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The fossil American lion (*Panthera atrox*) in South America: Palaeobiogeographical implications

*Le lion américain fossile (Panthera atrox) en Amérique du Sud :
implications paléobiogéographiques*

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ABSTRACT

By the late 19th and early 20th centuries, authors described several specimens belonging to a very large felid, the size of a lion, from some Late Pleistocene localities at southern Chile and Argentina. These remains were considered as belonging to large and now extinct subspecies of jaguar. In the present contribution based on qualitative and quantitative postcranial and cranial characters, we conclude that the “Patagonian *Panthera*” should be considered as representing remains of the American Cave Lion *Panthera atrox*. Evidence at hand indicates that *Panthera atrox* was a very large lion-like felid, with reddish skin, that inhabited dry open habitats. Furthermore, in contrast to living jaguars, transported and accumulated its preys in rocky dens. The presence of at least two pantherine lineages (i.e. *P. onca* and *P. atrox*) in the Pleistocene of South America indicates that the lineage has a long and complex history in the New World, and that the history of the clade in this landmass is still far from being well understood.

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R É S U M É

À la fin du XIX^e siècle et au début du XX^e, des auteurs ont décrit plusieurs spécimens appartenant à un très grand félin, de la taille d'un lion, dans différentes localités du Pléistocène supérieur du Chili méridional et d'Argentine. Ces restes ont été considérés comme appartenant à une sous-espèce de grande taille du jaguar, aujourd'hui disparue. Dans le

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présent article, nous concluons, sur la base de caractères crâniens et post-crâniens, à la fois qualitatifs et quantitatifs, que la « *Panthera patagonienne* » devrait être considérée comme représentant les restes du lion des cavernes américain, *Panthera atrox*. Il est évident, sur la base des éléments en notre possession, que *Panthera atrox* était un très grand félin de type lion à pelage rougeâtre, habitant les zones sèches ouvertes. Au contraire des jaguars actuels, il transportait et accumulait ses proies dans des tanières rocheuses. L'existence d'au moins deux lignées de panthérines (c'est-à-dire *P. onca* et *P. atrox*) dans le Pléistocène d'Amérique du Sud indique que la lignée a une histoire longue et complexe dans le Nouveau Monde, et que celle du clade est encore loin d'être bien comprise dans ce continent.

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1. Introduction

Panthera atrox Leidy, 1853, has frequently been considered as an exclusively North American lion, closely related to the extinct Eurasian cave lion (*Panthera spelaea*) and the extant African lion (*Panthera leo*) (Barnett et al., 2009; Christiansen, 2008b; Christiansen and Harris, 2009; Kurtén, 1965, 1973, 1985; Turner and Antón, 1997). Furthermore, some authors consider that *P. atrox* is a mere subspecies of *P. leo* (Anderson, 1989; Burger et al., 2004; Diedrich and Rathgeber, 2012; Kurtén and Anderson, 1980; Montellano-Ballesteros and Carbot-Chanona, 2009; Nagel et al., 2003; Turner and Antón, 1997). On the contrary, some authorities proposed that was more nearly related in skull shape to the living South American Jaguar (*P. onca*) (Christiansen and Harris, 2009; Merriam and Stock, 1932; Simpson, 1941). This uncertainty is probably due to the strong similarities shared by the four living species of the genus *Panthera*, which are difficult to distinguish because of their strong osteological homogeneity. In fact, the skulls of living tigers and lions are nearly indistinguishable (Christiansen, 2008a; Sunquist and Sunquist, 2002), and thus, the taxonomy of pantherines is far confusing. However, the recent detailed analysis of craniomandibular morphometric and anatomical evidence published by Christiansen and Harris (2009) allow distinguishing, based on quantitative and qualitative characters, the four living species of the genus (i.e., *Panthera leo*, *P. atrox*, *P. onca*, *P. tigris*).

Roth (1899) described the remains of a large felid from the Late Pleistocene of “Cueva del Milodón”, in Última Esperanza, southern Chile. These specimens were collected by expeditions of the collector Rodolfo Hauthal to Patagonia. In the original description of these remains, Roth (1899) coined the new name *Iemish listai*, which consisted on isolated postcranial remains. This genus was considered by Roth as the largest felid from South America, and he completed his description of this mysterious animal with some local traditions and legends regarding its external aspect and behavior. Later, Nordenskjöld (1900) and Smith Woodward (1900) based on new fossil remains and the re-study of some of the specimens, concluded that *Iemish* was nearly related or belonged to the genus *Felis*. Lately, Roth (1904) reviewed all available evidence and hypothesized that this large felid belonged to a giant species of the genus *Felis* comparable in size with the African lion *F. leo*. Thus, he eliminates the name *Iemish* and renamed the felid as *Felis listai*. Posteriorly, Cabrera (1934) re-analyzed

Roth's specimens and concluded that they belonged to a large extinct subspecies of the extant jaguar *F. onca*. Furthermore, he found that *F. listai* (Roth, 1899) was a not an available name and re-named it as *Felis onca mesembrina*. Since this influential work, the large extinct felid from Patagonia was considered as a subspecies of extant Jaguar, a criterion followed by all subsequent authors.

The aim of the present paper is to review all available evidence regarding *Felis onca mesembrina*, to evaluate its phylogenetic affinities and its validity as a subspecies of *Panthera onca*.

Institutional abbreviations. CFA-Ma, Colección de Mastozoología, Fundación de Historia Natural “Félix de Azara”, Universidad Maimónides, Ciudad Autónoma de Buenos Aires, Argentina; MACN-Ma, Departamento Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP, Colección Paleontología Vertebrados, Museo de La Plata, Buenos Aires, Argentina.

2. Referred material

Roth (1899) described as belonging to *Iemish listai* from the Caverna del *Myiodon* in Última Esperanza the distal end of right humerus, distal end of incomplete right femur, two incomplete metatarsals, and possibly a fragmentary pelvis (see also details in Smith Woodward, 1900). Later, the same author (Roth, 1904), referred the anterior half of a skull, two incomplete mandibles, isolated teeth, ribs, and claws. Moreover, he found isolated portions of skin that belong to this species (Roth, 1904; see also Lehmann-Nitsche, 1899). The skull and one of the mandibles were later described in more detail by Cabrera (1934). Regrettably, the skull, which constituted the holotype of *Felis onca mesembrina* Cabrera, 1934 (MLP 10-90) is currently lost (Prevosti and Reguero, 2000). Additional material was mentioned by Emperaire and Laming (1954), consisting on a left maxillary fragment.

More recently, several authors found isolated material referred to *P. onca mesembrina*. Nami (1985; see Nami and Menegaz, 1991; Prieto, 1991) illustrated a left mandibular ramus coming from the Cueva del Medio, at Última Esperanza, Chile. From the same site, Nami and Menegaz (1991) also report an isolated metatarsal and a left M2. From Cueva of Sofía Lake, Última Esperanza, Chile, Martín (2008, 2013) described an incomplete right mandible, left maxilla, left i3 of juvenile specimen, and a left P4 of adult individual. From Cueva de los Chingües, Pali Aike, Chile,

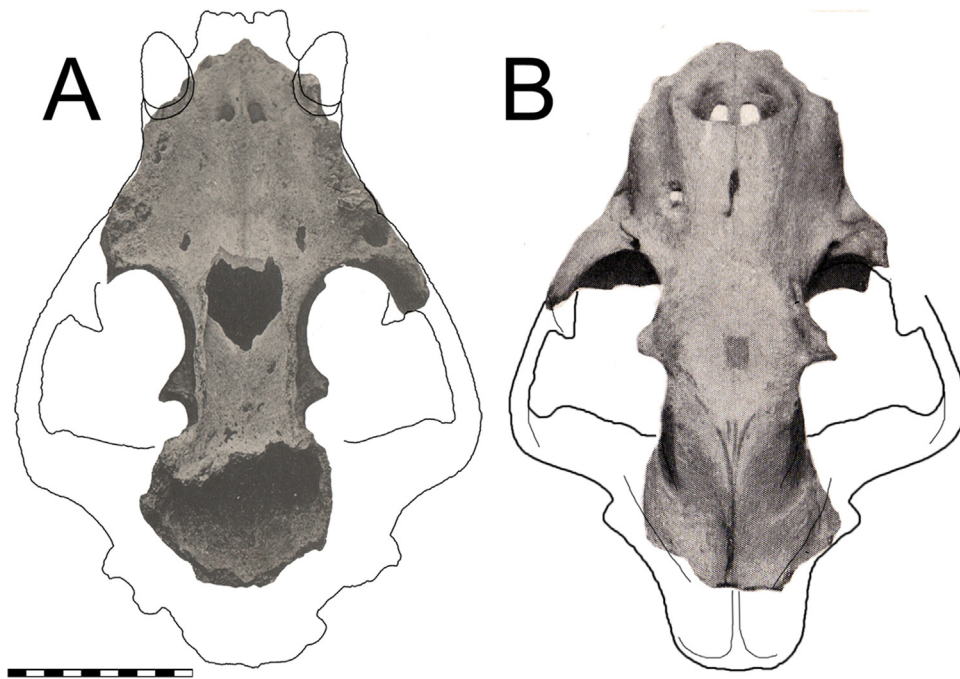


Fig. 1. The skulls of “*Panthera onca mesembrina*” in palatal (A); and dorsal (B) views. Scale bar: 100 mm

Fig. 1. Crâne de « *Panthera onca mesembrina* » en palatale (A) ; et dorsale (B) vues. A, selon Roth (1904), B, selon Cabrera (1934). Barre d'échelle : 100 mm.

