Rev. bras. paleontol. 11(3):199-206, Setembro/Dezembro 2008

doi: 10.4072/rbp.2008.3.06

NEW POSTCRANIAL REMAINS OF *SMILODON POPULATOR* LUND, 1842 FROM SOUTH-CENTRAL BRAZIL

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ABSTRACT – The postcranial remains of the saber-toothed cat *Smilodon populator* dealt with here corresponds to the first occurrence of the taxon in the State of São Paulo, filling a gap in its geographical distribution. The fossils were collected in Abismo Iguatemi, a karstic fissure located in the municipality of Apiaí, upper Ribeira River valley. Given that the described specimens share equivalent size, similar preservation, and were found relatively close to one another, without duplicated elements, it is suggested that these belong to a single individual. Concerning the accumulation, this animal might have entered the fissure partially or completely articulated, either trapped or dragged by pluvial flood as a carcass. In this context, the fragmentation and weathering of the fossils seem related to reworking inside the cave. Comparative measurements show that the studied material dimension is, on average, larger than North American forms and approximate to other South American specimens, that are admittedly larger and more robust.

Key words: *Smilodon populator*, megafauna, Quaternary, Abismo Iguatemi, São Paulo State, Brazil.

RESUMO – Os elementos pós-cranianos do tigre-dentes-de-sabre *Smilodon populator* aqui tratados correspondem à primeira ocorrência do táxon no estado de São Paulo, o que vem a preencher uma lacuna em sua distribuição geográfica. Os fósseis provêm do Abismo Iguatemi, depressão de origem cárstica localizada no município de Apiaí, Alto Vale do Ribeira. Dado que os elementos esqueletais apresentam tamanho equivalente, preservação similar e foram encontrados próximos uns aos outros, sem elementos duplicados, assume-se que pertençam a um único indivíduo. Quanto ao modo de acumulação, infere-se que o material tenha adentrado o abismo parcial ou completamente articulado, por queda acidental do animal ainda vivo ou arraste da carcaça pela água pluvial. Neste contexto, a fragmentação/abrasão dos fósseis se relacionaria ao retrabalhamento dentro da caverna. Medidas comparativas revelaram que as dimensões do material estudado são, em média, maiores que aquelas de formas norte americanas e aproximam-se daquelas de outros espécimes sul americanos, reconhecidamente maiores e mais robustos.

Palavras-chave: *Smilodon populator*, megafauna, Quaternário, Abismo Iguatemi, São Paulo, Brasil.

INTRODUCTION

The South American saber-toothed cat is known since the middle of the 19th century (Lund, 1842), and represents one of the better known components of the Quaternary faunas of that continent (Burmeister, 1866; Churcher, 1967; Berta, 1985). In Brazil it has been registered in Pleistocene-Holocene deposits of Minas Gerais (Paula-Couto, 1980a; Piló & Neves, 2003), Paraíba (Paula-Couto, 1980b), Ceará (Paula-Couto, 1980b; Gomide *et al.*, 1987; Bergqvist *et al.*, 1997), Goiás (Gomide *et al.*, 1987), Bahia (Cartelle & Abuhid, 1989; Cartelle & Hartwig, 1996; Lessa *et al.*, 1998), Rio Grande do Sul (Lessa *et al.*, 1998; Rodrigues *et al.*, 2004), Rio Grande do Norte (Lessa *et al.*, 1998; Porpino *et al.*, 2004), Piauí (Guerin *et al.*, 1999), Pernambuco (Silva *et al.*, 2003) and Sergipe (Dantas *et al.*, 2003; Dantas & Zucon, 2004). The studied material corresponds to the first occurrence of a saber-toothed cat in São Paulo State (Ferreira & Karmann, 2002; Hingst-Zaher *et al.*, 2003; Castro, 2005), filling a gap in the geographical distribution of these animals.

The species composition of the genus *Smilodon* is controversial. Paula-Couto (1979) defined a single species, *S. populator* Lund, 1842, with two subspecies, *S. populator populator* and *S. populator californicus*, respectively corresponding to the South and North American members of the genus. Other authors (e.g., Kurtén & Anderson, 1980)

