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First occurrence of *Panthera atrox* (Felidae, Pantherinae) in the Mexican state of Hidalgo and a review of the record of felids from the Pleistocene of Mexico

Victor Manuel Bravo-Cuevas[1], Jaime Priego-Vargas[2], Miguel Ángel Cabral-Perdomo[1], and Marco Antonio Pineda Maldonado[3]

[1]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, Mexico
[2]Área Académica de Biología, Doctorado en Biodiversidad y Conservación, Universidad Autónoma del Estado de Hidalgo, Ciudad del Conocimiento, Carretera Pachuca-Tulancingo km 4.5, CP 42184, Pachuca, Hidalgo, Mexico
[3]Área Académica de Biología, Maestría en Biodiversidad y Conservación, Universidad Autónoma del Estado de Hidalgo, Ciudad del Conocimiento, Carretera Pachuca-Tulancingo km 4.5, CP 42184, Pachuca, Hidalgo, Mexico

Correspondence to: Victor Manuel Bravo-Cuevas (vmbc1@yahoo.com)

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Abstract. *Panthera atrox* was a common large-sized cat in North America during the late Pleistocene. An isolated lower canine and a fifth metacarpal bone referable to this species were recovered from fluvial Quaternary deposits that outcrop in southeastern Hidalgo, central Mexico. Associated fossil material belonging to *Bison* indicates a Rancholabrean North American Land Mammal Age; the age assignment is corroborated by the presence of *P. atrox*. A comparative study with selected specimens of *Panthera* and *Smilodon* indicates that the Hidalgoan sample shares the following diagnostic features with *P. atrox*: a large, robust, and non-strongly curved lower canine; a large and relatively slender fifth metacarpal with a well-developed projection on the palmar side at the proximal end, narrow articulating surface for the unciform; a narrow notch on the articulating surface for the fourth metacarpal; and a diaphysis that at the middle is oval in cross section. The record supplements the evidence of *P. atrox* in central Mexico and represents the first reported occurrence of this cat species in the state of Hidalgo. By the same token, the known geographic distribution of *P. atrox* in the Mexican territory suggests that it was relatively common in temperate areas of central Mexico between 19 and 24° N at an altitudinal range from 1500 to 2250 m a.s.l. The large size (mean body mass of 300 kg) and hypercarnivorous adaptations of the American lion suggest it was the top predator of the mammalian community recorded at southeastern Hidalgo, displacing other members of the carnivore guild at the mesopredator level, such as the dire wolf (*Canis dirus*), which has been also reported in the area. The high diversity of large herbivores recorded at southeastern Hidalgo, which in turn could represent potential prey of *P. atrox*, suggests that some areas that now are part of central Mexico were suitable hunting sites for this large-sized cat.

A review of the Pleistocene record of Felidae from Mexico revealed that it encompasses 87.5 and 73.3 % of generic and specific diversity known for North America, respectively, including seven genera (*Felis*, *Miracinonyx*, *Panthera*, *Puma*, *Lynx*, *Leopardus*, and *Smilodon*) and 11 species (*Felis rexroadensis*, *Miracinonyx inexpectatus*, *Panthera atrox*, *Panthera onca*, *Puma concolor*, *Puma yagouaroundi*, *Lynx rufus*, *Leopardus pardalis*, *Leopardus wiedii*, *Smilodon fatalis*, and *Smilodon gracilis*). The majority of these taxa have been reported from numerous late Pleistocene localities; in particular, *Panthera atrox* was relatively common and widely distributed across the Mexican territory.

1 Introduction

The subfamily Pantherinae is a group of large-sized cats that originated in Asia (probably in some part of what is now China) during the end of the Miocene and at the beginning of the Pliocene (10.8–3.8 Ma) (Johnson et al., 2006; Davis et al.,

2010; Tseng et al., 2016). This group of felids includes six extant species in the genera *Panthera* (*P. leo* (African lion), *P. tigris* (tiger), *P. onca* (jaguar), and *P. pardus* (leopard)), *Uncia* (*U. uncia* (snow leopard)), and *Neofelis* (*N. nebulosa* (clouded leopard)) (Davis et al., 2010; King and Wallace, 2014); all of these species are considered to be vulnerable, endangered, and/or threatened (IUCN, 2015). Extinct pantherines include the Pleistocene species *P. gombaszoegensis* (eastern Africa), *P. fossilis* (Eurasia), *P. youngi* (northeastern China), *P. spelaea* (Eurasia and Alaska), and *P. atrox* (North America) (Kurtén and Anderson, 1980; Lange, 2002; Kurtén, 2009; Tseng et al., 2016). The oldest known pantherines are those referable to *P. blytheae* from the late Miocene–early Pliocene of the Himalayan region (Tseng et al., 2016) and *P. palaeosinensis* from the Plio-Pleistocene of China (Mazák, 2010).

The late Pleistocene species *P. atrox* was a common large-sized cat in the North American subcontinent, which has been traditionally referred to as the American lion (Kurtén and Anderson, 1980). Ancestors of the American lion apparently crossed from Asia to Alaska sometime during the Illinoian glacial stage (191 000 to 130 000 years ago) (Lange, 2002) at the beginning of the Rancholabrean North American Land Mammal Age (NALMA). Early representatives of *P. atrox* appeared during the Sangamonian interglacial stage, reaching areas of southern temperate North America in a relatively short time (ca. 125 000 years ago) (Kurtén and Anderson, 1980; Lange, 2002). In the Wisconsinan (75 000–10 000 years ago) at the end of the Rancholabrean NALMA, *P. atrox* spread across the United States and Mexico (Kurtén and Anderson, 1980), and its southernmost occurrence has been recorded in tropical areas of the Mexican territory (Montellano-Ballesteros and Carbot-Chanona, 2009; Carbot-Chanona and Gómez-Pérez, 2014).

