



First record of *Smilodon fatalis* Leidy, 1868 (Felidae, Machairodontinae) in the extra-Andean region of South America (late Pleistocene, Sopas Formation), Uruguay: Taxonomic and paleobiogeographic implications

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ABSTRACT

The Felidae are known in South America from the Ensenadan Stage/Age onwards. Among them, machairodonts of the genus *Smilodon* stand out. Three species are recognized, and all three are present on the continent: *S. gracilis* from the early-middle Pleistocene in north-east Venezuela; *S. fatalis*, found only in Lujanian sediments on the west side of the Andes (north-west of Peru and south-west of Ecuador); and *S. populator*, which inhabited the eastern part of the Andes during the Ensenadan and Lujanian. This distribution has led to the suggestion that the last two felids were allopatric during the Lujanian. Here, we report the first evidence of *S. fatalis* in the eastern part of the continent (Sopas Formation, late Pleistocene of Uruguay), based on an almost complete skull. This finding not only enlarges its distribution in South America but questions the idea of allopatric distribution. It also adds a new component to the mammalian predator trophic level of Uruguay, with the capacity to predate large South American herbivores and megaherbivores. A revision of materials previously assigned to *S. populator* in the extra-Andean zone of South America will be required.

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1. Introduction

The fossil record of carnivorous land mammals (order Carnivora) in South America began in the late Miocene and exhibits a remarkable dispersion around 3 million years ago (mya), when the Isthmus of Panama arose in an event known as the Great American Biotic Interchange (G.A.B.I.) (see Soibelzon and Prevosti, 2007; Woodburne, 2010; Rincón et al., 2011; Ubilla et al., 2011; Cione et al., 2015). This amalgamation of faunas occurred as dispersal pulses, mainly in two stages according to the fossil record (late Pliocene and early Pleistocene) (Soibelzon and Prevosti, 2007; Woodburne, 2010). Other events where carnivorous land mammals entered the continent took place during the middle and late Pleistocene but were less important (Woodburne, 2010). Once in South America, an adaptive radiation of the immigrant clades occurred, along with extinction events, leading to the origin of the diverse native species that inhabit the continent today (Soibelzon and Prevosti, 2007).

The fossil record for large felids in South America is quite scarce, relative to other mammalian carnivores and compared with other continents. They are reliably known since the Ensenadan (early-middle Pleistocene) (Prevosti and Pomi, 2007; Soibelzon and Prevosti, 2007; Rincón et al., 2011; Chimento et al., 2014 and references therein). At least seven taxa have been identified: *Smilodon populator* Lund, 1842; *S. fatalis* (Leidy, 1868); *S. gracilis* Cope, 1880 (Fig. 1A); *Homotherium venezuelensis* Rincón et al., 2011; *Xenosmilus* Martin et al., 2000; *Panthera onca* Linnaeus, 1758; and *Puma concolor* (Linnaeus, 1771) (Méndez-Alzola, 1941; Churcher, 1967; Currier, 1983; Seymour, 1989; Kurtén and Werdelin, 1990; Mones and Rinderknecht, 2004; Prevosti and Pomi, 2007; Rincón et al., 2011).

In Uruguay, remains (mostly fragmentary but still informative) belonging to *Panthera onca*, *Puma concolor* and the machairodonts *Smilodon populator* and cf. *Xenosmilus* sp. have been found (Mones and Rinderknecht, 2004; Ubilla et al., 2011; Ubilla and Martínez, 2016).

