Castañeda 2010), and the Irvingtonian (1.9–0.15 Ma) of the Southern Great Basin (Sonora, northern Mexico) (Croxen et al. 2007; White et al. 2010); and *H. macrocephala* from various Late Blancan–Late Rancholabrean (2.5–0.01 Ma) localities in Mexico and the United States (Kurten and Anderson 1980; Morgan and Hulbert 1995; Webb and Stehli 1995).

“*Hemiauchenia*” *minima* was reported from the Late Clarendonian to Hemphillian (13.6–4.9 Ma) of the Gulf Coast of Florida (Webb et al. 1981). However, its taxonomic status is controversial, and it is possible that the taxon should be placed in a new genus (Webb et al. 1981). Finally, “*Hemiauchenia*” *vera* from the Late Hemphillian (ca. 6.5–4.9 Ma) of the Gulf Coast (Florida), the Great Basin (California Basin, Arizona, New Mexico, and Guanajuato) and the Great Plains (Nebraska and Kansas) (Honey et al. 1998) was recently referred to *Pleiolama* (Webb and Meachen 2004; Hulbert and Whitmore 2006).

In Mexico, *Hemiauchenia* is represented by three species, making it the second most diverse group of Pleistocene lamines after *Camelops* (Ferrusquía-Villafranca et al. 2010). The most common species here is *H. macrocephala*, which has been recovered from several localities in northern and

central Mexico (Hibbard 1955; Guenther and Bunde 1973; Ferrusquía-Villafranca and Torres-Roldán 1980; Arroyo-Cabral et al. 2002). Recently, *H. gracilis* (gracile llama) and *H. cf. blancoensis* (blanco llama) were reported to form part of the El Golfo de Santa Clara Fauna from the Irvingtonian of Sonora (Croxen et al. 2007; White et al. 2010), although detailed descriptions of this material have not yet been published. Finally, the El Cedazo Fauna from the Irvingtonian of Aguascalientes also includes the remains of both a small and a large species of *Hemiauchenia* (Mooser and Dalquest 1975).

Here, we describe material of a small *Hemiauchenia* recovered from three Late Pleistocene (Rancholabrean) localities of the state of Hidalgo (central Mexico), compare them to the Plio-Pleistocene North American species formally included in the genus, and comment on the paleobiological significance of this new material.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; F:AM, Frick Collection at AMNH; IGM, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, México; KU, University of Kansas, Kansas, USA; TMM, Vertebrate Paleontology Laboratory Collection, University of Texas at Austin, Texas, USA; UAHMP, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo, Hidalgo, México; UF, Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; UNSM, University of Nebraska State Museum, Nebraska, Lincoln, USA.

Anatomical abbreviations.—Bd, breadth of distal end; Bp, breadth of proximal end; C/c upper/lower canine; GL, greatest length; I/i, upper/lower incisor; L, tooth length; M/m, upper/lower molar; MDL, mandibular diastema length; P/p, upper/lower premolar; SD, smallest breadth of diaphysis; UTRL, upper tooth row length; W, tooth width.

Other abbreviations.—Ka, thousand years; Ma, million years; n, number of specimens.

Geological setting

The material studied here was recovered from Barranca del Berrendo (HGO-28) (20°01'20.7" N, 98°37'37.9" W), Barranca San Agustín (HGO-29) (20°00'27.7" N, 98°37'59.9" W), and El Barrio (HGO-47) (20°07'41" N, 98°56'02.7" W), three nearby localities located in southeastern Hidalgo, central Mexico (Fig. 1). These localities are characterized by outcrops of Tertiary to Quaternary volcanic and volcano-sedimentary rocks (INEGI 1992). The latter include unnamed Quaternary fluvio-lacustrine deposits consisting of poorly to moderately consolidated clays and silts, which are irregularly intercalated with volcanic gravels of mafic composition (Bravo-Cuevas 2002). The fossil material was recovered from these deposits (Fig. 2).

The associated mammalian fauna includes rodents, bears, dire wolves, giant ground sloths, giant armadillos, horses, antilocaprids, cervids, bison, mammoths, and mastodons (Castillo-Cerón et al. 1996; Bravo-Cuevas 2001, 2002; Cabral-Perdomo 2001; Bravo-Cuevas et al. 2009a, b), with the presence of *Bison* being indicative of the Rancholabrean North American Land Mammal Age (Bell et al. 2004).

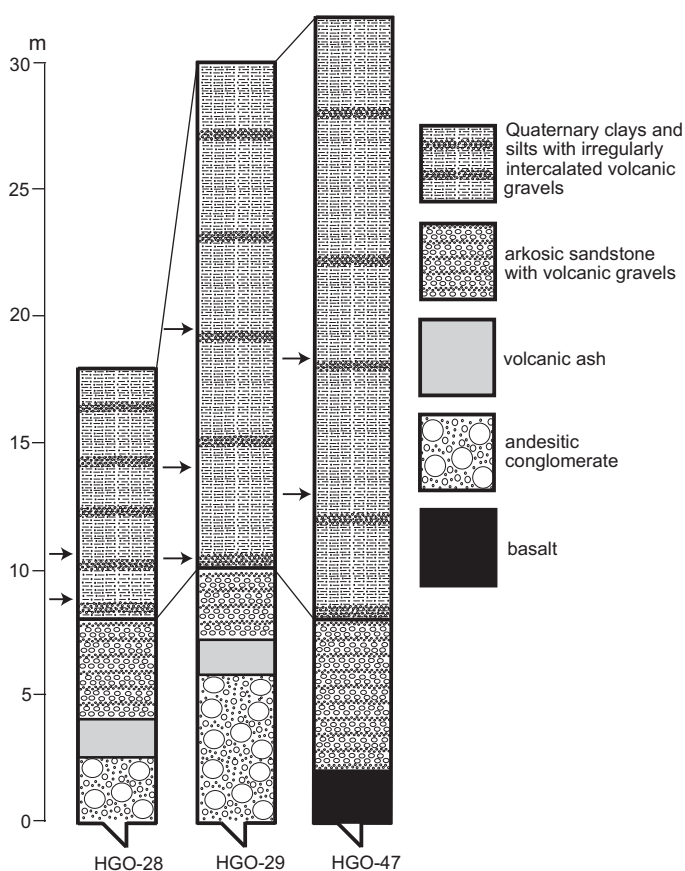


Fig. 2. Stratigraphic sections of the localities of Barranca del Berrendo (HGO-28), Barranca San Agustín (HGO-29), and El Barrio (HGO-47); the correlation of the fossiliferous sedimentary sequence is shown. Arrows indicate the levels which have yielded the specimens.