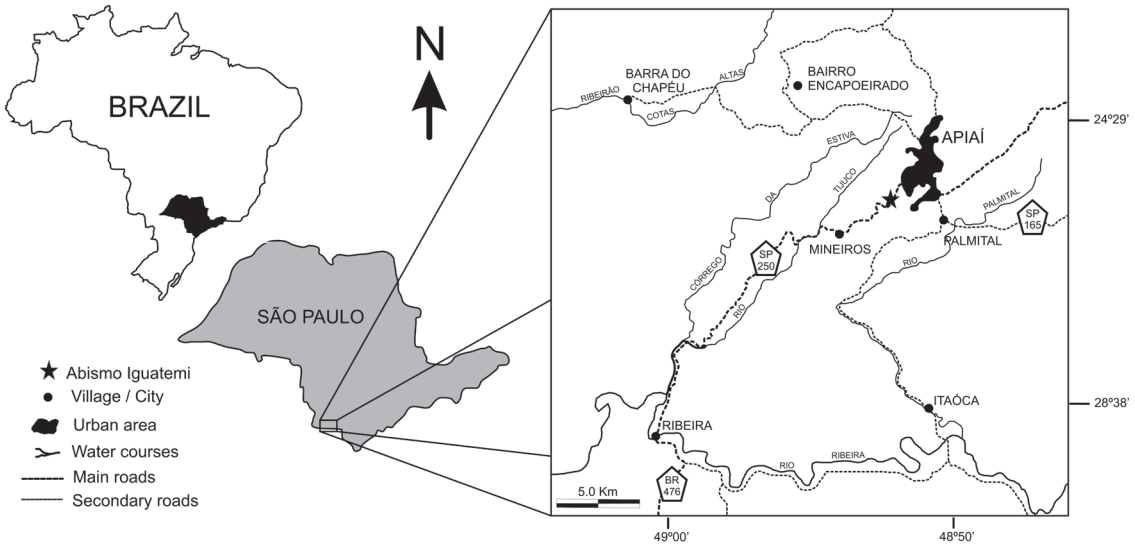

Figure 1. Location map of Abismo Iguatemi locality, in São Paulo State, Brazil.

accept a specific differentiation between these forms, applying the name *S. fatalis* Leidy, 1869, to the North American form, given its priority over *S. californicus* Bovard, 1907. More recently, *S. gracilis* Cope, 1880 was acknowledged as a third and more basal taxon, restricted to the Late Pliocene-Middle Pleistocene of North America (Kurtén & Werdelin, 1990). This paper will adopt the scheme proposed by Berta (1985), in which *Smilodon populator* represents the only South American saber-toothed cat. In any case, even in the three-species scheme proposed by Kurtén & Werdelin (1990), all the cis-Andean *Smilodon* forms (including the Brazilian ones) are referred to *S. populator*. The nomenclatural status of *S. populator* is also questionable (see Burmeister, 1866; Lund, 1950; Churcher, 1967), given the possible priority of other specific names such as "*Hyaena*" *neogaea* Lund, 1839 and "*Felis*" *protopanther* Lund, 1839. Yet, we will follow the orthodoxy (Paula-Couto, 1979; Berta, 1985; Kurtén & Werdelin, 1990) and refer the Brazilian saber-toothed cat to *S. populator*.

The fossils described here have been collected in the 44 m in plan and 15 m deep karstic fissure known as Abismo Iguatemi (Figure 1). This was formed in the intensively folded rocks of the Açungui Group (Middle Proterozoic) that includes metamorphized dolomitic limestones intercalated with insoluble lithologies (Auler & Farrant, 1996). The fissure was initially explored by Ferreira & Karmann (2002), who named the site and retrieved paleontological material, including a skull and both mandibular rami possibly associated with the specimens described herein. This skull presents prominent post-orbital process, long post-canine diastema, and absence of the second premolar teeth (Hingst-Zaher *et al*., 2003). The cave deposits are mainly composed of a black to reddish clay associated with larger clasts of limestone, filite and calcite crusts. Concerning the age of this material, recent C^{14} AMS (Accelerator Mass Spectrometry) dates of *Smilodon populator* were given as 14,580 years BP (Alex Hubbe; verbal comm. 30/05/2008).

MATERIAL AND METHODS

The skeletal remains described here were collected by members of the Museu de Zoologia of the Universidade de São Paulo and are deposited at the fossil collection (MZSP) of that institution. Given the rarity of comprehensive osteological descriptions of Brazilian saber-toothed cats (Cartelle & Abuhid, 1989), the main reference adopted for anatomical nomenclature and measurements was the study of Merriam & Stock (1932) on *S. fatalis* from Rancho La Brea, with complementary data from Cartelle & Abuhid (1989) and Rodrigues *et al.* (2004). For anatomical terminology, Nomina Anatomica Veterinaria (ICVGAN, 2005) was followed whenever possible.

SYSTEMATIC PALEONTOLOGY

CARNIVORA Bowdich, 1821
FELIDAE Fischer, 1817
MACHAIRODONTINAE Gill, 1872
Smilodon populator Lund, 1842
(Figures 2-5, Tables 1-3)

Specific assignation. The diagnosis of *S. populator* (Paula-Couto, 1955; Berta, 1985; Kurtén & Werdelin, 1990) includes characters that can not be observed in the specimens of Abismo Iguatemi. However, the possibly associated skull falls into the morphometric range of that taxon (Hingst-Zaher *et al.*, 2003). Additionally, Paula-Couto (1955) stated that the South American saber-toothed cats usually have longer and stouter long bones than those of North America, a condition observed in the material described here.

