

PANTHERA LEO ATROX (MAMMALIA: CARNIVORA: FELIDAE) IN CHIAPAS, MEXICO

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ABSTRACT—A well-preserved right lower jaw with complete P₃-M₁ and an isolated canine of a large felid was found in the southern state of Chiapas, Mexico. It is identified as the American lion *Panthera leo atrox*. Its presence in Chiapas documents its southernmost distribution in North America.

RESUMEN—Una mandíbula derecha bien conservada de un gran félido con P₃-M₁ y un canino aislado fueron encontrados en el estado sureño de Chiapas, México. Fue identificado como león americano *Panthera leo atrox*. Su presencia en Chiapas documenta la distribución más al sur del continente americano.

In 1950, Eliseo Palacios-Aguilera first reported the mammalian fossil remains of edentates and proboscideans recovered from the Quaternary deposits of Villaflores and Villa Corzo, these municipalities are located in central Chiapas. Recovery of fossils was sporadic until 2004, when the staff of the Museo de Paleontología del Instituto de Historia Natural started a systematic study in those areas. As a result of paleontological field surveys, remains of *Mammuthus*, *Cuvieronius*, *Eremotherium*, *Glyptotherium*, *Equus*, *Odocoileus*, and *Bison* have been recovered (Carbot-Chanona et al., 2004; Carbot-Chanona and Vázquez-Bautista, 2006; Montellano-Ballesteros and Carbot-Chanona, in press). One of the most important fossil specimens collected is a fragmentary lower jaw of a large felid that is the object of this note. Taxonomic history of the genus and species is complex, Leidy (1853) originally described *Felis atrox*. In 1873, he described *Felis imperialis* as a smaller separate species. However, Kurtén and Anderson (1980) synonymized *F. imperialis* with *P. leo atrox*. Merriam (1909) and Frick (1930) described the subspecies *F. atrox bebbi* and *F. atrox alaskensis*, respectively. With the detailed study of Merriam and Stock (1932) on the fossil-felid material from Rancho La Brea, California, it has been possible to examine morphological variation within the population. They synonymized *F.*

imperialis with *F. atrox* and considered as *nomina dubia* the proposed subspecies *bebbi* and *alaskensis*. Simpson (1941) moved *F. atrox* to the genus *Panthera* and suggested that *P. atrox* was not a lion, but might be a giant jaguar. He considered it to be distinct from *P. onca* and named it *P. jaguarius atrox*. Currently, the genus *Felis* includes small felids, while *Panthera* includes large cats such as lions, tigers, and leopards (Turner and Antón, 1997). The abbreviations used in the paper are: IHNFG, Instituto de Historia Natural, Fósil Geográfico, Tuxtla Gutiérrez, Chiapas; C, canine; M, molar; P, premolar (measurements are in millimeters).

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Felidae Gray, 1821

Subfamily Pantherinae Pockock, 1917

Genus *Panthera* Oken, 1816

Panthera leo atrox Leidy, 1853

Type: *Felis atrox* Leidy, 1853:319. Left lower jaw with broken C and P₃-M₁ from Pleistocene at Natchez, Mississippi.

Felis imperialis Leidy, 1873:259. Type: upper jaw with P₃, from Pleistocene gravels at Livermore Valley, California.

Felis imperialis Matthew, 1902:321.

Felis atrox bebbi Merriam, 1909:301.

Felis atrox Freudentberg, 1910:33.

Felis imperialis Freudentberg, 1910:31.

