

The large jaguar that lived in the past of México: a forgotten fossil

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In the 1970's, Oswald Mooser delivered to the Instituto de Geología, Universidad Nacional Autónoma de México, a fossil jaw recovered from the Chapala region, Jalisco, that he identified as *Panthera onca*. The collection label indicates doubts about this taxonomic assignment; an issue that remains unsolved. The aim of this work is to study the taxonomy and biogeographic implications of this material. With this aim, morphological and morphometric comparisons were made using fossil and current feline specimens. Additionally, a review of the fossil record of *Pa. onca* in Mexico was carried out using the material deposited in collections and reported in the literature. Our results indicate that the jaw from Jalisco belongs to a large Pleistocene form of jaguar historically called *Pa. onca augusta*. With the present record, there is a total of 10 paleontological localities in México where fossil jaguar records have been reported. Curiously, only one of these locations matches with the current distribution of this feline in North America, the San Josecito Cave in Nuevo León. With this information, there is evidence to confirm that the range distribution of the jaguar has been reduced significantly since the Pleistocene to the present.

En los 70, Oswald Mooser entregó al Instituto de Geología, Universidad Nacional Autónoma de México, una mandíbula fósil recuperada de la región de Chapala, Jalisco, que identificó como *Panthera onca*. La ficha de colección señala dudas sobre esta asignación taxonómica, un tema que no se ha resuelto. El objetivo de este trabajo fue estudiar la taxonomía y las implicaciones biogeográficas de este material. Para esto, se realizaron comparaciones morfológicas y morfométricas utilizando especímenes de felinos fósiles y actuales. Adicionalmente, se realizó una revisión del registro fósil de *Pa. onca* en México utilizando el material depositado en colecciones y reportado en la literatura. Nuestros resultados indican que la mandíbula de Jalisco pertenece a una forma grande de jaguar del Pleistoceno que históricamente ha sido llamado *Pa. onca augusta*. Con este registro, hay un total de 10 localidades paleontológicas en México donde se han reportado jaguares fósiles. Curiosamente, solo uno de estos lugares coincide con la distribución actual de este felino en América del Norte, la Cueva de San Josecito en Nuevo León. Con esta información, hay evidencia para confirmar que el rango de distribución del jaguar se ha reducido significativamente desde el Pleistoceno hasta el presente.

Key words: distribution; felid; San Josecito Cave; Chapala; *Panthera onca augusta*.

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Introduction

Jaguar is the common name of the big New-World felid *Panthera onca* (Linnaeus 1758). This species is the only American extant species of the pantherine lineage ([Seymour 1989](#); [Barnett et al. 2016](#)). The jaguar is characterized by its similar appearance with the African leopard, *Pa. pardus*; both have spots and rosettes on their skin, but the jaguar is slender, and its teeth are smaller ([Seymour 1989](#)). Phylogenetically, *Pa. onca* is more related to the leopard *Pa. pardus*, the lion *Pa. leo*, the extinct lion cave *Pa. spelaea*, and the American lion *Pa. atrox*, than to the snow leopard *Pa. uncia*, the tiger *Pa. tigris*, the extinct *Pa. palaeosinensis*, and *Pa. blytheae* ([Johnson et al. 2006](#); [Mazák et al. 2011](#); [Tseng et al. 2014](#)). Nevertheless, the origin of the jaguar is not yet clear. Some authors have indicated that there were forms

that lived in Eurasia and part of Africa during most of the Pleistocene, under two subspecies: *Pa. onca gombaszoegensis* and *Pa. onca georgica* ([Shultz et al. 1985](#); [Hemmer and Kahle 2005](#); [Hemmer et al. 2001](#); [2003](#); [2010](#)); but other authors differed from this taxonomic scenario, and considered the Eurasian jaguar-like animal as a different species, *Pa. gombaszoegensis* ([Arroyo-Cabrales 2002](#); [O'Regan 2002](#); [Marciszak 2014](#); [Stimpson et al. 2015](#)).

