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A roe deer from the Pliocene of Hidalgo, central Mexico

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Mexican Pliocene cervids are very poorly known. We report on new fossil material of the roe deer *Capreolus constantini* recovered from the Pliocene Atotonilco El Grande Formation of Santa María Amajac, Hidalgo (central Mexico). The specimens were collected from a series of layers of friable to moderately indurated polymictic conglomerate supported by a sandstone-tuffaceous-calcareous matrix. This species was formerly known only from the late Pliocene of Udunga, Russia, thus implying a dispersal event to North America around 4.0 Ma. This cervid is one of the very small number of mammals recorded from the poorly sampled Pliocene temperate deposits of Mexico.

Key words: Mammalia, Cervidae, *Capreolus*, Hidalgo, Pliocene, Mexico.

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Introduction

Cervidae are one of the most diverse families of artiodactyls (Groves 2007). Having originated in Eurasia during the Early Miocene, they had dispersed to North America by the early Pliocene (Prothero and Schoch 2002), as shown by the occurrence of *Eocoileus gentryorum* in the latest Hemphillian of Florida (Webb 2000). Yet, within the territory of Mexico, the fossil record of Pliocene cervids is exceedingly poor, and currently restricted to *?Odocoileus* from the early Blancan of Chihuahua (Lindsay 1984). Here, we expand the Mexican record by describing the fossil remains of a cervid recovered from Pliocene sediments of eastern Hidalgo, central Mexico, and comment on the biogeographical significance of this new material.

Institutional abbreviations.—GIN, Geological Institute, Ulan-Ude, Russia; INAH, Colección Osteológica del Laboratorio de Arqueozoología, Instituto Nacional de Antropología e Historia, México City, México; IPHES, Institut Català de Paleoecología Humana i Evolutio Social, Tarragona, Spain; LCBE, Laboratorio de Colecciones Biológicas, campus Puerto Escondido, Universidad del Mar (UMAR), Puerto Escondido, Mexico; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCN-UNS, Colección del Museo de Ciencias Naturales de la Provincia de Salta,

Universidad Nacional de Salta, Salta, Argentina; MLP, Colección de Mastozoología de la Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; UAHMP, Museo de Paleontología, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Pachuca, México

Other abbreviations.—L, length; W, width.

Geological setting

The fossil material was recovered from the upper part of the Atotonilco El Grande Formation, in the Santa María Amajac area, at 20°17'56.4" N and 98°46'43.2" W (Fig. 1). Previous paleontological work in its basal part indicated an early Blancan (Blancan I) North American Land Mammal Age for this part of this formation, which has yielded the remains of horses and gomphotheres (Carranza-Castañeda 2006; Bell et al. 2004). This estimate is in agreement with a radiometric ⁴⁰Ar/³⁹Ar date of 4.57 ± 0.02 Ma and a fission-track date of 4.2 ± 0.3 Ma (early Pliocene) for volcanic ash exposed at Santa Cruz de Amajac, which is at the base of this sequence (Locality HGO-12; Kowallis et al. 1998; Flynn et al. 2005).

The fossil locality exposes a sequence of thinly bedded, yellowish gray, moderately indurated clayey marls, which

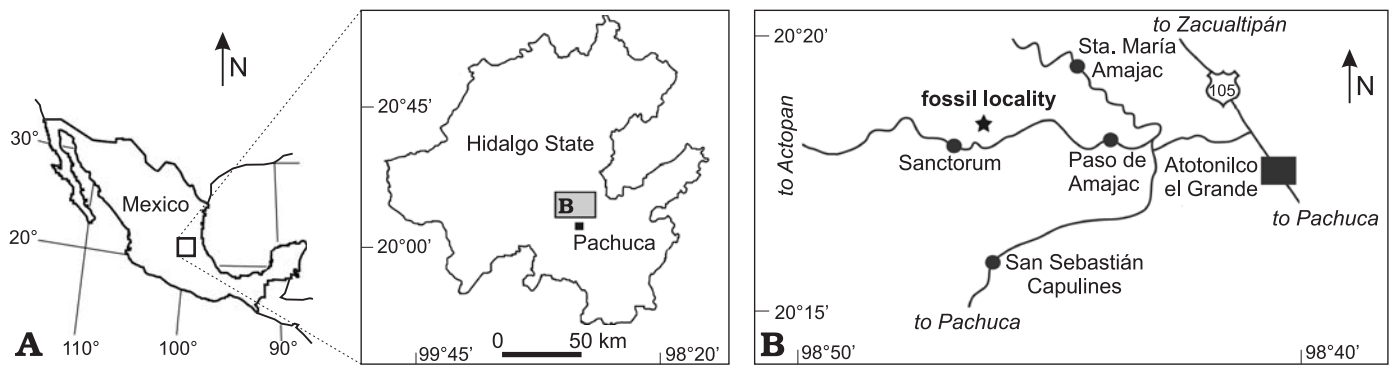


Fig. 1. Location of the studied area in the state of Hidalgo, central Mexico (A), map of the Santa María Amajac area (B).