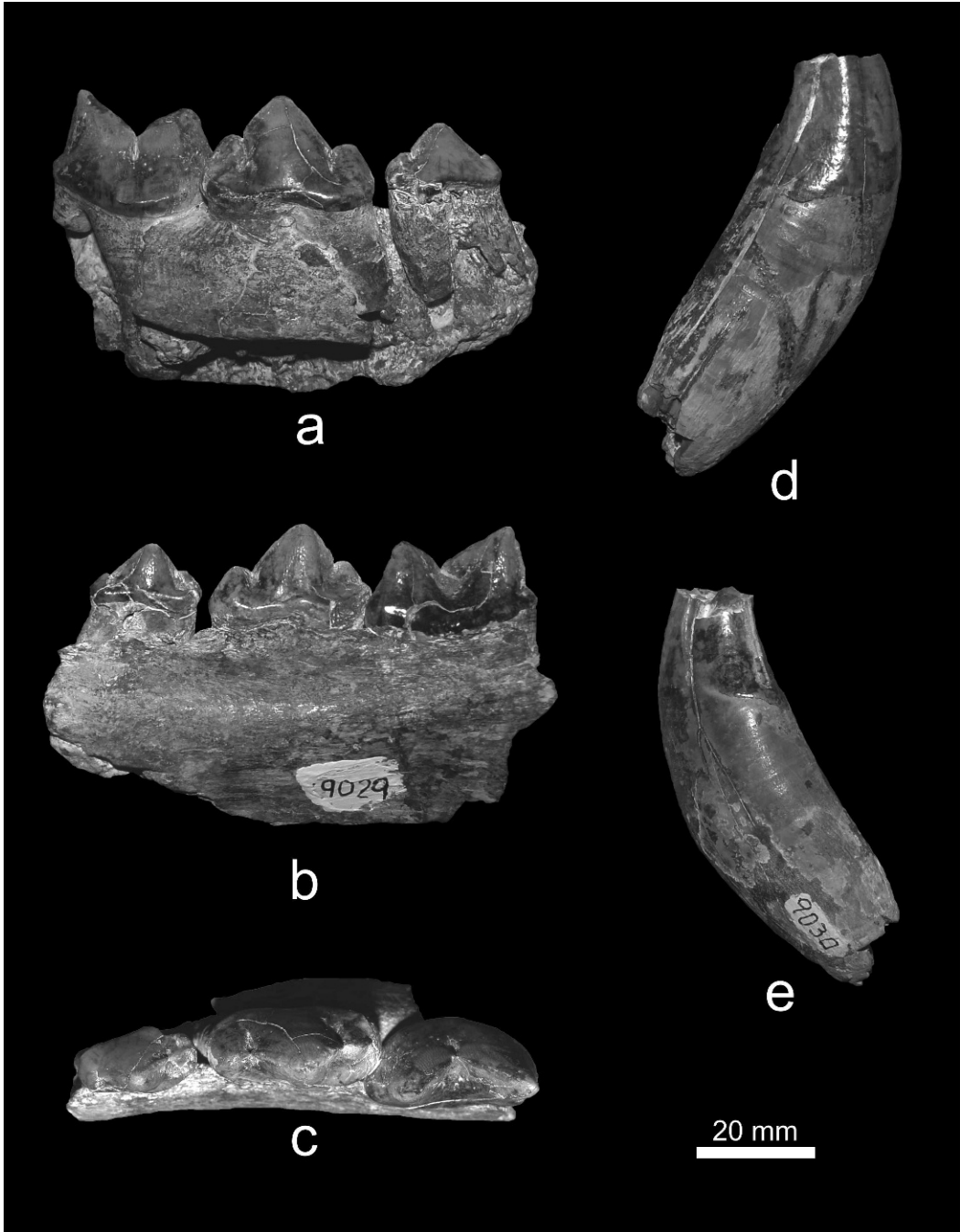


FIG. 1—Views of the partial right lower jaw of *Panthera leo atrox* with P_3 - M_1 (IHNFG-2678): a) lingual; b) labial; c) occlusal; an isolated canine d) outer, e) inner.

Referred Specimen—The specimen is a partial right lower jaw with complete P_3 - M_1 and an isolated canine that probably belongs to the same individual (IHNFG-2678; Fig. 1).

Locality and Age—The fossil specimen was from La Tejería, which is a quarry for construction materials. This site is near the town of San Pedro Buenavista, in the Municipio of Villa Corzo,

TABLE 1—Comparative measurements (mm) of lower dentitions of *Panthera leo atrox* from Mexico (Chiapas and Tequiquiac) and Rancho La Brea, California.