The phylogenetic status of *Panthera atrox* is controversial, given that some authors have considered it to have been closely related to jaguars (Simpson, 1941; Christiansen and Harris, 2009) and others that it was a subspecies of the extant lion (Kurtén and Anderson, 1980). Recent studies on the phylogenetic relationship of *P. atrox* with other members of the genus *Panthera* indicate that it should be considered as a separate species closely related to lions (*P. leo*) and tigers (*P. tigris*) (Barnett et al., 2009; Christiansen and Harris, 2009; King and Wallace, 2014).

Information regarding the fossil material, description, and formal taxonomic characterization of Mexican specimens referable to *P. atrox* is unknown in many instances. Hence, the purpose of this study is to formally describe the dental and postcranial material belonging to *Panthera atrox* from the late Pleistocene of southeastern Hidalgo, central Mexico, as well as to discuss some ecological and geographic aspects of the record. Furthermore, a review of the record of felids from the Pleistocene of Mexico is provided.

2 Study area

The material considered here has been recovered from a locality formally known as El Barrio (HGO-47: 20°07′41″ N, 98°56′02.7″ W) in the southeastern region of Hidalgo, central Mexico (Fig. 1a). In this region Tertiary to Quaternary volcanic and volcano sedimentary rock units crop out (INEGI, 1992). The fossil-bearing strata consist of heterogeneous clastic material, including clay, silt, sand, and scarce conglomeratic lenses, setting in a fluvial depositional environment (Fig. 1b).

The associated mammalian fauna includes dire wolves (*Canis dirus*), giant armadillos (*Glyptotherium floridanum*), giant ground sloths (*Paramylodon* cf. *harlani*), llamas (*Hemiauchenia gracilis* and *Camelops* sp.), horses (*Equus conversidens*), pronghorns (*Stockoceros conklingi* and *Capromeryx minor*), deer (*Odocoileus* cf. *virginianus*), bison (*Bison* sp.), gomphotheres (*Cuvieronius* sp.), and mammoths (*Mammuthus* sp.) (Bravo-Cuevas, 2001, 2002; Bravo-Cuevas et al., 2009, 2011, 2012, 2013). There is evidence of material belonging to the genus *Bison*, including a horn core fragment and an isolated tooth; the presence of this taxon is indicative of a Rancholabrean NALMA (Bell et al., 2004). The biochronological age of the fossil assemblage is supported by the presence of material belonging to *Panthera atrox* (present study).

3 Materials and methods

The sample consists of an isolated canine and a metacarpal bone. The material is housed at the Sección de Macrovertebrados, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo, México, with the catalogue numbers UAHMP-4221 and UAHMP-4222, respectively.

The anteroposterior and transverse diameters of the isolated tooth were measured. The measurements of the metacarpal are those of Merriam and Stock (1932: table 62, p. 134). Measurements in millimeters were taken using 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 order to assess the taxonomic identity of the dental and postcranial remains from Hidalgo, we performed a comparative study with selected specimens of *Panthera atrox* housed at the George C. Page Museum, La Brea Discoveries, Museum of Natural History of Los Angeles County (LACM), California, USA. Additional comparisons were done with specimens belonging to the extant species *P. leo* (OCMP-080) and *P. tigris* (OCMP-077) housed at the Osteological Collection of the Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo. Furthermore, the Hidalgoan material was compared with specimens described and figured in Merriam and Stock (1932), Whitmore and Foster (1967), and Montellano-Ballesteros and Carbot-Chanona (2009).

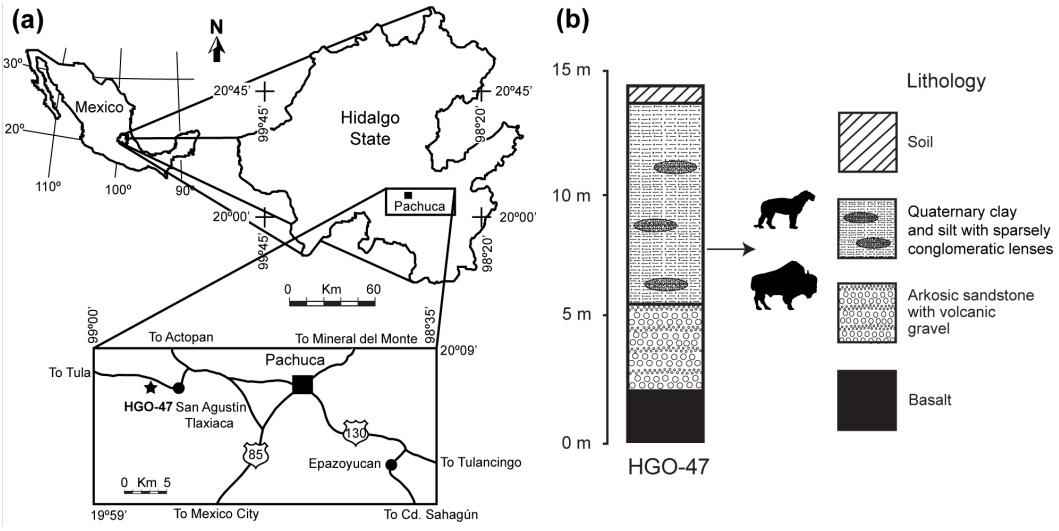

Figure 1. (a) Index map showing the study area in southeastern Hidalgo, central Mexico; the capital of the state (Pachuca) and the late Pleistocene locality El Barrio (HGO-47) are depicted. **(b)** Stratigraphic section of the El Barrio locality (HGO-47); the arrow indicates the fossil-bearing level.