Martin (2013) described a left anterior portion of a juvenile jaw of “*F. o. mesembrina*”. A large felid claw from the same site may be referred to “*F. o. mesembrina*” (San Roman et al., 2000). Furthermore, Borrero (2001) illustrated feces of *P. o. mesembrina*, coming from the Caverna del Mylodon in Última Esperanza. A single isolated metatarsal was recovered in Tres Arroyos 1 site (Latorre, 1998; Martin, 2013; Massone, 2004; Massone et al., 1998) at Tierra del Fuego, Argentina. Further material was recovered in Cueva del Puma, at Pali Aike, Chile (Martin et al., 2004), but a detailed information is still wanting.

All the fossil material comes from Late Pleistocene strata, and available dates indicates it was present by 11.085 ± 70 AP (Massone, 2004), 10.840 ± 60 AP (Martin, 2012), and $13.560 \pm 180/10.200 \pm 400$ AP (Tonni et al., 2003).

The most relevant specimen of “*F. o. mesembrina*” is the holotype skull MLP 10-90. This material was studied in detail by Roth (1904) and Cabrera (1934) whom figured the skull in dorsal and ventral views, and give a large amount of cranial measurements, but this specimen is currently lost (Prevosti and Reguero, 2000). Thus, our comparisons and interpretations on skull morphology of “*F. o. mesembrina*” must rely on Roth (1904) and Cabrera (1934) measurements, illustrations, photographs, and descriptions.

Material examined. MLP 94-VIII-10-92, third upper premolar (P3); MLP 94-VIII-10-13, posterior fragment of hemimandible; MLP 94-VIII-10-15 (previously under collection number MLP 10-96), distal fragment of right humerus; MLP 94-VIII-10-16, distal end of metapodial; MLP 94-VIII-10-17, fourth left metatarsal; MLP 94-VIII-

10-69, incomplete sacrum; MLP 94-VIII-10-70, isolated claw; MLP 94-VIII-10-71, fragment of skin; MLP 94-VIII-10-91 (previously under collection number MLP 10-93), first lower molar (m1) with part of maxillary bone; MLP 94-VIII-10-93, isolated non-ungual phalanx.

3. Description

In this section, we briefly describe the more remarkable features of each analyzed element of “*Felis onca mesembrina*”, and we made special reference to the traits that are taxonomically relevant. It is worthy to note that, as indicated above, and recognized by most authors (e.g., Cabrera, 1934; Roth, 1904), specimens of “*F. o. mesembrina*” are very large and robust, comparable only with lions and related taxa of the genus *Panthera* (i.e., *Panthera leo*, *P. atrox*, *P. spelaea*, *P. tigris*), and thus, main comparisons are carried out with these species (Fig. 1).

Specimen MLP 94-VIII-10-92. It corresponds to a complete left P3. It presents a narrow cingulum along labial and lingual sides of the crown. Both cingula contact each other at the distal margin of the tooth. On the lingual side the cingulum is linguallly projected at the metastyle level. The mesial cusp (parastyle) is very low and is located at the lingual edge. The main cusp (paracone) is large, conical, and presents a strong crest in the mesial and distal margins. The distal cusp (metacone) is taller than the anterior cusp, and is located in the central surface of the crown. In the distal end of the crown, the junction of the lingual and labial cingula forms a prominent shelf (Fig. 2A–C).

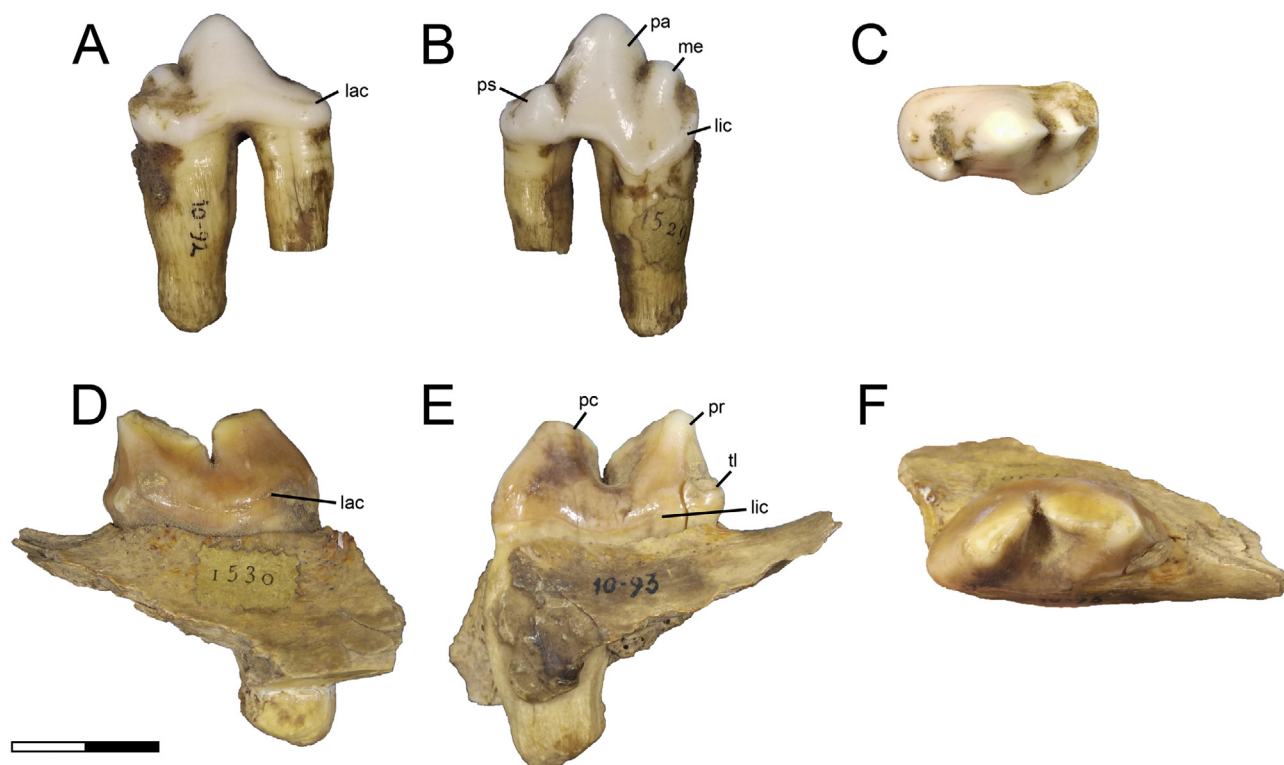


Fig. 2. MLP 94-VIII-10-92, left P3 (A–C) and MLP 94-VIII-10-91, right m1 (D–F) of “*P. onca mesembrina*” from Cueva Última Esperanza in labial (A and D), lingual (B and E) and occlusal views (C and F). Scale bar: 20 mm

Fig. 2. MLP 94-VIII-10-92, P3 gauche (A–C) et MLP 94-VIII-10-91, (m1 droite D–F) de « *P. onca mesembrina* » de la grotte Cueva Última Esperanza en vues labiale (A et D), linguale (B et E) et occlusale (C et F). Barre d'échelle : 20 mm

Table 1

Measurements (in mm) of the *Panthera* lineage in the New World.