Character	Chiapas ^a IHNFG-2678	Tequiquiac ^b 102	Rancho La Brea, California ^c
Length of canine	21.9	—	21.8–30.4
Width of canine	15.6	—	15.1–22.0
Length of P ₃	17.5	—	17.0–21.6
Width of P ₃	9.7	—	8.9–13.2
Length of P ₄	26.2	23.5–24	25.8–32.3
Width of P ₄	12.5	—	12.0–16.9
Length of M ₁	26.7	24–25	26.9–33.9
Width of M ₁	13.2	—	13.0–17.5

^a Herein.
^b Freudentberg (1910).
^c Merriam and Stock (1932).

Chiapas. The fossil was collected by Misael Nanduca, owner of the La Tejería, from a 20-cm thick layer of a dark, fine-grained, sandy clay. The Pleistocene age is suggested based on presence of an unknown species of *Glyptotherium* sp., *Equus conversidens*, and probably *Cuvieronius tropicus*.

Description and Comparisons—The canine has the occusal end broken. P₃ is double rooted with the posterior root more robust. Tooth crown bears a distinct small anterior and a slightly larger posterior basal tubercle. Apex of the main cuspid is slightly posterior to the middle of the cuspid. Posterior edge of the main cuspid is sharp. Talonid of P₃ is small with a shallow basin. Merriam and Stock (1932) mentioned that the anterior basal tubercle is present in most P₃s of

Panthera leo atrox from Rancho La Brea. P₄ shows anterior and basal tubercles of nearly equal size, separated from the main cuspid by a notch. Posterior tubercle is divided in the type specimen (Merriam and Stock, 1932:figure 133). Principal cuspid of P₄ is higher than long and the anterior slope is longer than the posterior slope; in the lingual side of the basal posterior tubercle, there is a shallow basin. This tooth is bordered posterolingually by a distinctive cingulum. M₁ also is double rooted, with talonid exhibiting a cingulum as in the material from Rancho La Brea. Protoconid is slightly longer anteroposteriorly and higher than the paraconid. These cuspids meet medially to form a well-defined carnassial notch. In comparison to the material from Rancho La Brea, California, no significant morphological difference was noted. Measurements are in Table 1 and Fig. 2; size of the specimen from Chiapas is in the size range of the sample from Rancho La Brea.

Geographic Distribution of Panthera leo atrox in Mexico—The American lion, *P. l. atrox* is distinguished easily from other Pleistocene felines by its great size and relatively long and slender bones (Kurtén and Anderson, 1980). It was widely distributed in Canada and United States, reaching Mexico during Rancholabrean times; however, it is not known where it occurred in Mexico (Bell et al., 2004). Kurtén and Anderson (1980) mentioned its presence in Peru, but Seymour (1983, in Yamaguchi et al., 2004) reinterpreted the material as a jaguar (*P. onca*) of large size.

Freudentberg (1910) in his work on the carnivores of the Plio-Pleistocene Mexican faunas,

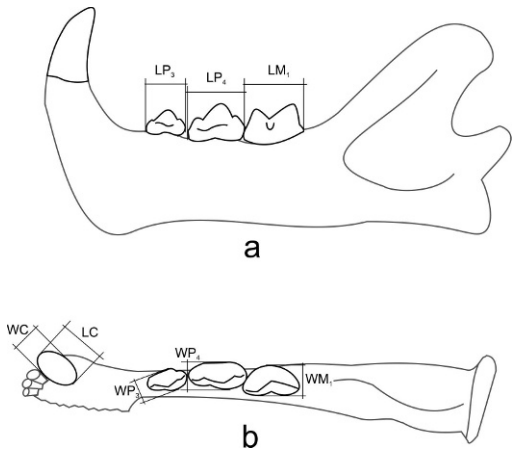


FIG. 2—Measurements (mm) taken from specimen IHNFG-2678: L, length; W, width; P, premolar; M, molar; C, canine.