Material and methods

The specimens consist of a partial skull, a mandible fragment and several postcranial elements, and are housed at the Colección de Macromamíferos, UAHMP.

Our dental nomenclature follows Honey (2004). Comparisons of the dental morphology of the specimens from Hidalgo with selected species of *Hemiauchenia* were performed at comparable wear stages, following Breyer (1977: 529). Measurements were taken with a digital caliper with a measuring range of 0–150 mm, a resolution of 0.01 mm, and an accuracy of 0.003 mm. In some instances, limb measurements were taken using a 3 m flexible tape measure.

The taxonomic identity of the fossil material from Hidalgo was assessed by evaluating a set of key morphological and metric features commonly used to identify llama taxa (Webb 1965, 1974; Breyer 1977), and comparing it to selected *Hemiauchenia* specimens housed at AMNH, F:AM, IGM, KU, TMM, UF, and UNSM.

Systematic paleontology

Order Artiodactyla Owen, 1848

Family Camelidae Gray, 1821

Subfamily Camelinae Gray, 1821

Tribe Lamini Webb, 1965

Genus *Hemiauchenia* Gervais and Ameghino, 1880

Type species: Hemiauchenia paradoxa Gervais and Ameghino, 1880, Pampean region of Argentina, Lujanian (Late Pleistocene).

Hemiauchenia gracilis Meachen, 2005

Figs. 3–7, Tables 1–4.

Type material: UF210707, holotype, a right mandibular fragment including p4–m3 (Meachen 2005).

Type locality and horizon: De Soto Shell Pit 5 in De Soto County, Florida, Caloosahatchee Formation, latest Blancan (UF locality DE011).

Referred material.—Locality of Barranca del Berrendo (HGO-28): UAHMP-357, distal portion of a metatarsal; UAHMP-1142, partial skull. Locality of Barranca San Agustín (HGO-29): UAHMP-419, distal part of a left scapula; UAHMP-515, distal portion of a left tibia. Locality of El Barrio (HGO-47): UAHMP-1144, fragmentary left mandible preserving p4–m3 in situ, as well as the alveoli for i1–i3 and c; UAHMP-962, metatarsal fragment; UAHMP-954, two proximal phalanges of the same individual.

Emended diagnosis.—Small-sized llama (mean UTRL = 91.08 mm); moderately hypsodont teeth (mean molar crown height along mesostyle ~20 mm); both upper and lower molariforms covered by cementum; well-developed parastyle and mesostyle on M1–M3; upper molars with U-shaped fossettes; lack of p1 and p3; robust posterolophid on m3; and gracile limbs.

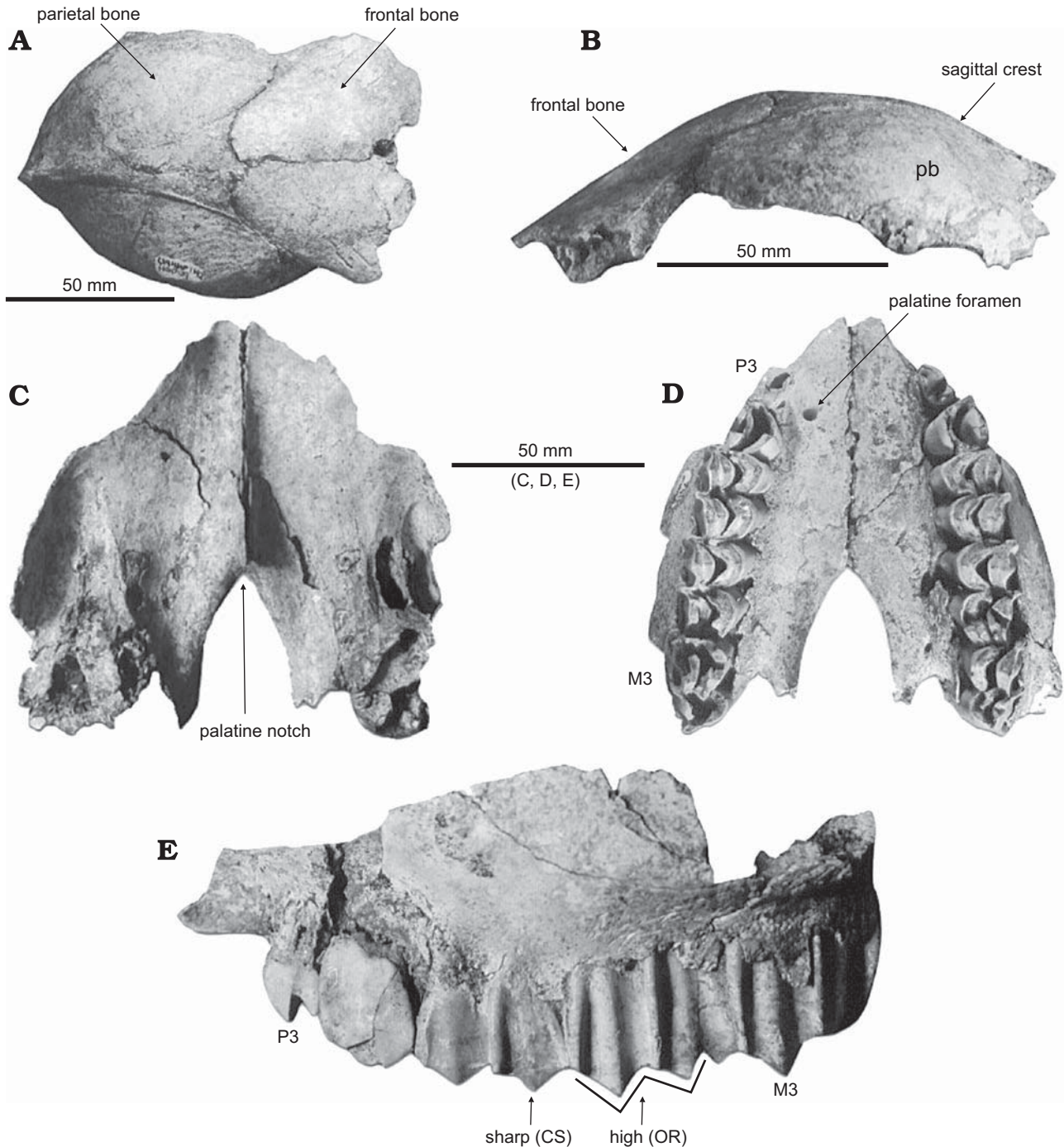


Fig. 3. Skull and upper dentition of the camelid *Hemiauchenia gracilis* Meachen, 2005 from the Late Pleistocene (Rancholabrean) of Hidalgo, central Mexico. Cranial vault (UAHMP-1142) in dorsal (A) and lateral (B) views. Dorsal (C), ventral (D), and lateral (E) views of maxillary fragment. The arrows in E indicate mesowear patterns: high occlusal relief (OR) and sharp cusp shape (CS).