The oldest fossil record of *Pa. onca* in North America comes from the Middle Pleistocene of northern United States ([Shultz et al. 1985](#); [Seymour 1989](#)), and the species became abundant during the Late Pleistocene ([Kurtén 1973](#)). Some authors argued that it was probably present in the continent since the Late Pliocene or Early Pleistocene times ([Johnson et al. 2006](#)).

The distribution of this species in the past ranged from Washington, United States, to Chilean Tierra del Fuego (Seymour 1989; Soibelzon and Prevosti 2013; Arias-Alzate et al. 2017; Prevosti and Forasiepi 2018). Nowadays, its distribution is restricted from northern México to northern Argentina, but it should be noted that this distribution is constituted mostly patchy (Seymour 1989; de la Torre et al. 2017; Quigley et al. 2017; Arias-Alzate et al. 2017; Jędrzejewski et al. 2018). Curiously, laying México in the northern part of the current species distribution, the fossil record in this country is poorly represented (Arroyo-Cabrales 2002), unlike in United States (Kurtén 1973).

In order to contribute to the knowledge of the evolutionary history of the jaguar in North America and specifically in México, this study focuses on a fossil right jaw of a this feline (Figure 1) from San Luis Soyatlán, a town sitting in the southern border of the Chapala Lake, in the State of Jalisco. This specimen was donated to the Museum of the Instituto de Geología, Universidad Nacional Autónoma de México, by Osvaldo Mooser (swiss dentist and amateur paleontologist) in 1977 (Figure 2), but was never studied thoroughly and officially entered the IGM Paleontological Collection. Despite its fragmentary nature, its study provides relevant evolutionary and taxonomic information. Additionally, to the study of this material, a review of the fossil record of *Pa. onca* for México is presented with the biogeographic and ecological implications.

Materials and Methods

The fossil material (IGM 9518) is housed at the Colección Nacional de Paleontología, Museo Ma. Del Carmen Perrilliat (IGM), at the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM) in México City, México.

Comparison. Specimen IGM 9518 was compared with material of *Leopardus* spp.: from the Museo Estación Biológica de Rancho Grande, Venezuela: EBRG 563, 589, 1183, 1374, 1493, 1617, 3017, 2214, 3159, 9609, 805, 1618, 1904, 3200, 17585; *Panthera leo*: from the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Mastozoología, Argentina: MACN-Ma 23.1; Argentinean *Pa. onca*: from the Museo de La Plata, Argentina: MLP 10-9, and from MACN 26.217; Venezuelan *Pa. onca*: EBRG 3196 (female), 20224 (female), 20238 (male), 21702 (female), 21703 (male), 22467; *Puma concolor*: EBRG 128, 275, 1418, 1705, 1902, 2304, 17059, 20787, 22400.

Also, some comparison data were obtained from bibliographic sources, as Carbot-Chanona and Gómez-Pérez (2014), Hemmer et al. (2001; 2010), Kurtén (1973), Merriam and Stock (1932), Montellano-Ballesteros and Carbot-Chanona (2009), Simpson (1941), and Rufolo (1998).

Size was evaluated by a scattered plot using the mesiodistal length and buccal-lingual width of the lower canine. Measurements were taken with an analog caliper (± 0.1 mm, max. 150 mm) and are given in millimeters (mm). Dental abbreviations are as follows: lower canine, c1; third lower premolars, p3; fourth lower premolar, p4; and first lower molar, m1.

Results

Order Carnivora Bowdich 1821
 Family Felidae Fischer de Waldheim 1817
 Subfamily Pantherinae Pocock 1917
 Genus *Panthera* Oken 1816
Panthera onca (Linnaeus 1758)
Panthera onca augusta (Leidy 1872) (Figure 1)

Referred material. IGM 9518 is an incomplete right jaw (Figure 1), with preserved c1, but with broken crown, p3, p4, and m1.