In the present contribution, an almost complete skull from late Pleistocene sediments from northern Uruguay (Sopas Formation) (Fig. 1B) is described, which belonged to the saber-toothed cat *Smilodon fatalis*. This is the first evidence of this species on the

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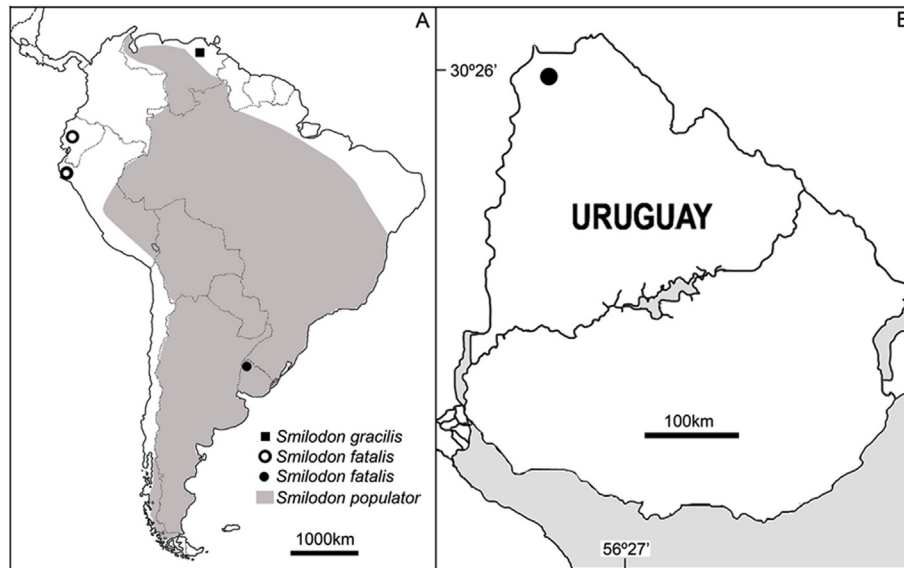


Fig. 1. A) Distribution of *S. gracilis* (according to Rincón et al., 2011), *S. fatalis* (according to Kurtén and Werdelin, 1990) and *S. populator* (according to Berta, 1985; Kurtén and Werdelin, 1990; Soibelzon and Prevosti, 2007, 2013; Shockey et al., 2009; Prieto et al., 2010) in South America. B) Geographic location of the zone of the discovery: Tres Cruces Grande Creek, Department of Artigas (Sopas Formation).

eastern slope of the Andes. The implications that this discovery has for taxonomy and paleobiogeography are discussed based on the present state of knowledge.

2. Geological context

The Sopas Formation, located in northern Uruguay, is characterized by conglomerates with clay and calcareous matrices, conglomerate-sandstones, siltstones and sandy siltstones. This unit is predominantly brownish with a 5–8 m thickness (Martínez and Ubilla, 2004; Ubilla et al., 2016). The bearing outcrop comprises sandy siltstones with an intercalated conglomerate level with channel geometry and alternating sandy layers with planar and convolute stratification. At the top of the section are carbonatic levels (Appendix A). Based on the mammalian assemblage, this unit is correlated with the Lujanian Stage/Age (late Pleistocene–early Holocene) (Ubilla et al., 2011). Multiple absolute dates based on radiocarbon and OSL/TL methods indicate that this unit is correlated mainly with MIS-3 (60–25 ka), with some outcrops at approximately 14 ka (Ubilla et al., 2016). Based on the paleontological content of the Sopas Formation, a wide range of environments can be suggested (lacustrine-fluvial, open areas, semi-forested and dense vegetation) (Ubilla and Martínez, 2016). In this unit, several taxa of the order Carnivora are recorded. The large Felidae include *P. concolor*, *P. cf. P. onca* and *S. populator* (Ubilla et al., 2016).

3. Materials and methods

3.1. Institutional abbreviations

CBM, Colección particular Brum-Martínez, Montevideo, Uruguay; **FC-DPV**, Facultad de Ciencias- Colección Paleontológica (Vertebrados fósiles), Montevideo, Uruguay; **MNHN-P**, Museo Nacional de Historia Natural, Departamento de Paleontología, Montevideo, Uruguay.

3.2. Comparative sample

For comparative analysis, materials of *S. populator* housed in the Colección Paleontológica (Vertebrados fósiles) of the Facultad de Ciencias (UdelaR) and the Museo Nacional de Historia Natural (Montevideo) were used. Bibliographic material for *S. gracilis*, *S. fatalis* and *S. populator* according to Merriam and Stock (1932), Méndez-Alzola (1941), Churcher (1967), Berta (1985, 1987, 1995), Kurtén and Werdelin (1990) and Rincón et al. (2011) were also used. Dental nomenclature follows Berta (1987).