In order to review the Pleistocene record of Felidae from Mexico, we performed a bibliographic search in primary sources (journal articles, books, and book chapters), secondary sources (abstracts, catalogs, and theses), and databases (The Paleobiology Database (https://paleobiodb.org) and the Mexican Quaternary Mammals Database; Arroyo-Cabrales et al., 2005). The collected data were arranged in terms of its generic and specific diversity, representing the basis of a distribution map of the known (so far) Pleistocene felids from the Mexican territory.

4 Systematic paleontology

- Order Carnivora Bowdich, 1821
- Family Felidae Fischer, 1817
- Subfamily Pantherinae Pockock, 1917
- Genus *Panthera* Oken, 1816
- *Panthera atrox* Leidy, 1853

Referred material. El Barrio locality: UAHMP-4221, left lower canine; UAHMP-4222, left fifth metacarpal.

Distribution and age. The American lion was widely distributed across North America from Alaska (Whitmore and Foster, 1967) to southern Mexico (Montellano-Ballesteros and Carbot-Chanona, 2009; Carbot-Chanona and Gómez-Pérez, 2014); some records from Alaska and western Canada maybe represent members that are more closely related to the cave lion (*P. spelaea*) (Barnett et al., 2009). It is a taxon limited to the Rancholabrean NALMA (Kurten and Anderson, 1980; Lange, 2002).

4.1 Description

The canine UAHMP-4221 is large and robust (Table 1). A thin layer of enamel (< 1 mm thick) covers the first third of the tooth. The tip has broken anterolaterally after death (given that it does not show wear) and is subacute in shape. The specimen is moderately curved, and in cross section it is oval to oval-elongate toward to the base. The lateral surface of the tooth is slightly convex, whereas the medial surface is flattened (Fig. 2).

The metacarpal UAHMP-4222 is slender and long, showing a relatively gracile appearance (Table 2, Fig. 3). The shaft is oval in cross section and without sharply defined borders between the dorsal and palmar surfaces. At the proximal end, the articular surface for the unciform is narrow. The medial face presents the articular surface for metacarpal IV, formed by a large projection ("ear-shaped projection" of Merriam and Stock, 1932) and a narrow notch placed on the palmar side. The lateral surface presents a convex tuberosity. At the distal end, the lateral tuberosity is more prominent than the medial tuberosity. The distal articulation surface is situated at a 10° angle from the axis of the shaft and a prominent palmar keel is apparent.

4.2 Taxonomic assessment

The deciduous lower canine of felids is distinguished by having an accessory cusp situated on the anterolingual side of the tooth (Salles, 1992). The specimen UAHMP-4221 does not show this condition, indicating that it is a permanent tooth; furthermore, it resembles the lower canine of pantherines in the absence of a lingual cavity (a widespread condition among felids), and differs from an upper canine in the ab-

Table 1. Comparison of measurements (in mm) in UAHMP-4221 and lower canine specimens of *Panthera atrox* (a–d) and the extant species *P. tigris* (e) and *P. leo* (f). Rancholabrean localities: (a) El Barrio, southeastern Hidalgo, central Mexico (present study); (b) Lost Chicken Creek, Alaska, United States (Whitmore and Foster, 1967: table 1, p. 250); (c) Rancho La Brea, California, United States (Merriam and Stock, 1932: table 94, p. 177); and (d) La Tejería, Chiapas, southern Mexico (Montellano-Ballesteros and Carbot-Chanona, 2009: table 1, p. 219). Abbreviations: AD, anteroposterior diameter; TD, transverse diameter.

	(a) UAHMP-4221 Left	(b) USNM-23619 Right	(c) Rancho La Brea (N= 11)	(d) IHNFG-2678 Right	(e) OCMP-077 Left	(f) OCMP-080 Right/left
AD	30.1	30.0	21.8–30.4	21.9	20.8	21.0/20.7
TD	21.6	21.5	15.1–21.6	15.6	14.2	13.9/13.7

Table 2. Comparison of measurements (in mm) between UAHMP-4222 and fifth metacarpal specimens of *Panthera atrox* from Rancho La Brea (RLB), late Pleistocene of California, United States (Merriam and Stock, 1932: table 62, p. 134). The observed range in the specimens from Rancho La Brea is in parentheses.

	UAHMP-4222 Left	RLB Right	RLB Left
Greatest length	105.9	$x = 105$ (90.6–115.3)	$x = 106.6$ (91.7–113.0)
Greatest transverse diameter of proximal end	28.4	28.7 (25.1–27.7)	$x = 27.8$ (24.9–30.0)
Greatest dorsoventral diameter of proximal end	26.8	$x = 31.3$ (27.0–30.8)	$x = 29.8$ (27.3–33.2)
Transverse diameter at middle of shaft	17.0	$x = 17.0$ (14.2–15.8)	$x = 16.3$ (14.2–17.6)
Dorsoventral diameter at middle of shaft	13.9	$x = 15.0$ (13.2–15.2)	$x = 14.1$ (12.2–15.8)
Greatest transverse diameter at distal end of shaft	23.5	$x = 24.9$ (21.2–25.2)	$x = 24.8$ (22.2–25.2)

sence of a lingual ridge (Salles, 1992) and in being more robust. By contrast, the lower canine of *Smilodon* is smaller and slender, strongly curved, and shows a median lateral ridge (Merriam and Stock, 1932).