Description

Skull and upper dentition.—Specimen UAHMP-1142 (Fig. 3A–E) is a partial skull comprising parts of the cranial vault, as well as the palatines, maxillae (preserving both left and right P3–M3), and several unidentifiable fragments. The frontal bones are directed forwards and downwards, transversely narrow and rounded posteriorly, and expanding transversely towards their anterior borders. The cranial suture between the frontals is well delineated. The parietal

bones are dorsally convex and separated by a narrow, triangular sagittal crest (Fig. 3A, B). The palatines are slightly concave ventrally and bear a prominent sagittal crest on their dorsal side. The suture between each maxilla and palatine is V-shaped, pointing anteriorly. The palatine foramina are located in line with the posterior border of P3, while the palatine notch is sharply V-shaped and extends anteriorly to the level of the anterior portion of M2 (Fig. 3C, D).

The mean UTRL of specimen UAHMP-1142 is ca. 90

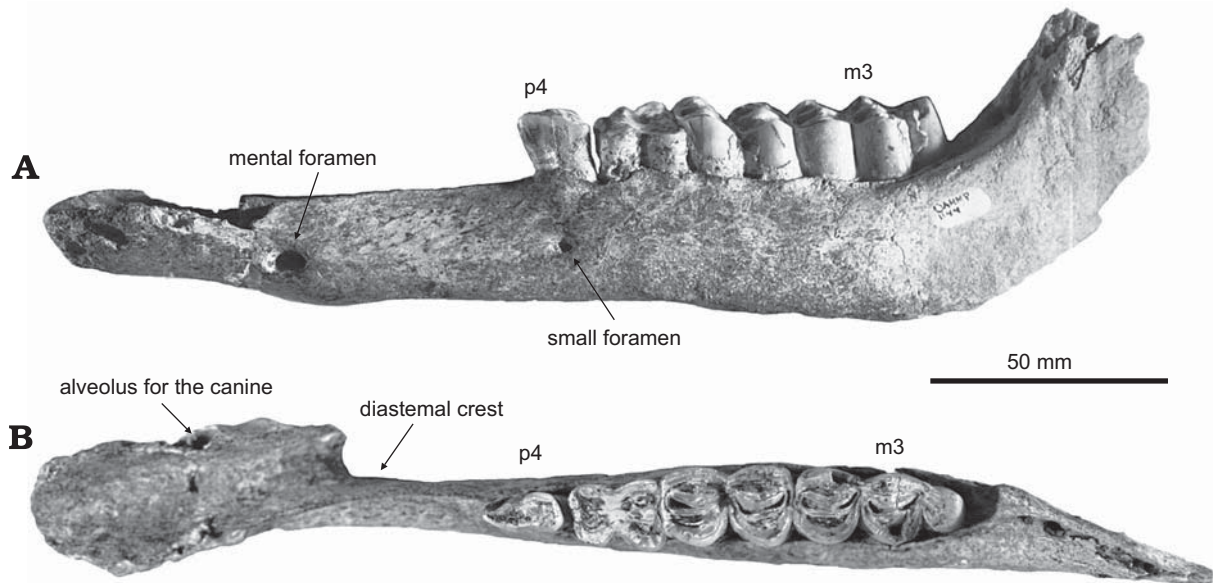


Fig. 4. Mandible and lower dentition of the camelid *Hemiauchenia gracilis* Meachen, 2005 from the Late Pleistocene (Rancholabrean) of Hidalgo, central Mexico. Partial mandible (UAHMP-1144) in lateral (A) and occlusal (B) views.

mm, indicating a small-sized individual, while the molari-forms are in moderate to late-moderate stages of tooth wear, suggestive of a young adult. The cheek teeth show little crenulation and are transversely compressed, with a mean molar crown height (along the mesostyle) of ca. 20 mm. The P3 is small, unworn and resembling a blade, two-rooted, and shows two small lingual ridges located at the base of the tooth. Its occlusal surface is situated below the crown height of P4 or any of other upper molars, indicating that this tooth was non-functional. In occlusal view, the P4 is subquadrangular in outline, with a rounded lingual and a straight labial border, and a single U-shaped fossette. The parastyle is rounded and well developed, while the metastyle is relatively poorly developed. A faint, rounded rib is present on the ectoloph. M1–3 are distinguished by having prominent styles and ribs. The protocones and the metaconules are rounded and subequal in size, and the pre- and postfossetes are U-shaped. A thin layer of cementum is present on the ectoloph of the molars (Fig. 3D, E).

Mandible and lower dentition.—The mandibular fragment UAHMP-1144 (Fig. 4A, B) is shallow and slender. A relatively short diastema, 49.2 mm long, is located between the alveoli for the canine and p4. The alveolus for the canine is large, subovoid, and deep. The diastemal crest is sharp. The mandibular depth increases anteroposteriorly (depth below anterior p4 = 23.6 mm; depth below posterior m3 = 34.8 mm). A large and well-developed mental foramen is situated below the alveolus for the canine, while a second, small foramen occurs below the midpoint of p4 (Fig. 4A).

While p4 and m1 exhibit a late stage of tooth wear, m2 is at an early late stage of wear, and m3 at a late moderate stage, with the wear on the molar series as a whole corresponding to wear stage three of Breyer (1977). Taken together, this wear stage and the full eruption of m3 are indicative of an adult in-

dividual. The length of the p4–m3 dental series is approximately 82 mm. A thin layer of cementum, most evident at the base of dental crown, is present on the cheek teeth. The p1 and p3 are absent. The p4 is triangular in occlusal view and bears two fossettids at the posterior end of the occlusal surface, with the more anterior fossettid being the larger one. The m1 is quadrangular and marked by a hypoconid much broader than the protoconid. The m2 is rectangular, with the protoconid and hypoconid being rounded and subequal in