Material. MZSP-PV 07, 08, thoracic vertebrae; MZSP-PV 09-14, 16, 18, 19, 21, ribs; MZSP-PV 05, right ulna; MZSP-PV 04 left radius; MZSP-PV 02,03 left and right innominates; MZSP-PV 01, left femur; MZSP-PV 06, right astragalus. MZSP-PV 15, 17, 20, anatomically indeterminate elements that may not

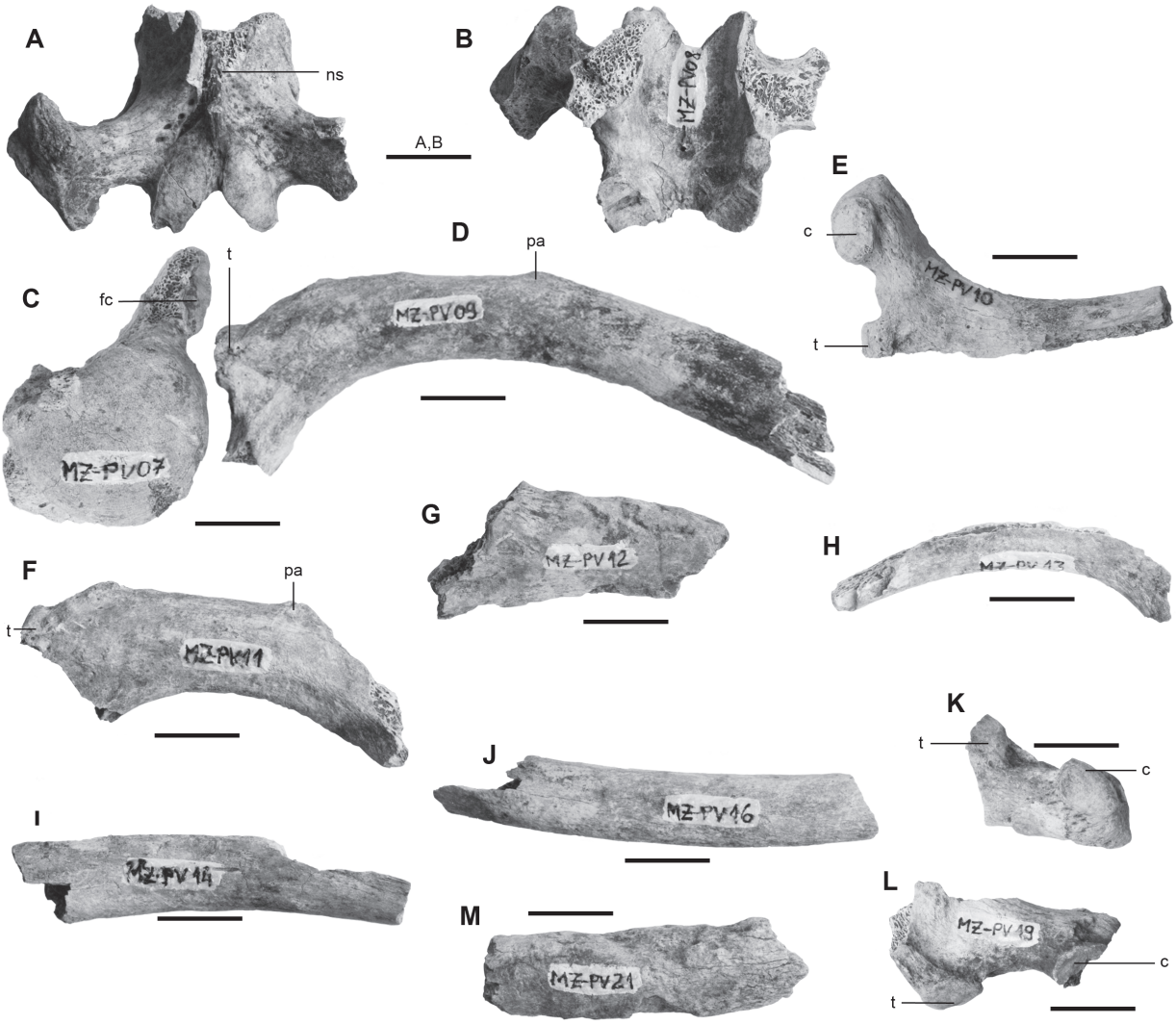

Figure 2. *Smilodon populator* from Abismo Iguatemi, vertebrae (A-C) and rib fragments (D-M): **A**-**B**, MZSP-PV 08 in dorsal (**A**) and ventral (**B**) views; **C,** MZSP-PV 07; **D**, MZSP-PV 09; **E**, MZSP-PV 10; **F**, MZSP-PV 11; **G**, MZSP-PV 12 (**C**-**G** in cranial view); **H**, MZSP-PV 13; **I**, MZSP-PV 14; **J**, MZSP-PV 16; **K**, MZSP-PV18 in caudal view; **L,** MZSP-PV19 in cranial view; **M**, MZSP-PV 21. **Abbreviations: c**, capitulum; **fc**, facet for the capitulum of rib; **ns**, neural spine; **pa**, posterior angle; **t**, tuberculum. Scale bars = 20 mm.

belong to *S. populator*, although they were found together with the other specimens and share similar preservation.

Locality. Abismo Iguatemi, about 5 km southwest of Apiai town, upper Ribeira River valley, São Paulo State, Brazil (Figure 1).