3.3. Analyses

Body mass estimations were made based on allometric equations formulated for extant felids (Van Valkenburgh, 1990) (Appendix B), using measurements of the skull according to the preservation of the material. Bivariate graphs were used to highlight quantitative differences between taxa. The multivariate analyses (principal components analysis or PCA, and hierarchical cluster) were performed on the variance-covariance matrix measurements, using the statistical program PAST Version 2.09 (Hammer et al., 2001). The data for *S. gracilis*, *S. fatalis* and *S. populator* came from the literature (Merriam and Stock, 1932; Méndez-Alzola, 1941; Churcher, 1967; Berta, 1987, 1995; Kurtén and Werdelin, 1990; Prieto et al., 2010; Rincón et al., 2011) and from this paperwork (see Appendix C).

3.4. Measurements

All measurements were taken by one of us (A. M.) following Méndez-Alzola (1941), Churcher (1967) and von den Driesch (1976), with manual calipers accurate to 0.01 mm and expressed in millimeters (Appendix D).

Skull measurements: total length (TL), condylobasal length (CBL), orbito-occipital length (OOL), zygomatic width (ZW), rostral width (RW), interorbital width (IOW), width at the post-orbital constriction (PCW), greatest mastoid breadth (GMB), greatest breadth at the occipital condyles (GBC), greatest breadth of the foramen magnum (FMB), height of the foramen magnum (FMH).

Dental measurements (right side): tooth row length I1-PM4 (TRL I1-PM4), diastema canine-PM3 (Diast), antero-posterior diameter of the canine (CAP), transverse diameter of the canine (CML), crown height of the canine (CH), antero-posterior diameter of the PM3 (PM3AP), transverse diameter of the PM3 (PM3ML), antero-posterior diameter of the PM4 (PM4AP), transverse diameter of the PM4 (PM4ML).

4. Results

4.1. Systematic paleontology

Carnivora Bowdich, 1821
 Felidae Fischer de Waldheim, 1817
 Machairodontinae Gill, 1872
 Smilodontini Kretzoi, 1929
Smilodon Lund, 1842
Smilodon fatalis Leidy, 1868

4.2. Referred material

CBM 13, almost complete skull (Fig. 2).