are infrequently intercalated with diatomite (Fig. 2); both lithologies are typical of lacustrine environments (Tucker 2001). In the lower part of the section, there are two 0.5 m beds of light greenish-gray tuff. The cervid material was contained in a series of layers of friable to moderately indurated polymictic conglomerate, supported by a sandstone-tuffaceous-calcareous matrix turning laterally into a sandstone-calcareous-tuffaceous matrix. These sediments accumulated without a preferred orientation or imbrication of epiclasts in normally to inversely graded stratification cycles, indicating fast deposition events occurring near their original source, such as lacustrine deltaic environments (Tucker 2001). The fossil specimens were found without any associated fauna in a bed located ca. 60 m above the $4.2 \pm$

0.3 Ma dated tuff (Fig. 2), thus indicating a slightly younger age. We tentatively suggest the latter to be Blancan III, based on the occurrence of conspecific material in the late Pliocene (MN16, correlating with Blancan III) of Udunga, Russia (Vislobokova et al. 1995; Valli 2010).

Material and methods

The maximum length and width at the occlusal surface of the tooth were measured using calipers with 0.01 mm accuracy. The dental nomenclature is that of Bärmann and Rössner (2011), the postcranial terminology that of Webb (1965) and Schmid (1972). Postcranial measurements follow von den Driesch (1976). All measurements are in mm.

The taxonomic identity of the studied material was assessed through comparisons with a diverse array of typical American Capreolinae and Cervinae, including *Odocoileus virginianus*, *O. hemionus*, *Mazama* spp., *Pudu* spp., *Blastocerus dichotomus*, *Ozotoceros bezoarticus*, *Navahoceros fricki*, *Hippocamelus antisensis*, *H. bisulcus*, and *Cervus canadensis* (see for catalogue numbers SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app60-Jimenez-Hidalgo_Bravo-Cuevas_SOM.pdf).

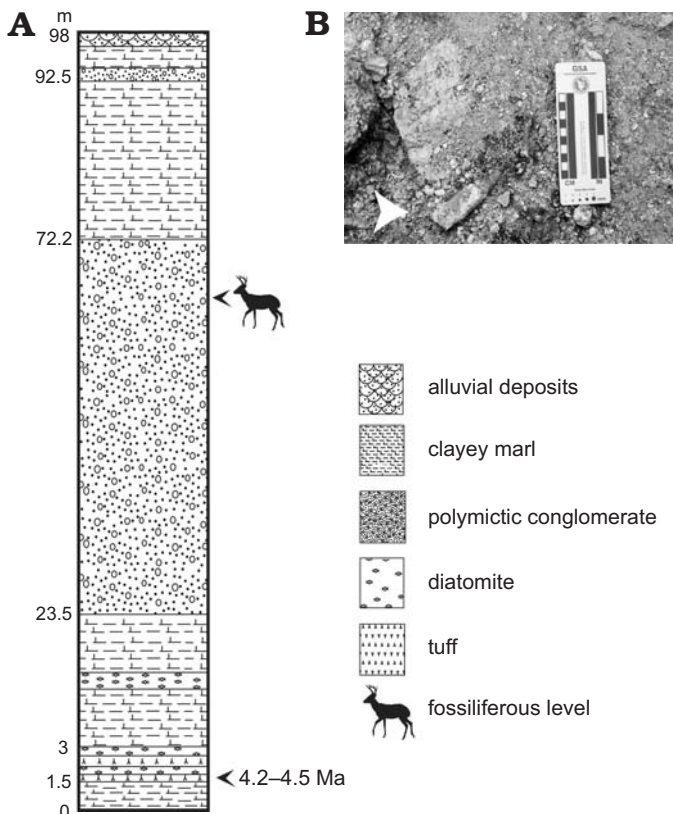


Fig. 2. A. Stratigraphic column of the fossil locality at Santa María Amajac. B. Field photograph of the UAHMP 481 (left mandible).