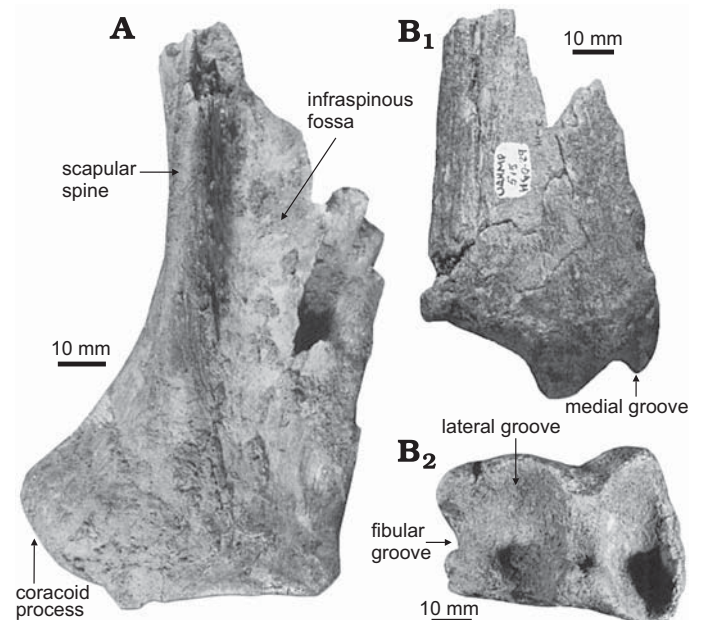


Fig. 5. Postcranial elements of the camelid *Hemiauchenia gracilis* Meachen, 2005 from the Late Pleistocene (Rancholabrean) of Hidalgo, central Mexico. A. Distal end of left scapula (UAHMP-419) in lateral view. B. Distal end of left tibia (UAHMO-515) in anterior (B₁) and distal (B₂) views, showing the articular surface.

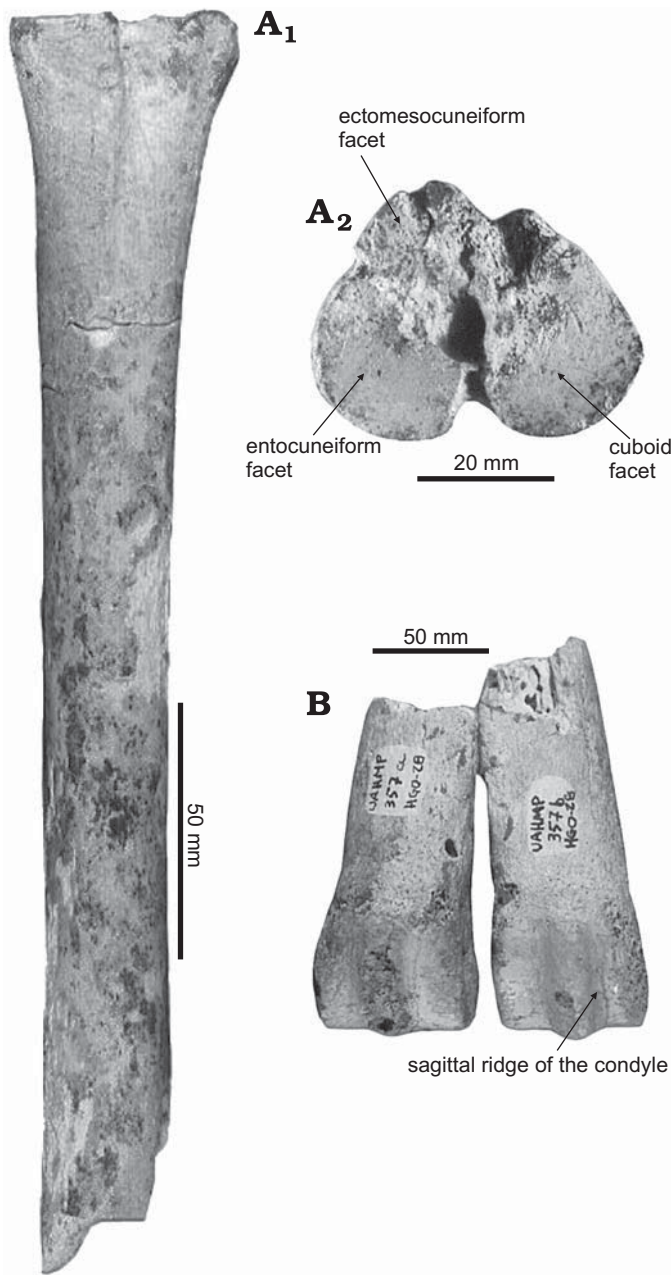


Fig. 6. Hind limb of the camelid *Hemiauchenia gracilis* Meachen, 2005 from the Late Pleistocene (Rancholabrean) of Hidalgo, central Mexico. **A.** Left metatarsal (UAHMP-962) in anterior (A_1) and proximal (A_2) views, showing the articular surface. **B.** Distal portions of metatarsals III and IV (UAHMP-357) in anterior view.

size, and is the only tooth showing a weak anteroexternal styloid (“llama buttresses”). A robust and well-differentiated hypoconulid is present on m3 (Fig. 4B).

Postcranial elements.—Specimen UAHMP-419 (Fig. 5A) represents the distal end of a left scapula. The infraspinous fossa is very large near the distal end of the shaft. The scapular spine is straight and overhangs the infraspinous fossa. The scapular neck is broad and thick, and the glenoid cavity large and subcircular in ventral view. The lateral and medial edges

of the glenoid cavity are rounded, and a small tuberosity is present adjacent to the lateral edge. The coracoid process is massive and rugose.

Specimen UAHMP-515 (Fig. 5B) represents the distal end of a left tibia, marked by a dorsoventrally compressed diaphysis. The lateral and medial grooves on the distal articular surface are subovoid, strongly concave, limited by malleoli, and separated by a sagittal ridge, which terminates anteriorly in a prominent, blunt tongue. The lateral groove is shallower and wider than the medial one, suggesting a llama-like style of articulation with the proximal trochlea of the astragalus (Webb 1965). The fibular groove is U-shaped and limited by two small malleoli. The lateral and medial sides of the distal end of the shaft are slightly convex.

Specimen UAHMP-962 (Fig. 6A) consists of the proximal portion of a left metatarsal with a length of 24.6 cm. Approximately 75% of the bone are preserved, suggesting a total length of about 33 cm. The proximal articular surface is trapezoidal, with a central deep concavity and three articular facets. The latter include (i) the large, slightly convex, and subovoid cuboid facet; (ii) the bean-shaped entocuneiform facet, slightly smaller than the cuboid facet; and (iii) the small, subrounded ectomesocuneiform facet, separated from the entocuneiform facet. The slender and transversely compressed diaphysis bears a short, narrow channel, extending on to the proximal quarter of the shaft. While the lateral and medial sides of the bone are flattened, its dorsal side is slightly convex and smooth. By contrast, its ventral side is concave, thus forming a wide, deep groove along the shaft.

