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Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t917000010>

New saber-toothed cat records (Felidae: Machairodontinae) for the Pleistocene of Venezuela, and the Great American Biotic Interchange

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Online publication date: 21 March 2011

To cite this Article Rincón, Ascanio D. , Prevosti, Francisco J. and Parra, Gilberto E.(2011) 'New saber-toothed cat records (Felidae: Machairodontinae) for the Pleistocene of Venezuela, and the Great American Biotic Interchange', Journal of Vertebrate Paleontology, 31: 2, 468 – 478

To link to this Article: DOI: 10.1080/02724634.2011.550366

URL: <http://dx.doi.org/10.1080/02724634.2011.550366>

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NEW SABER-TOOTHED CAT RECORDS (FELIDAE: MACHAIRODONTINAE) FOR THE PLEISTOCENE OF VENEZUELA, AND THE GREAT AMERICAN BIOTIC INTERCHANGE

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ABSTRACT—The Machairodontinae fossil record in South America is not very diverse. Until now, only the genus *Smilodon* (Smilodontini) has been reported, with likely a single species, *S. populator*. A second taxon of Machairodontinae was referred to Homotheriini and to the genus *Xenosmilus*, but the age to which it was assigned, early to middle Pleistocene, is uncertain, because it was recovered out of stratigraphic context. At present, the Venezuelan saber-toothed cat record is limited to the late Pleistocene, and consists of fossils found in Mene de Inciarte (state of Zulia), and from Zumbador cave deposit in the state of Falcón. Here we report a new species of Machairodontinae *Homotherium venezuelensis*, nov. sp., as well as the first record of *Smilodon gracilis* in South America. Both were found in El Breal de Orocuai, a tar seep in the state of Monagas, northeastern Venezuela. The age of the deposit has been interpreted as early to middle Pleistocene by thermoluminescence dating. We have been able to identify 30 vertebrate taxa, suggesting a paleoenvironment similar to the Venezuelan llanos today: an extensive savanna with rivers and patches of gallery forest. The saber-toothed cats described here demonstrate that the biogeography of Neotropical felids is more complex than previously thought, and allow us to identify new invasions and delimit the times during which they occurred. The fossils from Orocuai represent the first record of *Homotherium* for South America, indicating that scimitar-toothed cats invaded this continent as early as the early–middle Pleistocene.

INTRODUCTION

South America was isolated approximately 65 million years during the Cenozoic, but around 2.5 to 3 Ma ago geological activity of the Pacific tectonic plates caused Central and South America to be linked (Duque-Caro, 1990; Coates and Obando, 1996; Iturralde Vinent and MacPhee, 1999; Coates et al., 2004), resulting in the Great American Biotic Interchange (GABI), which allowed significant faunal and floral exchange between the Americas (Webb, 1976; Stehli and Webb, 1985; Pascual, 2006; Woodburne et al., 2006). Campbell et al. (2010) suggested the GABI started earlier. This land bridge functioned as an ecologically selective dispersal corridor (Patterson and Pascual, 1972; Webb, 1978, 1985, 1991, 2006; Simpson, 1980; Reig, 1981; Marshall et al., 1982; Pascual, 2006; Woodburne et al., 2006).

Our knowledge of the GABI comes mostly from the fossil record of southern South America at one end of the continent, and U.S.A. and Mexico at the other. In Central America and northern South America, however, there is a hiatus of paleontological information. Thus our interpretation of the GABI could be greatly biased by the absence of fossil Plio-Pleistocene localities near the connection between Central and South America.

In this paper we describe two new North American immigrant elements (Felidae: Machairodontinae) to South America: a scimitar-toothed cat (*Homotherium venezuelensis*), and the early dirk-toothed cat (*Smilodon gracilis*), from an early Pleistocene tar seep deposit in northern South America (Eastern Venezuela). These finds constitute the first records of the genus *Homotherium* and *S. gracilis* for South America, and confirm the inva-

sion of scimitar-toothed cats, which are different from the better known dirk-toothed cat *Smilodon*. These discoveries confirm that the biogeographic history of felids in South America is complex (Prevosti, 2006; Soibelzon and Prevosti, 2007). Moreover, they demonstrate that regions that are poorly known from a paleontological perspective, such as the northern part of South America and Central America, can enrich our understanding of the GABI.

The felids were one of the most successful groups of placental carnivores (Order Carnivora) to participate in GABI event, invading South America from Central and North America (Johnson et al., 2006; Prevosti, 2006). Their success is evident in the recent and past diversity of South American felids; at least seven felid lineages invaded South America, and subsequently some clades underwent adaptive radiations (Sunquist and Sunquist, 2002; Johnson et al., 2006; Prevosti, 2006; Soibelzon and Prevosti, 2007).

MATERIALS AND METHODS

We took dental and cranial measurements (Tables 1–3) with a digital caliper recording data to ± 0.01 mm. We studied specimens from different collections (see Institutional Abbreviations below), and have included some published measurements as well. Descriptions mainly follow the nomenclature used by Berta (1987). We used bivariate graphs to highlight quantitative differences among taxa.

The biogeographical reconstruction was based on available information of felid phylogeny, fossil record, and DNA divergence dates (see Turner and Antón, 1997; Martin, 1998; Antón

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et al., 2004; Barnett et al., 2005; Johnson et al., 2006; Prevosti, 2006; Soibelzon and Prevosti, 2007; Slater and Van Valkenburgh, 2008).

Institutional Abbreviations—**ANSP**, The Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; **BIOPSI**, Babi-arz Institute of Paleontological Studies, Inc., Phoenix, Arizona, U.S.A.; **BRD**, Brazil deposit collections at MNHN; **F:AM**, Frick Collection of fossil vertebrates, American Museum of Natural History, New York, U.S.A.; **FSL**, Faculty of Science, The University Claude Bernard Lyon 1, Lyon, France; **IMNH**, Idaho Museum of Natural History, Pocatello, Idaho, U.S.A.; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **OR**, El Breal de Orocuál collection, hosted in Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; **PET**, Perrier-Etouaires collection at MNHN; **TMM**, Texas Memorial Museum, Austin, Texas, U.S.A.; **UF**, Vertebrate Paleontology Collection, Florida Museum of Natural History, Gainesville, Florida, U.S.A.

Thirty taxa have been identified at this location; many aquatic or semiaquatic taxa, such as *Caiman* sp., Anatiidae, aff. *Recurvirostridae*, *Tapirus*, and Hydrochaeridae, are consistent with a fluvio-deltaic interpretation for the Mesa Formation. There are also elements from the forest-savanna ecotone: Testudine taxa, aff. *Geochelone*, Colubridae, Cathartidae, Accipitridae, *Didelphis* sp., *Eremotherium* sp., Megalonychidae, Mylodontidae, *Propaopus sulcatus*, *Pachyarmatherium* cf. *P. leiseyi*, *Tayassu* sp., *Platygonus* sp., *Mixotoxodon larensis*, Proboscidea, and *Protocyon* sp. Also, *Glyptodon* sp., aff. *Hoplophorus*, *Holmesina occidentalis*, *Pampatherium humboldtii*, *Hippidion* sp., and *Paleolama* sp. suggest a savanna paleoenvironment, with Erethizontidae and *Proechimys* sp. as arboreal components. This faunal assemblage suggests that the El Breal de Orocuál paleoenvironment was similar to that of the Venezuelan llanos today: an extensive savanna with rivers and patches of gallery forest (Rincón, et al., 2007, 2009).

