

Occurrence of the sabretooth cat *Smilodon populator* (Felidae, Machairodontinae) in the Cuvieri cave, eastern Brazil

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ABSTRACT

The saber-toothed cat *Smilodon populator*, typical of the Pleistocene of South America, is known for its teeth, cranial bones, and post-cranial bones (humerus, radius, ulna, femur, tibia, fibula, astragalus, and phalanges). A specimen found in the Cuvieri Cave in Brazil based on small bones (calcaneal, ectocuneiform, and phalanges) is described and commented here. The osteological material has a complete calcaneal and an ectocuneiform that adds data on *S. populator*. The specimen is comparable in size to that of an adult lioness and represented the largest predator in the region. The associated fauna and age obtained for the material were also discussed.

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INTRODUCTION

The Cuvieri cave is part of the Lagoa Santa karst complex, consisting of two passages, one obstructed and the other with 1.5 m height and 1 m width, giving access to its interior. The cave has three small vertical cavities, natural traps, which were called *Locus* 1, 2, and 3, with 16 m, 4 m, and 8 m depth, respectively (Hubbe et al., 2011). Since 1974, with the discovery of terrestrial sloth *Catonyx cuvieri*, the Cuvieri Cave has been the target of scientific interest which is reflected in the work done

on dating, paleontology, taphonomy, and comparison with other paleontological and archaeological sites (Hubbe et al., 2011; Haddad-Martim et al., 2017).

The Felidae family emerged in South America since the American Faunal Interchange of the Late Pliocene. Currently only three genera occur in South America, *Puma*, *Panthera*, and *Leopardus*. However, after the faunal exchange three other genera attributed to the Machairodontinae subfamily were reported, *Smilodon*, *Homotherium* (Mones

and Rinderknecht, 2004), and *Xenosmilus* (Rincón et al., 2011), the first being the most common in the fossil record.

The genus *Smilodon* is part of the Machairodontinae, an extinct subfamily of Felidae, and includes three species; *S. gracilis*, *S. fatalis*, and *S. populator*. The main diagnostic feature of this subfamily is the very elongated canine teeth compared to other predators, from which its colloquial name “saber tooth cats” originates. The *Smilodon populator* species is, so far, the largest and the last to be extinct (Antón, 2013; Christiansen and Harris, 2005; Chimento et al., 2019).

Remains of *Smilodon populator* have been registered in almost all countries in South America (Berta, 1985, Kurtén and Werdelin, 1990; Ubilla et al., 2004; Rincón, 2006; Prieto et al., 2010). Studies developed by Hubbe et al. (2011) named the presence of a large Felidae, initially identified as *Smilodon populator*. The purpose of this contribution is the presentation with comments on the osteological material of this specimen and its identification.

MATERIAL AND METHODS

The osteological material of the Cuvieri Cave (Figure 1) collected comes from “Locus” 2. According to Hubbe et al. (2011) the sediment found in this location was poorly consolidated, which favored excavation and more careful exploration, with detailed stratigraphy and taphonomy data being obtained.

The specimen presented a small number of materials for study, identification, and classification. According to Hubbe et al. (2011) the distribution of these bones was more concentrated in the corners and extremities of “Locus” 2, despite this scattering bone parts can be considered as belonging to the same individual, since they are compatible in size to those of a large feline, and there are no repeated bone parts. The specimen is represented by only 11 bone parts that were scattered throughout the cavity. An ectocuneiform bone, CVL2-13122, was dated and was 10790 ± 60 BP at $14C$ yr BP and $12.880 - 12.720$ cal yr BP.

The material and registration numbers are deposited at the Laboratório de Estudos Evolutivos Humanos (LEEH) of the Universidade de São Paulo.

SYSTEMATIC PALAEOLOGY

Order CARNIVORA Bowdich, 1821

Family FELIDAE Gray, 1821

Subfamily MACHAIRODONTINAE Gill, 1872

Tribe SMILODONTINI Kurtén, 1963

Genus *SMILODON* Lund, 1842

Figure 2, Figure 3, Figure 4, Figure 5

Type species. *Smilodon populator* Lund, 1842

Material. The identified material consists of a fragmented right calcaneal (CVL2 15315), complete left calcaneal (CVL2 12157), complete proximal phalanx (CVL2 14207), four intermediate phalanges (CVL2 13300, CVL2 13333, CVL2 13400,