The size of the tooth is comparable to that observed for lower canines belonging to *Panthera atrox*, including USNM 23619 (right lower jaw with c, p3–m1) from Lost Chicken Creek, Rancholabrean of Fairbanks, Alaska; it falls in the upper limit of the observed range in specimens from Rancho La Brea, California, United States; and it is nearly 25 % larger than the specimen IHNFG-2678 (isolated lower canine) from Chiapas, southern Mexico (Table 1). The difference in size between the specimens from Hidalgo and Chiapas could be explained by intraspecific variation (related to age and/or sex), considering that UAHMP-4221 shows dimensions comparable to the larger lower canines from Rancho La Brea, whereas the dimensions of IHNFG-2678 correspond to those of the smaller ones (Table 1). It should be stated that the specimen UAHMP-4221 is significantly larger (ca. 33 %) than lower canines of *Panthera leo* and *P. tigris*; however, the size of this tooth between those extant species is similar (Table 1).

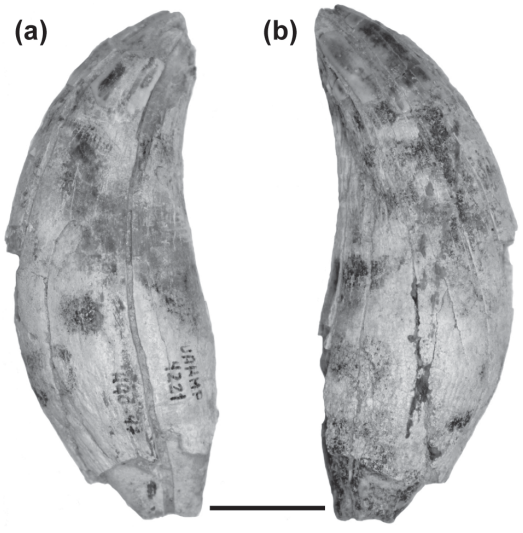

Figure 2. Isolated left lower canine (UAHMP-4221) of *Panthera atrox* from the late Pleistocene of southeastern Hidalgo, central Mexico. **(a)** Labial and **(b)** lingual views. Scale bar equals 2 cm.

Figure 3. Left fifth metacarpal (UAHMP-4222) of *Panthera atrox* from the late Pleistocene of southeastern Hidalgo, central Mexico. **(a)** Ventral, **(b)** dorsal, **(c)** medial, **(d)** lateral, **(e)** proximal, and **(f)** distal views. Scale bar equals 2 cm.

Among felids, the morphology of the limb elements is somewhat homogeneous, including the metacarpals. In general, the metacarpal bones of felids are characterized by being short and robust with a broad and curved diaphysis as well as broad proximal and narrow distal ends (Morales-Mejía and Arroyo-Cabrales, 2012). All these features are observed in the specimen UAHMP-4222, indicating its felid condition. In particular, the fifth metacarpal from Hidalgo resembles those of *Panthera atrox* in the following characters: (1) well-developed projection on the palmar side at the proximal end; (2) the articulating surface for the unciform is narrow; (3) the diaphysis is relatively slender; (4) the notch on the articulating surface for the fourth metacarpal is narrow; and (5) the diaphysis at the middle is oval in cross section (Merriam and Stock, 1932). Furthermore, the size of UAHMP-4222 (greatest length = 105.9 mm) is within the observed range of fifth metacarpals of *P. atrox* from Rancho La Brea, California, United States (Table 2); however, it is about 25 % larger than the fifth metacarpal of OCMP-077 belonging to *P. tigris* (greatest length = 80.3 mm). It should be noted that the fifth metacarpal of *Smilodon* is distinguished in having a poorly developed projection on the palmar side at the proximal end, a broad articulating surface for the unciform, and a relatively stout diaphysis (Merriam and Stock, 1932).

The comparative study indicates that the size and morphology of dental and postcranial remains from Hidalgo are closely comparable to those observed in specimens belonging to *Panthera atrox*. Hence, the studied sample is formally assigned to that large-sized cat species.

5 Paleobiological significance

5.1 Paleoecology

The American lion was one of the largest cats that inhabited North America during the late Pleistocene (Kurtén and Anderson, 1980; Lange, 2002). Body size estimations indicate that this felid had a mean body mass of 300 kg, ranging from 200 to 400 kg (Van Valkenburgh et al., 2016). It has been observed that prey body size tends to increase with the predator size (Sinclair et al., 2003). Therefore, it should be expected that large mammalian herbivores were common prey of *Panthera atrox*. Van Valkenburgh et al. (2016: fig. 2, p. 865) predicted a typical prey size ranging from 60 to 900 kg for the American lion, and the maximum prey size could have been about 1000 kg.