Systematic paleontology

Order Artiodactyla Owen, 1848

Suborder Ruminantia Scopoli, 1777

Family Cervidae Gray, 1821

Subfamily Capreolinae Brookes, 1828

Genus *Capreolus* Gray, 1821

Type species: Cervus capreolus Linnaeus, 1758; Recent, Europe.

Capreolus constantini Vislobokova, Dmitrieva, and Kalmykov, 1995

Figs. 3, 5, 6, Tables 1, 2.

Referred material.—Partial skeleton consisting of UAHMP 481, left mandible fragment with roots of p2, p3–m2 in situ,

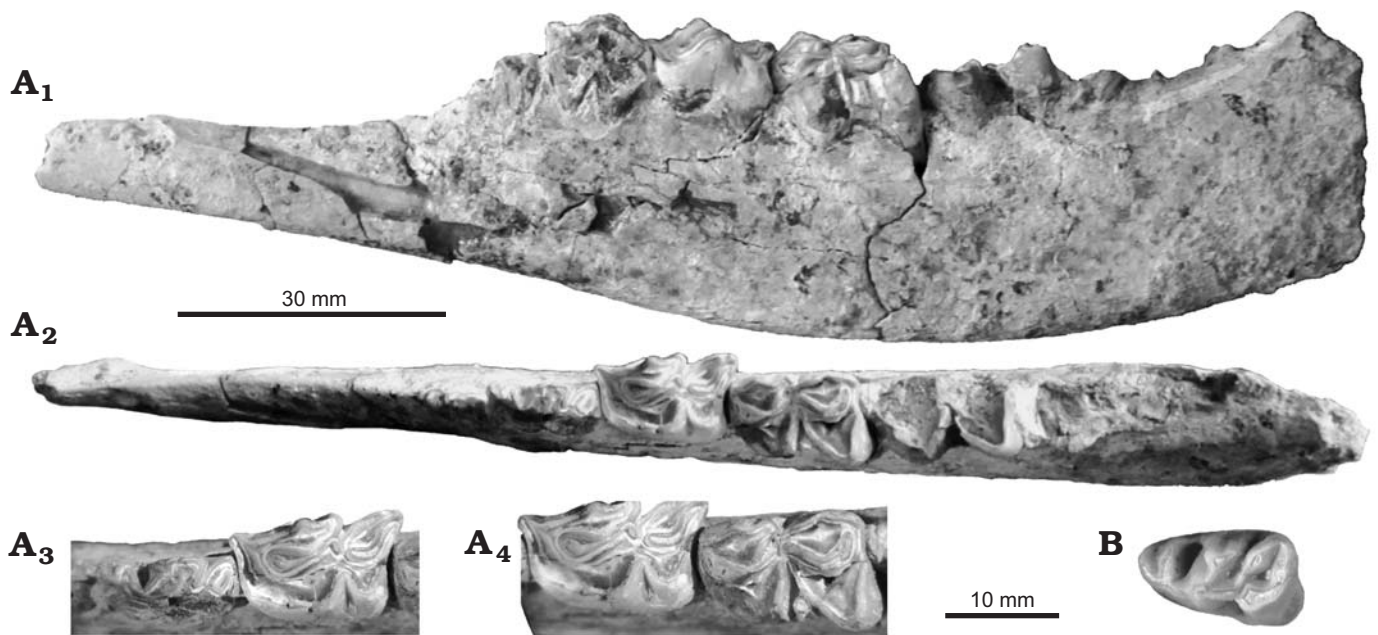


Fig. 3. Mandible and teeth of the cervid mammal *Capreolus constantini* Vislobokova, Dmitrieva, and Kalmykov, 1995 from the Pliocene of Hidalgo, Mexico. A. UAHMP 481, left mandible fragment in lateral (A₁) and occlusal (A₂) views; partial p3 and p4 in occlusal view (A₃); p4 and m1 in occlusal view (A₄). B. UAHMP 432, p3 in occlusal view.

and m3 alveolus; UAHMP 484 and UAHMP 485, humeri; UAHMP 490, olecranon process of ulna; UAHMP 486, left tibia; UAHMP 488, metacarpal; UAHMP 433, proximal fragment of metatarsal; UAHMP 487, left patella; and UAHMP 489, first right phalanx of digit IV of forelimb. UAHMP 432, p3; UAHMP 434, fragment of m3. All from Santa María Amajac, Hidalgo, Mexico; Pliocene.