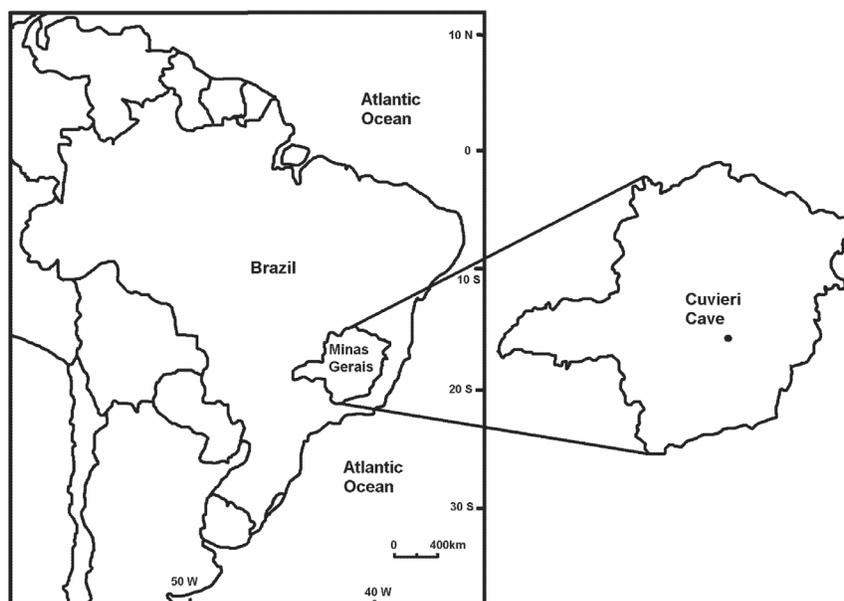


FIGURE 1. Location of the Cuvieri Cave, Lagoa Santa region. State of Minas Gerais, Brazil.

CVL2 15187), two fragmented distal phalanges (CVL2 14309, CVL2 14532), distal part of metatarsal (CVL2 12475) and one right ectocuneiform bone (CVL2 13122).

General characteristics and comparison. It is possible to compare the osteological material found with large species attributed to the genus *Panthera*. In Figures 2-4 the calcaneal and ectocuneiform bones were compared to the equivalents of an adult lioness (*Panthera leo*).

Calcaneal. Comparing the calcaneal, the specimen found in the Cuvieri Cave has the most robust and dense tuberosity (*tuber calcis*), and the astragalar facets are larger, wider and slightly closer to the cuboid rim than in that of the lioness.

The sustentacular facets, As2 and As3 (Figure 2), have great contact with each other, and As3 basically represents an extension of As2. Compared to the genus *Panthera*, it has a small extension that links these facets (Figure 3A-D). The process supporting the second facet (As2) or support is more robust and prominent in proportion to the total size of the calcaneal, mainly seen in dorsal view (Figure 3).

The As3 astragalar facet is larger and more evident than in the lioness and extends to the cuboid facet. The navicular facet (Na) is next to the As3 facet and both are in direct contact with the cuboid articular facet.

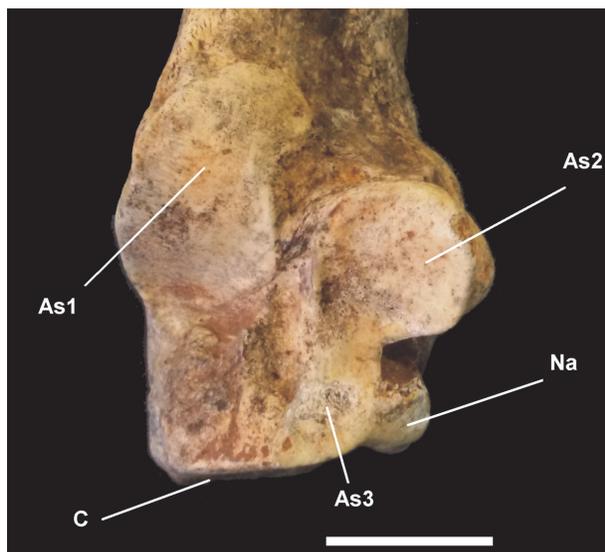


FIGURE 2. Detail of the right calcaneal articular region CVL2 15315. As1 - External astragalar facet or ectal facet; As2 and As3 - internal astragalar facets or sustentacular facets; Na - facet articulate with the navicular; C - Articulation facet with cuboid. Scale bar equals 20 mm.