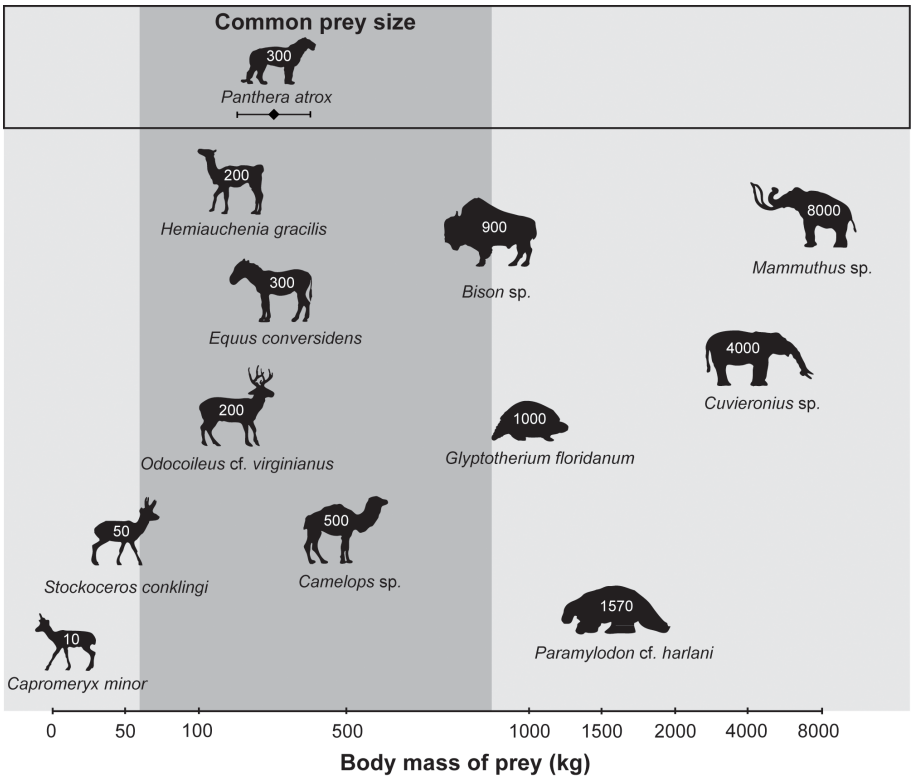

Figure 4. Potential common prey-size range for *Panthera atrox* from the late Pleistocene of southeastern Hidalgo, including the herbivores that have been reported at the El Barrio locality (HGO-47). Diamond and line indicate the mean and observed range of body mass (from Van Valkenburgh et al., 2016).

Given the above and considering the taxonomic mammalian composition known at the El Barrio locality, it seems that potential prey for *Panthera atrox* in that site could include adult individuals of llamas (*Hemiauchenia gracilis* and *Camelops* sp.), deer (*Odocoileus* cf. *virginianus*), horses (*Equus conversidens*), and even bison (*Bison* sp.); the body mass among these herbivores is estimated to have been 200 to 900 kg (Fig. 4). Hunting in groups increases the upper range of available prey size; consequently, it has been suggested that large-sized Pleistocene cats (such as *Panthera atrox*) were able to kill prey with a body mass of about 6000 kg (Van Valkenburgh et al., 2016). Assuming a hunting group behavior and potential presence of other individuals belonging to *Panthera atrox* at southeastern Hidalgo during the late Pleistocene, it is also probable that adult individuals of glyptodonts (*Glyptotherium floridanum*) and ground sloths (*Paramylodon* cf. *harlani*), as well as young and/or subadult individuals of proboscideans (*Cuvieronius* sp. and *Mammuthus* sp.), could represent other, perhaps occasional prey.

The American lion was the second largest carnivore in the late Pleistocene ecosystems of North America, exceeded by only the short-faced bear *Arctodus simus* (Kurtén and Anderson, 1980). The large size and restricted dietary behavior of *Panthera atrox* (a carnivore that feeds mostly on meat, i.e., a hypercarnivore) suggest that this extinct cat occupied the top of the trophic chain, considering that both conditions are typical of extant top predators (Ritchie and Johnson, 2009). At the El Barrio locality, it is probable that the individual of *P. atrox* described here had the ecological role of the top predator, displacing other carnivores of small to medium size, such as the dire wolf (*Canis dirus*) to the mesopredator guild.

5.2 Geographic distribution

By the late Pleistocene, the American lion was widely distributed from Alaska to southern Mexico. The earliest known occurrences are from the Sangamonian interglacial stage, including localities in the western of the United States, as well as northern and central Mexico (Kurtén and Anderson, 1980; Van Devender et al., 1985), indicating that this large-sized cat reached regions of southern temperate North America in a relatively short time. Subsequently, the American lion spread its distribution to the Great Plains, the Great Basin, the California Coast, the Gulf Coast, and Mexico during the Wisconsinan (Kurtén and Anderson, 1980; Lange, 2002). Based on the known geographic distribution of *Panthera atrox*, it seems that it was a common inhabitant of temperate areas of central-western North America, although it was able to reach tropical areas that now are part of southern Mexico (Fig. 5).

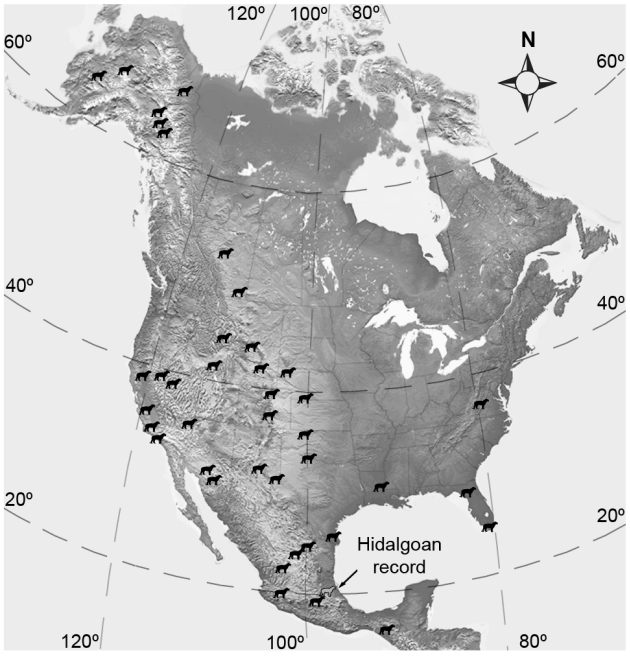

Figure 5. Geographic distribution of *Panthera atrox* in North America during the late Pleistocene (main source: Kurtén and Anderson, 1980). The gray silhouette indicates the record from southeastern Hidalgo, central Mexico.