GEOGRAPHIC, CHRONOLOGICAL, AND PALEONTOLOGICAL CONTEXT

The new Machairodontinae remains come from El Breal de Orocuál, 20 km northwest of Maturin, Monagas state, Venezuela (Fig. 1). This deposit has been interpreted as a tar seep deposit lying in the Mesa Formation (Hackley et al., 2006), a unit that consists of fluvio-deltaic strata of early to middle Pleistocene age, based on thermoluminescence dates of 0.5 to 1.0 Ma (Carbón et al., 1992).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
 CARNIVORA Bowdich, 1821
 FELIDAE Fischer, 1817
 MACHAIRODONTINAE Gill, 1872
 HOMOTHERIINI (Fabrini, 1890)
HOMOTHERIUM Fabrini, 1890
HOMOTHERIUM VENEZUELENSIS, nov. sp.

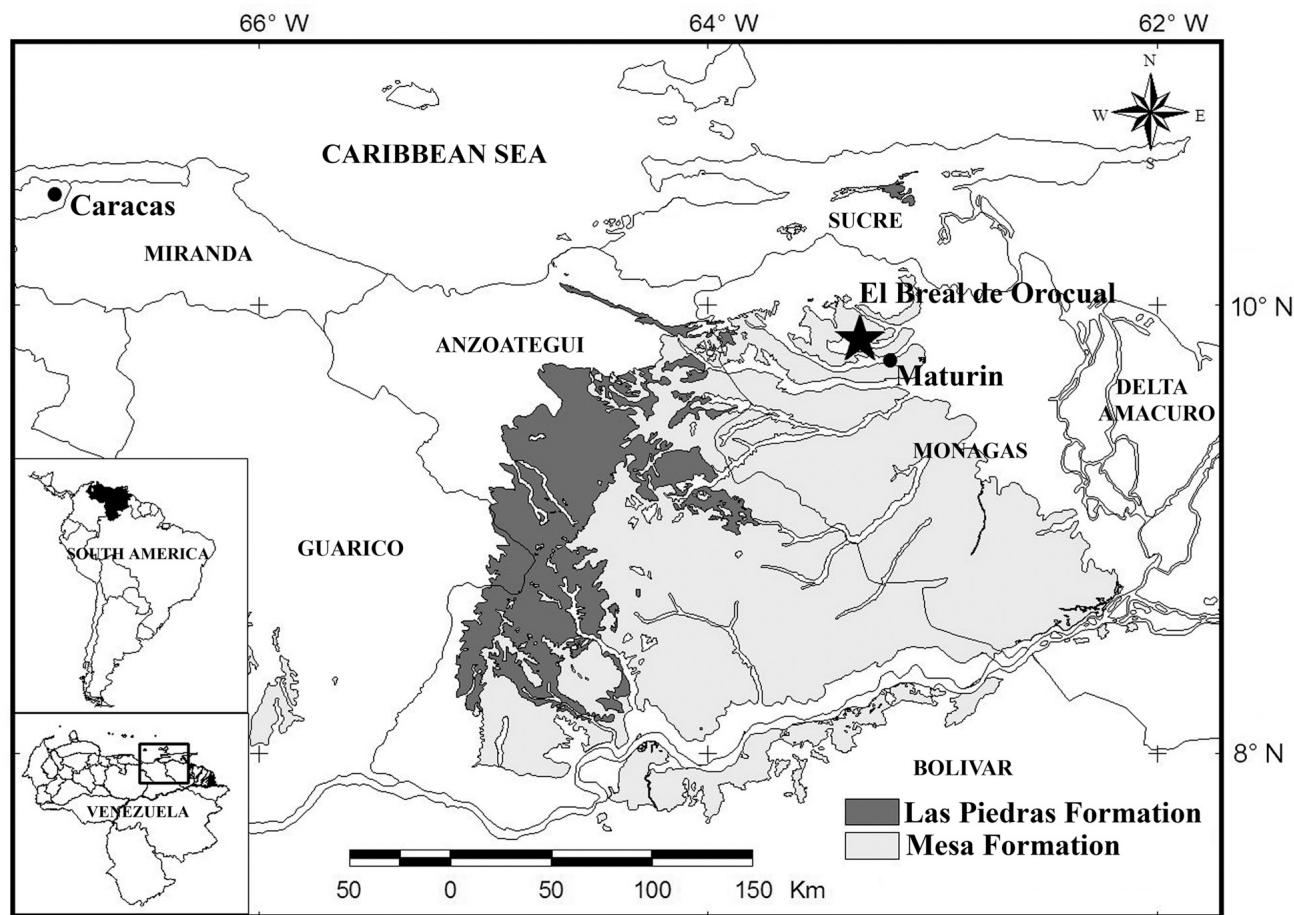


FIGURE 1. Geographical map showing the location of El Breal de Orocuál tar seeps, Monagas State, Venezuela, and the schematic geological map of eastern Venezuela, showing the main geological units, Mesa and Las Piedras Formations. (After Hackley et al., 2006.)