The ectal facet (As1) is larger, wider, and less elongated than observed in the genus *Panthera* and does not invade the tuberosity.

The cuboid facet (C) differs from the lioness since it occupies a larger area, reaching the plantar border, being straight and flat on this side to the central part (Figure 3E), but presents a concavity close to the contact with the navicular facets (Na) and of the astragalar facet (As3).

Ectocuneiform. The right ectocuneiform is more compressed in proximo-distal direction than those in recent large felines. The plantar projection with groove to the tendon of the long fibular muscle has an open hook shape and less prominent curvature than that of the lioness (Figure 4C-D).

The articulating facet with the navicular tapers and stretches to the plantar region, while observing a small projection on the lioness (Figure 4B).

The opposite facet, which articulates to the metatarsal III, is very similar in both (Figure 4A). The plantar projection of this surface is much shorter and relatively small compared to that of a lion of similar size (Figure 4C-E).

Viewed from the inside, the plantar facet of the second metatarsal spans the distal border near the dorsal part of the ectocuneiform. On the outer surface, the cuboid facet is larger than that of the lioness and extends along the proximal edge and approaches the dorsal edge.

Metatarsal and phalanges. The metatarsal and phalanges are indistinguishable in size to those from a recent large feline, such as tigers, lions, or jaguars, as observed in the single phalanx, CVL2 14207. The other specimens had wear, polish (Figure 5E-H), or many breaks, as in the case of the ungual phalanges and the metatarsal (Figure 5A, 5C-D).

The main measurements performed are available in Table 1.

Discussion. *Smilodon populator* was considered to be the sole representative of the genus *Smilodon* in South America until evidence was found in the Andean region of Ecuador and Peru, and recently in Uruguay of *S. fatalis* (Kurten and Werdelin, 1990; Manzuetti et al. 2018) and *S. gracilis* in the Venezuelan Andes (Rincón et al, 2011). Manzuetti et al. (op. cit.) suggested that *S. populator* and *S. fatalis* lived together at the same time and region and Christiansen and Harris (2005) commented that although *S. populator* is larger, it is not uncommon to find adult individuals of similar size to *S. fatalis*.

Comparing the ectocuneiform and calcaneal sizes it is possible to infer that the specimen is