DESCRIPTION

Thoracic vertebrae

Two thoracic vertebrae were collected: MZSP-PV 07 preserves most of the cranial portion of the centrum, and MZSP-PV 08 is a partial neural arch (Figure 2). The cranial articular surface of MZSP-PV 07 is nearly complete, together with the left facet for the capitulum of rib, the position of which suggests its identification as a mid thoracic vertebra. The ventral tip of the caudal articulation is preserved, allowing the measurement of the centrum length as 45 mm. A large nutrient foramen (about 7 mm wide) occurs in the center of the dorsal surface, as also seen in some specimens described by Merriam & Stock (1932). A 2 mm wide foramen is seen in the center of the opposite (ventral) surface.

MZSP-PV 08 preserves incomplete neural spine and left transverse process, somewhat fragmented pre- and post-zygapophyses, a nearly complete right transverse process with articular facet for the tuberculum, and part of the right articulation for the capitulum of rib. Series of foramina are present on the dorsal surface, flanking both sides of the neural spine: four on the right and three, more spaced, on the left. Another foramen is seen on the mid-caudal part of the ventral surface. The transverse process is more caudally projected than the pre-zygapophyses, which are just 15 mm apart from one another at their cranial tips. This suggests that MZ-PV 08 represents a caudal thoracic vertebra (see Merriam & Stock, 1932), although some variation might be expected.

Ribs

Ten rib fragments were recovered (Figure 2). Four of them (MZSP-PV13, 14, 16, 21) are non-articular shaft segments recognized as ribs only due to their cranial-caudal flattening. The others preserve dorsal portions of left (MZSP-PV 09, 11,

12) or right (MZSP-PV 10, 18, 19) ribs. The capitulum has two articular surfaces separated by a shallow notch, and the tuberculum includes the articular portion and a small lateral projection. The surface between tuberculum and capitulum is more excavated in MZSP-PV 10 and MZSP-PV 18. In the former, the caudal portion of that surface bears a tuberosity dorsal to a roughened area, while in the latter that portion possesses a number of foramina. The posterior angle is preserved in specimens MZSP-PV 9 and MZSP-PV 11.

Ulna

The partial right ulna (MZSP-PV 05) is broken at the distal portion of the interosseus ligament scar, so that about 70% of the bone is preserved (Figure 3). Also fragmented are the lateral surface of the olecranon, the tip of the coronoid process, and the cranial portion of the articular surface for the radius. Distal to the latter, a flattened area in the diaphysis represents the origin of the supinator muscle. A prominent tubercle is seen distal to the coronoid process. Lateral to this a large nutrient foramen is seen, whereas other foramina spread over the epiphysis and around the proximal portion of the sigmoid cavity.

Radius

The well preserved left radius (MZSP-PV 04) lacks only the proximal epiphysis and a small medial portion of the distal articulation (Figure 3), precluding the observation of grooves for mm. extensor ossis metacarpi pollicis and extensor communis digitorum. A wide nutrient foramen perforates the medial surface of the proximal-most part of the shaft, distal to which is located the tubercle for m. biceps brachialis. The middle part of the shaft is laterally flattened for the insertion of m. supinator. As pointed out by Merriam & Stock (1932),