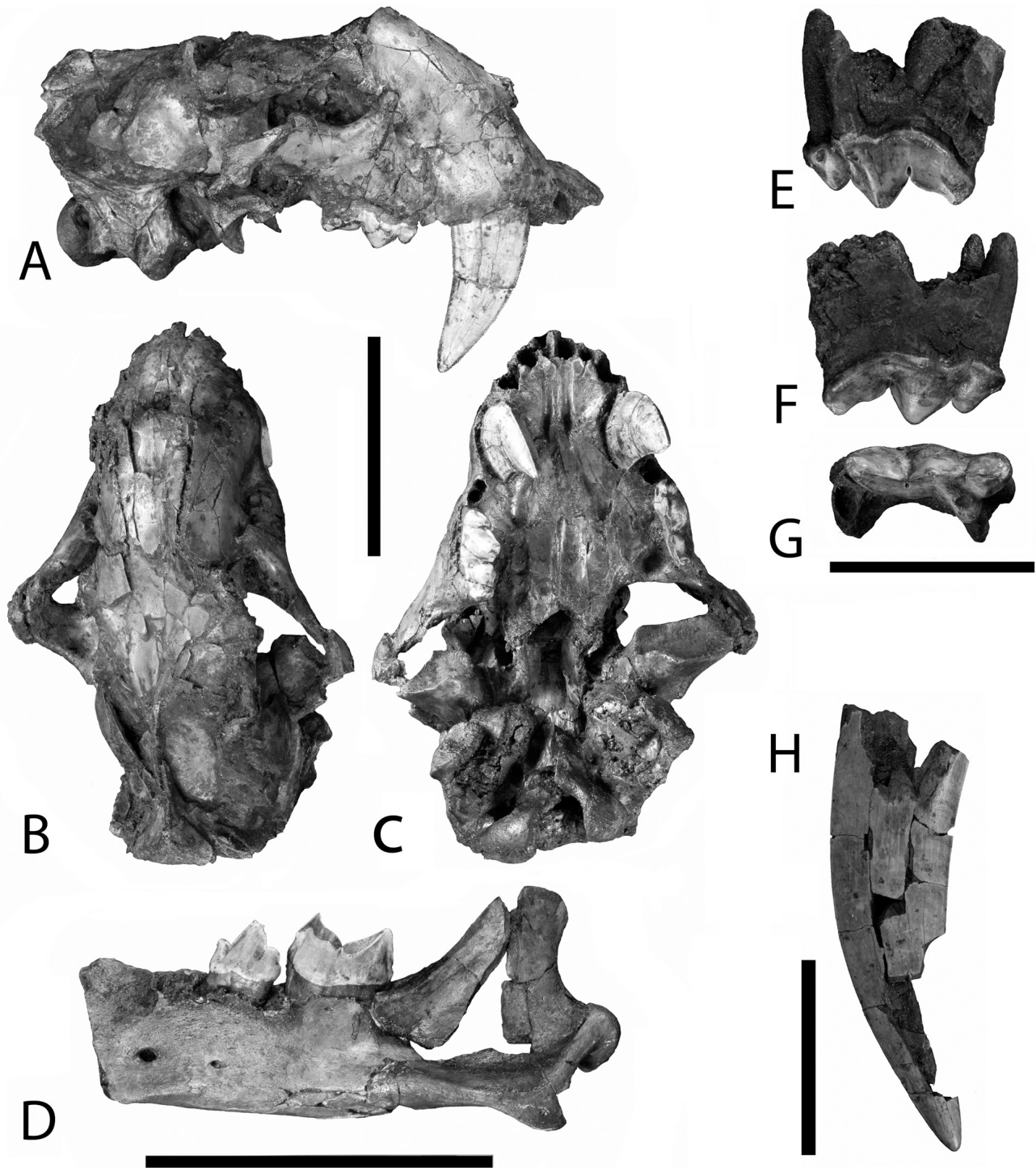


FIGURE 2. **A–D**, Holotype of *Homotherium venezuelensis*. Skull (OR-1352) in **A**, lateral view; **B**, dorsal view; **C**, ventral view; **D**, left mandible (OR-259) in lateral view. **E–H**, *Smilodon gracilis* from El Breal de Orocuál. **E**, right P4 (OR-1343) in lingual; **F**, labial view; **G**, occlusal view; **H**, upper left canine (OR-1342) in labial view. Scale bars equal 10 cm in A, B, C, D; scale bars equal 4 cm in E, F, G, H.

Etymology—To commemorate the discovery of this species in Venezuela.

Locality and Age—Venezuela, Monagas State. Mesa Formation, Plio-Pleistocene asphalt deposit. Type locality: El Breal de Orocuál, N09°50'48.3", W63°19'46.0".

Holotype—OR-1352, complete and compressed skull, lacks the upper incisors, left third premolar and left first molar (Figs. 2, 3, Tables 1, 2).

Hypodigm—Three upper canines, OR-712, OR-1349, OR-1350; four upper canine fragments, OR-080, OR-258, OR-1219,

TABLE 1. Jaw measurement comparisons among Machairodontinae (in mm): *Smilodon populator* (BRD 21-MNHN), *Smilodon fatalis* (TMM-30967-198), *Xenosmilus hodsonae* (BIOPSI 101), *Machairodus giganteus* (BIOPSI-S/N), *Machairodus coloradensis* (TMM-41261-8), *Homotherium ischyrius* (IMNH-900-11862), *Homotherium serum* (TMM 933-2456, TMM 933-1, TMM 933-1283, TMM 933-3353), *Homotherium venezuelensis* (OR-259), and *Homotherium crenatidens* (PET 2001b, FSL 210991, FSL 212939).

Measurements	BRD 21 MNHN		TMM 30967-198		BIOPSI 101		BIOPSI S/N		TMM-41261-8		IMNH 900-11862		TMM 933-2456		TMM 933-1		TMM 933-1283		TMM 933-3353		OR-259		PET 2001b		FSL 210991		FSL 212939					
Length p3-m1	69.7						71.6		80.9	63.2	62.9	64.5	68.1	62.8	67.4	66.9	64.7	62.8	67.4	66.9	64.7	62.8	67.4	66.9	64.7	62.8	67.4	66.9	64.7	62.8		
Length p4-m1	55.5						52.4		59.7	48.7	49.5	45.6	48.5	49	52.7	49.1	50.8	49	52.7	49.1	50.8	49	52.7	49.1	50.8	49	52.7	49.1	50.8	49		
Length m1	28.9		50				28.6		32	11.1	27.3	28.4	29.6	28.2	31	32.7	32.7	28.2	31	32.7	32.7	28.2	31	32.7	32.7	31.5	32.7	32.7	31.5	32.7		
Length p3	7.9						16.6		20	11.1	8.7	10	10.7	7.6	11.5	6.6	9.6	7.6	11.5	6.6	9.6	7.6	11.5	6.6	9.6	7.4	6.6	9.6	7.4	6.6		
Breadth p3	7.5						7.3		10	7.2	5.8	6.1	8.1	6.9	6.7	4.6	5.6	6.9	6.7	4.6	5.6	6.9	6.7	4.6	5.6	4.5	4.6	5.6	4.5	4.6		
Length p4	28.3						26.4		30.6	20.1	18.7	18.5	19.1	17	21.1	17.2	18.7	17	21.1	17.2	18.7	17	21.1	17.2	18.7	21.7	17.2	18.7	21.7	17.2		
Breadth p4	12.8						10.6		11.5	9.6	8.6	8.7	8.8	8.2	10.3	9.6	10.3	8.2	10.3	9.6	10.3	8.2	10.3	9.6	10.3	9.4	10.3	10.3	9.4	10.3	9.4	
Length m1	28.9						28.6		32	30.1	27.3	28.4	29.8	28.2	31	32.7	32.7	28.2	31	32.7	32.7	28.2	31	32.7	32.7	31.5	32.7	32.7	31.5	32.7	31.5	
Breadth m1	13.4						12.4		12.7	13	11.1	11.8	10.9	10.6	13.8	13.3	13	10.6	13.8	13.3	13	10.6	13.8	13.3	13	12.5	13.3	13	12.5	13.3	12.5	
Depth below p3 at lingual side							37.7		40.6	39.3	41.6	45.6	43.3	37.8	39.6	53	44	43.3	39.6	53	44	37.8	39.6	53	44	34.7	53	44	34.7	53	44	
Depth below p4 at lingual side							38.7		42.9	39.6	40.1	40.7	39.9	38.7	38	52.4	44.3	38.7	38	52.4	44.3	38.7	38	52.4	44.3	40.2	38	52.4	44.3	40.2	38	
Depth below m1 at lingual side							40.2		48.1	37.9	36.7	42.1	39.8	40.2	40.1	49.4	41.3	40.2	40.1	49.4	41.3	40.2	40.1	49.4	41.3	39	40.1	49.4	41.3	39	40.1	
Length masseteric fossa	65						65.2		73.7	75.3	56.1	67.2	63	40.2	66.8	75.9	61.5	40.2	66.8	75.9	61.5	40.2	66.8	75.9	61.5	74	66.8	75.9	61.5	74	66.8	
Depth masseteric fossa	32						45.5		51.2	42.2	36	32.3	63	32.3	43.7	40	38.7	32.3	43.7	40	38.7	32.3	43.7	40	38.7	46.9	43.7	40	38.7	46.9	43.7	
Height coronoid process	59.7						32		52.5	33	30.2	32.3	29	32.4	33.5	36.6	23.8	32.4	33.5	36.6	23.8	32.4	33.5	36.6	25.7	33.5	36.6	25.7	33.5	36.6	25.7	
Length diastema c1-p3	27.8						52.7		33.2	45.3	28.1	45.3	29	32.4	21.8	47.9	39	32.4	21.8	47.9	39	32.4	21.8	47.9	42.7	21.8	47.9	39	42.7	21.8	47.9	
Mandibular thickness at p3	22.5						15.3		18.7	16.7	17.1	15.9	16.8	16.1	17.1	22.8	17.9	16.1	17.1	22.8	17.9	16.1	17.1	22.8	16.7	17.1	22.8	16.7	17.1	22.8	16.7	17.1
Mandibular thickness at p4	23						16.3		18.8	17.6	18.4	17.8	18.4	19	19.7	24.2	19	16.1	19.7	24.2	19	16.1	19.7	24.2	17.6	19.7	24.2	17.6	19.7	24.2	17.6	19.7
Mandibular thickness at m1	22.5						16.7		18.3	18.2	17.8	18.9	19.7	18.8	18.2	24.3	18.3	18.8	18.2	24.3	18.3	18.8	18.2	24.3	18.3	18.8	18.2	24.3	18.3	18.8	18.2	24.3
Height of articular process	16.1						13.3		16.2	20.2	16.4	18.1	18.1	18.1	20.4	18.2	18.1	18.1	20.4	18.2	18.1	18.1	20.4	18.2	18.1	18.1	18.1	18.2	18.1	18.1	18.2	18.1
Breadth of articular process	48.4						41.3		43.8	49.3	33.5	41.2	41.2	41.2	39.5	50.6	38.8	41.2	39.5	50.6	38.8	41.2	39.5	50.6	38.8	38.8	39.5	50.6	38.8	39.5	50.6	38.8
Length articular to angular process	32.7						34.6		40.5	46.3	39.5	40.2	40.2	40.2	39.8	40.4	39.6	40.2	39.8	40.4	39.6	40.2	39.8	40.4	39.6	39.6	40.4	39.6	40.4	39.6	40.4	39.6
Length coronoid to angular process	58.2						79.6		91	83.9	71.8	80.1	80.1	80.1	72.7	62.6	54.6	80.1	72.7	62.6	54.6	80.1	72.7	62.6	54.6	54.6	62.6	54.6	62.6	54.6	62.6	54.6