Description.—The mandible is shallow dorsoventrally and little convex ventrally, but slightly increases in depth towards m3 (Fig. 3). Its depth is 21.30 mm below p2, 23.60 mm below p4–m1, and 28.70 mm posterior to m3. The diastema is long (35.0 mm), and its dorsal border is acute. The teeth are brachyodont, and combine to a total anteroposterior length (p2–m3) of 95 mm. The p2 has two roots. The p3 has a strong and narrow anterior stylid, and bears a narrow anterior conid which is separated from the mesolingual conid by a deep anterior valley (Figs. 3, 4A, B). In the slightly worn specimen UAHMP 432, the mesolingual conid has an anterolingual and a posterolingual cristid, while in the moderately worn p3 of UAHMP 481, these cristids have disappeared. The back valley is closed owing to the fusion of the posterior cristid and the posterior stylid (Figs. 3, 4A, B), which in turn is connected to the posterolabial conid via a cristid.

The p4 is molariform, and the largest of the premolars (Figs. 3, 4A). Its anterior stylid is well developed. The anterior conid is connected to the mesolingual conid via the anteriorly elongated anterolingual cristid, which closes the narrow anterior valley (Figs. 3, 4A). The posterior valley is reduced to a small notch owing to the posterior elongation of the posterolingual cristid. The anterior and posterior valleys are connected, creating an oblique, long, and narrow valley (Figs. 3, 4A). The posterior cristid and

the posterior stylid are very close, almost blocking the back valley. The mesolabial conid is separated from the posterolingual conid by a V-shaped notch. The transverse cristid is confluent with the mesolabial conid, but not with the mesolingual conid; instead, it forms a posterolingually directed projection that touches the posterolingual cristid (Figs. 3, 4A).

The mesostylid and entostylid of m1 are weakly developed, but the metastylid is well developed. The only preserved m2 is broken. On m3, the posterior fossetid and the back fossetid are united, and the entoconulid is poorly developed.

The humerus is robust (Fig. 5A) and bears a well-developed head, with the tuberosities being separated by a deep fossa. The distal trochlear surface extends somewhat into the olecranon fossa. Only the olecranon process of the ulna is preserved, and has a length of 38.06 mm and a width of 14.35 mm. The tibia is large and straight (Fig. 5B), bearing a well-developed tuberosity, U-shaped sulcus muscularis, and a prominent popliteal scar. The cnemial crest occupies about 1/3 of the total length of the preserved specimen, smoothly finishing toward its distal end. The patella has a triangular outline, with a width of 33.7 mm and an anteroposterior length of 20.11 mm.

The preserved metacarpal is robust, and shows a wide palmar sulcus, large distal foramina in the diaphysis, and a fused intertrochlear notch (Fig. 6A). The proximal fragment of the metatarsal has a squared outline, with a transverse width of 23.72 mm and a proximodistal length of 20.29 mm. The first right phalanx is straight (Fig. 6B). Its proximal articular facets are high and dorsoventrally concave, with a deep and wide sulcus. The lateral facet is dorsoventrally