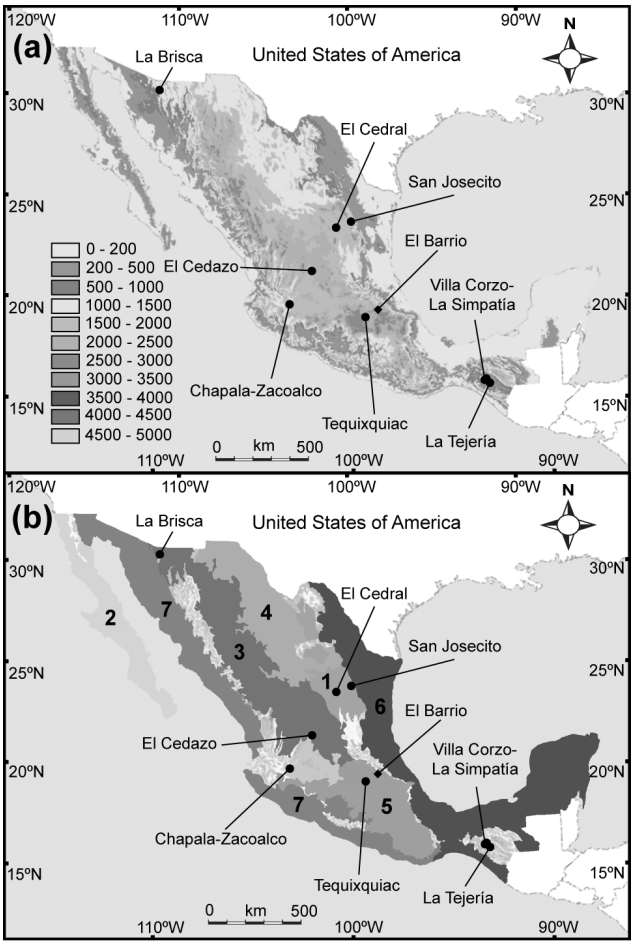

Figure 6. Mexican Pleistocene localities with records of *Panthera atrox*, considering **(a)** a hypsometric base and **(b)** the Mexican biogeographic corridors (sensu Ceballos et al., 2010). Diamond indicates the record from southeastern Hidalgo, central Mexico. Biogeographic corridors: 1, eastern US–Sierra Madre Oriental; 2, western US–Baja California; 3, Rocky Mountains–Sierra Madre Occidental; 4, central US–northern Mexico; 5, Transvolcanic Belt–Sierra Madre del Sur; 6, Tamaulipas–Central America Gulf Lowlands; and 7, Sonora–Central America Pacific Lowlands.

Previous to this study, the American lion *Panthera atrox* has been reported from nine Mexican localities in northern (La Brisca (Sonora); Arroyo-Cabrales et al., 2005), central (San Josecito (Nuevo León), El Cedral (San Luis Potosí), El Cedazo (Aguascalientes), Chapala–Zacoalco (Jalisco), Tequixquiac (State of Mexico); Freudenberg, 1910; Mooser and Dalquest, 1975; Lorenzo and Mirambell, 1981; Arroyo-Cabrales and Polaco, 2003; Arroyo-Cabrales et al., 2005; Lucas, 2008), and southern (La Simpatía, La Tejería y Villa Corzo (Chiapas); Aviña, 1969; Montellano-Ballesteros and Carbot-Chanona, 2009; Carbot-Chanona and Gómez-Pérez, 2014) areas of the country. The record reported here supplements its presence in central Mexico, specifically in areas that now are part of southeastern Hidalgo. It is noted that most of the localities where *Panthera atrox* has been reported are located in central Mexico, between 19 and 24° N at an altitude from 1500 to 2250 m a.s.l. (including El Barrio locality at 2184 m a.s.l., Hidalgo (present study)), whereas the occurrences in northern (La Brisca, Sonora) and southern (Chiapasan localities) Mexico are located at a mean altitude of 750 m a.s.l. (Fig. 6a).

According to the major biogeographic corridors of Ceballos et al. (2010), the records of *Panthera atrox* from northwestern and central Mexico (including the Hidalgoan record considered in the present study) indicate that this felid used the corridors of the Rocky Mountains–Sierra Madre Occidental and/or central US–northern Mexico, which correspond to the southern Rocky Mountains–Sierra Madre Occidental branch and to the Great Plains–western Chihuahua/Central Plateau corridors, respectively (after Ferrusquía-Villafranca et al., 2010). Furthermore, it used the corridor of the Tamaulipas – Central America Gulf Lowlands (i.e., Gulf Coastal Plain corridor (after Ferrusquía-Villafranca et al., 2010)) for reaching southern tropical areas of the Mexican territory (Fig. 6b).