Measurements. c1 length and width: 19.2 mm, 16.8 mm; p3 length and width: 15.1 mm, 7.5 mm; p4 length and width: 20.0 mm, 10.2 mm; m1 length and width: 21.1 mm, 10.9 mm. Length dental system (p3-m1): 56.3 mm. Height of the mandibular ramus at the level of p3: 33.8 mm. Height of the mandibular ramus at the level of m1: 31.2 mm.

Locality. IGM 9518 comes from the vicinity of San Luis Soyatlán, Arandas Municipality, Jalisco State (IGMloc 1442). San Luis Soyatlán is located on the southwestern border of the Chapala Lake. Although the exact point of origin of IGM 9518 is unknown, Lucas (2008) mentions for San Luis



Figure 1. Buccal (left) and lingual (right) views of the specimen of *Panthera onca* IGM 9518.

Soyatlán the presence of Quaternary deposits outcrops. The museum label (Figure 2) indicates that this fossil comes from the Early Pleistocene, however this has not been confirmed yet. If it were true, this would be one of the oldest known jaguars in the America continent.

Description and comparison. The specimen represents a large feline (Figure 3). Because c1 is conical and robust it belongs to the pantherine group, unlike the machairodontines where this tooth is more acute and slightly compressed. Also, c1 is larger than those of specimens of in *Puma* and living jaguars; its size matches with Pleistocene jaguars (*Pa. onca augusta* and *Pa. onca georgica*), but it is not as big as in *Pa. atrox* (Figure 3). Lateral sides of the crown are smooth, while in *Pa. atrox*, *Pa. spelaea*, and *Pa. leo* a crest running along the crown is usually appreciated (see "Discussion" for further explanation). The p3 and p4 have three cusps, where the central cusp (*i. e.*, protoconid) is the largest. A well differentiated posterior cingulum is also present in these teeth. This morphology is also observed in other species of the genus *Panthera* and *Puma*; although in *Pa. atrox* the p4 cingulum is more differentiated. The m1 is robust as in other species of *Panthera* and *Puma*, and less blade-like than in machairodontines. The diastema between c1 and p3 is less broad than in *Pa. leo* and *Pa. atrox*.

CATALOGO TAXONOMICO		U. N. A. M. C. U. INSTITUTO DE GEOLOGIA MUSEO PALEONTOLOGICO DE VERTEBRADOS	
TAXONOMIA		COLOCACION	
CLASE	Mammalia Carnivora	EJEMPLAR	Unico
ORDEN	Carnivora	ESTANTE	
GEN. Y SP.		GAVETA	
NO. DE REGISTRO	LOCALIDAD Y EDAD	MATERIAL	
	San Luis Soyatlán	Una mandíbula	
	Lago de Chapala,	con molares y	
	Jalisco.	canido de un	
	Edad: Pleistoceno	félido de gran	
	Temprano?	tamaño.	
	FECHA 23-II-77		
Enviado por el Dr. Osvaldo Mooser de Aguascalientes.			

El Dr. Mooser identificó este ejemplar como *Panthera Onca*, pero la identificación resulta dudosa porque el tamaño y la masividad de los dientes parece mucho mayor que la de un jaguar.

Figure 2. Museum label from 1977, with collecting information of the fossil jaguar (IGM 9518) from San Luis Soyatlán, Jalisco (México). This label shows the doubts of O. Mooser identification: "Dr. Mooser identified this specimen as "*Panthera Onca*", but the identification is doubtful because the size and massiveness of the teeth seems much greater than that of jaguar" (author's translation).

Discussion

Taxonomic notes. In the Figure 3 it can be noticed that IGM 9518 is a large felid. In the American continent big felids are represented by pantherines, cougars, and the extinct long-teeth machairodontines (Turner 1997). IGM 9518 differs from machairodontines by its rounded canine and premolars. Also, is larger than any *Puma concolor* analyzed. Although the Soyatlán jaw is not complete, it can be certain that it belongs to *Panthera* because its size and dental morphology.