Tableau 1

Mesures (en mm) de la lignée de *Panthera* dans le Nouveau Monde.

	<i>Panthera onca mesembrina</i>		<i>Panthera atrox</i>		<i>Panthera onca</i> fossils NA		<i>Panthera onca</i> fossils SA		<i>Panthera onca</i>	
	OR	N	OR	N	OR	N	OR	N	OR	N
PL	150	1	161.2–185	4	113	1	110	1	91.8–115.3	12
PW	132	1	110–147.8	17	96–108	3	95–118	5	74.3–102.5	12
APD c	26	1	21.4–33	40	19.6–26	8	18–21.4	3	13.2–22.6	11
LLD c	20	1	13.9–21.5	17	15.4–22	8	14.5–16.4	3	9–17	11
APD p3	20	1	17–21.6	17	13.7–18.2	9	17–18.2	2	11.8–16.9	11
LLD p3	15	1	8.9–13.2	17	7.8–9	8			4.3–9.2	11
APD p4	24	1	25.8–32.3	17	20.6–25	15	22–24.2	3	15.5–22.2	11
LLD p4	13	1	12–16.9	17	10–13	15	11.2	1	6.3–10	11
APD m1	30.2	1	25.1–34	51	20.7–22.6	5	22.4–23.5	6	15.4–22.5	11
LLD m1	14.4	1	12.5–17.9	50	11–11.6	4	11–12.5	6	6.7–11.4	11
APD C	28	1	25.2–38.1	17	19.5–21.5	6	19–22	3	15–23.8	12
LLD C	24	1	18–25.7	17	16.1–18.8	6	15.5–18	3	11.4–18.9	12
APD P3	24.7	1	22.8–30.6	22	16.9–22.3	6	19.5–22	5	14.8–21.3	12
LLD P3	13.9	1	12–18.1	22	9.2–11.8	8	10	1	5.9–10	12
MHB	45	1	46–67.1	16	37.3–46	5	26–39.5	6	28.1–40.1	11

APD: anterior-posterior diameter; LLD: lingual-labial diameter; MHB: height of mandibular body at the proximal border of the m1; OR: observed range; PL: palatal length; PW: palatal width. Sources in [Supplementary Material](#).

Remarks. In spite that the P3 lacks relevant taxonomical traits, its total length (24.76 mm) corresponds to the size range of *P. atrox* (Harington, 1971; Kurtén, 1965; Merriam and Stock, 1932) and is outside to the range of the *P. onca* (recent and fossil) of North and South America (Cabrera,

1934; Jefferson, 1983; Kurtén, 1965, 1973; Simpson, 1941: Table 1).

Specimen MLP 94-VIII-10-91. It is a complete right m1 with a fragment of the dentary bone. The cusps are complete and present some wear. The mesial cusp

(paraconid) is notably mesiodistally shorter than the distal cusp (protoconid). Both lingual and labial faces of the paraconid are smooth. The protoconid is large, slightly higher and mesiodistally longer than the paraconid, and has large crests on both labial and lingual sides. In the distal edge of the protoconid there is a thin and acute dorsoventral ridge. A small talonid is present in the posterior edge of the tooth. At lingual and labial sides, long cingula run along the entire length of the crown (Fig. 2D–F).

Remarks. The total length value (30.20 mm) of MLP 94-VIII-10-91 is higher than the range observed in fossil and living *P. onca* (see Table 1; Cabrera, 1961; Kurtén, 1965; Simpson, 1941). On the contrary, it is nested within the *P. atrox* size range (Carbot-Chanona and Gómez-Pérez, 2014; Kurtén, 1965, 1973, 1985; Merriam and Stock, 1932; Montellano-Ballesteros and Carbot-Chanona, 2009; Whitmore and Foster, 1965). The morphology of the m1 crown in species of *Panthera* is very similar among all species, being the size the main difference between *P. atrox* and *P. onca* (Carbot-Chanona and Gómez-Pérez, 2014). In spite of that, a paraconid much shorter than the protoconid is a trait typical of most *P. atrox* specimens (Merriam and Stock, 1932; Montellano-Ballesteros and Carbot-Chanona, 2009), while in *Panthera onca* the paraconid is nearly equal in size to the protoconid.

Specimen MLP 94-VIII-10-15. It is a well-preserved distal end of right humerus. In anterior view, a large elongated supracondyloid foramen is present proximally to the medial epicondyle. In *P. onca*, this foramen is proportionally smaller and is located at the level of the epicondyle. The capitulum and trochlea are well developed, and the proximal margins of trochlea and capitulum are at the same level. In *P. onca* the trochlea is much smaller than the capitulum, and the proximal edge is low. The medial epicondyle is well developed, being anteroposteriorly expanded. In posterior view, the large olecranon fossa shows a well-developed lateral edge delimited in part by an acute and prominent proximodistal ridge. In distal view, the lateral ridge of the capitulum does not possess the medial invagination observed in *Panthera onca*. The lateral epicondyle is nearly smooth, whereas in *P. onca* it forms a shelf-like platform. The lateral epicondyle crest is straight, and in lateral view, is very high and anteriorly directed.

Remarks. Harington (1969) enumerated four humeral traits typical of the humerus of *P. atrox*: (1) general robustness comparable to *Smilodon* and *Homotherium*; (2) great anteroposterior expansion of the medial epicondyle; (3) sharp, posteriorly directed crest below the medial epicondyle when the specimen is viewed laterally; and (4) the outward flair of the lateral condyloid crest, which is concave to straight in *Smilodon*. All these features are present in MLP 94-VIII-10-15, but are absent in *Panthera onca*. Additionally, as indicated above, the general shape of the distal trochlea, the form and size of the supracondyloid foramen, the ridge delimiting the lateral edge of the olecranon fossa, and the morphology of the lateral epicondylar crest in lateral view, are features that may prove useful to differentiate *P. atrox* from *P. onca* (Fig. 3).

Specimen MLP 94-VIII-10-69. It is an incomplete sacrum preserving the first two vertebral centra and the left apophysis of the first sacral vertebra. The sacrum is

proportionally more robust than that of *P. onca*, and similar to that of *P. leo*. The prezygapophyses are strong, and reach the level of the spinal process, in a similar fashion to *P. atrox* (Merriam and Stock, 1932). Both large anterior dorsal foramina are observed. The anterior articular surface with ilium is stout and proportionally wide. In ventral view two large anterior foramina are present. In anterior view, only part of the centrum surface is preserved; the neural canal is transversely wide and dorsoventrally low. The articular surface and prezygapophyses are dorsally projected, more than in *P. onca*, and in a similar fashion to *P. leo* and *P. atrox* (Merriam and Stock, 1932). In sum, the proportions and the general features of MLP 94-VIII-10-69 are similar to those of *P. atrox* and *P. leo*, and differ from those of the smaller *P. onca* (Fig. 4).

Specimen MLP 94-VIII-10-17. It is a nearly complete left metatarsal fourth. This element is large and robust. In anterior and medial views, the cuboid facet is straight (convex in *P. onca*). In medial view, the dorsal facet for metatarsal III is observed. This facet is proportionally larger and more distally extended than in *P. onca*. The dorsal facet for metatarsal V is flat and proportionally large. In proximal view, this facet is rounded, being similar in this aspect to *P. onca*. In lateral view, the dorsal metatarsal V facet is more proximally projected than in *P. onca*. In lateral and medial views, the shaft is nearly straight, contrasting with the bowed condition of *P. onca*. In the proximal half of shaft, the ventral side presents an oval-shaped, large, and rugose surface, with well-defined edges. In contrast, in *P. onca* this surface is feebly developed. The distal end in distal view, shows subparallel medial and lateral edges, while that in *P. onca* both margins are posteriorly divergent projected (Fig. 5).

Remarks. The proportions of MLP 94-VIII-10-17 are similar to those of the remains of *P. atrox* described by Merriam and Stock (1932). In spite of that the size of present specimen (111.2 mm) is slightly lower than the range noticed for *P. atrox* (166.9–135.1 mm), it is far larger than the values reported in fossil and living *P. onca* (see Kurtén, 1965).

Other analyzed specimens (MLP 94-VIII-10-13, MLP 94-VIII-10-16, MLP 94-VIII-10-70, MLP 94-VIII-10-71, MLP 94-VIII-10-93; Fig. 6) lack diagnostic characters and are referred to *P. atrox* only because of their large size, being larger than specimens of *P. onca*.