TABLE 2. Upper tooth row and cranial measurement comparisons among Homotheriini (in mm): *Homotherium ischyryus* (IMNH-900-11862), *Xenosmilus hodsonae* (BIOPSI 101), *Homotherium serum* (TMM 933-3582, TMM 933-3444), *Homotherium crenatidens* (PET 2000a, FSL 210991), and *Homotherium venezuelensis* (OR-1352).

Measurements	IMNH-900-11862	BIOPSI 101	TMM 933-3582	TMM 933-3444	PET 2000a	FSL 210991	OR-1352
Length C1–P4	103.1	98.6	87.1	103.8	114.4	98.5	84.4
Length C1 anteroposterior	35.3	37.3	31.5	34.1	39.1	50.1	34.1
Labial-lingual width C1	14.6	18.2	13.5	14.5	18.4	33.6	18.6
Length P3	14	9.1	9.4	10	10.2	14	13
Width P3	6.8	7.5	7	6.7	6.6	8.5	7.2
length P4	38.5	41.3	38.4	39.7	41.7	42.5	40.7
Width P4	13	13.7	13.3		13.4	13.1	14.2
Width C1–C1	73.5	84.9	85.7	76.7	85.8	75	72.8
Width P3–P3	76.2	95	98.3	84.3	92.7	90.3	85.2
Width P4–P4 (between protocones)	94.4	106.4	105.7	97.6	104.3	104	95.1
Width P4–P4 (between labial border at its posterior part)	107.3	117.7	127.8	112.2	116.8	98.3	102.2
Greatest palatal width: P4–P4 (between protocones)	103	108.4	97.1	103.2	107.9	98.3	99.7
Palatal length (incisor–posterior border of P4)	127.4	123	113.7	129.4	128	124.8	101.9
Length P4–ptergoides wing	48	53.3	63.9	69.9	67		49 approx.
Width of glenoid surface	52.6	47	43.4	46.6	50.9	47.8	52.9
Length of glenoid surface	28.6	25.1	22.9	22.8	25.9	24.9	25.5
Greatest mastoid process width	115.5	121.4	113.7	105.7	117	110.9	114.8
Greatest paraoccipital process width	82.2	104	94.5	83	93.4		95.1
Greatest width of the occipital condyles	64.5	67.8	60.9	60.5	71.8	60.7	70 approx.
Width of the tympanic bullae	29	28.2	25.4	28.7	23	28.3	26
Greatest diameter of the tympanic bulla	43.7	47.4	47.2	44.5	47.6	43.8	42.7
Zygomatic width	184	180	177	175.7	204	199.1	175
Greatest width of frontal post orbital process	122.1	77.3	118.6		118.8	116.6	
Length of sagittal crest	80	122	88.8	95.6	84.4	86	76.7
Length of temporalis fossa	135	155.2	137.8	142.1	143.3	129.2	
Height of temporalis fossa	83.2	93.8	99.2	114.8	104.1	83.4	
Height of basicranium–sagittal crest	107.4	121.1	108.8	121.3	101.2	99.4	90.3
Length between mastoid and paraoccipital process	51.3	45.5	36.7	44.1	51.7	46.1	45.9
Height of external nares	45.1	52	67.6		55.5	51.8	37.2
Greatest width of external nares	40.5	40.5	58.3	68	45.8	40.6	38.2
Greatest width of the muzzle at infraorbital foramen	69.4	72.1	88.5	88.5	83.4	73.5	75.2
Greatest width of the muzzle at orbits	87.4	66.8	93.5		91	77.9	76.3
Greatest neurocranium width	79	87	82.7	81.2	83.8	82.9	
Basal length	267.1	261.4	245.1	267.1	290.1	258.3	200
Total length	308	330	332.6	346.1	306.7	282	230 approx.

OR-1386; right I3, OR-256; two right P4, OR-255, OR-1390; two left dentaries, OR-259, OR-330; two dentary fragments, OR-710, OR-711; left lower canine, OR-254; two right lower canines, OR-771, OR-1221; left m1, OR1389; left i3 and lower canine associate, OR-1166; right i1 crown, OR-081; left i1, OR-1385; right i2, OR-1381; right i3, OR-1220; left i3 crown, OR-785; two left p4, OR-257, OR-1384.