Specimen UAHMP-357 (Fig. 6B) consists of the distal ends of the proximally fused metatarsals III and IV, with both bones preserving their respective condyles. The lateral sides

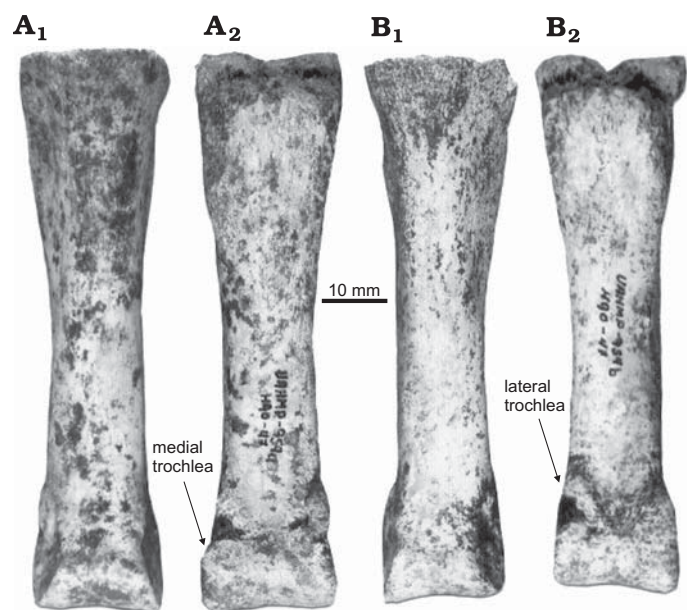


Fig. 7. Proximal phalanges of the camelid *Hemiauchenia gracilis* Meachen, 2005 from the Late Pleistocene (Rancholabrean) of Hidalgo, central Mexico. **A.** UAHMP-954 (right) in anterior (A_1) and posterior (A_2) views. **B.** UAHMP-954 (left) in anterior (B_1) and posterior (B_2) views.

of the bones are convex, whereas their medial, dorsal and ventral sides are flattened. The large condyles bear prominent sagittal ridges, which extend dorsoventrally on to the distal portion of the shaft.

Finally, UAHMP-954 consists of two proximal phalanges of a single individual (Fig. 7). In both specimens, the proximal epiphysis is not completely ossified, suggesting a relatively young individual. The diaphysis is subrounded in cross section, with convex dorsal and flattened ventral sides. The depressions for the collateral ligaments are rough and large. The proximal posterior surface is rough and bears a W-shaped scar for the insertion of the suspensory ligament, which extends on to the proximal quarter of the shaft. Distally, the bones terminate in a dorsoventrally expanded articular surface formed by two trochleae, with the lateral trochlea being relatively larger than the medial one.

Geographic and stratigraphic range.—Blancan III or Early Blancan (approximately 4.1–3.0 Ma) of Guanajuato, central Mexico (Jiménez-Hidalgo and Carranza-Castañeda 2010) and Idaho, USA (Ruez 2009); Late Blancan (2.5–1.3 Ma) of Florida (Meachen 2003, 2005), Arizona, and New Mexico, USA (White and Morgan 2005); Irvingtonian (1.3–0.15 Ma) of Sonora, Northern Mexico (Croxen et al. 2007; White et al. 2010); and Rancholabrean (160–9.5 ka; following Bell et al. 2004) of Hidalgo, central Mexico (this study) (Fig. 8).

Discussion

The fossils from Hidalgo show several features typical of lamines, including a high-domed cranium with a weak sagittal

crest, reduced premolars, anteroexternal stylids (“llama buttresses”) on the lower molars, a lack of both P2 and p2, a sharp diastemal crest on the mandible, and fused metatarsals. However, the material from Hidalgo differs in several respects from other Pleistocene North American (NA) and South American (SA) lamines, including *Palaeolama* (NA and SA), *Camelops* (NA), *Lama* (SA), and *Vicugna* (SA).

The mandible and postcranial elements of *Palaeolama* differ from the Hidalgo specimens in possessing: (i) a P4 with V-shaped crescents; (ii) a mandible consistently deeper below p4 than below m1 and m2; (iii) a p4 with complex infolding; and (iv) short and robust metatarsals. Similarly, *Camelops* differs from the specimens described here in (i) a very deep and robust mandible; (ii) robust metatarsals; (iii) proximal phalanges with a raised suspensory ligament scar extending almost to the center of the shaft; and (iv) its larger size. Finally, in contrast to the specimens from Hidalgo, a p3 may sometimes be present in the South American genera *Lama* and *Vicugna*. In addition, the genus *Lama* is distinguished by having strong anteroexternal stylids on the lower molars, as opposed to the much weaker stylid restricted to m2 in the material from Hidalgo (Webb 1965, 1974; Honey et al. 1998; Meachen 2003).

The specimens from Hidalgo described in the present study share with *Hemiauchenia* the following suite of diagnostic characters: (i) cement-covered cheek teeth; (ii) a mandible increasing in depth from p4 to m3; (iii) a simple and triangular p4; (iv) a sharply V-shaped palatine notch; (v) long and slender metatarsals; and (vi) proximal phalanges with a W-shaped suspensory ligament scar (Webb 1974; Honey et al.

Table 1. Upper cheek teeth measurements (in mm) of the material from Hidalgo and selected species of *Hemiauchenia* from the Plio-Pleistocene of North America. Abbreviations: CH, crown height; L, length; W, width. For UAHMP-1142, the first value represents right, the second left teeth. Data are from ^a Meachen (2005: 438, table 1), ^b Meachen (2003: 20), ^c Montellano-Ballesteros (1989: 361, table 1), ^d Webb (1974: 190, table 9.3), ^e The Paleobiology Database (PDBD) (5 July, 2010), and ^f Jiménez-Hidalgo and Carranza-Castañeda (2010: 54, table 2).

		P3	P4	M1	M2	M3
Hidalgo specimen	UAHMP-1142*	11.3/11.8L 6.5/6.3W 9.7/9.5CH	14.0/14.0L 11.4/11.4W ---/16.5CH	21.8/22.4L 15.4/15.4W 11.5/13.2CH	23.6/25.6L 15.0/14.7W	24.4/23.4L 15.3/12.3W 24.4/23.9CH
<i>Hemiauchenia gracilis</i> ^a	UF 210714		13.8L 10.9W 14.5CH			
	UF 45493			17.8L 12.7W 7.1CH	22.2L 15.7W 19.5CH	
<i>Hemiauchenia edensis</i> ^b			11.6L 9.3W			
<i>Hemiauchenia macrocephala</i>	UMMP 46086 ^c		14.0L	23.0L	28.0L	27.5L
	UF 8902 ^d	15.0L 9.0W	16.0L 16.5W	22.0L 21.5W	24.5L 22.0W	28.0L 21.5W
	PDBD ^e			22.0L 21.3W	27.4L 19.9W	29.1L 17.9W
<i>Hemiauchenia blancoensis</i> ^f	KU 71141			28.0L 18.0W	29.0L 14.0W	27.4L 15.4W
	IGM 2342-1				21.5L 18.7W	
	IGM 2342-2					25.6L 17.5W