6 Review of the felid record from the Pleistocene of Mexico

In Mexico, Pleistocene felid fossils are uncommon and fragmentary. Nevertheless, this group of carnivores was relatively diverse, including seven genera (*Felis*, *Miraci-*

Table 3. The record of felids from the Pleistocene of Mexico. The morphotectonic provinces are those of Ferrusquía-Villafranca (1993). Morphotectonic provinces: NW, Northwestern Plains and Sierras; CH-CO, Chihuahua–Coahuila Plateaus and Ranges; SMOr, Sierra Madre Oriental; CeP, Central Plateau; TMVB, Trans-Mexican Volcanic Belt; GCP, Gulf Coastal Plain; SMS, Sierra Madre del Sur; CHI, Sierra Madre de Chiapas; YPL, Yucatan Platform. Localities: 1, El Golfo (Sonora); 2, La Brisca (Sonora); 3, Terapa (Sonora); 4, Cuatro Ciénegas (Coahuila); 5, Cueva de Jiménez (Chihuahua); 6, Cueva de San Josecito (Nuevo León); 7, El Cedral (San Luis Potosí); 8, Mina San Antonio (San Luis Potosí); 9, El Cedazo (Aguascalientes); 10, Chapala–Zacoalco (Jalisco); 11, Tequixquiac (State of Mexico); 12, Tlapacoya (State of Mexico); 13, Tlailotlacan (State of Mexico); 14, El Barrio (Hidalgo, present study); 15, Valsequillo (Puebla); 16, Mixtequilla (Veracruz); 17, San Agustín (Oaxaca); 18, La Simpatía (Chiapas); 19, La Tejería (Chiapas); 20, Villa Corzo (Chiapas); 21, Cueva de Loltún (Yucatán); 22, Hoyo Negro (Quintana Roo).

	NW			CH-CO		SMOr			CeP	TMVB						GCP	SMS	CHI			YPL	
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Panthera atrox		X				X	X		X	X	X			X				X	X	X		
Panthera onca		X		X		X		X	X	X												
Panthera cf. *P. onca*	X																					
Puma concolor				X	X	X				X	X					X	X				X	
Puma yagouaroundi						X															X	
Lynx rufus			X	X	X	X		X	X		X	X										
Leopardus pardalis																					X	
Leopardus wiedii													X									
Smilodon fatalis						X			X	X	X											X
Smilodon sp.															X							
Felis rexroadensis	X																					
Miracinonyx inexpectatus	X																					

nonyx, *Panthera*, *Puma*, *Lynx*, *Leopardus*, and *Smilodon*) and 11 species (*Felis rexroadensis*, *Miracinonyx inexpectatus*, *Panthera atrox*, *Panthera onca*, *Puma concolor*, *Puma yagouaroundi*, *Lynx rufus*, *Leopardus pardalis*, *Leopardus wiedii*, *Smilodon fatalis*, and *Smilodon gracilis*) (Table 3). The Mexican record of Pleistocene felids includes 87.5 % and 73.3 % of generic and specific diversity known for North America, respectively.

As far as we know, the only record of felids from the early Pleistocene of Mexico consists of three species (*Felis rexroadensis*, *Miracinonyx inexpectatus*, and *Panthera* cf. *P. onca*) from El Golfo, State of Sonora, in the Northwestern Plains and Sierras morphotectonic province (Lindsay, 1984; Croxen III et al., 2007). By contrast, the late Pleistocene record of Mexican felids is represented by at least eight species whose material has been recovered from several localities across the country (Fig. 7).

Fossil material that has been referred to *Panthera atrox* (the American lion), *P. onca* (jaguar), *Lynx rufus* (bobcat), *Puma concolor* (cougar), and *Smilodon fatalis* (saber-toothed cat) is somewhat numerous. These species are known from several late Pleistocene localities in the following morphotectonic provinces: Northwestern Plains and Sierras (*P. atrox* and *P. onca*; Arroyo-Cabrales et al., 2005; Ferrusquía-Villafranca et al., 2010), Chihuahua–Coahuila Plateaus and Ranges (*P. onca*, *L. rufus*, and *P. concolor*; Gilmore, 1947; Messing, 1986), Sierra Madre Oriental (*P. atrox*, *P. onca*, *L. rufus*, *P. concolor*, and *S. fatalis*; Lorenzo and Mirambell, 1981; Arroyo-Cabrales and Álvarez, 2003; Arroyo-Cabrales et al., 2005, 2010; Ferrusquía-Villafranca et al., 2010), Central Plateau (*P. atrox*, *P. onca*, *L. rufus*, and *S. fatalis*; Mooser, 1959; Mooser and Dalquest, 1975), Trans-Mexican Volcanic Belt (*P. atrox*, *P. onca*, *P. concolor*, and *S. fatalis*; Freudenberg, 1910; Aviña, 1969; Rufolo, 1998; Lucas, 2008; Ferrusquía-Villafranca et al., 2010), Gulf Coastal Plain (*P. concolor*; Arroyo-Cabrales et al., 2005; Ferrusquía-Villafranca et al., 2010), Sierra Madre del Sur (*P. concolor*; Arroyo-Cabrales et al., 2005; Ferrusquía-Villafranca et al., 2010), Sierra Madre de Chiapas (*P. atrox*; Montellano-Ballesteros and Carbot-Chanona, 2009; Carbot-Chanona and Gómez-Pérez, 2014), and Yucatan Platform (*P. concolor* and *S. fatalis*; Álvarez and Polaco, 1982; Collins et al., 2015). The present study adds an occurrence of *Panthera atrox* from a late Pleistocene locality in southeastern Hidalgo, central Mexico, within the Trans-Mexican Volcanic Belt morphotectonic province.

The species *Puma yagouaroundi* (jaguarondi) is known from the Sierra Madre Oriental and Yucatan Platform morphotectonic provinces (Arroyo-Cabrales and Johnson, 1998; Arroyo-Cabrales and Álvarez, 2003). By the same token, the species *Leopardus pardalis* (ocelot) and a saber-tooth cat with an uncertain specific identity (referred to as *Smilodon* cf. *S. gracilis*) have single occurrences from localities in the Yucatan Platform and Trans-Mexican Volcanic Belt morphotectonic provinces, respectively (Kurtén, 1967; Arroyo-Cabrales and Álvarez, 2003; Ferrusquía-Villafranca et al., 2010).