In North America, three species of *Panthera* have been reported: the extinct cave lion *Pa. spelaea*, the American lion *Pa. atrox*, and the still present jaguar *Pa. onca* (Seymour 1989; Barnett et al. 2016). Recently, a new pantherine species, called *Pa. balamoides*, was reported for the Pleistocene of a Quintana Roo cenote in México (Stinnesbeck et al. 1918), but in our opinion its morphology remember that of ursids, not that of a pantherine; for this reason we do not consider it in our study.

The morphology of IGM 9518 is relatively similar to that of American pantherines species, except for the absence of a crest in the lower canine. Nelson and Goldman (1933) indicate that *Pa. onca* typically lacks a longitudinal ridge (or groove) in the canines. However, we observe that in the lower canines of some South American members this ridge is present (*e. g.* MLP 10-9 and MACN 26.217 from Argentina). But, this crest is always present in all the *Pa. atrox* and *Pa. spelaea* observed. So, the absence of this crest allows us to refer IGM 9518 to *Pa. onca* and not *Pa. atrox* neither *Pa. spelaea*.

In 1977, O. Mooser reached the same taxonomical conclusion, however, in the museum's label it can be read that there is a doubt about this assignation; "...the identification is doubtful because the size and massiveness of the teeth seems much greater than that of a jaguar" (Figure 2). Our morphometric analyses corroborate this observation; this specimen does not match in size with any living jaguar, male and female even (see Figure 3). Curiously, this condition was previously observed in other Pleistocene jaguars. Simpson (1941) considered that Pleistocene forms from North America were morphologically similar to the living ones but different in size. Simpson (1941) assigned the fossil specimens to the subspecies *Pa. onca augusta* (Leidy, 1872), which is 15 to 20 % larger than the living forms (Kurtén 1973; Seymour 1989). Although the subspecies concept is debatable (Wilson and Brown 1953), the usage of subspecific taxa is useful to describe the historical change in size of the *Pa. onca*. Seymour (1993) shown that in North America, the living and fossil members of *Pa. onca* differ in size cranially and postcranially. Also, the material from San Luis Soyatlán is not the only Mexican material that presents a large size. This condition is also present in specimens from San Josecito Cave in Nuevo León, as can be seen in Figure 3.

Past and present range distribution in México. México has few reports of fossil jaguar. Torres (1995), Arroyo-Cabrales (2002), Arroyo-Cabrales (2002), Morales-Mejía et al. (2009),

and Ferrusquía-Villafranca *et al.* (2010), listed nine localities; the record here presented adds one additional locality, totaling 10 localities (Table 1; Figure 4). However, not all of these reports have been confirmed as corresponding to *Panthera onca*. The localities with confirmed material are five: 1) El Cedazo (Aguascalientes), 2) Loltún Grottoes (Yucatán), 3) Mina de San Antonio (San Luis Potosí), 4) San Josecito Cave (Nuevo León), and 5) Soyatlán/Chapala region (Jalisco).

Today, the Mexican jaguar is almost restricted to environments with closed vegetation in the Sierra Madre Occidental-Sierra Madre Sur, Sierra Madre Oriental, Sierra de Tamaulipas, and the Southern part of the country including the Yucatan Peninsula (Ceballos 2014; de la Torre *et al.* 2017; Quigley *et al.* 2017; Figure 4). It is important to highlight that only one fossil locality, San Josecito Cave, lies within the current range of the jaguar (see Figure 4). In other words, the only place known in North America where the jaguar has remained since the Pleistocene time is in the Sierra Madre Oriental of Nuevo León, México. Certainly, there are localities that do not match with the range distribution of the living jaguar reported by de la Torre *et al.* (2017) and Quigley *et al.* (2017), but they are in areas with a large probability of occurrence of this pantherine (*sensu* Jędrzejewski *et al.* 2018) like El Golfo and Rancho La Brisca (Sonora), Cuatro Ciénagas (Coahuila), Mina de San Antonio (San Luis Potosí), and Loltún Grottoes (Yucatán). Despite this, there are four fossil Mexican localities with low probability of occurrence of living jaguars: Brechas Coloradas (San Luis Potosí), Arroyo Cedazo (Aguascalientes), and Zacoalco and Soyatlán (Jalisco; Figure 4).