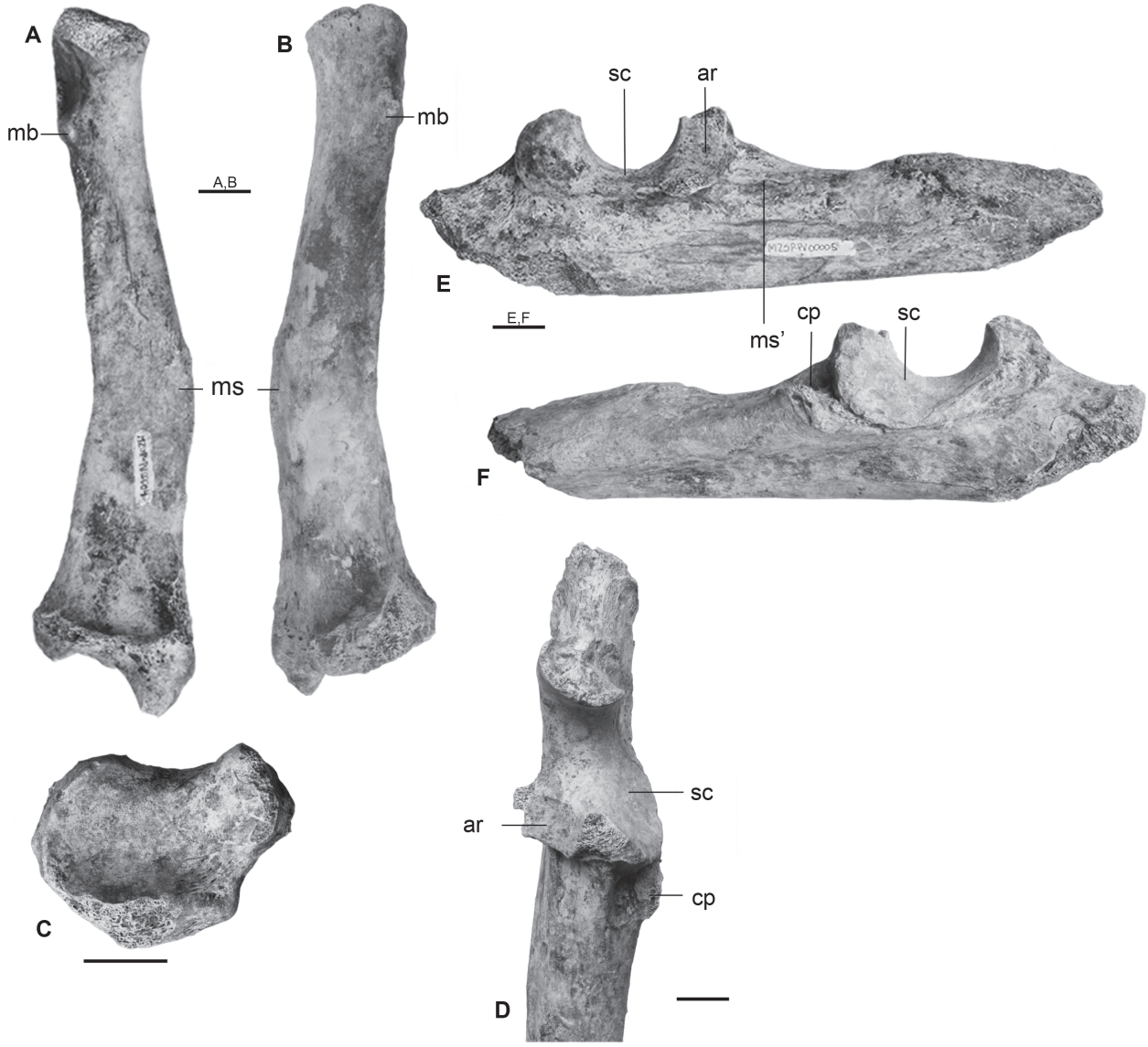

Figure 3. *Smilodon populator* from Abismo Iguatemi. **A**-**C**, MZSP-PV 04, left radius in cranial (**A**), caudal (**B**) and distal (**C**) views; **D**-**F,** MZSP-PV 05, right ulna in medial (**D**), cranial (**E**) and caudal (**F**) views. **Abbreviations: ar**, articulation for the radius; **cp**, coronoid process; **mb**, tubercle for m. biceps brachialis; **ms**, flatness for the m. supinator; **ms'**, origin of m. supinator; **sc**, sigmoid cavity. Scale bars = 100 mm.