Table 2. Lower cheek teeth measurements (in mm) of the material from Hidalgo and selected species of *Hemiauchenia* from the Plio-Pleistocene of North America. Abbreviations: L, length; W, width. Data are from: ^a Meachen (2005: 438, table 1), ^b Webb (1974: 190, table 9.3), ^c The Paleobiology Database (PDBD) (5 July, 2010), ^d Jiménez-Hidalgo and Carranza-Castañeda (2010: 54, table 3), and ^e Hulbert and Webb (2001: 26, fig. 13.28A).

		p3–m3	p4–m3	p4	m1	m2	m3	depth at p4	depth at m3
Hidalgo specimen	UAHMP-1144		82.0L	13.6L 7.1W	15.4L 12.3W	22.5L 13.5W	28.8L 13.1W	23.6	34.8
<i>Hemiauchenia gracilis</i> ^a	UF 210707		76.3L		13.9L 9.90W	19.9L 12.1W	29.4L 11.7W	22.2	33.3
	UF 210715						26.5L 11.8W		
	UF 210717						28.2L 11.1W		
<i>Hemiauchenia macrocephala</i>	UF 11420 ^b	108.0L	96.5L	17.0L 8.5W	20.6L 13.2W	26.0L 15.5W	35.7L 14.1W	42.0	65.0
	PDBD ^c				20.1L 14.3W	16.2L 15.8W	15.1L 14.5W		
<i>Hemiauchenia blancoensis</i>	UF 11555 ^b	106.0L	95.0L	16.0L	21.0L 14.8W	22.5L 16.5W	36.5L 16.3W	38.5	55.0
	TMM 31181-126 ^d		115.0L	18.0L 8.9W	26.6L 15.4W	32.5L 16.8W	40.0L 15.0W		
	UNSM 4707-39 ^d		95.7L	16.0L 7.0W	18.7L 15.0W	27.5L 14.0W	38.8L 10.6W		
<i>"Hemiauchenia" minima</i>	AMNH 41200 ^e	72.2L	66.1L	10.2L	15.4L	17.0L	21.7L	19.7	26.6

1998; Hulbert and Webb 2001). More specifically, the length of the upper premolar-molar tooth row (P3–M3) of UAHMP-1142 (mean UTRL = 91.08 mm) is indicative of a small-sized form, which may indicate its affinity with relatively small species, such as *H. gracilis* and *H. edensis* (Meachen 2003, 2005; Webb et al. 2008), rather than the medium-sized *H. macrocephala* or the large *H. blancoensis* (Webb 1974; Breyer 1977; Kurtén and Anderson 1980).

The morphology of the upper cheek teeth of UAHMP-1142 resembles that of *H. gracilis* and *H. macrocephala* in the presence of a two-rooted P3, molars covered by a thin layer of cementum, U-shaped molar selenes, well-developed styles and ribs, and a small degree of crenulation (Meachen 2003, 2005). However, *H. macrocephala* differs from the Hidalgo material in having a subtriangular and relatively large P4 (as compared to the molars) (Webb 1974), as well as larger and more robust molars, resembling *H. blancoensis* in this regard (Table 1). In *H. edensis*, the cheek teeth lack cementum and the molar selenes are V-shaped (Meachen 2003, 2005; Jiménez-Hidalgo and Carranza-Castañeda 2010).

Breyer (1977) demonstrated the significance of mandibular morphology in the recognition of different species of *Hemiauchenia*. The mandible from Hidalgo (UAHMP-1144) resembles that of *H. gracilis* and *H. edensis* in being shallow and slender, while being deeper than that of *"Hemiauchenia" minima*, and considerably shallower than that of *H. macrocephala* and *H. blancoensis* (Table 2; Meachen 2003). The length of the diastema in UAHMP-1144 (ca. 49 mm) is relatively longer than in the holotype of *H. gracilis* from the Blancan of Florida (UF 210707, MDL = 39.2 mm) (Meachen 2003), but shorter than in the holotype of *H. macrocephala* from the Irvingtonian of Texas (TMM 18621, MDL = 61 mm), or the specimens referred to *H. blancoensis* from the

Blancan of Nebraska (e.g., UNSM 21382, MDL = 67.3 mm; UNSM 213890, MDL = 70.8 mm) (see Breyer 1977: fig. 2B, D). The length of the lower tooth row in UAHMP-1144 is similar to that of *Hemiauchenia gracilis* (UF 210707, right mandibular fragment with p4–m3 from De Soto Shell Pit site, Late Blancan of Florida), longer than that of *"H." minima* and *H. edensis* (72 mm, including the p3) (Meachen 2003), and shorter than that of *H. blancoensis* and *H. macrocephala* (Table 2).

UAHMP-1144 resembles *H. gracilis* in the lack of p1 and p3, the presence of cementum on the lower molars, and a robust posterolophid on m3 (Meachen 2003, 2005). Unlike UAHMP-1144, the material of *H. gracilis* from Florida is marked by the presence of a very prominent "llama buttress" on m3 (see Meachen 2003, 2005). This difference may be explained in two ways: (i) it is possible that throughout the evolution of *H. gracilis* there was an evolutionary trend towards a decrease in the anterolingual development of the stylids, resulting in their near or complete loss in the Rancholabrean forms; or (ii) the posterior margin of m2 in the material from Hidalgo closely approximates the anterolabial margin of m3, thus possibly preventing the complete development of the latter. A much larger fossil sample is needed to properly address these questions.

The lower cheek teeth of *H. edensis* differ from those from Hidalgo in a lack of cementum (Webb et al. 2008), whereas the lower molars of *H. blancoensis* and *H. macrocephala* are distinguished by having strong anteroexternal stylids. Furthermore, a two-rooted p3 may sometimes be present in the latter two species (Webb 1974; Breyer 1977).

The lamines generally resemble each other in terms of their postcranial morphology, with only a few characters, such as the size and proportion of the limb elements, showing

Table 3. Measurements (in mm) of the metapodials of the material from Hidalgo and selected species of *Hemiauchenia* from the Plio-Pleistocene of North America. Abbreviations: GL, greatest length; Bp, breadth of proximal end; Bd, breadth of distal end; SD, smallest breadth of diaphysis. * estimate. Data are from ^a Meachen (2003: 41, table 8), ^b Meachen (2005: 444), and ^c Hulbert and Webb (2001: 264, fig. 13.29D).