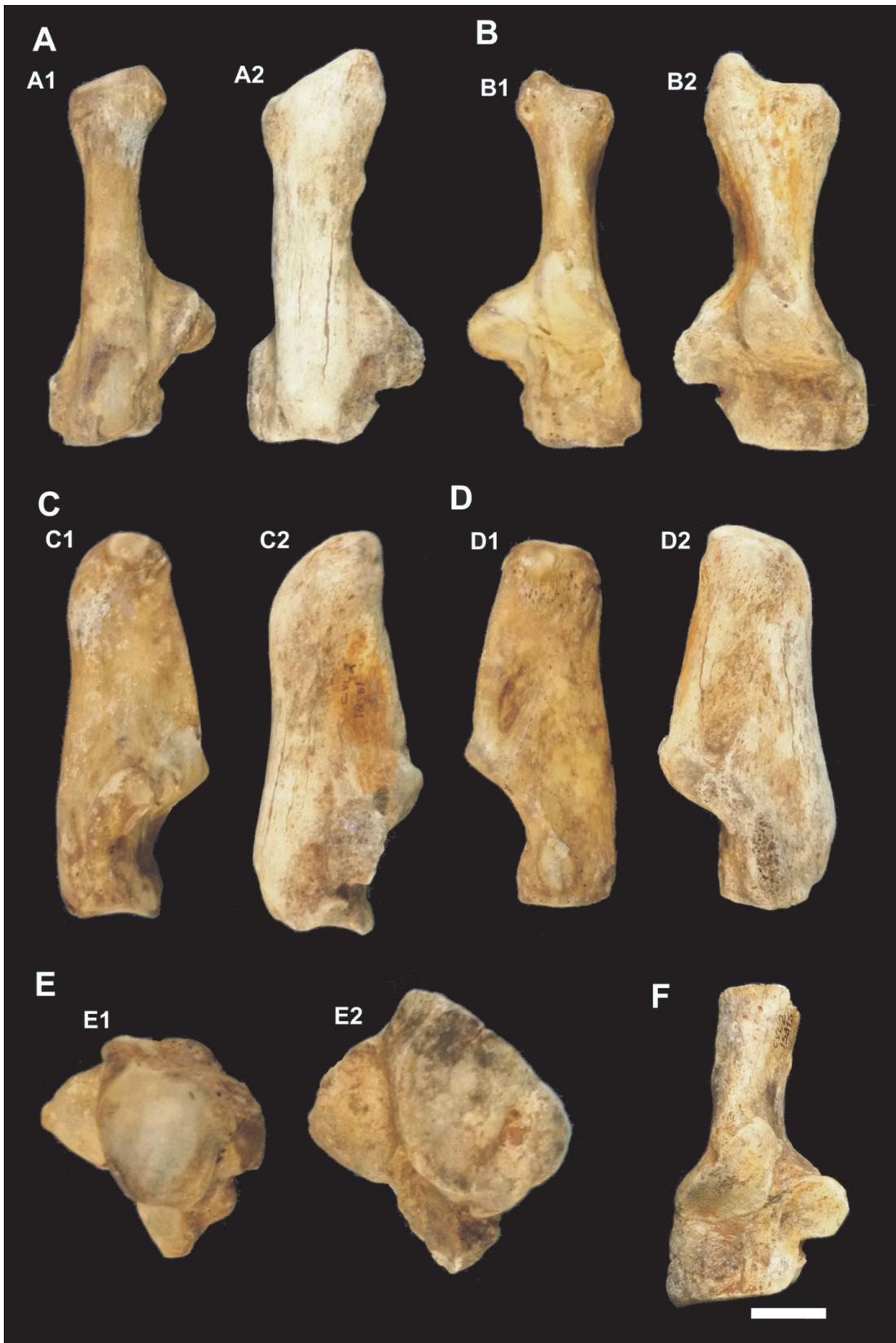


FIGURE 3. Calcaneus. A-F) Left Calcaneus. A) Dorsal view; B) Astragalar view; C and D) Lateral view; E) Distal view; F) Right Calcaneus. A.1-E.1) Adult lioness (*Panthera leo*) A.2-F) *Smilodon populator*. Scale bar equals 20 mm.