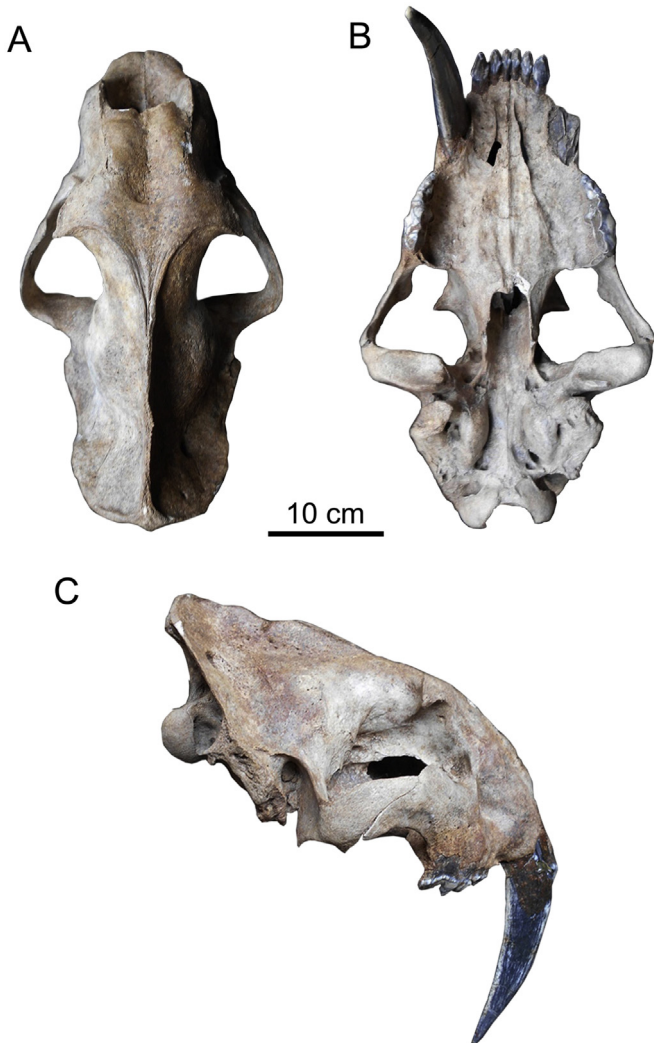


Fig. 2. Skull of *Smilodon fatalis* (CBM 13) in A) dorsal, B) ventral and C) right lateral view. Scale 10 cm.

4.3. Geographic and stratigraphic location

Tres Cruces Grande Creek (Department of Artigas, Uruguay). Sopas Formation, late Pleistocene.

4.4. Comparative description

Dorsal view: elongated and rather narrow skull with rostral region shorter than postorbital region, more similar to *S. populator* than to *S. fatalis*. Skull with a small braincase, wide postorbital region and marked postorbital constriction. Nasals are anteriorly wide and the naso-frontal suture is “U”-shaped. Lateral view: differing from *S. populator* and similar to *S. fatalis*, nasals are not high and the large lambdoid crest is anteroventrally straight, converging in the same plane as the mastoid process (Fig. 3). Ventral view: anteriorly narrow and elongated palatine foramina; antero-posteriorly elongated and transversely compressed auditory bullae. Tooth rows very well preserved but lacking M1 and with cracked left canine. Conical and prominent principal cusp in the incisors, which are slightly posteriorly recurved and procumbent and accompany the alveolar margin of the anteriorly oriented premaxilla. The preserved canine has the typical blade shape of smilodontins (antero-posteriorly wide, laterally compressed, posteriorly curved and highly hypertrophied) (Merriam and Stock, 1932; Méndez-Alzola, 1941). It is longer, curved and much more trenchant than in *S. gracilis*. The PM3 is tricuspidate and slightly

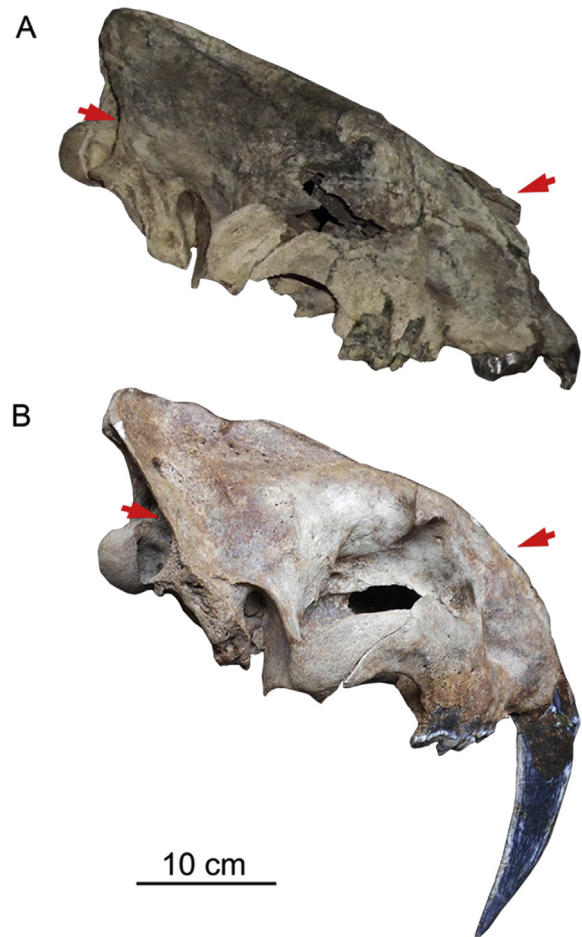


Fig. 3. Comparison, in right lateral view, of the skull of A) *S. populator* (MNHN-P 957) and B) *S. fatalis* (CBM 13). The arrows shows the main differences between both of them. Explanation in section 4.4. Scale 10 cm.