The reduction in the geographic distribution of jaguar has been previously mentioned. Seymour (1989) and Arias-Alzate *et al.* (2017) shown that during the Middle Pleistocene the range of *Pa. onca* extended to Canada. Then, during the Late Pleistocene this range was reduced to the United States, probably at the latitude of Virginia and Northern California. Historical data indicates that by the decade of 1950's the jaguar extended to California, Arizona, Nuevo México, and Southeastern Texas, with an already absence in the Mexican Central Plateau (Hall 1959). Quigley *et al.* (2017) showed that for 2008 the North American distribution was already restricted only to México, and that from 2008 to 2015 a 20 % of declination in the jaguar range. Jędrzejewski *et al.* (2018) mention that historically the jaguar had a range that covered *ca.* 1660 thousand km²; currently, this range is of *ca.* 339 thousand km². Variation in the distribution and structure of populations have been attributed to climatic changes occurred during the Pleistocene-Holocene (Barnosky *et al.* 2003; Koch and Barnosky 2006; Arroyo-Cabrales *et al.* 2007; Barnosky 2008; Ceballos 2014; Arias-Alzate *et al.* 2017). Kurtén and Anderson (1980) and Arias-Alzate *et al.* (2017) pointed out that the reduction in the range distribution of the jaguar was the product of the influence of glacial and interglacial shifts. In addition, given that the range reduction continues nowadays, it is necessary to consider and discuss other variables, in particular anthropogenic pressure and emerging diseases.

In general, the diversity of the American Quaternary carnivores was deeply affected, where some became completely extinct (*e. g.*, hyenas, long-teeth felines, American