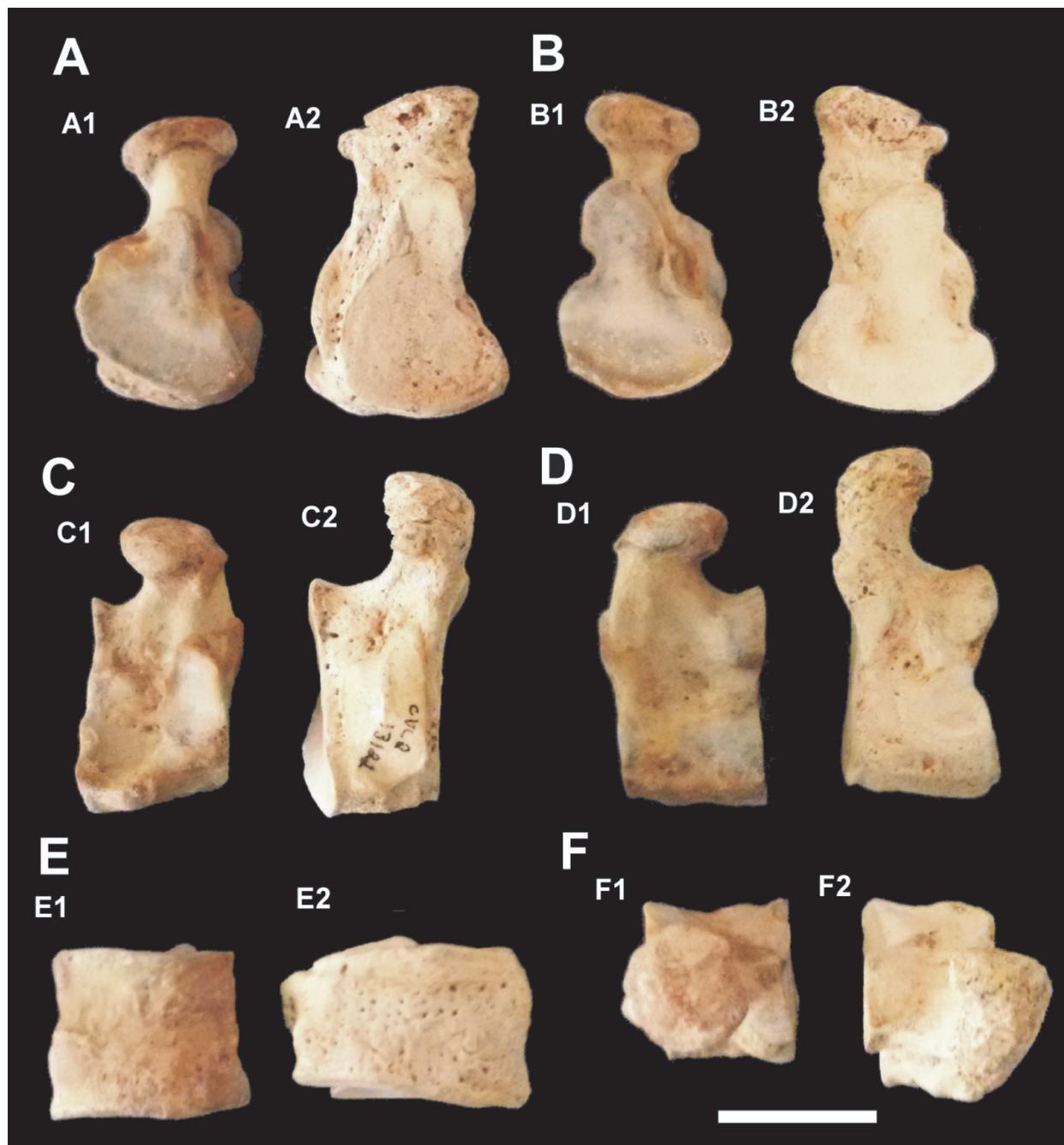


FIGURE 4. Right Ectocuneiform. A) Distal view; B) Proximal view; C) Internal view; D) External view; E) Dorsal view; F) Plantar view. A1-F1) Adult lioness (*Panthera leo*); A2-F2) *Smilodon populator*. Scale bar equals 20 mm.

close to the Pleistocene felines *Smilodon fatalis*, *S. populator* and *Panthera gombaszogensis*, and *P. onca augusta* (Merriam and Stock, 1932; Hemmer et al., 2010, Argant and Argant, 2011; Baryshnikov, 2011; Scaferla et al., 2013) in length and width and smaller than that of large extinct felines such as *P. atrox* and *P. fossilis* (Merriam and Stock, 1932; Sabol, 2014; Chimento and Agnolin, 2017).

The proportions of left calcaneal and right ectocuneiform width and length measurements of the Cuvieri Cave specimen with those described for *S. fatalis*, by La Brea by Merriam and Stock (1932), the Brazilian specimen is slightly more robust than would be expected for a *S. populator* of similar size to *S. fatalis*.