referred a fragmented skull with I³, C, P³-P⁴ as *Felis imperialis*; a mandible with P₄-M₁ to *Felis* cf., *imperialis* and an upper-jaw fragment without teeth to *Felix* (= *Panthera*) *atrox*. Simpson (1941) suggested that some of the material described by Freudenberg (1910) as *Felis* cf., *imperialis* was a jaguar (*P. onca*), and that the rest belonged to a small *F. atrox* or to a large extinct Mexican race of *P. onca*. Simpson (1941) could not find reliable differences between *P. onca* and *P. atrox* in the preserved elements. Unfortunately, all fossil material described by Freudenberg is lost and, therefore, cannot be restudied. Miller (1943) and later, Arroyo-Cabrales and Polaco (2003) mentioned *Felis* (*Panthera*) *atrox* as part of the megafauna collected in the San Josecito Cave, Nuevo León, but neither of them mentioned material that was collected. Aviña (1969) reported a P² from Villa Corzo, Chiapas, which was identified by Alvarez as *F. (P.) atrox*. The illustrated tooth in Aviña does not correspond to a P² but to a P³, and the catalog number is different from that labeled in the figure. Compared to the P³ figured in Merriam and Stock (1932:plate 33:figures 2 and 2a) and size of material from California, this specimen from Chiapas is similar to *F. (P.) atrox*. In the El Cedazo local fauna, Aguascalientes, Mooser and Dalquest, (1975) referred a radius to this cat as *F. (P.) atrox* because of its large size. Lorenzo and Mirambell (1981) mentioned this felid at Rancho La Amapola, San Luis Potosí. Rufolo (1998) questionably referred an incomplete distal end of a humerus of a juvenile to ?*P. leo atrox*, which was in the collection from Lago de Chapala housed at the Los Angeles County Museum.

From information presented above, it is evident that the current record of this felid is scarce. The record at La Tejería confirms the southernmost record of this big cat in North America. It is absent in local faunas described for Central America (Cisneros, 2005).

Systematic History of Panthera leo atrox—Comparative morphological analysis of Pleistocene and Holocene lions of different geographic populations suggests existence of two evolutionary lines: the *spelaeae* group (Europe) and the *leo* group of Africa and southern Asia. Some authors favor the taxonomic combination of these groups within *Panthera leo* (Kurtén, 1965; Turner and Antón, 1997) and others prefer a taxonomic separation at the species level in *P. spelaeae* and *P. leo* (Baryshnikov and Boeskorov,

2001; Burger et al., 2004). In their attempt to reconstruct the phylogenetic position of *P. leo spelaeae* (Pleistocene European cave lion), Burger et al. (2004) used mitochondrial cytochrome-b genes and suggested that this extinct lion is the sister clade of extant lions, and that this feline lineage was isolated from the African and Asian lions since their dispersal over Europe ca. 600,000 years ago. They concluded that the question of whether extinct cave lions of Europe and extant lions of Africa and Asia should be recognized as different species may be a matter of convention. The same controversy exists with the Pleistocene American lion; some authors considered *P. atrox* as a subspecies of the African lion *P. leo* (e.g., Kurtén and Anderson, 1980; Anderson, 1989; Turner and Antón, 1997); others considered that it is distinct from *P. leo spelaeae*, which lived in Eurasia during the Pleistocene (e.g., Simpson, 1941; Whitmore and Foster, 1967; Martin and Gilbert, 1978; Wheeler and Jefferson, 2003). There is no molecular study dealing with the Pleistocene American lion that would provide clarification of lineages.

The fossil record of felids in Mexico is scarce, so geographic and temporal distribution and paleodiversity are not possible to determine at present. This attests to the geographical importance of the find. The fossil material described here is identified as *P. l. atrox*, which indicates that the most southern distribution documented for this lion in the Pleistocene was Chiapas. Its assignment as a subspecies of *P. leo* follows the idea that sometime during the Pleistocene, the species *P. leo* dispersed from Africa, invading Europe and Asia where *P. l. spelaeae*, *P. l. vereshchagini*, and *P. l. fossilis* are known. It later crossed Beringia and reached North America, living there in open habitats.

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