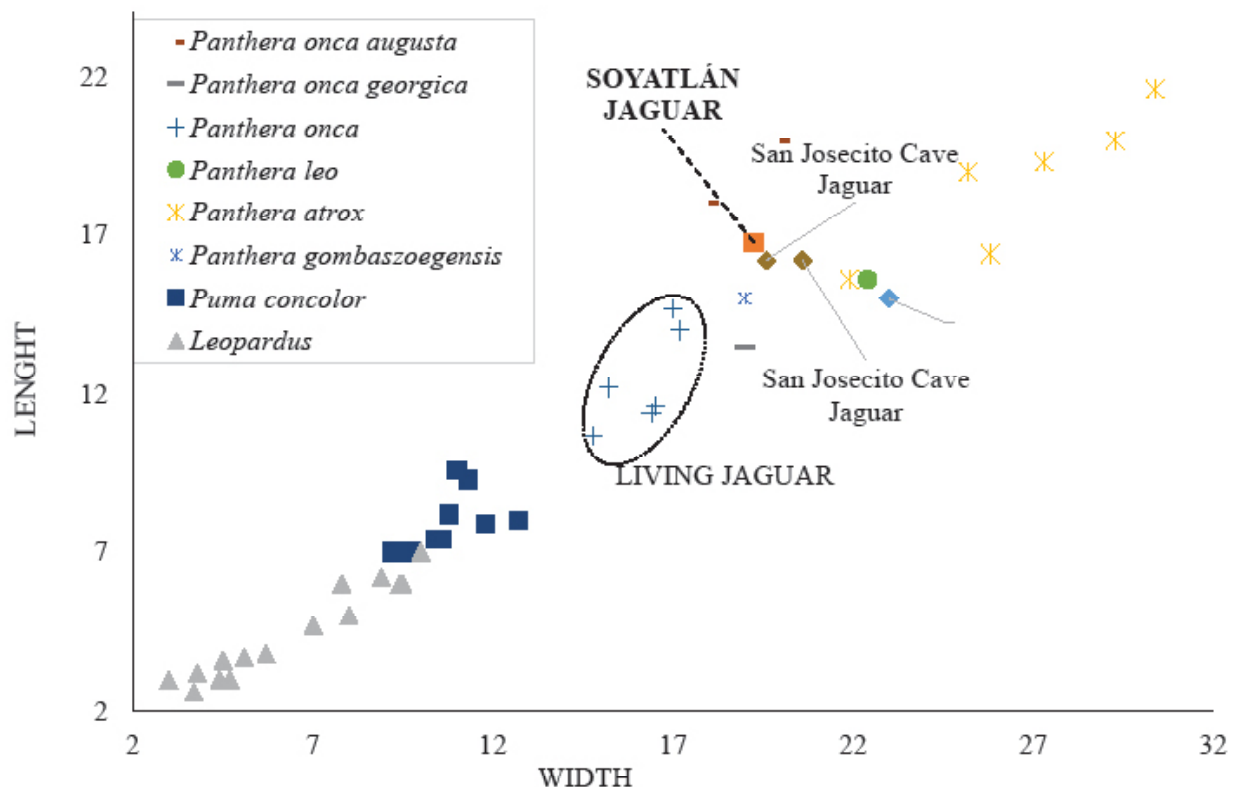


Figure 3. Size relationship (in mm) of the lower canine (c1) of specimen IGM 9518 with respect to other felids. Abbreviations: S. L., San Josecito cave.

lion, and Dire wolf), others modified their distribution (*i. e.*, local extinction), and few went through phenotypic changes (Koch and Barnosky 2006; Ceballos *et al.* 2010). In the case of the jaguar, there are evidences of the last two situations: 1) changes in its distribution (Figure 4), and 2) changes in its phenotype (they became smaller).

The fossil record of jaguar in the central part of México is evidence that the conditions in the past were favorable for its presence there. The extant jaguar mainly lives in tropical rainforests, sub-deciduous and deciduous forests, and mangroves, and less frequently in conifer or oak forests, and xeric environments (Seymour 1989; Linares 1998; Ceballos 2014). Likely, the localities where fossil jaguars have been recorded during Pliocene-Pleistocene times were areas of close vegetation and environments that favored hunting opportunities (Stinnesbeck *et al.* 1982; Ceballos *et al.* 2010). For example, Arroyo El Cedazo, Aguascalientes, central México, currently has a vegetation associated with deserts and high human presence, but during the Rancholabrean time, it was an extensive grasslands or prairie capable of supporting herds of large grazing mammals, where gallery forests probably existed nearby (Mooser and Dalquest 1975). These habitat types are described as suitable hunting area for the jaguar (Crawshaw and Quigley 2002).

Another possibility, compatible with the previous one, is that the potential jaguar prey migrated to the tropical areas where jaguar habits today in México, and that caused the current distribution of this feline, as happened with other carnivores (Ripple *et al.* 2014).

Curiously, many large mammals became extinct around the World during the Quaternary extinction (Koch and Barnosky 2006; Barnosky 2008; Arias-Alzate *et al.* 2017), and México was not an exception. Proboscidean (Gomphotheriidae and Mammutidae), xenanthran (Glyptodontidae, Megatheriidae, and Mylodontidae), felids (machairodontines and American lion), and canids (Dire wolf), are completely extinct, while Pleistocene camels (Camelidae), and horses (Equidae) became locally extinct (Arroyo-Cabrales *et al.* 2007; 2010; Ceballos *et al.* 2010; Arias-Alzate *et al.* 2017). *Pa. onca augusta* is not present today in North America, so this large form of the jaguar became locally extinct too, probably due to the same phenomenon of megafauna extinction (Arias-Alzate *et al.* 2017).