Remarks on skull remains referred to *P. o. mesembrina*: The cranial and dental remains from Patagonia formerly referred to “*Felis onca mesembrina*” are similar to those of *P. leo* and *P. atrox*, and differ from *P. onca* and *P. tigris* based on some diagnostic features recognized by Christiansen and Harris (2009). Regrettably, as explained above, the more relevant specimens are currently lost, including a well-preserved skull and some complete mandibles illustrated and described in detail by Roth (1904) and Cabrera (1934). Thus, the analysis of cranial and mandibular characters that follows is based on data published by those authors.

In dorsal view, the nasals of *P. leo* and *P. atrox* withdrawn from the nasal basin. This results in that the incisive foramina are clearly visible in dorsal view, usually exposed

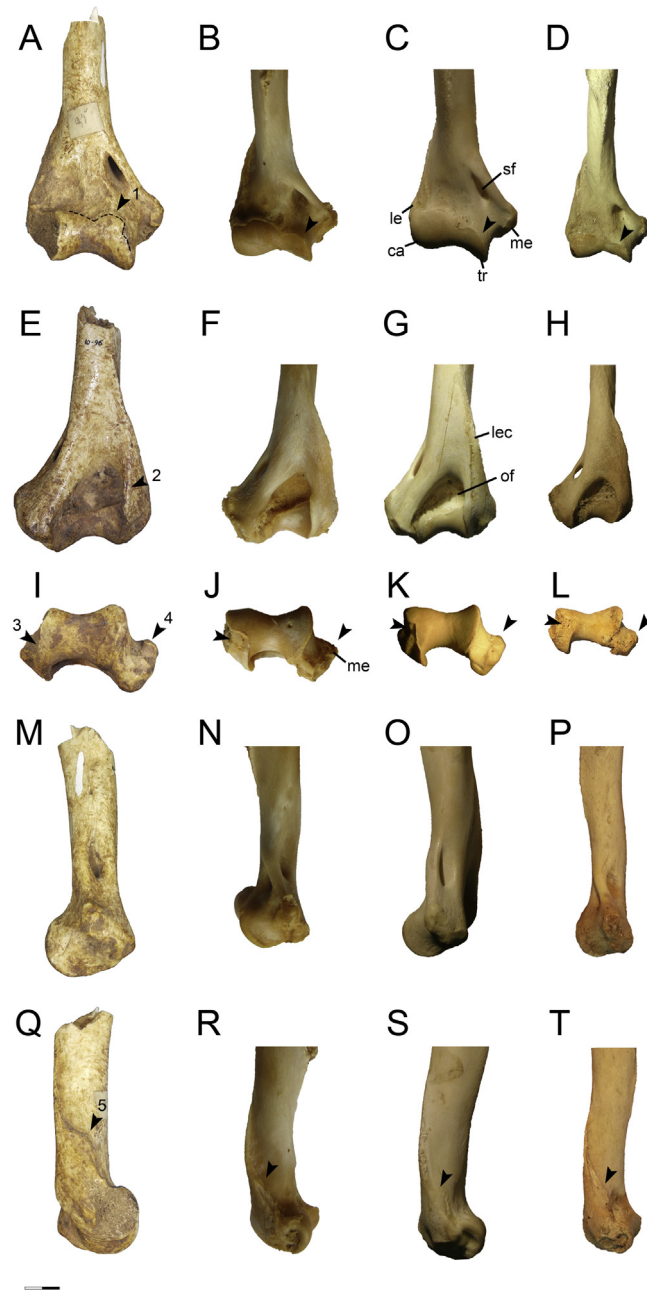


Fig. 3. Right humerus (MLP 94-VIII-10-15) from Cueva Última Esperanza compared with recent specimens of *Panthera onca* in anterior (A–D), posterior (E–H), distal (I–L), medial (M–P), and lateral views (Q–T). Arrows and numbers indicate features discussed in the text: 1, relationship between the proximal margins of trochlea and capitulum; 2, presence/absence of a well-developed ridge delimiting the lateral edge of the olecranon fossa; 3, presence/absence of the medial notch in the lateral ridge of the capitulum; 4, anteroposterior expansion of the medial epicondyle; 5, morphology of the lateral epicondylar crest in lateral view. Abbreviations: ca: capitulum; le: lateral epicondyle; lec: lateral epicondylar crest; me: medial epicondyle; of: olecranon fossa; tr: trochlea; sf: supracondylar foramen. A, E, I, M, Q, MLP 94-VIII-10-15; B, F, J, N, R, CFA 12823; C, G, K, O, S, MACN 51147; D, H, L, P, T, MACN 29.911. Scale bar: 20 mm

Fig. 3. Humérus droit (MLP 94-VIII-10-15) de la grotte Última Esperanza, comparé à ceux de spécimens récents de *Panthera onca* en vues antérieure (A–D), postérieure (E–H), distale (I–L), médiale (M–P) et latérale (Q–T). Les flèches et les numéros indiquent les caractères discutés dans le texte : 1, relation entre les marges proximales de la trochlea et du capitulum ; 2, présence/absence d'une ride bien développée délimitant le bord latéral de la fosse olécranienne ; 3, présence/absence de l'encoche médiale dans la ride latérale du capitulum ; 4, expansion antéro-postérieure de l'épicondyle médial ; 5, morphologie de la crête épicondylaire latérale en vue latérale. Abréviations : ca : capitulum ; le : épicondyle latéral ; lec : crête épicondylaire latérale ; me : épicondyle médial ; of : fosse olécranienne ; tr : trochlea ; sf : foramen supracondylaire. A, E, I, M, Q, MLP 94-VIII-10-15 ; B, F, J, N, R, CFA 12823 ; C, G, K, O, S, MACN 51147 ; D, H, L, P, T, MACN 29,911. Barre d'échelle : 20 mm