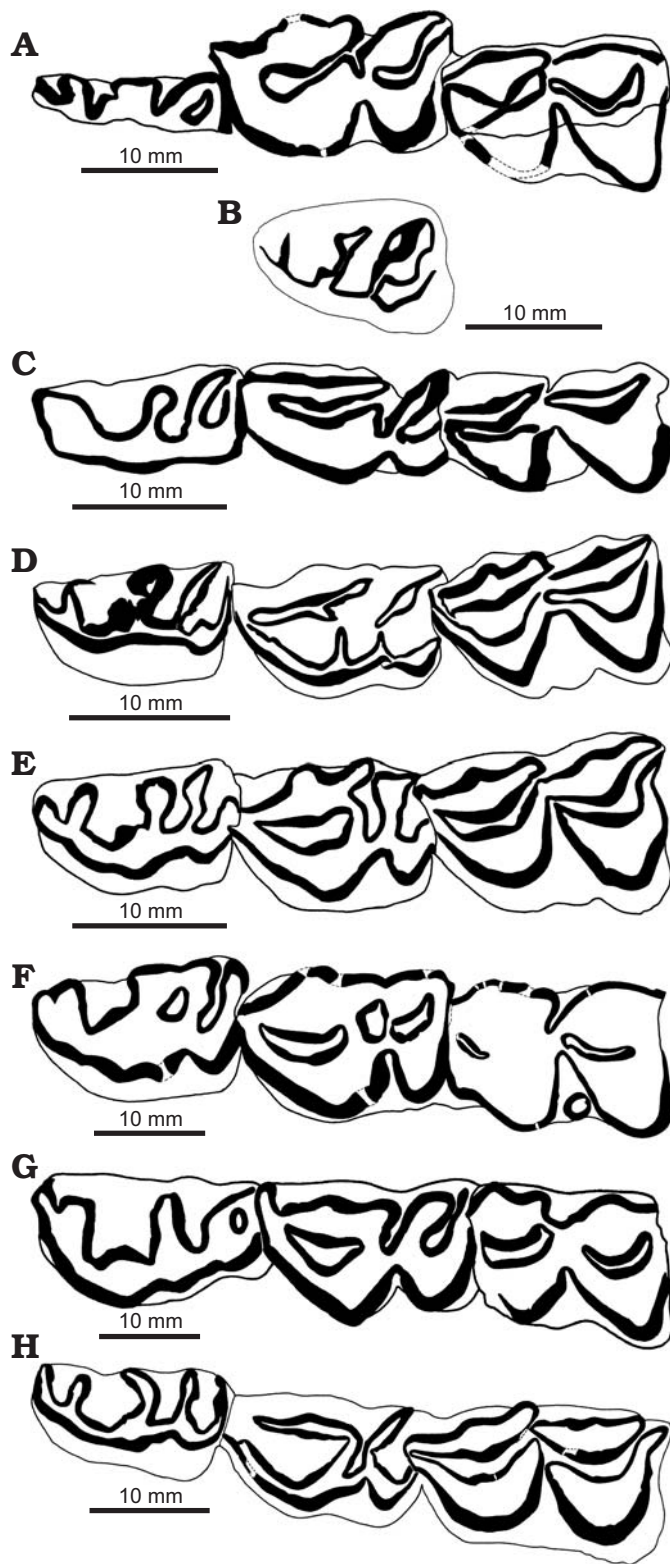


Fig. 4. Comparison of occlusal views of p3–m1 of the cervid mammal *Capreolus constantini* from the Pliocene of Hidalgo, Mexico, with selected extant cervids. **A, B.** *Capreolus constantini*. **A.** UAHMP 481. **B.** UAHMP 432, isolated p3. **C.** *Capreolus capreolus*, IPHES O-241. **D, E.** *Odocoileus virginianus*. **D.** INAH 16897, slightly worn. **E.** INAH 663, moderately worn. **F.** *Navahoceros fricki*, INAH 1082 (reversed), heavily worn. **G.** *Cervus canadensis*, INAH 1227 (reversed), moderately worn. **H.** *Hippocamelus bisulcus*, MLP 1364 (reversed), slightly worn.

shorter than the medial one, indicating that the phalanx likely belonged to digit IV (Morejohn and Dailey 2004). The distal articular surface is relatively wide. The phalanx has a proximodistal length of 43.12 mm, and a transverse width of 16.38 mm and 13.27 mm across the proximal articular surface and the distal trochlea, respectively.

Geographic and stratigraphic range.—Late Pliocene (MN16) of Udunga, Western Trans-Vaikal, Russia; and Pliocene (Blancan ?III) of Santa María Amajac, Hidalgo, Mexico.

Discussion

Taxonomic assessment.—Detailed morphological comparisons between the fossil specimens from Amajac, Hidalgo and a variety of cervids reveal that the present material considerably differs from extant American cervids (Fig. 4; see SOM for detailed comparisons), but closely resembles Eurasian *Capreolus*. Shared characters include a p3 with an anterior styloid, a deep, V-shaped anterior valley, a narrow and oblique posterior valley, and an oblique and almost closed back valley (Figs. 3, 4A–C); a molarized and bilobed p4 with connected anterior and posterior valleys, a narrow and oblique back valley, a narrow and nearly absent posterior valley, and a transverse cristid that does not fuse with the mesolingual conid, but instead forms a posterolingually directed projection almost reaching the posterolingual cristid (Figs. 3, 4A–C; see also Janis and Lister 1985); a cnemial crest that gently finishes towards its distal end, and a prominent popliteal scar on the tibia; metacarpals with a fused distal notch; and a robust phalanx with a well-developed distal trochlea (Figs. 5, 6; see SOM for detailed comparisons).

Within *Capreolus*, the material from Hidalgo differs from *Capreolus capreolus* in having a p4 that is larger than p3, as well as in having somewhat larger teeth overall. It further differs from *C. pygargus* in having a strong anterior styloid on p3,

Table 1. Measurements (in mm) of the teeth of *Capreolus constantini* from the Pliocene of Santa María Amajac, Hidalgo (central Mexico) and Udunga (Russia). Data for Udunga specimens were taken from Vislobokova et al. (1995). Abbreviations: e, estimated; L, length; W, width.