Diagnosis—Large size and presence of hypertrophied C1 with coarse serrations on mesial and distal crests as in derived Homotheriini (i.e., *Machairodus*, *Xenosmilus*, *Homotherium*); C1 proportionally shorter but mesiodistally longer than in Smilodontini; P2 absent; P3/p3 more reduced than in *Machairodus*; P3 with two roots and two cusps (has one root in *H. serum* and *H. crenatidens*, and three cusps in *Machairodus* and *H. ischyryus*); p3 present and double to single rooted (absent in *Xenosmilus*); short temporalis fossa and wider frontals as in *Homotherium serum*, *Homotherium latidens*, or *Homotherium crenatidens*, wider than in *Xenosmilus* or *Machairodus*; shorter sagittal crest than in *Xenosmilus* or *Machairodus*; angular process very well developed as in *Xenosmilus*, but not hypertrophied as in *H. serum*, *Homotherium johnstoni*, or *H. latidens*; very shallow masseteric fossa on the mandible, without the anterior ‘pocket’ present in *H. serum* and *H. latidens*; coronoid process short and inclined (*H. latidens*, *H. ischyryus*, and *X. hodsonae* have a straighter process); shorter muzzle than in other Homotheriini, without diastema between C1 and P3; palate as wide as long, proportionally shorter than in other Homotheriini; paraoccipital process well developed; short occipital height mandibular condyle at the same level as the lower tooth row.

Description and Comparison—Teeth coarsely serrated; upper incisor arranged in an arc, and very precumbent compared to the rest of Homotheriini; upper canine shorter than in Smilodontini; no diastema between the third upper premolar and the upper canine; palate as wide as long, relatively shorter than in other Homotheriini; third upper premolar double rooted, with a principal cusp and a smaller posterior cusp; P4 long and extremely compressed in lateral dimension, with an exceedingly reduced protocone; frontals wide as in *H. serum*, *H. latidens*, or *H. crenatidens*, and broader than *Xenosmilus*; sagittal crest short as in *Homotherium* and shorter than in *Xenosmilus*; paraoccipital process very well developed; mastoid process fused with the tympanic bullae; short temporalis fossa; the mandibular ramus is deeper and massive as in other Homotheriini; the masseteric fossa in OR-259 is shallow and not pocketed anteriorly as in *Homotherium ischyryus*, *H. johnstoni*, *H. crenatidens*, *Homotherium problematicus*, and *Xenosmilus hodsonae* (in *H. serum* and *H. latidens* it is deep and anteriorly pocketed); the alveolus for the third lower premolar is present and is single to double rooted; p4 has a short posterior cingulum and a strong mesial accessory cusp; the m1 is elongated and laminated and the paraconid and protoconid blades are the same size; in OR-259, the coronoid process is lower, broad, rectangular in shape, and posteriorly inclined as in *H. serum* and *H. crenatidens*, and differs from *H. latidens*, *H. ischyryus*, and *X. hodsonae* where the coronoid process is straight, relatively slender, and not posteriorly inclined.

Remarks—*Homotherium venezuelensis* has hypertrophied upper canines with robust and very coarse serrations, a mandible with a strong ramus at the symphysis, deeper and more massive

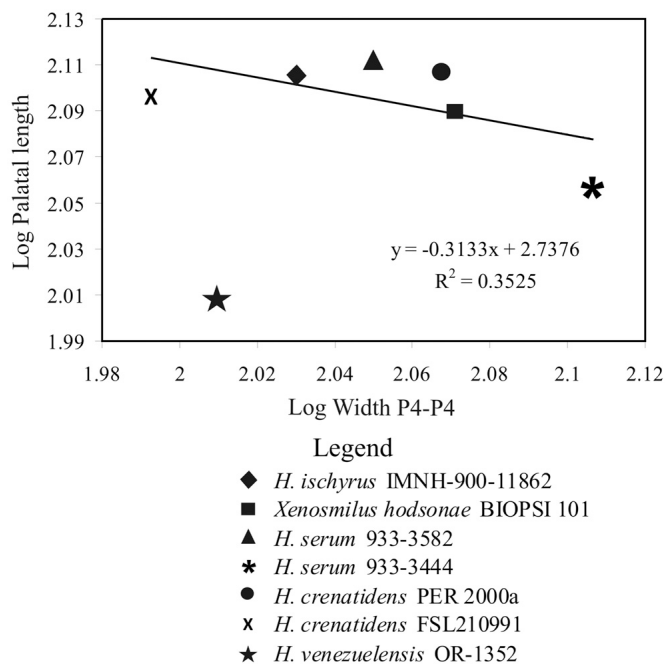


FIGURE 3. Comparative biplot of palatal length (incisor to posterior border of fourth upper premolar) versus width fourth upper premolar (at its posterior part) in *Xenosmilus hodsonae*, *Homotherium serum*, *Homotherium crenatidens*, *Homotherium venezuelensis*, and *Homotherium ischyryus*.

mandibles than in Smilodontini, a very reduced or non-existent protocone, and proto- and paraconid blades of equal size on the lower carnassial. Most of these characters are diagnostic of a large homotheriine cat (Meade, 1961; Berta, 1987; Rawn Schatzinger, 1992; Martin, 1998).

Machairodus differs from *Homotherium* by the following features: P3 relatively large with three small cusps; p3 with three well-developed cusps and p4 with four; the lower carnassials display a rudimentary talonid; the upper carnassials have retained a well-developed protocone with an independent root; the metastyle is shorter than the parastyle (De Bonis, 1976). *Lokotunjailurus* differs from other Homotheriini in that the P2 although present is small and peglike (Werdelin, 2003).

The P3 in both *Homotherium* and *Xenosmilus* is smaller than *Machairodus*, and has one small cusp. *Homotherium* and *Xenosmilus* also share the following features: p4 with three well-developed cusps; the lower carnassials do not have a talonid; in the upper carnassials the protocone is fused with the tooth, and the protocone root disappears; the metastyle and parastyle blades are of equal size (Meade, 1961). *Xenosmilus* differs from *Homotherium* in the following features: p3 is absent; narrower frontals; temporal fossa and sagittal crest are elongated; limbs are shortened and robust (Martin et al., 2000).

The combination of characters observed in the Orocuai specimens (wide frontals; a short sagittal crest; p3 present and single to double rooted; a short temporal fossa; p4 with three well-developed cusps; the protocone in P4 is absent) allows us to refer them to the genus *Homotherium*.