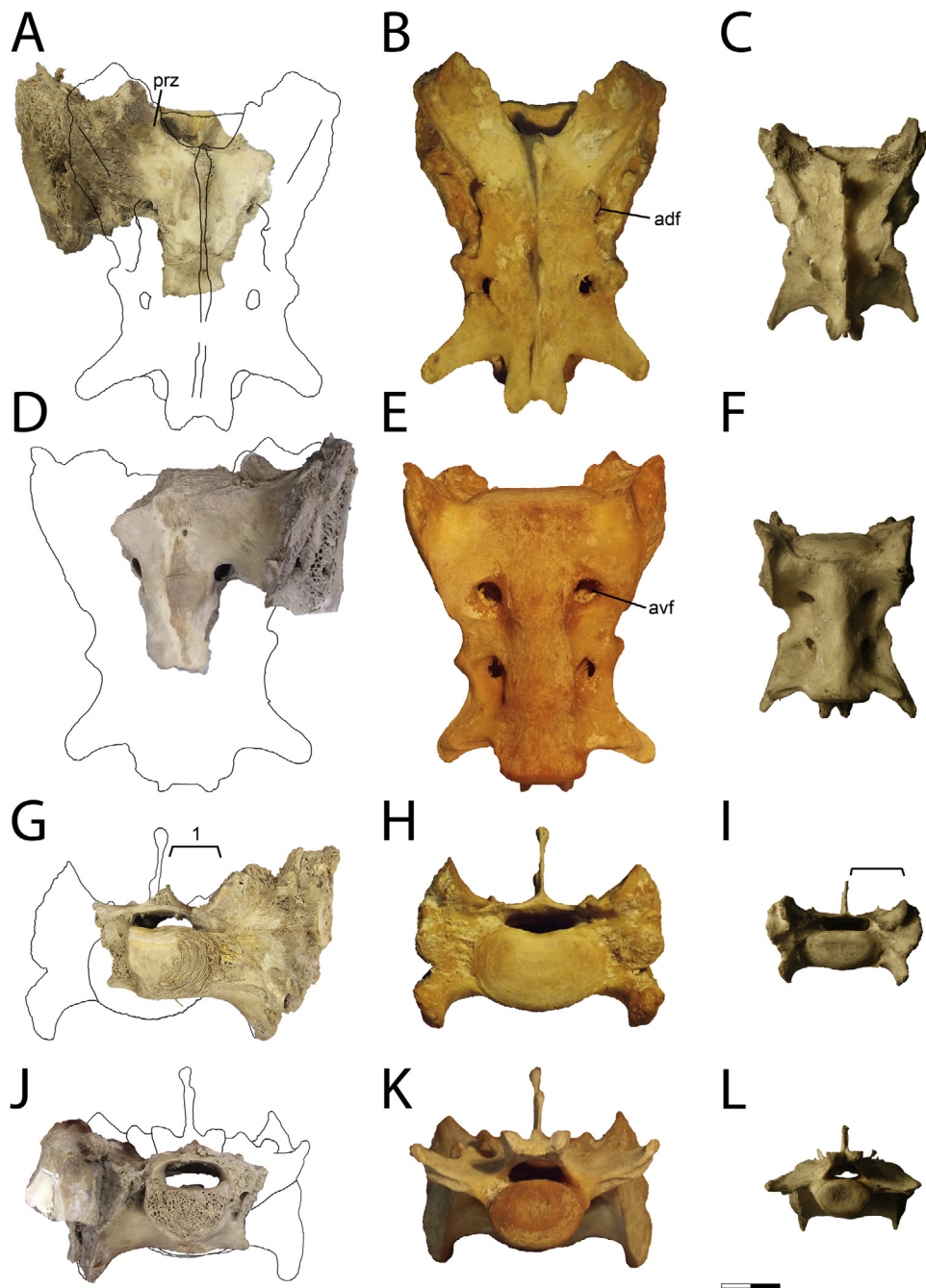


Fig. 4. Sacrum MLP 94-VIII-10-69 (A, D, G, J) compared with living *Panthera leo* (B, E, H, K) and *Panthera onca* (C, F, I, L) in dorsal (A–C), ventral (D–F), anterior (G–I), and posterior views (J–L). Abbreviations: adf: anterior dorsal foramen; avf: anterior ventral foramen; prz: prezygapophysis; 1: distance between the neural spine and the lateral edge of the prezygapophysis. B, E, H, K, MACN 22.3; C, F, I, L, MACN 29.911. Scale bar: 20 mm.

Fig. 4. Sacrum MLP 94-VIII-10-69 (A, D, G, J), comparé avec celui de *Panthera leo* vivante (B, E, H, K) et *Panthera onca* (C, F, I, L) en vues dorsale (A–C), ventrale (D–F), antérieure (G–I) et postérieure (J–L). Abréviations : adf : foramen antérieur dorsal ; avf : foramen antérieur ventral ; prz : prézygapophyse ; 1 : distance entre l'épine neurale et le bord latéral de la prézygapophyse. B, E, H, K, MACN 22,3 ; C, F, I, L, MACN 29,911. Barre d'échelle : 20 mm.

on most of their length. On the contrary, in *P. onca* and *P. tigris* the incisive foramina are totally obscured by the nasals, or only the anterior tip is exposed when viewed dorsally (Christiansen and Harris, 2009). In the photographs of skull published by Cabrera (1934: plate IV) illustrating “*F. o. mesembrina*”, the incisive foramina are clearly visi-

ble in dorsal view in most of their length. Furthermore, the nasals are short and caudally retracted, and the narial opening is wide and with a convex dorsal margin. This nasal retraction and correlated large narial aperture are traits also present in *P. leo* and *P. atrox*, being absent in living *P. onca* (Christiansen and Harris, 2009).

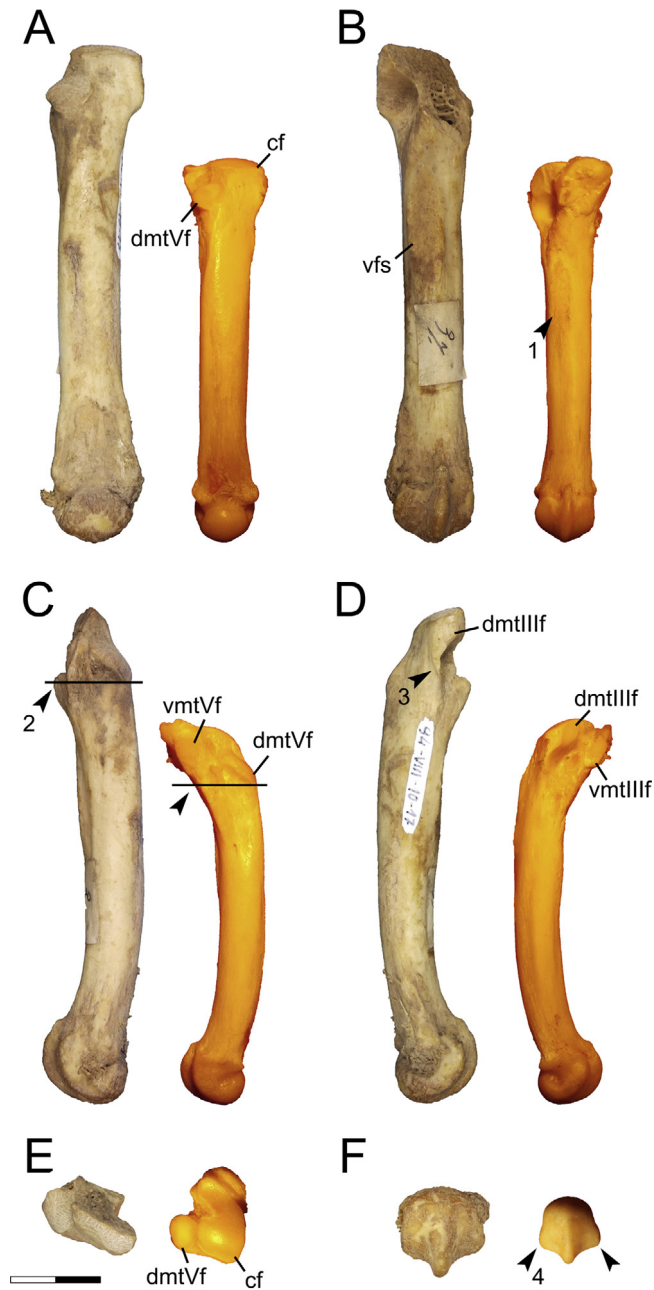


Fig. 5. MLP 94-VIII-10-17 (left) compare with the left metatarsal IV of living *Panthera onca* (MACN 51.147) (right) in dorsal (A), ventral (B), medial (C), lateral (D), proximal and anterior (E) and distal and posterior views (F). Abbreviations: cf: cuboid facet; dmtIIIcf: dorsal metatarsal III facet; dmtVf: dorsal metatarsal V facet; vmtIIIcf: ventral metatarsal III facet; vmtVf: ventral metatarsal V facet; vfs: ventral flat surface. Arrows indicate: 1: differences in ventral surfaces; 2: position of the dorsal metatarsal V facet; 3: elongation and distal extension of the dorsal metatarsal III facet; 4: projections of medial and lateral edges of the distal end. Scale bar: 20 mm.

Fig. 5. MLP 94-VIII-10-17 (à gauche), à comparer avec le métatarsien IV gauche de *Panthera onca* vivante (MACN 51.147, à droite), en vues dorsale (A), ventrale (B), médiale (C), latérale (D), proximale et antérieure (E), distale et postérieure (F). Abréviations : cf : facette cuboïde ; dmtIIIcf : facette dorsale du métatarsien III ; dmtVf : facette dorsale du métatarsien V ; vmtIIIcf : facette ventrale du métatarsien III ; vmtVf : facette ventrale du métatarsien V ; vfs : surface ventrale plate. Les flèches indiquent : 1 : les différences dans les surfaces ventrales ; 2 : la position de la facette dorsale du métatarsien V ; 3 : l'élongation et l'extension distale de la facette dorsale du métatarsien III ; 4 : les projections des bords médiaux et latéraux de la terminaison distale. Barre d'échelle : 20 mm.