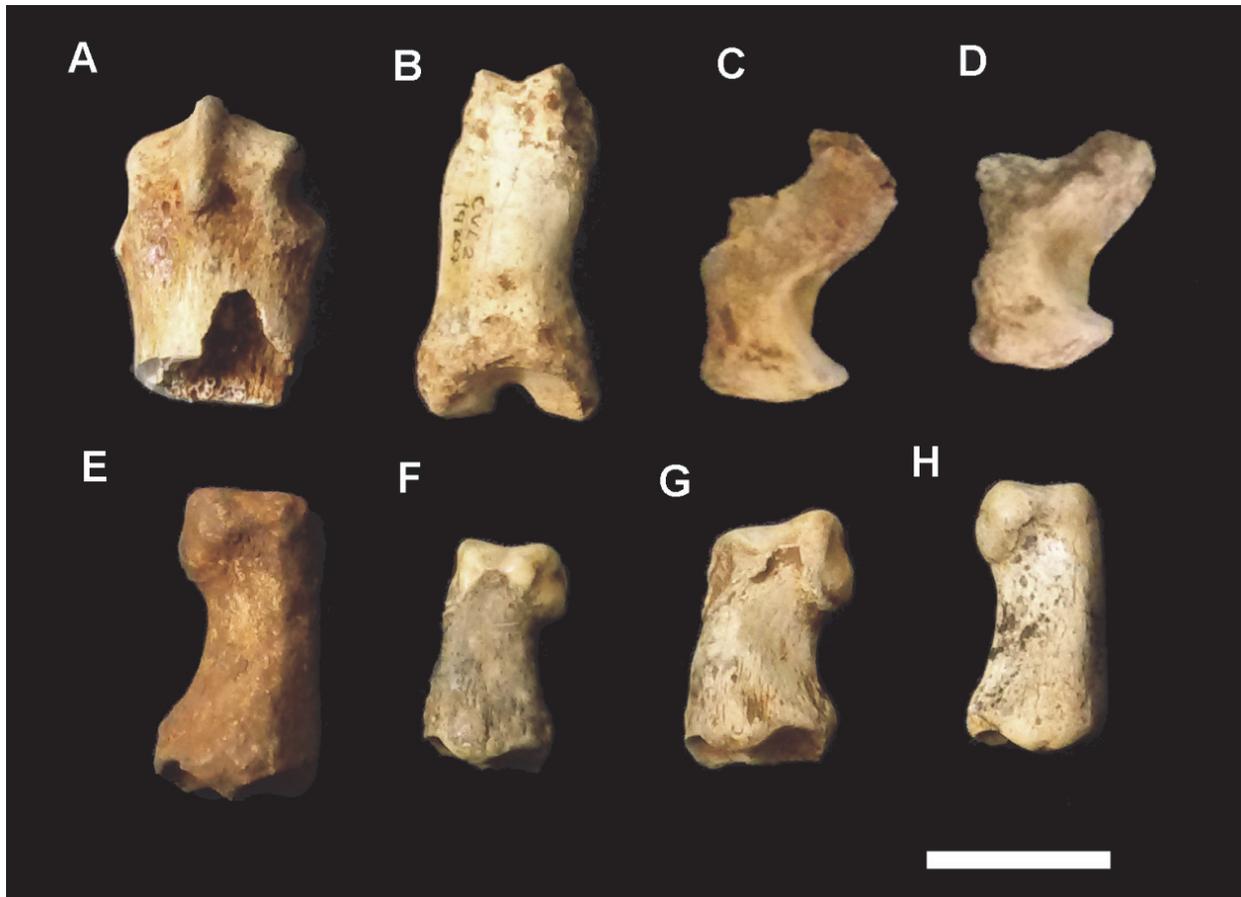


FIGURE 5. Identified osteological material. A) Distal part of metatarsal (CVL2 12475); B) Proximal phalanx (CVL2 14207); B-C) Ungual phalanges (CVL2 14532; CVL2 14309) E-H) Intermediate phalanges (CVL2 15187; CVL2 13333; CVL2 13400; CVL2 13300). Scale bar equals 20 mm.

Smilodon populator occurrences are common in southeastern Brazil. Lund (1842) originally identified and described this species in the Lagoa Santa region, where several specimens were found in various caves, including phalanges and large canine teeth. Other specimens were dated and described, being the specimen found in the Abismo Iguatemi Cave, State of São Paulo, which presented the best specimen with the skull and several preserved bone parts (Ferreira and Karmann, 2002; Castro and Langer, 2008, 2011; Hubbe et al., 2013), revealing important information about the species.

The existence of several specimens of *Smilodon populator* allowed the registration of various ages for several specimens in South America, and it is clear that the specimens occurred during the late Pleistocene, especially in the last 100,000 years from the Pleistocene to the Early Holocene. Most of the reported ages ranged from 25,000-9,000 years (Berta, 1985; Kurtén and Werdelin,

1990; Hubbe et al., 2013; Prevosti and Martin, 2013; Prevosti et al., 2013; Bocherens et al., 2016), with one exception coming from northeast Brazil dating from 93,900 years, using the ESR method, being the oldest of this species (Kinoshita et al., 2017).

ASSOCIATED FAUNA

The osteological material found in Cuvieri Cave consists mainly of animals of recent fauna, such as Tayassuidae, Cervidae, rodents, small reptiles and anurans, and few occurrences of extinct animals. Among the extinct animals found there are two species of Xenarthra Scelidotheriinae typical of the Lagoa Santa region, *Catonyx cuvieri* and *Valgipes bucklandi* (Hubbe et al., 2011), the Cuniculidae *Cuniculus rugiceps* (Mayer et al., 2016) and a new species of Vulturidae *Pleistovultur nevesi* (Alvarenga et al., 2008).

TABLE 1. Measurements (in millimeters) of osteological material found in Cuvieri Cave.