Tooth		Udunga specimens	UAHMP 481	UAHMP 432	UAHMP 434
p2	L	9.00–9.50	7.37e		
	W	5.00–6.30	–		
p3	L	11.40–12.40	12.27	13.90	
	W	6.70–7.60	–	7.22	
p4	L	12.30–13.90	15.80		
	W	8.30–9.30	8.46		
m1	L	11.80–13.60	14.56		
	W	8.60–9.00	10.51		
m2	L	13.00–14.60	14.50		
	W	9.70–10.40	9.77		
m3	L	18.60–21.00	20.00e		
	W	10.00–10.70	9.42e		10.19

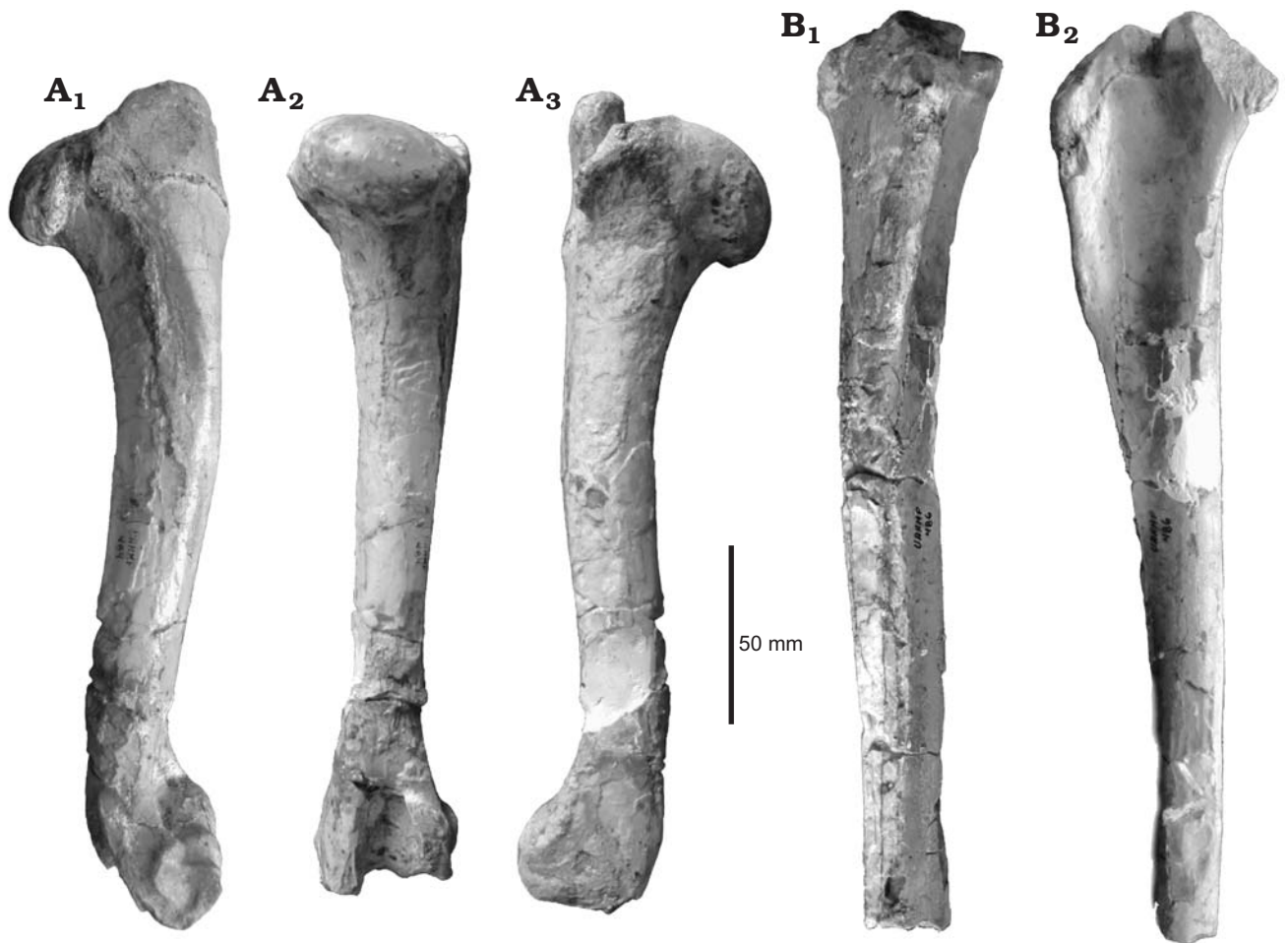


Fig. 5. Humerus and tibia of the cervid mammal *Capreolus constantini* Vislobokova, Dmitrieva, and Kalmykov, 1995 from the Pliocene of Hidalgo, Mexico. **A.** UAHMP 432, right humerus, in lateral (A₁), anterior (A₂), and medial (A₃) views. **B.** UAHMP 436, left tibia, in anterior (B₁) and lateral (B₂) views.

as well as less molarized premolars. However, the new specimens are close in both morphology and size to *C. constantini* (Tables 1, 2) from Russia, and share with it the following features: a narrow anterior conid, a strong and narrow anterior stylid, a wide anterior valley, and a closed back valley on p₃; a distinctly molarized p₄ that is the largest premolar, and is

characterized by a deep, V-shaped notch between the mesolabial and the posterolabial conid, as well as an anterior conid connecting with the mesolingual conid via the anterolingual cristid, a closed back valley owing to the fusion of the posterior cristid and the posterolingual stylid, and an anterior lobe almost twice the length of the second lobe; and an m₁ bearing