		GL	Bp	Bd	SD
Hidalgo specimens	UAHMP-357			43.2	
	UAHMP-962	330*	39.7		25.3
<i>Hemiauchenia gracilis</i> ^a	UF176935	320	33.0	39.4	19.1
<i>Hemiauchenia edensis</i> ^b	specimens from the UF collection (n = 2)	279.5			17.5
<i>Hemiauchenia macrocephala</i> ^c	UF133908	342.9	45.1	51.4	28.2
<i>Hemiauchenia blancoensis</i> ^b	specimen from the F:AM collection	470			33.5

Table 4. Measurements (in mm) of the proximal phalanges of the material from Hidalgo and selected species of *Hemiauchenia* from the Plio-Pleistocene of North America. Abbreviations as in Table 3. Data are from ^a Meachen (2003: 41, table 9), ^b Breyer (1974: 77, table 1), and ^c Jiménez-Hidalgo and Carranza-Castañeda (2010: 53, figs. 2.10, 2.11). The GL:SD ratios shown in parentheses are from Meachen (2005: 455).

		GL	Bp	Bd	SD	GL:SD
Hidalgo specimens	UAHMP-759a	82.7	20.3	19.3	13.7	6.04
	UAHMP-759b	80.9	28.9	18.7	13.4	6.04
<i>Hemiauchenia gracilis</i> ^a	UF179638	82.6	18.5	16.0	10.7	7.72
	UF179639	84.2	19.6	14.6	11.1	7.59
<i>Hemiauchenia edensis</i>						(6.1)
<i>Hemiauchenia macrocephala</i> ^b	specimens from the Irvingtonian of Nebraska (n =10)	110	34			
<i>Hemiauchenia macrocephala</i>						(5.4)
<i>Hemiauchenia blancoensis</i> ^c	IGM2338	103.2	28.8	24.0	17.0	6.07

some taxonomically significant variation (see Webb 1974; Honey et al. 1998). The estimated length of UAHMP-962 is comparable to that of UF176935 (Table 3), a complete metatarsal of *Hemiauchenia gracilis* from the Late Blancan locality of Inglis 1A, Florida (Meachen 2003, 2005). By contrast, UAHMP-962 is longer than the metatarsal of *H. edensis*, and shorter than those of *H. macrocephala* and *H. blancoensis* (Meachen 2005). The length/width ratio of UAHMP-962 is indicative of a long and slender metatarsal, pointing to a gracile individual. The metatarsals of *H. edensis* are short and slender (GL: SD, 16.0), those of *H. macrocephala* are long and slender (GL: SD, 12.2), and those of *H. blancoensis* are long and robust (GL: SD, 14.0), whereas those of *H. gracilis* are very long and slender (GL: SD, 16.7) (Meachen 2005: 455). The limb proportion of UAHMP-962 is similar to that of *H. macrocephala* and *H. blancoensis*; nevertheless, the metatarsal from Hidalgo is shorter and has a smaller diameter, indicating a less stout-legged form (Table 3).

The proximal phalanges from Hidalgo (UAHMP 954a, b) are of comparable size to those of *Hemiauchenia gracilis*, as represented by UF179638 and UF179639, two proximal phalanges from the locality of Inglis 1A, Late Blancan of Florida (Meachen 2003). By contrast, the specimens from Hidalgo are shorter than proximal phalanges assigned to *H. blancoensis* and *H. macrocephala* (Table 4). The length/width ratio of the specimens from Hidalgo is 6.0 (GL:SD), giving the phalanges a gracile appearance. This proportion is comparable to that of *H. edensis* (6.1), relatively shorter than that of *H. gracilis* (~ 7.1), and larger than that of *H. macrocephala* (5.4) (Meachen 2003, 2005).

The size and slenderness of UAHMP 419 (distal part of scapula; maximum distal width of 79.1 mm [including the coracoid process]) and UAHMP 515 (tibial fragment; maximum distal width of 56.31 mm) (Fig. 5), are suggestive of small-sized individuals with gracile extremities.

Overall, the comparison of the postcranial material from Hidalgo with selected species of *Hemiauchenia* does not seem to provide much useful taxonomic information, owing to its relatively homogenous morphology and size. Nevertheless,

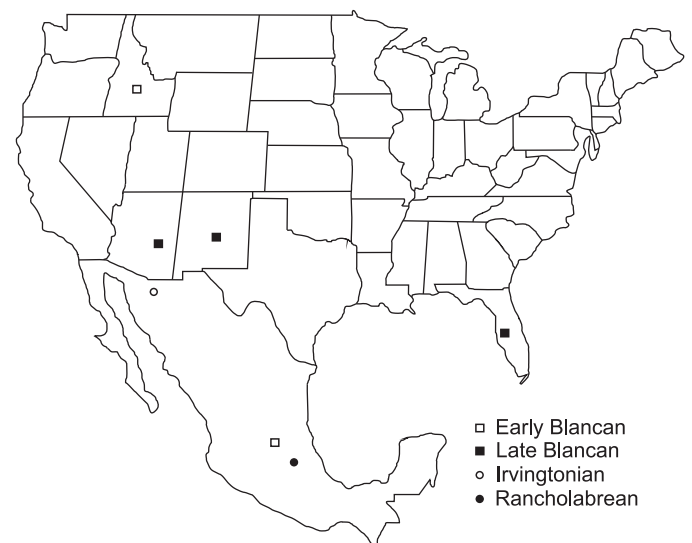


Fig. 8. North American Plio-Pleistocene localities with records of *Hemiauchenia gracilis* Meachen, 2005, including those from the Late Pleistocene (Ranchoabrean) of Hidalgo, central Mexico, described in the present study.