The absence of a recent systematic revision of *Homotherium*, plus its wide geographic distribution, has resulted in a large number of published species, some of dubious validity. Several North American species are in this situation. For example, it is very

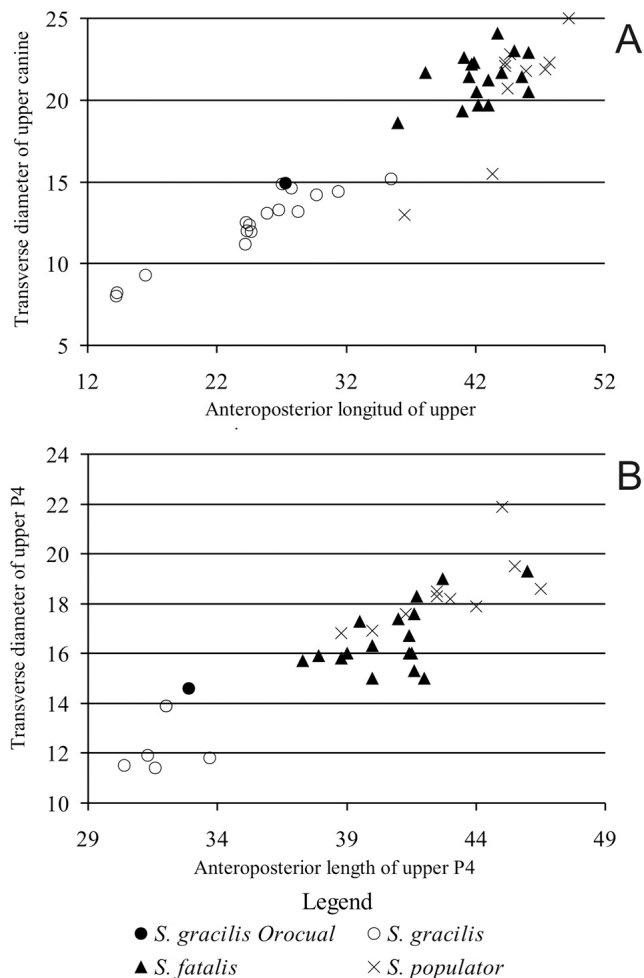


FIGURE 4. **A**, comparative biplot of transverse diameter of upper canine versus anteroposterior length of upper canine of Orocuai Smilodontini material, *Smilodon gracilis*, *Smilodon fatalis*, and *Smilodon populator*; **B**, comparative biplot of transverse diameter of upper fourth premolar versus anteroposterior length of upper fourth premolar of Orocuai Smilodontini material, *Smilodon gracilis*, *Smilodon fatalis*, and *Smilodon populator*.

difficult to separate *Homotherium ischyryus* from *Homotherium crusafonti* or *Homotherium idahoensis*, and the subtle differences between these species could be interpreted as intraspecific variation (i.e., ontogenetic or geographical variation or sexual dimorphism). It is important to note that these species are only known from a few incomplete specimens, most of them type specimens, and it is possible that *H. crusafonti* and *H. idahoensis* are junior synonyms of *H. ischyryus*. It is also impossible to morphologically differentiate *H. ischyryus* from *H. crenatidens* (Merriam 1905; Balleisio, 1963), although the validity of *H. ischyryus* may be presumed for biogeographic reasons, until further material of this species appears. *H. ischyryus* differs from *H. johnstoni* in having one posterior cusp on p4 rather than two (Mawby, 1965).

Homotherium ischyryus, *H. johnstoni*, *H. crenatidens*, and *H. problematicus*, as well as *Xenosmilus hodsonae* and *H. hadarensis*, all have anteriorly unpocketed masseteric fossa (Fabrini, 1890; Merriam, 1905; Balleisio, 1963; Collings, 1972; Martin et al., 2000), as in *H. venezuelensis*. In *H. latidens* and *H. serum*,

however, the anterior part of the masseteric fossa is pocketed. In the last species the temporal zygomatic process is perpendicular to the midline of the cranium as in *H. venezuelensis*, and in *Homotherium hadarensis* this structure is inclined frontally (Meade, 1961; Ballester, 1963; Petter and Howell, 1988).

Homotherium serum shares the following features with *H. latidens*: a diastema between C1 and P3 as in *H. problematicus*; a relatively longer muzzle as in *H. crenatidens*, *H. ischyryus*, and *H. hadarensis*; and the frontal part of the masseteric fossa is pocketed. *H. venezuelensis* does not have a diastema between C1 and P3, the masseteric fossa is unpocketed, and the muzzle is shorter than for other *Homotherium* species.

The shape of the P3 in *H. venezuelensis* is elliptical in occlusal view and double rooted—characteristics it shares with *H. ischyryus*. *H. venezuelensis*, however, differs from *H. ischyryus* in that the latter has one principal cusp with anterior and posterior cusplets, whereas *H. venezuelensis* has a very well developed principal cusp, but only a single posterior cusplet. In *H. crenatidens* the P3 is circular in occlusal view, single rooted, and displays two very reduced cusplets. This last characteristic is shared with *H. serum*.

In conclusion, and even though the systematic status of most species of *Homotherium* remain unclear, the Orocual specimens have a distinct combination of characters that sustain the creation of a new species.

SMILODONTINI Kurtén, 1963
SMILODON Lund, 1842
SMILODON GRACILIS Cope, 1880

Referred Materials—Upper incisor, OR-1346; fractured left upper crown of canine, 1342; left P3, 1344; right P3, 1347; right P4, 1343; left P4 fragments, 1345 (Figs. 2, 4; Table 3).

Description and Comparisons—The specimens from Orocual consisted of incomplete upper cheek teeth, but with nonetheless a very diagnostic morphology.

The Orocual fossils display the following characteristics: upper canines very elongated, laterally compressed, and recurved; P3 reduced; P4 protocone reduced, ectoparastyle enlarged and anteriorly directed, all of which allow us to assign this material to Smilodontini (sensu Berta and Galiano, 1983).

Two genera comprise Smilodontini: *Smilodon*, with fine serrated upper teeth, and *Megantereon*, with unserrated upper canines (Berta, 1987; Palmqvist et al., 2007). The presence of fine serrations on C1 suggests that the Orocual specimens belong to *Smilodon*.

The canine is hypertrophied, long and transversally narrowed as in other saber-toothed cats, but considerably shorter, and less recurved than *Smilodon populator* or *Smilodon fatalis*. The crown is curved distally and shows very fine serrations on its margins (as opposed to the longer and coarser serrations of the upper canines in *S. populator* or *S. fatalis*; Berta, 1987). The P4 is elongated and transversally narrowed, with a large metastyle and parastyle, and a small ectoparastyle. The protocone is present but small and low; P3 is double rooted.

The size of these teeth is smaller than *S. populator* and *S. fatalis*, and fall in the range of *Smilodon gracilis* (see Table 3 and Fig. 4).

Remarks—The morphology and size of these teeth are concordant with those of *Smilodon*, and as the teeth of *S. populator* and *S. fatalis* can be distinguished from *S. gracilis* on the basis of larger size, degree of recurving of the upper canines and the presence of coarser serrations on the teeth, as well as a P4 with a relatively reduced protocone (Berta, 1987), the combination of the dental morphology and measurements suggest that the Orocual specimens can be appropriately assigned to *Smilodon gracilis*.

DISCUSSION AND CONCLUSIONS

Previous paleontological (Kurtén and Werdelin, 1990; Prevosti 2006) and molecular (Johnson, et al., 2006) studies show that several felid lineages have invaded South America in independent immigration waves since the rise of the Panamanian land bridge around 3 million years ago. The oldest records of felids in South America come from the early–middle Pleistocene (Ensenadan) when the sabertooth (*Smilodon populator*), the jaguar (*Panthera onca*), the mountain lion (*Puma concolor*), and small felids of the ‘ocelot clade’ (“*Felis*” *vorohuensis*, *Leopardus colocolo*) are recorded (Berta, 1985; Kurtén and Werdelin, 1990; Berman, 1994; Cione and Tonni, 2005; Prevosti, 2006; Prevosti et al., 2006; Fig. 5).