Table 2. Postcranial measurements (in mm) of *Capreolus constantini* from Hidalgo, Mexico (UAHMP specimens) and *C. constantini* and *C. pygargus* from Udunga, Russia (after Vislobokova et al. 1995). DTdi, distal transverse diameter; DAPdi, distal anteroposterior diameter; DTpr, proximal transverse diameter; DAPpr, proximal anteroposterior diameter; GL, greatest length; Hw, head width; BP, greatest width of the proximal end; SD, smallest diameter.

Bone	Specimen/taxon	DTdi	DAPdi	DTpr	DAPpr	GL	Hw	BP	SD
Humerus	UAHMP 484	40.52	38.23			240.00	52.00		
	UAHMP 485		39.00			242.00	51.50		
	<i>Capreolus constantini</i>	31.00–33.20	31.40						
	<i>Capreolus pygargus</i>	32.00	31.00						
Metacarpals	UAHMP 488	29.60	18.17						
	<i>Capreolus constantini</i>	17.40	19.00						
	<i>Capreolus pygargus</i>	24.60	16.00						
Metatarsals	UAHMP 433			23.36	19.57				
	<i>Capreolus constantini</i>			23.80–25.00	25.20–26.20				
	<i>Capreolus pygargus</i>			22.05	23.20				
Tibia	UAHMP 486					275.00		59.50	24.70

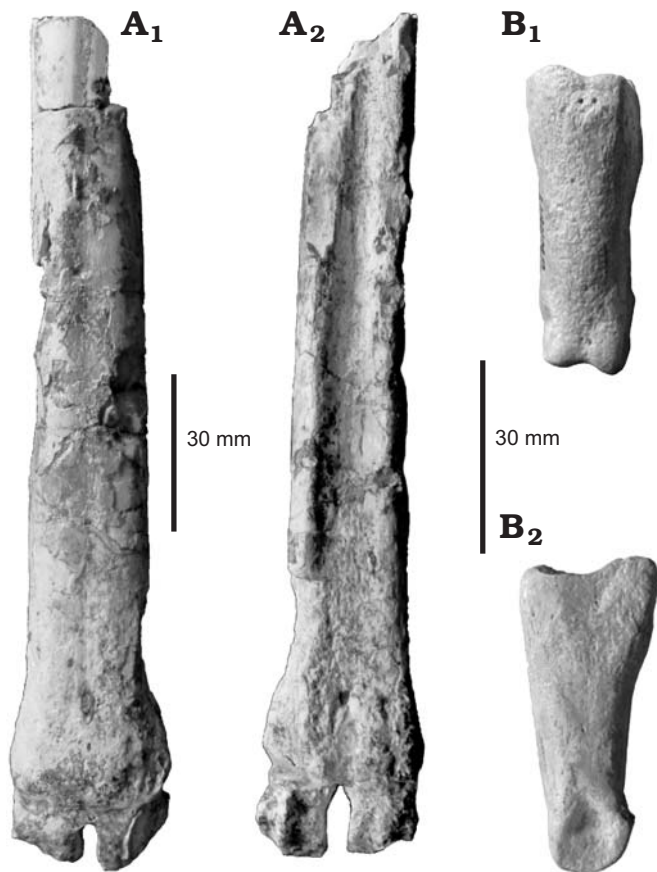


Fig. 6. Metacarpal and first phalanx of the cervid mammal *Capreolus constantini* Vislobokova, Dmitrieva, and Kalmykov, 1995 from the Pliocene of Hidalgo, Mexico. **A.** UAHMP 488, metacarpal, in anterior (A₁) and posterior (A₂) views. **B.** UAHMP 489, first phalanx, in anterior (B₁) and medial (B₂) views.