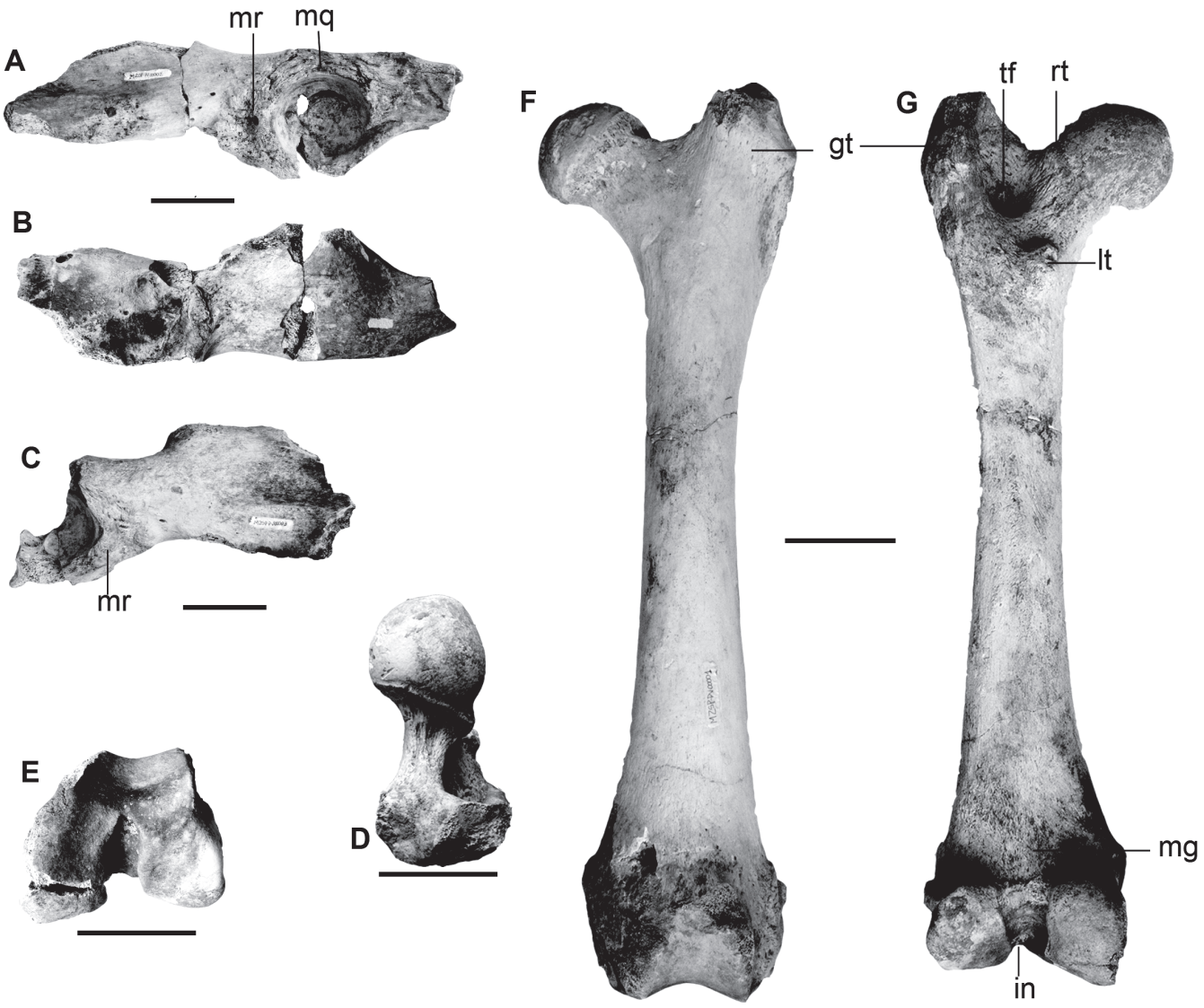

Figure 4. *Smilodon populator* from Abismo Iguatemi. **A**-**B**, MZSP-PV 02, left innominate in lateral (**A**) and medial (**B**) views; **C**, MZSP-PV 03, right innominate in lateral view; **D**-**G,** MZSP-PV 01, left femur in proximal (**D**), distal (**E**), cranial (**F**) and caudal (**G**) views. **Abbreviations: gt**, greater trochanter; **in**, intercondylar notch; **lt**, lesser trochanter; **mg**, origins of m. gastrocnemius; **mq**, origin of m. quadratus femoris; **mr**, origin of m. rectus femoris; **mv**, scar for the m. vastus intermedius; **rt**, rounded tuberosity; **tf**, trochanteric fossa. Scale bars = 50 mm.

the radius is distinctively stouter than that of modern large felines, especially in the distal half of the bone. The groove for mm. extensor carpi radialis longus and brevis is broad and deep.

Pelvis

The left innominate (MZSP-PV 02) preserves the ilium (except the dorsocranial margin of the crest), the cranial half of the ischium, and the acetabular portion of the pubis (Figure 4). A prominent rugose surface for the origin of m. rectus femoris is seen cranial to the iliac rim of the acetabulum, dorsocranial to which lie three wide nutrient foramina. Caudal to the ischiatic rim of the acetabulum a rugose area might represent the origin of m. quadratus femoris. The pubis and the iliac crest are more complete in the right innominate (MZSP-PV 03), but the bone in general is less complete than its counterpart (Figure 4). The distribution pattern of foramina is different in the two bones, and only one large foramen is seen dorsal to the rectus femoris rugosity in MZSP-PV 03.

Femur

The left femur (MZSP-PV 01) is complete and well preserved, with signs of abrasion at the tip of the greater trochanter and caudal surface of the inner tibial condyle (Figure 4). The greater trochanter rises proximal to the level of the head and its obliquely truncated lateral surface extends farther distally. The caudal surface of the neck bears a rounded and prominent tuberosity between the trochanteric fossa and the head. The diaphysis is narrower at the middle, expanding gradually towards the extremities. A large nutrient foramen pierces the caudal surface of the bone, midway between the lesser trochanter and the distal articulation,