It is important to mention that despite the reduction in the habitat of the jaguar, this species is extremely successful compared to other big extinct felids (*i. e.*, long-teeth felines and American lion). One hypothesis used to explain the extinction of other big felines, is focused on the degree

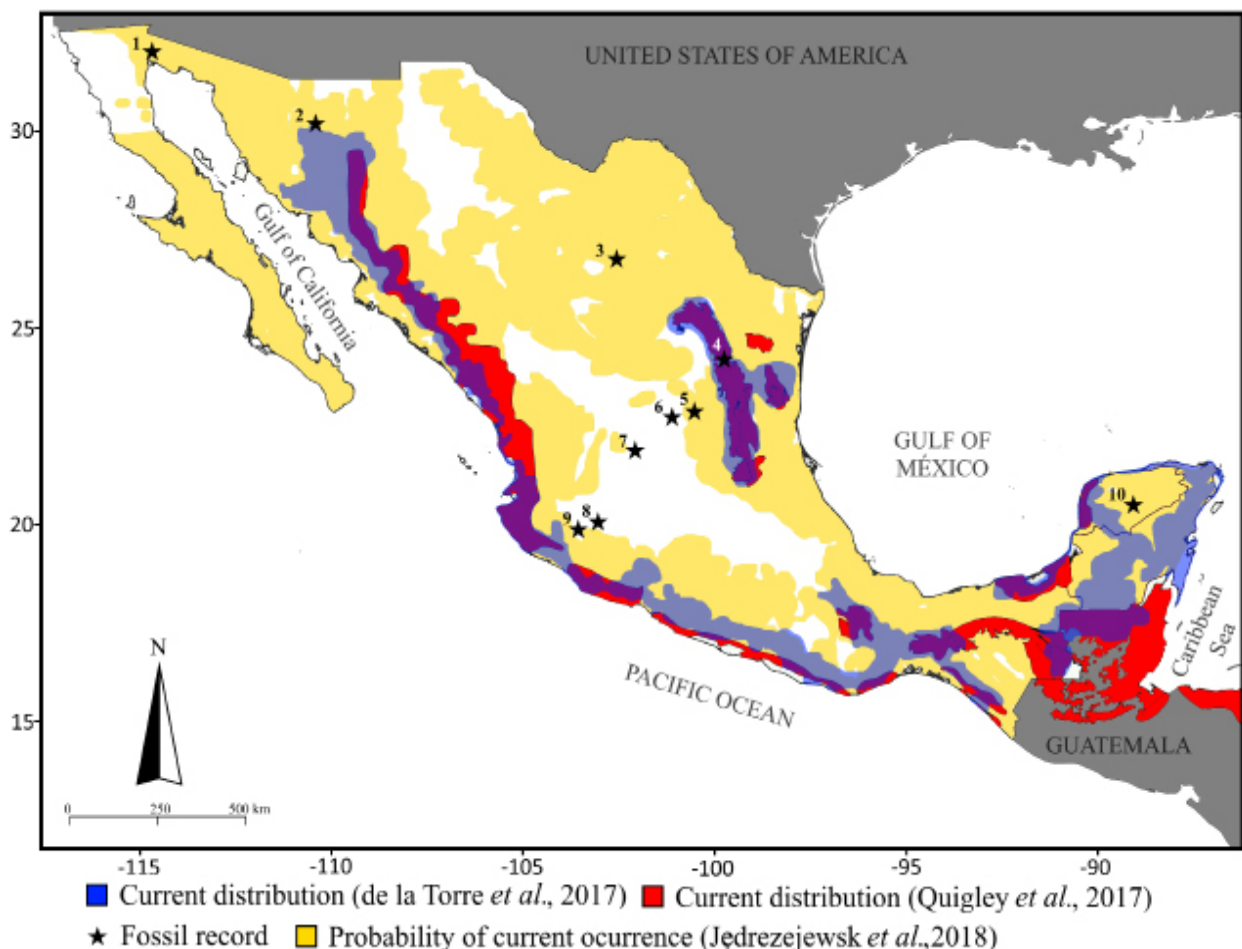


Figure 4. Past and present Mexican distribution of *Panthera onca*. Current distribution taken from de la Torre *et al.* (2017) and Quigley *et al.* (2017). Probability of current occurrence taken from Jędrzejewski *et al.* (2018). Fossil localities: 1) El Golfo; 2) Rancho La Brisca, Sonora; 3) Cuatro Ciénagas, Coahuila; 4) San Jocesito Cave, Nuevo León; 5) Mina de San Antonio; 6) Brechas Coloradas, San Luis Potosí; 7) El Cedazo, Aguascalientes; 8) Zacoalco; 9) Soyatlán, Chapala, Jalisco; 10) Loltún Grottoes, Yucatán. Fossil localities are those of Table 1.