oblique with respect to the corresponding PM4, with a dominant central cusp along with anterior and posterior minor cusps. In occlusal view, the posterior half is wider than the mesial half. The PM4 is secodont and has the typical configuration of the genus (Appendix E). The principal cusps are well preserved, the secondary ectoparastyle is anterior to the parastyle. The protocone is reduced like in *S. fatalis* and *S. populator* compared with *S. gracilis*. Judging from the degree of wear of the teeth, specially PM4, the analyzed specimen belongs to an adult.

4.5. Remarks

The body mass estimations calculated over measurements of the skull are consistent with this taxon, averaging around 165 kg (see section 5.1., see also Appendix F). Bivariate analysis based on dentition (Fig. 4), shows significant differences with the comparative set of *S. gracilis* and with *S. populator*. In terms of size, the canine and PM4 are smaller than in *S. populator* (Méndez-Alzola, 1941) and larger than in *S. gracilis* (Berta, 1987, 1995) falling

within the size variability of *S. fatalis* (Merriam and Stock, 1932). The PCA and cluster analyses performed over several skull measurements are congruent with the above-mentioned results (see Appendix G).

4.6. Measurements (in mm)

Skull measurements: TL, 319.6; CBL, 289.5; OOL, 183; ZW, 188; RW, 94; IOW, 88; PCW, 61; GMB, 128; GBC, 67.5; FMB, 30; FMH, 21.

Dental measurements (right side): TRL I-PM4, 143; Diast, 22.5; CAP, 42; CML, 21; CH, 140; PM3AP, 16.5; PM3ML, 8; PM4AP, 35; PM4ML, 14.5.

5. Discussion

5.1. Morphology and taxonomy

Within the genus *Smilodon*, and despite the controversies surrounding its specific taxonomy, three species are now recognized:

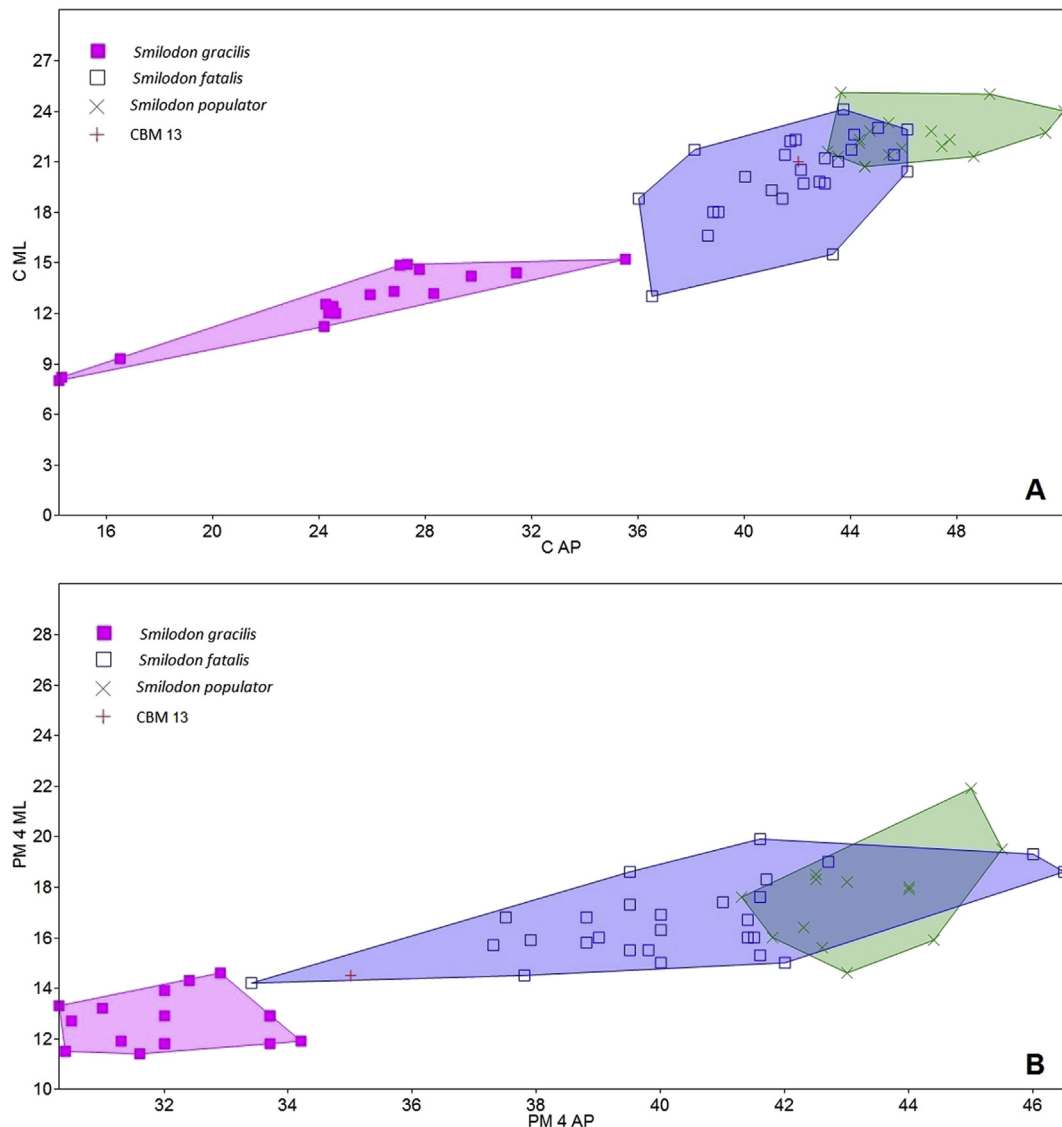


Fig. 4. Bivariate graphs for A) canine and B) PM4 for the material of *Smilodon fatalis* (CBM 13). The data of *S. gracilis* according to Berta (1987, 1995) and Rincón et al. (2011); *S. fatalis* according to Merriam and Stock (1932) and Kurtén and Werdelin (1990); *S. populator* according to Méndez-Alzola (1941), Churcher (1967), Kurtén and Werdelin (1990), Prieto et al. (2010) and this paperwork.

S. gracilis, *S. populator*, and *S. fatalis* (Kurtén and Werdelin, 1990; Turner and Antón, 1997).

According to body size, *S. gracilis* was similar to the extant jaguar (55–100 kg) (Christiansen and Harris, 2005), and was restricted mainly to the late Pliocene–middle Pleistocene of North America (Berta, 1985, 1987, 1995; Kurtén and Werdelin, 1990). It has also recently been recorded in northern South America (Venezuela), which, according to the age of the sediments, implies that it entered the continent at least in the early stages of the G.A.B.I. (early–middle Pleistocene) (Rincón et al., 2011). As noted by several authors, *S. populator* may have originated in South America from *S. gracilis* or from an ancestor common to both species (Turner and Antón, 1997; Rincón et al., 2011). *Smilodon populator*, endemic to South America, is the most frequently found on that continent, in Ensenadan to Lujanian deposits (early Pleistocene–early Holocene), particularly towards the center and east (Brazil, Bolivia, Paraguay, Venezuela, Argentina, Uruguay, southern Chile and eastern Peru) (Berta, 1985; Kurtén and Werdelin, 1990; Rincón, 2006; Soibelzon and Prevosti, 2007, 2013; Shockey et al., 2009; Prieto et al., 2010). This was the largest species of the genus, with a body mass of approximately 220–360 kg (Christiansen and Harris, 2005), although some individuals could exceed 400 kg (Christiansen and Harris, 2005; Sorkin, 2008). Finally, *S. fatalis*, from the mid–late Pleistocene of North America, has a mass intermediate between the aforementioned species, similar to that of the extant siberian tiger, weighing approximately 160–280 kg (Christiansen and Harris, 2005). This species has also been found in late Pleistocene sediments in northwestern South America (Coralito in Ecuador, and Talara in Peru, see Kurtén and Werdelin, 1990), which would have represented a new immigration, in this case late, of large felids to South America, along with other carnivores (for example *Canis dirus*) along the Pacific coast during the Lujanian (Kurtén and Werdelin, 1990; Soibelzon and Prevosti, 2007, 2013). Beyond sharing a common body plan in broad outline, these species differ from each other body size, as mentioned above, as well as in several other morphological characteristics. *Smilodon populator* is distinguished from *Smilodon fatalis* by a more elongated and narrow skull, with a postorbital region that is elongated compared to its facial region. Its nasals are prominent and determine a lateral rostral contour that is higher than in *S. fatalis*, while in its posterior region, an angle is formed between the lambdoid crest and the mastoid process (Kurtén and Werdelin, 1990). Based on these last two characteristics, the studied material presents a pattern congruent with that evidenced in *S. fatalis*. Nevertheless, the dorsal view shows a morphotype that is more similar to *S. populator*. This same cranial variation has already been observed in other specimens of *S. fatalis*, particularly among those recorded in Talara (Peru); therefore, it is interpreted as an intraspecific differentiation between these populations and those of North American *S. fatalis* (Kurtén and Werdelin, 1990). For the aforementioned species, the variant found here presents characteristics more consistent with those present in the sample of *S. fatalis* recorded in Talara (Peru) than with the purely North American lineage.