There is a report of *Leopardus wiedii* from a site known as Tlailotlacan, late Pleistocene of the State of Mexico (Arroyo-Cabrales et al., 2005, 2010). Furthermore, there are mentions of *Smilodon* sp., *Panthera* sp., and *Lynx* sp. from localities in the Sierra Madre Oriental (*Smilodon* sp.; Arroyo-Cabrales et

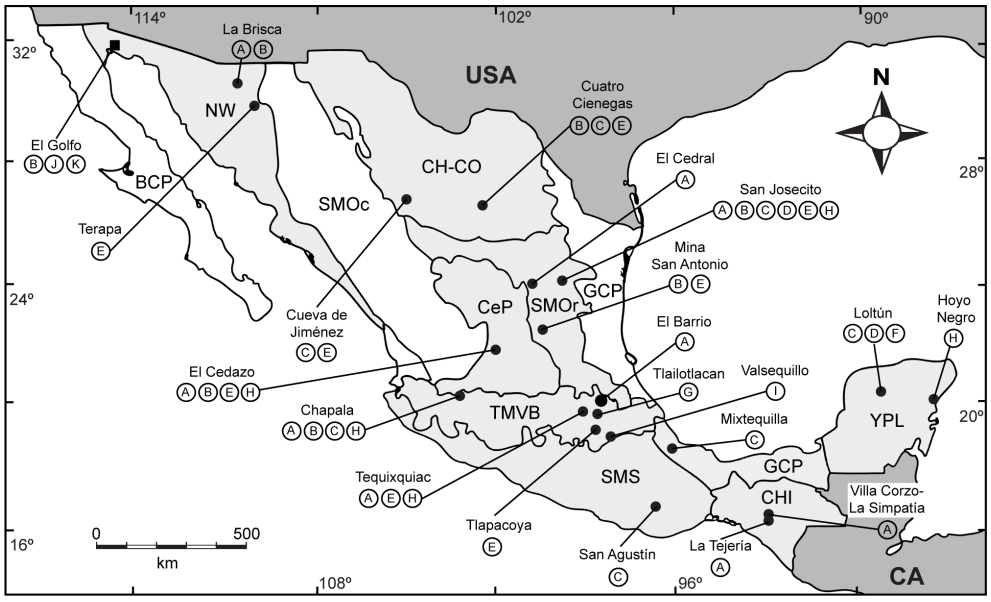

Figure 7. Mexican Pleistocene localities with records of felids. The map is regionalized in the morphotectonic provinces of Ferrusquía-Villafranca (1993). Abbreviations of the morphotectonic provinces as in Table 3. Squares indicate the early Pleistocene localities and circles the late Pleistocene localities. The felid record includes the following species: A: *Panthera atrox*; B: *Panthera onca*; C: *Puma concolor*; D: *Puma yagouaroundi*; E: *Lynx rufus*; F: *Leopardus pardalis*; G: *Leopardus wiedii*; H: *Smilodon fatalis*; I: *Smilodon* cf. *S. gracilis*; J: *Felis rexroadensis*; K: *Miracinonyx inexpectatus*.

al., 2005) and Trans-Mexican Volcanic Belt morphotectonic provinces (*Smilodon* sp., *Panthera* sp., and *Lynx* sp.; Arroyo-Cabrales et al., 2005; Bravo-Cuevas et al., 2009).

Clearly, felids were more diverse and widespread in their geographic distribution across the Mexican territory during the late Pleistocene. There are several areas in northern, central, and southern Mexico that testify to the presence of three to four species of felids, including Cuatro Ciénegas, Coahuila (*P. onca*, *P. concolor*, and *L. rufus*); El Cedazo, Aguascalientes (*P. atrox*, *P. onca*, *L. rufus*, and *S. fatalis*); Chapala–Zacoalco, Jalisco (*P. atrox*, *P. onca*, *P. concolor*, and *S. fatalis*), Tequixquiac, State of Mexico (*P. atrox*, *L. rufus*, and *S. fatalis*); and Cueva de Loltún, Yucatán, (*P. concolor*, *P. yagouaroundi*, and *L. pardalis*). The San Josecito Cave locality testifies to the presence of six species of felids. It is probable that the high diversity recorded there should be related to the nature of the site, which functioned as a shelter for maternity, resting, and/or feeding of several carnivore groups, including felids (Arroyo-Cabrales and Álvarez, 2003).

7 Conclusions

An isolated lower canine and a fifth metacarpal bone recovered from fluvial Quaternary deposits in southeastern Hidalgo, central Mexico, are formally described and assigned to *Panthera atrox*. A comparative study indicates that the Hidalgoan specimens share with that species the following diagnostic features: a large, robust, and non-strongly curved lower canine; a large and relatively slender fifth metacarpal with a well-developed projection on the palmar side at the proximal end; a narrow articulating surface for the unciform; a narrow notch on the articulating surface for the fourth metacarpal; and a diaphysis that at the middle is oval in cross section. The recovery of the American lion at the El Barrio locality suggests that this large-sized hypercarnivore was the top predator of the mammalian communities that inhabited southeastern Hidalgo during the late Pleistocene. In addition, it seems that some areas that now are part of central Mexico were suitable hunting sites for members of *P. atrox*, considering the high diversity of large mammalian herbivores (body mass ≥ 200 kg) that have been recorded there. In addition, *Panthera atrox* was relatively common in temperate areas of central Mexico between 19 and 24° N.

The Pleistocene record of Felidae from Mexico encompasses 87.5 and 73.3 % of total generic and specific felid diversity, respectively, known for North America.

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