Another feature distinguishing the snout of *P. leo* and *P. atrox* from *P. onca* and *P. tigris* consists on its gross shape. In dorsal view, the snouts of *P. onca* and *P. tigris* are short and heavy, and widen progressively towards the anterior

margin of the premaxilla. This results in snout margins laterally concave when viewed dorsally. On the contrary, in *P. leo* and *P. atrox* the snouts are longer, and taper slightly towards the anterior margin of the premaxilla, which

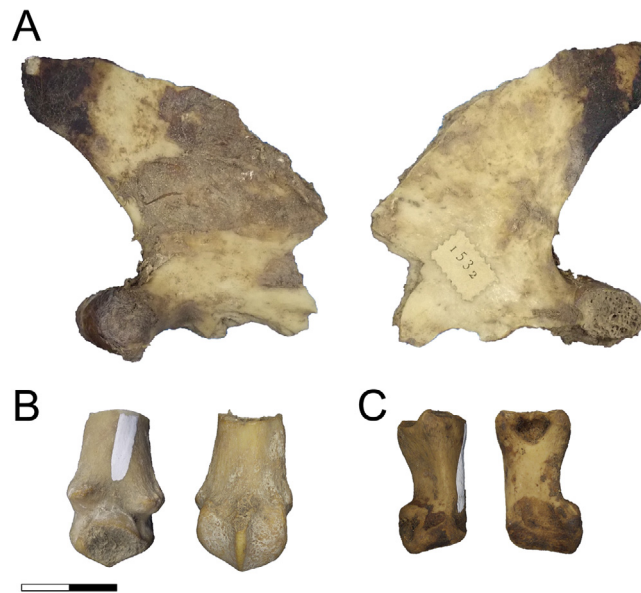


Fig. 6. Other bones of the “*P. o. mesembrina*” from Cueva Última Esperanza. **A.** MLP 94-VIII-10-13, posterior fragment of the hemimandible in medial (left) and lateral views (right). **B.** MLP 94-VIII-10-16, distal end of metapodial in dorsal (left) and ventral views (right). **C.** MLP 94-VIII-10-93, isolated non-ungual phalanx in dorsal (left) and ventral views (right). Scale bar: 20 mm.

Fig. 6. Autres os de « *P. o. mesembrina* » de la grotte d'Última Esperanza. **A.** MLP 94-VIII-10-13, fragment postérieur de l'hémimandibule en vues médiale (à gauche) et latérale (à droite). **B.** MLP 94-VIII-10-16 terminaison distale du métapode en vues dorsale (à gauche) et ventrale (à droite). **C.** MLP-94 VIII-10-93, phalange isolée non unguéale en vues dorsale (à gauche) et ventrale (à droite). Barre d'échelle : 20 mm.

results in laterally straight or slightly convex snout margins (Christiansen and Harris, 2009). In the photographs of the skull of “*F. o. mesembrina*” published by Cabrera (1934: plate IV), and Roth (1904: plate I, figure 2) the snout condition of this taxon is indistinguishable from that of *P. leo* and *P. atrox*.

There are some features in the mandibles referred to “*F. o. mesembrina*” that ally it with *P. atrox*, and distinguish it from other felids. As for example, the ventral margin of the mandibular ramus is convex on its mid-section, a condition present in *P. leo*, *P. onca*, and *P. atrox*, but absent in *P. tigris* (Boule, 1906; Christiansen and Harris, 2009; Whitmore and Foster, 1965). In the complete anterior dentary described and illustrated by Nami (1987) and Martin (2013) the mandibular symphysis is clearly set off from the horizontal ramus, a condition that distinguishes *P. atrox* from *P. leo* (Christiansen and Harris, 2009). Furthermore, it may be also distinguished from *P. leo* in having a non-tapering anterior end, and larger c1 alveolar width (Christiansen and Harris, 2009; see above).

Regarding the dentition, most features used by previous authors with the aim to distinguish species within *Panthera* have been proven strongly variable within each species by Christiansen and Harris (2009), and most dental measurements show at least partial overlapping among the species. However, Christiansen and Harris (2009) noted that in some proportions *P. atrox* and *P. leo* can be distinguished from tigers and jaguars. Although dental material is scarce in “*F. onca mesembrina*”, some of these dental proportions can be checked in available specimens. The lower first molar shows a protoconid height relative to

molar length ratio of 0.56, a number within *P. atrox* and *P. leo* ranges, far from *P. onca*, which shows proportionally smaller protoconid (Christiansen and Harris, 2009).

In addition, there are several measurements that may allow inclusion of “*F. o. mesembrina*” within *P. atrox*. The anteroposterior length of p3 range in *P. atrox* is of 17–21.6 mm (Kurtén, 1965; Merriam and Stock, 1932), whereas the size is much smaller in *P. onca*, which ranges from 11.8–16.9 mm. In the only available specimen of “*F. o. mesembrina*” is of 20 mm (Roth, 1904), being within the *P. atrox* range. The anteroposterior length of p4 range in *P. atrox* is of 25.8–32.3 mm (Merriam and Stock, 1932; Kurtén, 1965), in the only available specimen of “*F. o. mesembrina*” is of 24 mm (Roth, 1904), whereas the size is smaller in *P. onca*, which ranges from 19–23.2 mm (Kurtén, 1965). Finally, the anteroposterior length of m1 in *P. atrox* ranges from 25 to 33.7 mm (Carbot-Chanona and Gómez-Pérez, 2014; Kurtén, 1965, 1985; Merriam and Stock, 1932; Montellano-Ballesteros and Carbot-Chanona, 2009; Whitmore and Foster, 1965), between 26–31 in “*F. o. mesembrina*” (Cabrera, 1934; Roth, 1904), and from 18–24.8 mm in *P. onca* (Cabrera, 1934; Kurtén, 1965, 1973; Simpson, 1941). The upper canine alveolar width of “*F. o. mesembrina*” (24 mm) is within the range of *P. atrox*, different from the smaller canines known for *P. onca* and *P. leo* (Christiansen and Harris, 2009).

In sum, qualitative characters, proportions of dental elements, and size of teeth indicate that “*F. o. mesembrina*” is within the range of variation of *P. atrox*, and differs from other pantherines, including the jaguar *Panthera onca* (Table 1 and Fig. 7). Thus, on this basis, we here propose that