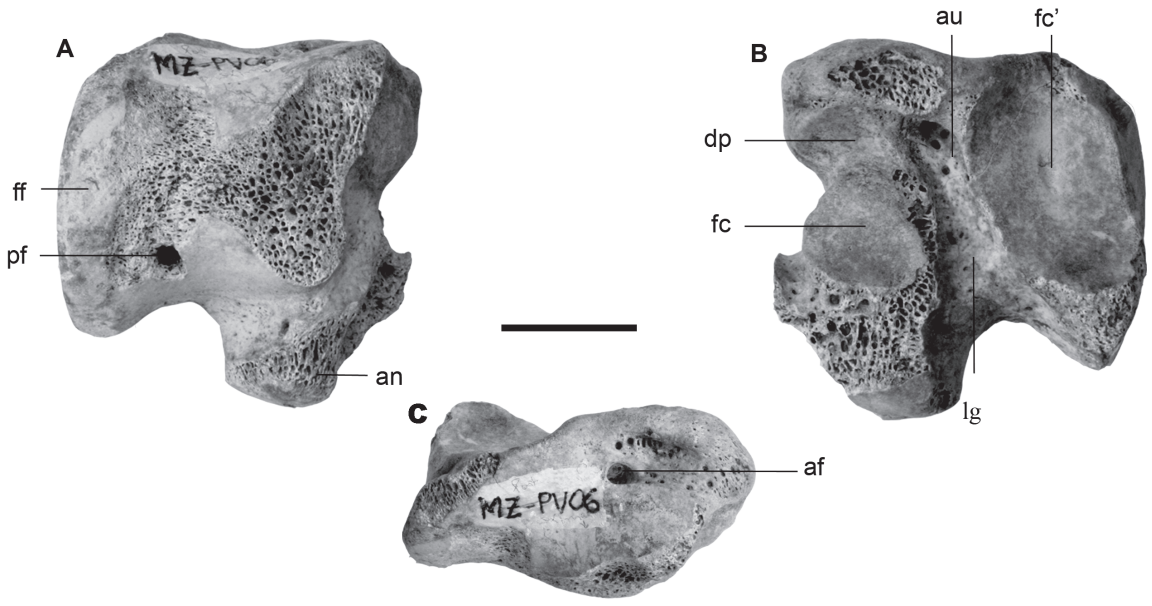

Figura 5. *Smilodon populator* from Abismo Iguatemi. **A**-**C**, MZSP-PV06, right astragalus in proximal (**A**), distal (**B**), and caudal (**C**) views. **Abbreviations: af**, astragalar foramen; **an**, articulation for the navicular; **au**, auxiliar foramina; **dp**, distoplantar projection; **fc**, medial facet for calcaneus; **fc'**, lateral facet for calcaneus; **ff**, articulation for the fibula; **lg**, longitudinal groove; **pf**, proximal foramen. Scale bar = 20 mm.

medial to which a scar for the m. vastus intermedius is seen. The inner tibial articulation is slightly larger than the outer, and both are separated by a narrow intercondylar notch. Directly proximal to the tibial condyles, the caudal surface of the femur bears prominent rugose areas for the origins of m. gastrocnemius.

Astragalus

The right astragalus (MZSP-PV 06) is a "short-necked" astragalus *sensu* Merriam & Stock (1932). It lacks the proximal margin of the trochlea, most of the articulation for the navicular, and the distal facet for the calcaneus (Figure 5). The articular surface for the fibula is broad and slightly concave. A deep longitudinal groove separates the lateral facet from the medial facet for the calcaneus, which is rounded and has a disto-plantar projection. Differently from those described by Merriam & Stock (1932) and Rodrigues *et al.* (2004), MZSP-PV 06 has a 3.5 mm astragalar foramen, a 4 mm foramen at the proximal surface, and several smaller auxiliary foramina scattered on the plantar surface, as well as surrounding the astragalar foramen.

COMMENTS ON THE SABER-TOOTHED CAT OF ABISMO IGUATEMI

Given that the specimens share equivalent size, similar preservation, and were found relatively close to one another without duplicated elements, it is suggested that these belong to a single individual. The animal might have entered the fissure partially or completely articulated, either trapped or dragged by pluvial flood as a carcass. Considering the nature of the deposits and the relief of Abismo Iguatemi, the fragmentation and weathering of the fossils seem related to reworking inside the cave.

The dimensions of the studied material are on average greater than those measured by Merriam & Stock (1932) on North American *Smilodon*, but approach those of other South American specimens (Burmeister, 1866; Churcher, 1967; Cartelle & Abuhid, 1989; Méndez-Alzola, 1941). The radius MZSP-PV 04 is subequal in length to that described by Burmeister (1866), but shorter than those measured by Kurtén & Werdelin (1990) and Méndez-Alzola (1941). It is also broader at the mid-shaft than the radius described by Cartelle & Abuhid (1989), as well as larger and more robust than the average measured by Meriam & Stock (1932; Table 1). Similarly, the acetabulum diameter "measured at right angles to long axis of internal notch" of MZSP-PV 02 (= 53.5 mm) is

Table 1. Measurements (mm) of *Smilodon populator* radia compared with the data from Merriam & Stock (1932). **Abbreviations: A**, greatest length; **B**, cranial-caudal dimension of the shaft at middle; **C**, lateral-medial dimension of the shaft at middle; **D**, greatest cranial-caudal dimension of the distal end; **E**, greatest lateral-medial dimension of the distal end; **e**, estimated measurement.

	MZSP-PV 04	Average (maxi-min)
A	270e	265.7 (295-235)
B	23	20.7 (24.6-16.5)
C	35	31.9 (38.8-26.0)
D	50	42.9 (48.2-35.6)
E	75	58.0 (67.3-49.4)
B/A x 10	0.85	0.78 (0.83-0.70)
C/A	0.13	0.12 (0.14-0.10)
D/A	0.19	0.16 (0.16-0.15)
E/A	0.28	0.22 (0.23-0.20)

Table 2. Measurements (mm) of *Smilodon populator* astragali. **Abbreviations: A**, greatest cranial-caudal dimension; **B**, greatest lateral-medial dimension; **C**, least distance across the neck.