Other species of *Leopardus* and a jaw of the jaguarondi (*Herpailurus*) have been recorded later in younger levels of the middle and late Pleistocene (Bonaerian–Lujanian; Prevosti, 2006). Earlier records of pre-Pleistocene felids have been dismissed due to the lack of good stratigraphic data, or as the result of incorrect taxonomy (Prevosti et al., 2006; Prevosti and Pomi, 2007). The North American saber-toothed *S. fatalis* has also been mentioned for late Pleistocene (Lujanian) sites in Perú and Ecuador (Kurtén and Werdelin, 1990). Lastly, there is a record of a scimitar-toothed cat (Homotheriini) for Uruguay (Mones and Rinderknecht, 2004), but its age is unknown and its generic assignment dubious because it is incomplete (an edentulous anterior portion of a ramus) and is very fragmented. In addition, the fossil record plus biogeographic, phylogenetic, and DNA-based analyses show that *Leopardus* diverged from other felids 2.91 Ma ago (a date concordant with the rise of the Panamanian bridge), and *Puma concolor* and *Herpailurus* diverged around 4.1 Ma (Johnson et al., 2006).

The information from all these sources indicates that at least seven independent invasions occurred: (1) *Panthera*, (2) *Puma*, (3) *Herpailurus*, (4) *Leopardus* (or its ancestor), (5) *S. populator* (or its likely ancestor *S. gracilis*), (6) *S. fatalis*, and (7) Homotheriini. The new fossils here described demonstrate that the biogeography of the Neotropical felids is more complex than previously thought, and allows us to identify new invasions and delimit the ages during which they occurred.

Smilodon is a North American genus, and the oldest records come from the Pliocene of the U.S.A. (Berta, 1985, 1987), represented by the species *S. gracilis* that until now has been restricted to the Pliocene–middle Pleistocene (late Blancan–late Irvingtonian) of the United States. Ferrusquía Villafranca et al. (2010) mention *S. gracilis* from the Pleistocene of Mexico, but insufficient detail is presented, and thus is not possible to corroborate their assignment. *Smilodon* has up until now been represented in South America by *S. populator*, reported for the late Pleistocene (Lujanian) of Brazil, Bolivia, Venezuela, and Argentina; and for the middle Pleistocene (Ensenadan) of Argentina (Berta, 1985; Kurtén and Werdelin, 1990; Berman, 1994; Rincón, 2004, 2006). *S. fatalis* was a North American species also reported for the latest Pleistocene of Perú and Ecuador (Kurtén and Werdelin, 1990). The fossils from Orocual constitute the first record of *S. gracilis* in South America (and outside the U.S.A.), and show that this species invaded South American at least during the early–middle Pleistocene. In this context, *S. populator* could have originated in South America from *S. gracilis* or from a common ancestor but *S. fatalis* originated in North America where there are older records (middle Pleistocene; Berta, 1985).

Records of Homotheriini are widespread throughout the world, and have been reported from Africa, Europe, Asia, North America, and most recently South America (Meade, 1961; Ficarella, 1979; Rawn-Schatzinger, 1992; Werdelin, 2003; Mones and Rinderknecht, 2004). This tribe contains four genera (*Machairodus*, *Homotherium*, *Xenosmilus*, and *Lokotunjailurus*),

TABLE 3. Upper teeth measurement comparisons between Orocuai Smilodontini material and *Smilodon gracilis*, *Smilodon fatalis*, and *Smilodon populator* (in mm).

Taxa and data source	Catalog number	APC	TC	APP3	TP3	APP4	TP4	
<i>Smilodon gracilis</i> (El Breal de Orocuai)	Or-1342	27.3	14.9					
	Or-1347			17.7	7.8			
	Or-1343					32.9	14.6	
<i>Smilodon gracilis</i> (Berta, 1987)	F:AM 95525	29.7	14.2	16.5	7.8	30.4	11.5	
	F:AM 95526	31.4	14.4					
	ANSP 44	35.5	15.2	16	6.5	33.7	11.8	
	ANSP 47	26.8	13.3					
	ANSP 46	25.9	13.1					
	UF 18099	16.5	9.3					
	UF 12927	14.3	8.2					
<i>Smilodon gracilis</i> (Natural History Museum of Florida)	UF 12928	14.2	8					
	UF 86843	24.5	12.39					
	UF 84189	24.34	12.01					
	UF 81722	27.02	14.85					
	UF 83655	28.29	13.17					
	UF 82251	24.17	11.21					
	UF 63654	24.23	12.53					
	UF 80182	24.61	11.98					
<i>Smilodon gracilis</i> (Berta, 1995)	UF 80111	27.75	14.6					
	UF 87243			14	6.2	31.3	11.9	
	UF 87246			13.5	6.3	31.6	11.4	
	UF 87238			14.7	7.2	32	13.9	
	UF 81700			14.7	7.2	32	13.9	
<i>Smilodon fatalis</i> (Merriam and Stock, 1932; RLB-LACMHC)	2001-24	46.1	22.9	18.5	10.6	46	19.3	
	2001-230	44	21.7	17.4	9.2	41.5	16	
	2001-225	43.7	24.1	19	9.7	39.5	17.3	
	2001-151	41.7	22.2	18	10.1	41.6	17.6	
	2001-111	41.9	22.3	17.4	9.5	41.6	15.3	
	2001-132	41.1	22.6	16.1	8.9	39	16	
	2001-288	45.6	21.4	15.7	9.4	40	16.3	
	2001-16	41.5	21.4	15.9	9	41.4	16.7	
	2001-181	43	21.2	15.5	9.3	37.3	15.7	
	2001-19	42.1	20.5	19.7	10.2	42.7	19	
	2001-65	46.1	20.5	16.8	9.8	38.8	15.8	
	2001-2	45	23	17.4	9.2	41.4	16	
	2001-307	38.1	21.7	15	8.4	40	15	
	2001-90	41	19.3	17.9	8.7	42	15	
	2001-131	43	19.7	18.5	9.1	41.7	18.3	
	2001-4	42.2	19.7	16.1	8.8	41	17.4	
	2001-256	36	18.6	16.1	8.4	37.9	15.9	
	<i>Smilodon populator</i> (Kurten and Werdelin, 1990)	KW2	44.5	20.7			45.5	19.5
		KW3	44.3	22.1	15.6	9	41.3	17.6
		KW4	47.7	22.3			44	17.9
KW5		45.9	21.8	16.4	8.9			
KW6				20.8	10.1	46.5	18.6	
KW7				17.6	8.8	40	16.9	
KW19		36.5	13	16	8	40.5		
KW20		43.3	15.5	14.5	8.6	38.9		
KW23				16.7	9.5	38.8	16.8	
KW26				18	10.8	43	18.2	
KW27		47.4	21.9					
KW28		49.2	25	18.9	11	42.5	18.5	
KW29		44.3	22.3			42.5	18.3	
KW30	44.7	22.8			45	21.9		