Table 1. Mexican localities with fossil records of *Panthera onca*. Numbers in parentheses correspond to the localities depicted in Figure 4.

	Locality	Material	Age	References
Sonora	El Golfo (1)	Not reported material, but the specimen was conferred to jaguar specie (<i>Panthera</i> sp. cf. <i>Pa. onca</i>)	Pleistocene (Irvingtonian)	Arroyo-Cabrales (2002); Croxen III <i>et al.</i> (2007); Ferrusquía-Villafranca <i>et al.</i> (2010)
	Rancho La Brisca (2)	Not reported material	Pleistocene (Rancholabrean)	Arroyo-Cabrales (2002); Ferrusquía-Villafranca <i>et al.</i> (2010)
Coahuila	Cuatro Ciénagas (3)	Not reported material, and Contreras-Balderas <i>et al.</i> (2007) points that the report is doubtful because the material could also belong to <i>Puma</i> .	Pleistocene (Rancholabrean)	Contreras-Balderas <i>et al.</i> (2007); Ferrusquía-Villafranca <i>et al.</i> (2010)
Nuevo León	San Josecito Cave (4)	LACM* 192/264; 192/9008. Cranial and postcranial material	27,000-45,000 YBP (Rancholabrean)	Kurtén (1973); Arroyo-Cabrales <i>et al.</i> (1995)
San Luis Potosí	Mina de San Antonio (5)	IGM 6705; 6706; 6707. Dental and postcranial material	Pleistocene (Rancholabrean)	Torres (1995); Ferrusquía-Villafranca <i>et al.</i> (2010)
	Brechas Coloradas (6)	Not reported material	Late Pleistocene-Holocene (Wisconsinian)	Arroyo-Cabrales (2002); Ferrusquía-Villafranca <i>et al.</i> (2010)
Aguascalientes	El Cedazo (7)	IGM 56-102; 56-190; FC** 613. Cranial and postcranial material	Pleistocene (Rancholabrean)	Mooser and Dalquest (1975); Arroyo-Cabrales (2002); Ferrusquía-Villafranca <i>et al.</i> (2010)
Jalisco Chapala Lake	Zacoalco ^a (8)	LACM 1757. Mandibular fragment conferred to jaguar specie (<i>Panthera</i> sp. cf. <i>Pa. onca</i>)	Pleistocene (Late Blancan)	Rufolo (1998); Lucas (2008); Arroyo-Cabrales (2002)
	Soyatlán (9)	IGM 9518. Mandibular fragment	Early? Pleistocene	New report in this work
Yucatán	Lultún Grottoes (10)	Under review material. Dental and postcranial material	Pleistocene (Rancholabrean)	Arroyo-Cabrales and Álvarez (2003); Morales-Mejía <i>et al.</i> (2009); Personal review

^aRufolo (1998) described this specimen but the exact provenance of this fossil is unknown. Arroyo-Cabrales (2002) referred to the Zacoalco town to indicate the origin of Chapala jaguar. But, Lucas (2008) indicates that most of the material described by Rufolo (1998) comes from the villages of Chapala and Ajijic towns or near to San Luis Soyatlán.

*LACM: Natural History Museum of Los Angeles County, California, United States.

**FC: Fauna Cedazo, México.

of specificity of the diet. *Pa. onca* is a generalist hypercarnivore, this means that it has the capacity to consume a great diversity of prey, even preys with hard shells, such as turtles or armadillos (Emmons 1989; Seymour 1989). This probably conferred advantages to *Pa. onca* at the time when the availability of large prey was declining. The same selection process probably happened with the cougar *Puma concolor*. Both, cougar and jaguar are generalist predators although they have prey separation (Chinchilla 1997).

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