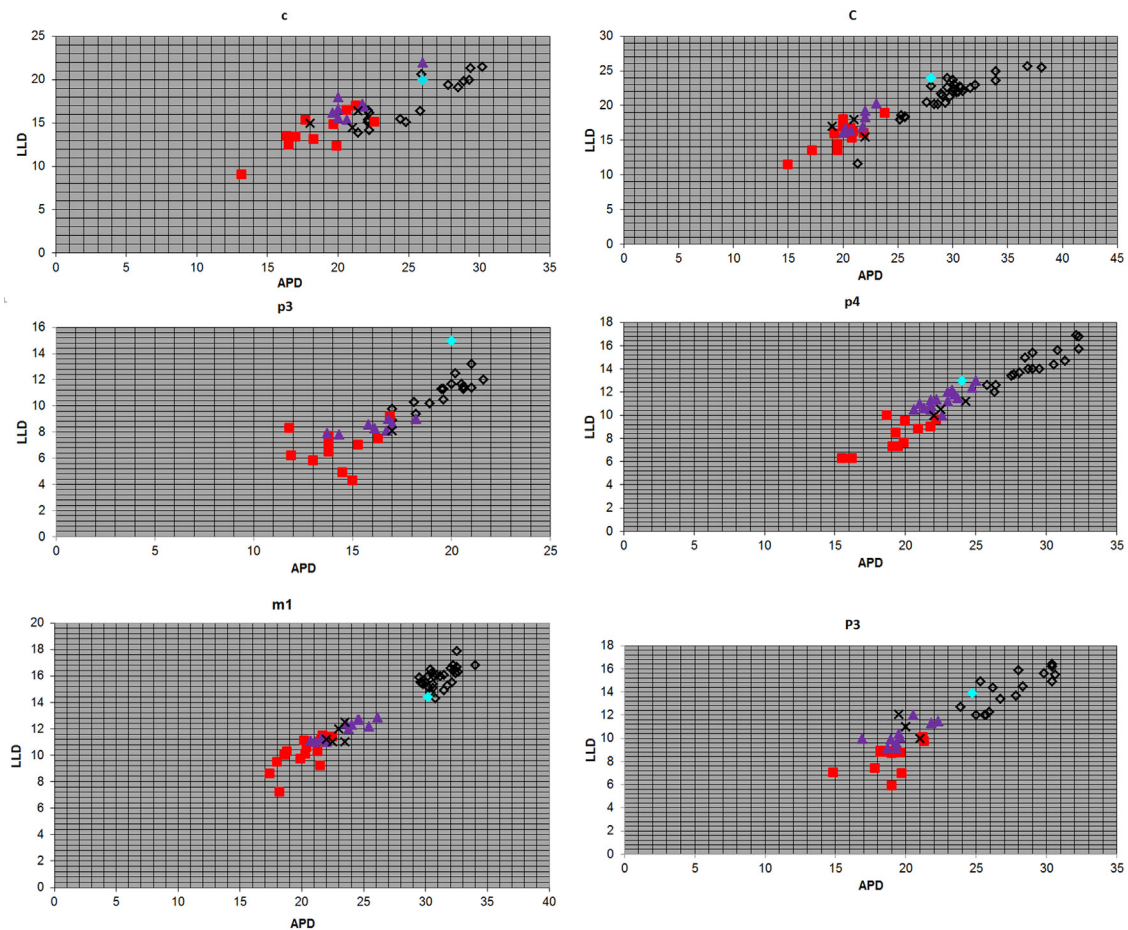


Fig. 7. Bivariate plots of dental remains of “*P. o. mesembrina*” (filled rhombus), *Panthera atrox* from North America (open diamond), *Panthera onca* from the Pleistocene of North America (triangles), *Panthera onca* from the Pleistocene of South America (cross) and recent specimens of *Panthera onca* (squares). Abbreviations: c: lower canine; C: upper canine; p3: lower third premolar; p4: lower fourth premolar; m1: lower first molar; P3: upper third premolar; APD: anteroposterior diameter; LLD: labiolingual diameter. Specimens analyzed and measurements indicated in the [Supplementary Material](#).
Fig. 7. Diagramme de restes dentaires de « *P.o. mesembrina* » (rhombes noirs), *Panthera atrox* d’Amérique du Nord (losanges blancs), *Panthera onca* du Pléistocène d’Amérique du Nord (triangles), et spécimens récents de *Panthera onca* (carrés). Abréviations : c : canine inférieure ; C : canine supérieure ; p3 : 3^e prémolaire inférieure ; p4 : 4^e prémolaire inférieure ; m1 : première molaire inférieure ; P3 : 3^e prémolaire supérieure ; APD : diamètre antéro-postérieur ; LLD : diamètre labio-lingual. Spécimens analysés et mesures indiqués en matériel supplémentaire.

Panthera onca mesembrina (Cabrera, 1934) should be considered as a junior synonym of *Panthera atrox* (Leidy, 1853).

4. Discussion

Body Mass estimation. The size of the m1 in the felid is the classic best gauge of body mass (Legendre and Roth, 1988; VanValkenburgh, 1990). We calculated the body mass (BM) of *P. o. mesembrina* using the m1 measurements, following the proposal of VanValkenburgh (1990) with the formula:

$$\log \text{BM} = 3.05 \times \log \text{m1L} - 2.15 = 231.2$$

We determined a body mass of 231.21 kg for “*Panthera onca mesembrina*”. This value is well within of the range of the males of *Panthera atrox* (Wheeler and Jefferson, 2009), whereas the values are much smaller in *Panthera onca* (Christiansen and Harris, 2005; Prevosti and Vizcaíno,

2006). Further, this body mass is within the range of largest felids, such as *Smilodon fatalis* and *S. populator* (Christiansen and Harris, 2005).

Recently, Prevosti and Martin (2014) made a mass calculation of “*P. onca mesembrina*” based on some unpublished fossil remains. They obtained values between 190 kg to 243 kg, based on the length of m1 of different individuals (see Prevosti and Martin, 2014: Supplementary data 1). It is worth mentioning that the living *P. onca* shows values near 100 kg (102 kg *sensu* Sunquist and Sunquist, 2002), and exceptionally upper values of 158 kg (Seymour, 1989). Further, the large extinct North American jaguar *P. onca augusta*, was 15 to 20% larger than living jaguar, being less than 190 kg (Seymour, 1989).

In this way, the mass calculation for “*P. o. mesembrina*” obtained by Prevosti and Martin (2014) and present paper points that the Patagonian *Panthera* was a felid that duplicates the size of living or extinct jaguars.

Additionally, based on body mass determination, it is possible to calculate the focused prey size of “*P. o. mesembrina*” on the basis of the following formula (Hemmer, 2004):

$$\log \text{PFM} = 1.917 \log \text{BM} - 1.710 = 663.4 \text{ kg}$$

This value is larger than that known for any living felid. In fact, the prey range in *P. leo* is between 15 to 1000 kg, whereas the focused prey size is of 200 kg (Christiansen and Harris, 2005; Sunquist and Sunquist, 2002). The values here calculated for “*P. o. mesembrina*” are within the range of ratios calculated for *Smilodon* (Christiansen and Harris, 2005; Prevosti and Vizcaíno, 2006; Sunquist and Sunquist, 2002).

On the other hand, the jaguar is a felid with a calculated maximum prey size of 582 kg (Prevosti and Vizcaíno, 2006), that preys upon large to mid-sized animals using ambush or stalk-short chase strategies (Eisenberg and Redford, 1999). In this regard, analyses regarding the paleoecological relationships of carnivorous and herbivorous mammals in the Pleistocene considered the “*P. o. mesembrina*” remains from Patagonia as belonging to living jaguar species, and consequently, were regarded as having the same prey-range (or a bit larger) than living specimens (e.g., Fariña, 1995; Fariña et al., 2013; Prevosti and Vizcaíno, 2006). However, Borrero (1994, 1997, 2001) and Borrero and Martin (1996) reported several lines of evidence indicating that the “Patagonia *Panthera*” preyed upon much larger animals than living jaguars. These authors indicate that, in addition to fossil horses (*Hippidion* sp.) and camelids, the extinct “*F. o. mesembrina*” predated upon Megafauna, such as *Myloodon listai*, which had a mass of 1000 kg (Fariña et al., 1998), which is much larger than the previously calculated maximum prey size, in agreement with the prey range here proposed. In this line, Borrero (1994, 2001), and Borrero and Martin (1996) indicate the presence of tooth marks referred to “*F. o. mesembrina*” in a femur referable to *Myloodon* coming from the site Dos Herraduras 3. In addition, Borrero (2001) illustrated and described from the “Cueva del Milodón” the presence of a large number of *Myloodon* dermal ossicles in a coprolite referable to “*P. o. mesembrina*”. Lately, Martin (2013) reported several *Myloodon* specimens, including a skull, showing deep tooth marks in the hind margin of the parietals, that may referable to a giant felid, in all probability to “*F. o. mesembrina*” (Martin, 2013).

This evidence suggests that *Panthera atrox* consumed very large preys, a fact that is in agreement with the prey size here calculated, and both indicate that this large felid may played a different paleoecological role than advocated previously.

Evidence of external aspect in *Panthera atrox*. *P. atrox* is not an uncommon member of the North American Pleistocene mammalian fauna, and is frequent in a large number of Rancholabrean assemblages (Kurtén and Anderson, 1980). Despite that, the species was only known of the basis of skeletal elements. With the inclusion of Patagonian remains within *P. atrox*, several lines of evidence allow us to recognize gross details of the external aspect in this species.

Lehmann-Nitsche (1899) mentioned the presence of some skin patches in the Pleistocene of “Cueva del Milodón” that pertained to “*F. o. mesembrina*”. Later, Roth (1904) described in detail a piece of skin adhered to the face and to the forelimb, as well as an isolated patch of leather. The skin of the face indicates a reddish brown tone (rufous), a color that constituted the background of available skin patches from the limbs and body (Fig. 8). Additionally, based on these remains, Roth (1904) indicates that the species probably exhibited dark and some yellowish color stripes, at least in the forelimbs.

In the same line of evidence, Cardich (1979, 1987) reported the illustration of a jaguar-like felid from the El Ceibo site, Santa Cruz province, Argentina. This author found among a large number of guanaco silhouettes and human hand representations, a very large feline illustration. This representation is very large (1.5 meters long) when compared to those of other animals found in the same site, suggesting that this taxon had some impressive aspect for the native people (Cardich, 1979). The coloration of the drawing includes a reddish background, with some black spots, and the forearm is slightly lighter than the rest of the body. This coloration is totally concordant with the small skins samples found in the “Cueva del Milodón”, and very probably pertain to the same taxon (Borrero, 2001; Cardich, 1979).

In sum, the patchy evidence here reported may allow us to recognize main coloration patterns for *P. atrox*. This felid was externally jaguar-like, with the body covered by black spots, but differed in having a deep reddish background and yellowish striped forelimbs.

Notes on the behavior of *Panthera atrox*. Regarding behavior, most evidence on the habits of *P. atrox* comes from the Rancholabrean deposits, and most data comes from skeletal frequencies and recognition of sexual dimorphism (see details in Wheeler and Jefferson, 2009).