an obliquely oriented metaconid, as well as an anterior crescent that is smaller than the posterior one, with both having a sharply triangular appearance (Figs. 3, 4A; Vislobokova et al. 1995: fig. 2).

The mandible of both the Russian and Mexican specimens is low and slightly increases in height posteriorly (Fig. 3). The ratio of p2–p4/m1–m3 of UAHMP 481 (0.728) falls within the reported range of *Capreolus constantini* (0.725–0.746; Vislobokova et al. 1995). Some dental and postcranial measurements of the material from Hidalgo are slightly larger than those of Russian specimens (Tables 1, 2). However, such subtle differences can be explained by taking into account different stages of dental wear, sexual dimorphism, and geographic variation, as demonstrated, for example, by a reported body mass variation of around 30 % within *Capreolus pygargus* (Danilkin 1995).

Neogene dispersals to North America and the arrival of *Capreolus* in Mexico.—During the Miocene and Pliocene, several dispersal events occurred between Eurasia and North America (e.g., Tedford and Harrington 2003; Wallace and Wang 2004; Mead and Taylor 2005). Numerous allochthonous, both herbivorous and carnivorous, mammals recorded

in the North American local faunas define the Hemphillian and Blancan North American Mammal Ages, as well as their subdivisions (Tedford et al. 2004; Bell et al. 2004). The oldest New World cervids are the late Hemphillian rangiferines *Eocoileus* and *Bretzia*, followed by *Odocoileus* and *Navahoceros* from the early Blancan or Blancan III (Webb 2000), and *Rangifer* from the early Pleistocene (Webb 2000). These observations imply at least one cervid immigration event to North America with subsequent diversification during the Pliocene (*Eocoileus*, *Bretzia*, *Odocoileus*, *Navahoceros*), and a further one (*Rangifer*) during the Pleistocene.

The Old World genus *Capreolus* includes the extant species *Capreolus pygargus* from Eastern Europe and Asia (Danilkin 1995) and *C. capreolus* from Europe and Asia Minor (Sempéré et al. 1996). Its oldest representative, *C. constantini*, is only known from the late Pliocene (MN16) of Udunga, Russia (Vislobokova et al. 1995; Valli 2010). Additional records of *Capreolus* sp. are also known from Moldavia (ca. 3.0 Ma; Lister et al. 1998), western Siberia (2.2–1.8 Ma; Valli 2010), and Slovakia (MN16, early Villafranchian; Valli 2010). The presence of *Capreolus* in the Pliocene of central Mexico thus hints at a previously unknown dispersal event of this genus into North America, additionally to the already known dispersal of Rangiferini. The occurrence of *Capreolus constantini* in the MN16 zone of Russia indicates that this dispersal likely occurred during the early Blancan or Blancan III, around 4.0 Ma, prior to the reopening of the Bering Strait in the late Pliocene (3.5–4.0 Ma) (Zhanxiang 2003). This agrees with molecular clock estimates dating the divergence of *Capreolus* and *Hydropotes* to about 4.2 Ma (Pitra et al. 2004: fig. 3).

Reconstructions based on floral assemblages from the Pliocene Santa María Amajac area indicate the presence of mesothermal woodland within a temperate humid climate, characterised by a mean annual temperature of 12–22°C (Velasco de León et al. 2010). These conditions match the habitat type of Quaternary and extant representatives of *Capreolus*, which includes cold to temperate forests and steppes (Danilkin 1995; Sempéré et al. 1996; Sommer et al. 2009). The material from Hidalgo thus represents one of a very small number of mammals recorded from the poorly sampled Pliocene temperate deposits of Mexico. It is noteworthy that *C. constantini* has not been recorded in coeval local faunas located in the United States or Canada. This may be related to the types of habitat available in those areas, which seem to have been mostly warm and savannah-like (Bell et al. 2004; Woodburne 2010), and therefore not suitable for this cervid.

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