Abbreviations: AP, anteroposterior length; TC, transverse length; C, canine; P3, third upper premolar; P4, fourth upper premolar.

and shows a high species diversity, although the number of species may be overestimated in the cases of *Machairodus* and *Homotherium* (Ficarelli, 1979; Pons-Moyà and Moyà-Solà, 1992; Sotnikova et al., 2002). The earliest *Homotherium* records come from the Odessa Catacombs (Ukraine) and the Nachukui Formation (Kenya), resulting in an indeterminate origin for this genus (Werdelin and Sardella, 2006). Up until now *Homotherium* fossil records have been distributed in the late Pliocene to late Pleistocene of Africa (*H. hadarensis*, *H. problematicum*), Europe, Asia (*H. latidens*, *H. crenatidens*), and North America (*H. serum*, *H. ischyurus*, *H. johnstoni*, *H. idahoensis*, *H. crusafonti*) (Merriam, 1905, 1918; Meade, 1961; Mawby, 1965; Schultz and Martin, 1970; Collings, 1972; Harris et al., 1988; Petter and Howell, 1988;

Rawn-Schatzinger, 1992; Jefferson and Tejada-Flores, 1993). The fossils from Orocuai represent the first records of *Homotherium* for South America, indicating that the scimitar-toothed cats invaded this continent at least during the early-middle Pleistocene.

The absence and scarcity of Homotheriini in other regions of South American during the Pleistocene could be due to biogeographic differentiation on this continent. On the other hand, the few known specimens from Venezuela and the only one from Uruguay (Mones and Rinderknecht, 2004) could be related to low population densities, something that agrees with the low frequency of *Homotherium* in the fossil record of other continents compared to other machairodonts (i.e., *Smilodon*).

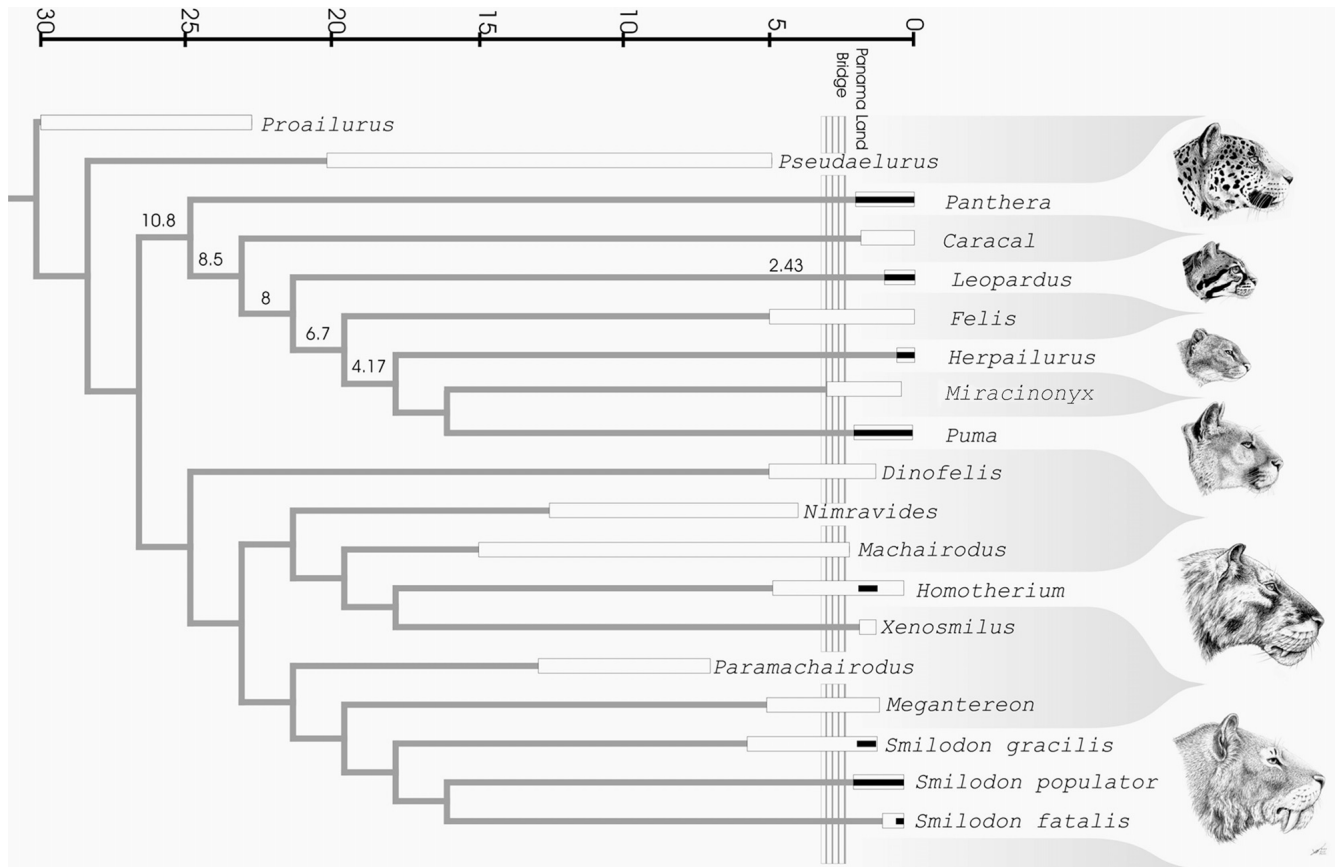


FIGURE 5. Phylogenetic relationships, fossil record, and DNA-based divergence dates of Felidae. White boxes represent the known fossil record for each taxa, black lines are the fossils recorded in South America, and the numbers on the nodes represent the DNA divergence dates in million years.

ACKNOWLEDGMENTS

We would like to thank J. Babiaryz (Babiaryz Institute of Paleontological Studies), T. Rowe and L. Murray (Texas Memorial Museum), A. Prieur and C. Guerin (Centre Commun des Collections de Géologie, Lyon), W. Akersten (Idaho Museum of Natural History), and P. Tassy and C. Argot (Muséum National d'Histoire Naturelle, Paris) for their help and permission to inspect their collections. We would also like to thank D. Orchard and E. Orchard, A. Fariñas, M. Fariñas, C. Bell, A. Vilorio, L. Lisett, and A. Nuñez for their work and companionship in the field and laboratory and L. Martin, L. Werdelin, T. Wheeler, L. dos Santos Avilla, J. Harris, C. Shaw, and B. Van Valkenburgh for providing much information and comments on earlier versions of the project. The photographs of this work were taken and edited by V. Monasterios. A. Solorzano made the map. M. T. Requena (Biblioteca, Institut de Paleontologia M. Crusafont) and C. Cordovez (Biblioteca Marcel Roche IVIC) provided help to find some literature. D. Fastovsky helped with the English. This study was supported by the Exploration and Production Unit of Petróleos de Venezuela S.A. (PDVSA) División Oriente and the Instituto Venezolano de Investigaciones Científicas, Science and Technology Ministry. We thank Marcos Ercoli for illustrations used in Figure 5.

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Submitted July 7, 2010; accepted December 7, 2010.

Handling editor: John Harris.