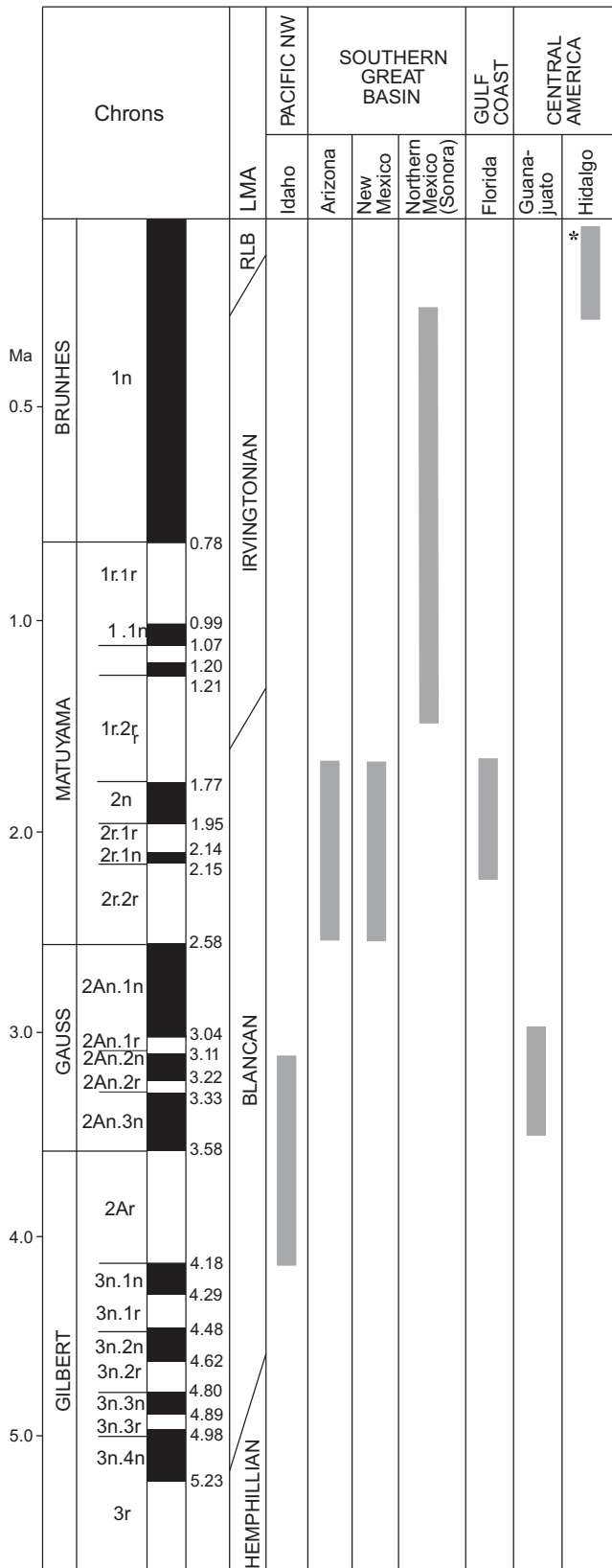


Fig. 9. Geographic distribution and geochronological range of *Hemiauchenia gracilis* Meachen, 2005 from the Plio-Pleistocene of Mexico and the USA. Biogeographic provinces after Janis (1998). LMA refers to North American Land Mammal Ages, modified from Bell et al. (2004). * present study. Abbreviations: RLB, Rancholabrean

we here consider these elements to belong to the same species, given their association with diagnostic cranial and dental material which can be confidently referred to *H. gracilis*.

Discussion

Geographic distribution.—The earliest occurrences of *Hemiauchenia gracilis* are from the Early Blancan of the Pacific Northwest (Idaho) (Ruez 2009) and central Mexico (Guanajuato) (Jiménez-Hidalgo and Carranza-Castañeda 2010), whereas in the Late Blancan (ca. 2.5 Ma) it is known from the southern Great Basin (Arizona and New Mexico) (White and Morgan 2005) and the Gulf Coast (Florida) (Meachen 2003, 2005).

By the Pleistocene, it seems that the geographic distribution of this llama had become restricted to the area of present-day Mexico, as indicated by an occurrence from the Irvingtonian of Sonora (Croxen et al. 2007; White et al. 2010) and another from the Rancholabrean of Hidalgo, described in the present study. The record of *H. gracilis* from Hidalgo extends its Pleistocene geographic distribution southwards, from northern to central Mexico, making it the southernmost within North America (Fig. 8). Both the youngest (reported here) and one of the oldest records (Guanajuato) of *H. gracilis* are known from localities in central Mexico (Jiménez-Hidalgo and Carranza-Castañeda 2010), suggesting that the species may have evolved in the southern temperate regions of North America.

Biochronology.—This study extends the Pleistocene record of *H. gracilis* from the Early Pleistocene (Irvingtonian) of northern Mexico (Sonora) to the Late Pleistocene (Rancholabrean) of central Mexico (Hidalgo). The material described here is also the youngest so far referred to this species, and extends its range from the Early Blancan to the Rancholabrean (Fig. 9).

The oldest record of South American lamines comes from the Barrancalobian subage, (Marplantan SALMA, around 3.0 Ma) (Woodburne et al. 2006). The morphological resemblance of *H. gracilis* to extant lamines may link it to the origins of South American llamas (Meachen 2005; Jiménez-Hidalgo and Carranza-Castañeda 2010). If so, *H. gracilis* would likely have migrated from Mesoamerica to South America shortly after its origins in North America at least 4 million years ago.

Paleoecology.—The population of *Hemiauchenia gracilis* from the Late Pleistocene (Rancholabrean) of Hidalgo shows a mesowear pattern marked by high occlusal relief and a sharp cusp shape in most cases (see Fig. 3E). This combination of characters is indicative of browsers (see Fortelius and Solounias 2000). Meachen (2003, 2005) proposed a mixed-feeding (including more browsing than grazing) dietary strategy for the population of *H. gracilis* from the Late Blancan of Florida, based on mesowear patterns and stable carbon isotope analysis. Here, we provide additional infor-

Table 5. Body mass estimates (in kg) for the material of *H. gracialis* from the Late Pleistocene of Hidalgo. The estimates are based on the equations of Janis (1990) using the length (a) and area (b) of the first lower molar, as well as those of Scott (1990) using the maximum length of the metatarsals (MT1) in all ungulates (c) and artiodactyls (d).

(a)	(b)	(c)	(d)	Mean value
88.51	134.58	251.18	316.22	197.62

mation regarding the feeding behavior of this small, gracile llama, which focused mainly on non-abrasive plant material.

Previous work demonstrated a marked increase in body size in Late Pleistocene specimens of *Hemiauchenia macrocephala* from Florida (Hulbert and Webb 2001). To test whether a similar trend may be evident in the closely related *H. gracilis* (Meachen 2005), we estimated the body mass of our specimens using the equations of Janis (1990), which were based on the size of ml, and Scott (1990), which were based on metatarsal length.

Although the results differed depending on which equation was used (Table 5), the estimates derived from the first lower molar area and metatarsal equations, as well as the mean estimate across all equations, are comparable to that reported by Jiménez-Hidalgo and Carranza-Castañeda (2010) for the Early Blancan material from Guanajuato (around 200 kg). It therefore appears that *H. gracilis* maintained approximately the same body mass throughout its biochronological range in central Mexico.

Conclusions

A collection of fossil camelid material from the Late Pleistocene (Rancholabrean) of Hidalgo is formally described and referred to *Hemiauchenia gracilis*. The record from Hidalgo extends the Pleistocene geographic distribution of this llama from northern to central Mexico, and represents the youngest occurrence of this species in North America.

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