5.2. Paleobiogeographical and chronological connotations

In South America, there are no records of coexistence between *S. fatalis* and *S. populator*, which has led to the interpretation of an allopatric distribution of these felids (see Fig. 1A), with the Mountain Range of the Andes acting as a barrier to dispersal (Kurtén and Werdelin, 1990; Turner and Antón, 1997; Soibelzon and Prevosti, 2007, 2013; Castro and Langer, 2008; Prieto et al., 2010). The finding reported here implies that the geographic range of *Smilodon fatalis* is expanded (in this case approximately 5000 km to the southeast of the continent). In addition, the idea of allopatric

distribution may also be discredited.

The radiocarbon ages available for the Talara deposits are 13–14 ka uncalibrated (Churcher, 1966), and there are no ages available for Coralito (Ecuador) (Lindsey and Seymour, 2015).

However, most of the Sopas Formation involves the interval 60 to 25 ka (Ubilla et al., 2016) and although numerical ages are not available for the levels of the Tres Cruces Creek, it is possible that the Uruguayan record may be older than that of Peru, or at least isochronous.

The predatory trophic level thus far described for the Sopas Formation comprises the above-mentioned felids and is accompanied by hypercarnivorous canids, short-faced bears and some birds (Prevosti et al., 2009; Ubilla et al., 2016). It is thus enriched by the presence of *S. fatalis*. The action of these large felids, like that of any carnivore, would have been decisive in exerting a regulatory effect, mainly by controlling prey populations (in this case, large herbivores and megaherbivores of the late Pleistocene) (Prevosti and Vizcaíno, 2006), and secondarily from other carnivores, thus maintaining the trophic structure in the respective environments they inhabited (Pérez Irineo, 2008 and references cited there).

Finally, based on this finding, it can not be ruled out that some materials previously determined as *S. populator* in the extra-Andean zone of South America might not belong to this species but to *S. fatalis*; so a review of these materials is necessary.

6. Conclusions

The saber-toothed cat cranium described in this paper is attributed to the extinct species *Smilodon fatalis*, from the late Pleistocene of Uruguay (Sopas Formation), based on several morphological characteristics that enable it to distinguish it from *S. populator*. These features include nasal bones that are not risen in a marked way and a lambdoid crest that forms a straight line to the mastoid process. The studied material also shows dental measures that fall in the range of size variability of *S. fatalis*. The specimen described here represents the first evidence of this taxon in the eastern part of South America and discredits the idea of allopatric distribution between the above-mentioned felids during the Lujanian. Based on this finding, a review of the materials of smilodontins in the extra-Andean zone of the continent is necessary.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quascirev.2017.11.024>.

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