Bone part	Number		Measurements (mm)
Left Calcaneal	CVL2 12167	Greatest length	96.8
		Greatest width measured across astragalar facets As1 and As2	42.1
		Greatest width across cuboid surface measured from astragalar facet As2 to outer side	47.9
		Greatest width of outer face measured normal to plantar Border and to edge of outer astragalar facet	44.7
		Calcaneal tuber length from top of ectal facet to most Uppermost point of calcaneal tuberosity	52.00
		Length from top of ectal facet to base of cuboid facet	44.00
		Projection of peroneal tubercle from midline	16.5
		Projection of sustentacular facet from midline	27.6
		Width of cuboid facet	31.00
		Mediolateral width of calcaneal tuber	29.00
		Anteroposterior width of tuber	32.00
		Length of ectal facet	31.5
		Width of ectal facet	17.00
		Length of sustentacular facet	24.8
		Width of sustentacular facet	19.9
		Tuber length from uppermost projection of sustentacular facet	48.9
		Width of calcaneal head at widest point including sustentacular facet	41.0
	Length from cuboid facet to bottom of sustentacular facet	17.0	
Right Calcaneal (Fragmented)	CVL2 15315	Greatest width measured across astragalar facets As1 and As2	42.3
		Calcaneal tuber length from top of ectal facet to most Uppermost point of calcaneal tuberosity	48.0
		Length from top of ectal facet to base of cuboid facet	~14.0
		Projection of peroneal tubercle from midline	29.0
		Projection of sustentacular facet from midline	31.0
		Width of cuboid facet	~23.0
		Mediolateral width of calcaneal tuber	32.0
		Length of ectal facet	27.6
		Width of ectal facet	18.4
		Length of sustentacular facet	25.0
		Width of sustentacular facet	18.9
			Length from cuboid facet to bottom of sustentacular facet
Right Ectocuneiform	CVL2 13122	Greatest dorsoplantar length	38.0
		Greatest proximodistal diameter	15.6
		Greatest width across metatarsal articulation	22.6
Metatarsal III	CVL2 12475	Greatest width in the distal part	23.0
		Greatest width of the joint	18.9
		Greatest dorsoplantar length	19.8
Phalanx 1	CVL2 14207	Greatest length	39.57
		Greatest width	19.8

TABLE 1 (continued).

Bone part	Number	Measurements (mm)	
Phalanx 2	CVL2 13333	Greatest length	25.0
		Greatest width	18.6
Phalanx 2	CVL2 15300	Greatest length	29.15
		Greatest width	14.6
Phalanx 2	CVL2 13400	Greatest length	29.0
		Greatest width	16.0
Phalanx 2	CVL2 15187	Greatest length	34.0
		Greatest width	17.7
Phalanx 3 (Fragmented)	CVL2 14309	Greatest dorsoplantar length	27.2
Phalanx 3 (Fragmented)	CVL2 14532	Greatest dorsoplantar length	25.0

The osteological material was found next to several carcasses of Cervidae, but none of them has predatory activity marks by large animals, and only rodent or small carnivorous marks, such as Canidae *Cerdocyon*, were observed. The same was found in other parts of the Cuvieri Cave. Probably the whole animal was there at some point and because of the period of exposure or fragmentation by other animals that subsequently fell there (pigs and deer), most of the bones that persisted are small or massive (calcaneal and phalanges), which are easily buried or protected, while bones with a larger surface area (femur, humerus, and scapula) and fragile bones (vertebrae and cranial bones) have been destroyed. Prevosti and Vizcaino (2006) suggest that *Smilodon populator* was at the top of the food web and could have captured an animal of 1 ton. All associated animals found would be potential prey.

CONCLUSIONS

The Cuvieri Cave was not used as a refuge for food or housing, as there was no evidence of gathering or hunting activity and the cavity probably served as a trap. Remains of *Smilodon popula-*

tor have been documented in Venezuela, Brazil, Paraguay, Uruguay, Argentina, Bolivia, and Chile. The age obtained by Hubbe et al. (2011) is very close to those measured in Chilean Patagonian specimens (Pietro et al., 2010), which are among the most recent of this species, in the Pleistocene-Holocene boundary.

Smilodon populator is the only species of *Smilodon* reported in Brazil, but with the discovery of *Smilodon fatalis* in Uruguay the hypothesis that both coexisted should not be disregarded. The specimen found is similar in size to that of a *S. fatalis* but is more robust. It would be in accordance with the proportions of a medium to small *S. populator*.

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