	MZSP-PV 06	average (max-min) Merriam & Stock (1932)	Rodrigues *et al.* (2004)	Méndez-Alzola (1941)
A	54	54.5 (61.2-44.6)	55.3/50.7	57
B	54	54.75 (61.2-46)	55.6/50.6	56.1
C	29	26.9 (29.5-23.3)	—	—

on the upper spectrum of the range measured by Merriam & Stock (1932) for North American forms, and it is close to Argentinean specimens (Méndez-Alzola, 1941; Churcher, 1967). Also the greatest lateral-medial dimension of the sigmoid cavity (43 mm) and the cranial-caudal dimension of the shaft at the proximal end of the interosseus ligament scar (41 mm) measured in MZSP-PV 05 are within the range of the North American specimens: 51.8 (60.2-41.5) and 39.8 (47.6-30.0), respectively (Merriam & Stock, 1932). The dimensions of astragalus also falls within the range of South and North American specimens (Table 2).

The femur (MZSP-PV 01) is larger than those measured by Burmeister (1866), Cartelle & Abuhid (1989), and Fariña *et al.* (1998), but more gracile than those studied by Churcher (1967) and smaller than specimens of Kurtén & Werdelin (1990) and Méndez-Alzola (1941). In relation to the sample measured by Merriam & Stock (1932), MZSP-PV 01 is always within both size and robustness ranges (Table 3), except when it comes to the lateromedial breadth of the proximal extremity, in which case the specimen in question exceeds maximum values of the North American sample. If compared to a specimen of similar length (2009 R-5) within the sample of Merriam & Stock (1932), MZSP-PV 01 has a much broader proximal extremity, but a narrower distal end. Applying the equations of Anderson *et al.* (1985) and Anyonge (1993) to MZSP-PV 01, the body mass of the specimen can be estimated as subequal to that of *Smilodon bonaerensis* in Fariña *et al.* (1998), i.e., around 285 kg. Such estimation is in the range of 220-360 kg predicted to *S. populator* by Christiansen & Harris (2005), who also concluded that this species is heavier than the congenerics *S. gracilis* and *S. fatalis* and also substantially larger than any extant felid.

Based on the cranial sutures, occipital morphology, and molars abrasion, it was proposed that the specimens studied by Hingst-Zaher *et al.* (2003) represents a subadult. On the contrary, assuming that the skull and postcranial belong to a single individual, the analysis of the postcranial elements suggests that it corresponds to an adult.

The above measurements and comparisons are in agreement with the observations of Paula-Couto (1955), that the South American *Smilodon* is larger and more robust than the North American form of this taxon. It agrees with the fact that the animal becomes progressively stouter with increased body size (Christiansen & Harris, 2005). Similar variations have been reported within single species of large living carnivores (Berta, 1985). Accordingly, as also proposed by other authors (Paula-Couto, 1955, 1979; Berta, 1985; Cartelle & Abuhid, 1989), comparative analysis of the saber-toothed cat of Abismo Iguatemi does not provide evidence for the separation of the South and North American *Smilodon* into different species.

Table 3. Measurements (mm) of *Smilodon populator* left femur. **Abbreviations: A,** greatest length parallel to longitudinal axis; **B**, cranial-caudal dimension of the head; **C**, greatest lateral-medial dimension of the proximal end; **D**, cranial-caudal dimension of the shaft at middle; **E**, lateral-medial dimension of the shaft at middle; **F**, greatest cranial-caudal dimension of the distal end; **G**, greatest lateral-medial dimension of the distal end; **H**, greatest lateral-medial dimension of the rotular surface; **I**, greatest lateral-medial dimension of the intercondylar notch; **J**, greatest lateral-medial dimension of the inner tibial articulation; **e**, estimated measurement.

	MZSP-PV01	average (max-min) Merriam & Stock (1932)	Churcher (1967)
A	382	367.7 (408-317)	354e-350
B	48	44.3 (50.7-39.1)	46.6/46.2
C	111	95.5 (108.8-82.7)	100.3e/96.8
D	34	31.5 (35.4-26.8)	34.2/31.3
E	38	35.8 (40.4-30.1)	41.5/37.9
F	72	73.0 (80.3-63.9)	77e/72.4
G	83	78.5 (90.2-65.2)	83.2e/81.1
H	42	50.4 (60-42)	49.8/55.7
I	22	19.7 (22.7-14.5)	21.2/15.5e
J	33	31.0 (35.7-24.9)	30.5/ -
B/A	0.126	0.121 (0.126-0.111)	0.132/0.131
C/A	0.290	0.260 (0.273-0.246)	0.277/0.283
D/A	0.089	0.086 (0.091-0.079)	0.089/0.097
E/A	0.099	0.098 (0.108-0.089)	0.108/0.117
F/A	0.188	0.199 (0.209-0.186)	0.207/0.217
G/A	0.217	0.213 (0.223-0.192)	0.232/0.235

ACKNOWLEDGMENTS

We gratefully acknowledge FAPESP for the financial support; H. El Dine Zaher (MZUSP) for the permission to study the material under his care; R. Fariña for the body mass estimation of MZSP-PV 01; and F. Machado and M. Brandão for contributing with the photos.

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Received in July, 2008; accepted in November, 2008.