P. atrox was described as a giant jaguar by Merriam and Stock (1932), Cabrera (1941), Simpson (1941), and Christiansen and Harris (2009). However, authors agree in that *P. atrox* inhabited open and dry environments rather than forested areas, in contrast to living *P. onca* (Sunquist and Sunquist, 2002). In fact, the highly cursorial morphology of *Panthera atrox* is probably convergent with that of *P. leo*, which is adapted to the Africa savannah. *Panthera atrox* effectively occupied open plains habitats exclusively, and probably developed its distinctive morphology as a result (Barnett et al., 2006, 2009; Martin et al., 1977; Wang and Martin, 1993; Wheeler and Jefferson, 2009). This is in agreement with the habitats were “*F. o. mesembrina*” was found, which consisted in open and very dry environments of southern Chilean and Argentinean Patagonia, very different from the habitats occupied by the living jaguar *P. onca* (Carman, 1984; Diaz, 2010).

Probably, one of the most interesting findings regarding the behavior of “*F. o. mesembrina*” was reported by Borrero (1997). He described a fossiferous site consisted on a deep cave and burrow with large accumulation of very large mammals including *Myloodon*, *Lama*, *Hippidion*, *Hippocamelus*, and others, with abundant tooth marks and broken bones. These authors analyzed in detail this discovery, and conclude that it belonged to a large felid burrow,



Fig. 8. MLP 94-VIII-10-70, isolated claw (top left) and MLP 94-VIII-10-71, fragment of skin.
Fig. 8. MLP 94-VIII-10-70, griffe isolée (en haut à gauche) et MPL 94 VIII-10-71 ; fragment de peau.

and was referred to “*F. o. mesembrina*” based on the size of tooth marks on preyed bones, and other taphonomical features of the site. It is worth to mention that in such sites the forelimbs of preys are much more frequent than other elements, which is in agreement with the model of consumption of living felids, which more commonly transport the hindlimbs to their burrows (Blumenshine, 1986; Blumenshine and Marean, 1993). Later, Martin (2008, 2013) corroborated such referral and added other localities bearing bone accumulation sites in burrows pertaining to “*F. o. mesembrina*”. The capacity of transport and accumulate carcass of preys is relatively uncommon in felids, and is present in a couple of species. Among pantherines it is present in lion and leopard (Egeland, 2007). As, for example, the leopard *Panthera pardus* employs caves as places of feeding and breeding, preferring dark enclosures for such object (Brain, 1981; De Ruiter and Berger, 2000; Sauqué et al., 2014). A similar behavior was also reported in extinct taxa, such as *Homotherium* (Dominguez-Rodrigo et al., 2007; Marean and Ehrhardt, 1995). In this regard, it has been reported that the jaguars only occasionally transport their prey to rocky burrows (Lewis, 1997; Martin, 2013) but this is uncommon nowadays. In any case, they do not accumulate remains of different preys in the same cave, contrasting with the giant Patagonian pantherine (Tonni et al., 2003).

Specimens of *P. atrox* from the latest Pleistocene have often been interpreted as having formed social groups (Turner and Antón, 1997; Yamaguchi et al., 2004). However, Wheeler and Jefferson indicate the absence of evidence arguing in favor or against social behavior of *P. atrox*. In this regard, the holotype skull of “*F. o. mesembrina*” shed some light in this respect. In jaguar skulls, both living and fossil, is common to find the presence of a shallow irregular pit on the lateral surface of the maxilla-nasal suture immediately posterior to the ascending process of the premaxilla; this represents a puncture by the canine made by other jaguar, healed during life (Simpson, 1941). As this author pointed out, all wild-collected specimens with such punctures were males, and no females with such scars were found everywhere. The presence of a puncture on the lateral surface of the skull in “*F. o. mesembrina*” described by Cabrera (1934) suggests that the specimen was a male. Furthermore, it also suggests that some kind of social behavior may have occurred among *Panthera atrox* individuals.

In sum, evidence at hand indicates that the behavior of *Panthera atrox* from Patagonia was different from *P. onca* and was more similar in this aspect to Old World *P. leo* and *P. leopardus*.

Palaeobiogeography. The phylogenetic affinities among pantherines, and specifically of *P. atrox* are in state

of flux. The most comprehensive morphological analyses including living and extant taxa are those of Christiansen (2008a) and King and Wallace (2014), and the molecular analysis of Barnett et al. (2009). Christiansen (2008b) proposes *P. onca* and *P. atrox* as successive stems towards the lion-cave lion-leopard clade. On the other hand, in King and Wallace (2014) phylogeny the position of both *P. atrox* and *P. onca* was not fully resolved. However, they propose a basal position for *P. onca* and a more derived position, nested within the lion lineage, for *P. atrox*. Barnett et al. (2009) also indicate that *P. atrox* was well-nested within the lion clade, whereas *P. onca* was considered as basal within the genus.

Fossil evidence of the *onca-leo* lineage began in the Villafranchian (1.9. Myr) in Europe (Hemmer et al., 2001), and the first presence of jaguar lineage in the Americas was reported as early Irvingtonian (Kurtén and Anderson, 1980) which is 1.5 Myr. Based on this fossil record and phylogenetic hypotheses, Christiansen and Harris (2009; see also Yamaguchi et al., 2004) propose that the *Panthera* lineage entered in North America by the early Pleistocene and later evolved in the modern jaguar, including extinct subspecies. Subsequently this lineage entered South America probably by late Pleistocene times (Yamaguchi et al., 2004). Christiansen and Harris (2009) further indicate that this palaeobiogeographical scenario is congruent with the geographical distribution of the modern jaguar, and its presence in the Rancho La Brea deposits (Merriam and Stock, 1932), a hypothesis that was followed by most recent authors.

However, most authorities do not discuss in detail the fossil record of the *Panthera* lineage in South America. At first, it is worthy to mention that remains assignable to *Panthera onca* are present in South America at least since the early-middle Pleistocene “Ensenadan” times (Ameghino, 1904; Berman, 1994; Cruz et al., 2012; Rusconi, 1929, 1949). In fact, Rusconi (1929) reported the presence of *Felis proplatensis* (= *Panthera onca*, sensu Cabrera, 1934) based on a single metatarsal III. This element was large-sized but relatively gracile, indicating, based on Rusconi’s data, that it certainly belongs to a *Panthera* species, the size of *P. onca*. Later, Rusconi (1949) confirmed the presence of *Panthera onca* (described by him under the name *Panthera proplatensis*) for the “Ensenadan” age based on a nearly complete mandible the size of a living jaguar. This suggests that the *Panthera* lineage has a longer history in South America, and blurs palaeobiogeographical hypotheses proposing not only its arrival time from North America, but also the place of origin of its lineage. Furthermore, if the phylogenetic hypothesis of Christiansen (2008b) is followed, the presence of the stem-lions *P. onca* and *P. atrox* in America may suggest that the lion lineage may have its origin in America rather than in the Old World as previously advocated (see Yamaguchi et al., 2004). However, evidence is still sparse, and more detailed studies and the finding of new material is needed to accept or refute palaeobiogeographical hypotheses regarding the origin and radiation of *Panthera* lineage in the Americas.

Regarding *P. atrox*, its confirmed presence south to the continental ice sheet in North America is first documented from the Rancholabrean (Kurtén and Anderson, 1980). In

this regard, purported Late Pleistocene Peruvian *P. atrox* were sustained by Kurtén and Anderson (1980; but see Seymour, 1983), and were considered as a late arrival of the species to South America by Yamaguchi et al. (2004). Further, Shockey et al. (2009) mention remains of a very large felid of the *Panthera* genus from the late Pleistocene at Jatun locality, Perú that may prove to belong to *P. atrox*. It is worthy to mention that based on the fossil record, the species *P. atrox* appears to be restricted to the Andean-Patagonian region, whereas remains of *P. onca* are usually found in eastern side of the Andes (see exceptions in Hoffstetter, 1949). This pattern of two dispersal corridors along South America was also recognized for herbivorous mammals, including proboscideans and equids (Gallo et al., 2013; Prado et al., 2005).

The presence of at least two pantherine lineages (i.e. *P. onca* and *P. atrox*) in the Pleistocene of South America indicates that the clade has a long and complex history in the New World, and that the history of the lineage in this landmass is still far from being well understood.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2017.06.009>.

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