The state of knowledge of the jaguar *Panthera onca* (Linnaeus, 1758) (Carnivora, Felidae) during the Quaternary in Uruguay

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ABSTRACT

Felids are the top predators in the environments they inhabit. They entered South America at the Pliocene-Pleistocene boundary, but their fossil record in Uruguay, although informative, is scarce. In the present contribution, three new materials (two hemimandibles and an isolated first lower molar) assigned to *Panthera onca* (Linnaeus, 1758) are described. This material came from Quaternary sediments (Sopas, Dolores, and Libertad Formations) from several localities in Uruguay. Based on this material, different aspects of the paleobiology and paleoecology of jaguars are discussed. Remains of these felids were previously listed but never described; thus, the material analyzed here is the first fossil records reliably determined for *P. onca* in Uruguay. These felids would have shared an ecological niche with other large carnivores during the late Pleistocene in Uruguay, such as saber-toothed cats (*Smilodon populator* Lund, 1842; *S. fatalis* Leidy, 1868), *Puma concolor* Linnaeus, 1771, and short face bears *Arctotherium* Burmeister, 1879; and they would have fed upon medium-sized herbivores, principally in vegetated environments.

KEY WORDS
Felidae,
Panthera onca,
Quaternary,
Uruguay.

RÉSUMÉ

L'état des connaissances du jaguar Panthera onca *(Linnaeus, 1758) (Carnivora, Felidae) au Quaternaire de l'Uruguay.*
Les félidés sont les principaux prédateurs des environnements qu'ils habitent. Ceux-ci sont arrivés en Amérique du Sud dans la limite Pliocène-Pléistocène, mais leur registre fossile pour l'Uruguay, bien qu'informative, est rare. Dans la présente contribution, trois nouveaux matériaux attribués à *Panthera onca* (Linnaeus, 1758) (deux hémimandibles et une première molaire inférieure isolée) sont décrits. Ce matériel provient de sédiments quaternaires (formations Sopas, Dolores et Libertad) de divers sites en Uruguay. Sur la base de ce matériel, différents aspects de la paléobiologie et de la paléoécologie des jaguars sont discutés. Les restes de ces félidés ont été précédemment répertoriés, mais jamais décrits, donc le matériiel analysé ici est le premier enregistrement fossile de *P. onca* clairement déterminé pour l'Uruguay. Ce félidé aurait pu partager une niche écologique avec d'autres grands carnivores du Pléistocène supérieur de l'Uruguay, tels que les tigres à dents de sabre (*Smilodon populator* Lund, 1842; *S. fatalis* Leidy, 1868), *Puma concolor* Linnaeus, 1771, et les ours à face courte *Arctotherium* Burmeister, 1879, se nourrissant principalement d'herbivores moyens dans des environnements de jungle.

MOTS CLÉS
Felidae,
Panthera onca,
Quaternaire,
Uruguay.

INTRODUCTION

Members of the family Felidae Fischer von Waldheim, 1817 are the best adapted for hunting and are more exclusively terrestrial carnivores within the order Carnivora Bowdich, 1821 (Kitchener 1991; Richard 2005; Prevosti & Forasiepi 2018). They entered South America from North America at the Pliocene-Pleistocene boundary (Ercoli *et al.* 2019; see also Rincón *et al.* 2011; Chimento *et al.* 2014), and also during the climax of the Great American Biotic Interchange (GABI), at approximately 1.8 Ma (early Ensenadan Stage/Age) and during other recent events (Soibelzon & Prevosti 2007, 2013; Woodburne 2010; Prevosti & Forasiepi 2018; Chahud & Okumura 2020). Subsequently, they underwent great diversification and were established as the dominant terrestrial predators of the continent (Chimento 2016; Rodriguez *et al.* 2018).

Several genera are registered in South America, such as the extinct *Smilodon* Lund, 1842; *Homotherium* Fabrini, 1890 and *Xenosmilus* Martin, Babiarz, Naples & Hearst, 2000; and the extant *Panthera* Oken, 1816; *Leopardus* Gray, 1842; *Puma* Jardine, 1834 and *Herpailurus* Severtzov, 1858 (see among others Berta 1985; Kurtén & Werdelin 1990; Mones & Rinderknecht 2004; Rincón *et al.* 2011; Chimento 2016; Prevosti & Forasiepi 2018; Manzuetti *et al.* 2018, 2020; Chahud 2020; Chahud & Okumura 2020).

The genus *Panthera* Oken, 1816 comprises five extant species in the New and Old World (Johnson *et al.* 2006; Werdelin *et al.* 2010). In the Americas, it is represented only by *Panthera onca* (Linnaeus, 1758), which is currently the largest carnivore on the continent (Seymour 1989; Diaz 2010; Labarca 2015; Rodriguez *et al.* 2018; Prevosti & Forasiepi 2018; Chahud & Okumura 2020). Widely geographically distributed in pre-1900 historical times (from southwestern United States to Patagonia in Argentina) (Seymour 1989; Swank & Teer 1989; Labarca & López 2006; Ferrero 2008; Zarrate-Charry *et al.* 2009; Moreno & Lima-Ribeiro 2015), its distribution has undergone a significant decline in recent times. Currently, it ranges from northern Mexico to northern Argentina, although with a patched distribution (Seymour 1989; Swank & Teer 1989; Ferrero 2008; Diaz 2010; Rodriguez *et al.* 2018; Ruiz-Ramoni *et al.* 2020), and is considered extinct in several countries, including Uruguay (Seymour 1989; Swank & Teer 1989; Diaz 2010; González *et al.* 2013; Pereira-Garbero *et al.* 2013; Pereira-Garbero & Sappa 2016; Chahud & Okumura 2020). Thus, the last record of a living jaguar in this country dates from 1901 from northeastern Uruguay (Department of Cerro Largo), which borders Brazil (Pereira-Garbero & Sappa 2016).

In the present contribution, three new fossil materials (two hemimandibles and an isolated m1) assigned to *Panthera onca* are described. This material were recovered from Quaternary sediments (the Sopas, Dolores, and Libertad Formations) of different localities from Uruguay (Santa Lucia River near San Ramon town, and Soca, which are both from the Department of Canelones; and Malo Creek from the Department of Tacuarembo) (Fig. 1). Based on this material, different aspects of the paleobiology and paleoecology of jaguars are discussed.

GEOLOGICAL CONTEXT

The Sopas Formation, which is located in northern Uruguay, is characterized by conglomerates with clay and calcareous matrices, conglomeratic sandstone, siltstone, and sandy siltstone. This unit is predominantly brownish with a thickness of 5-8 m and the sedimentary facies were developed mostly under fluvial and associated depositional contexts (Martínez & Ubilla 2004; Ubilla *et al.* 2016). Based on the mammalian fossil assemblage, this unit is correlated with deposits from the late Pleistocene sequence of the Pampean region (Lujanian Stage/Age, 126-7 ka) (Cione & Tonni 2005; Ubilla *et al.* 2011; Cione *et al.* 2015). Radiocarbon and optically stimulated luminescence (OSL) ages in some outcrops correlate mainly with MIS-3 (60-25 ka), and it also includes 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 & Martínez 2016).
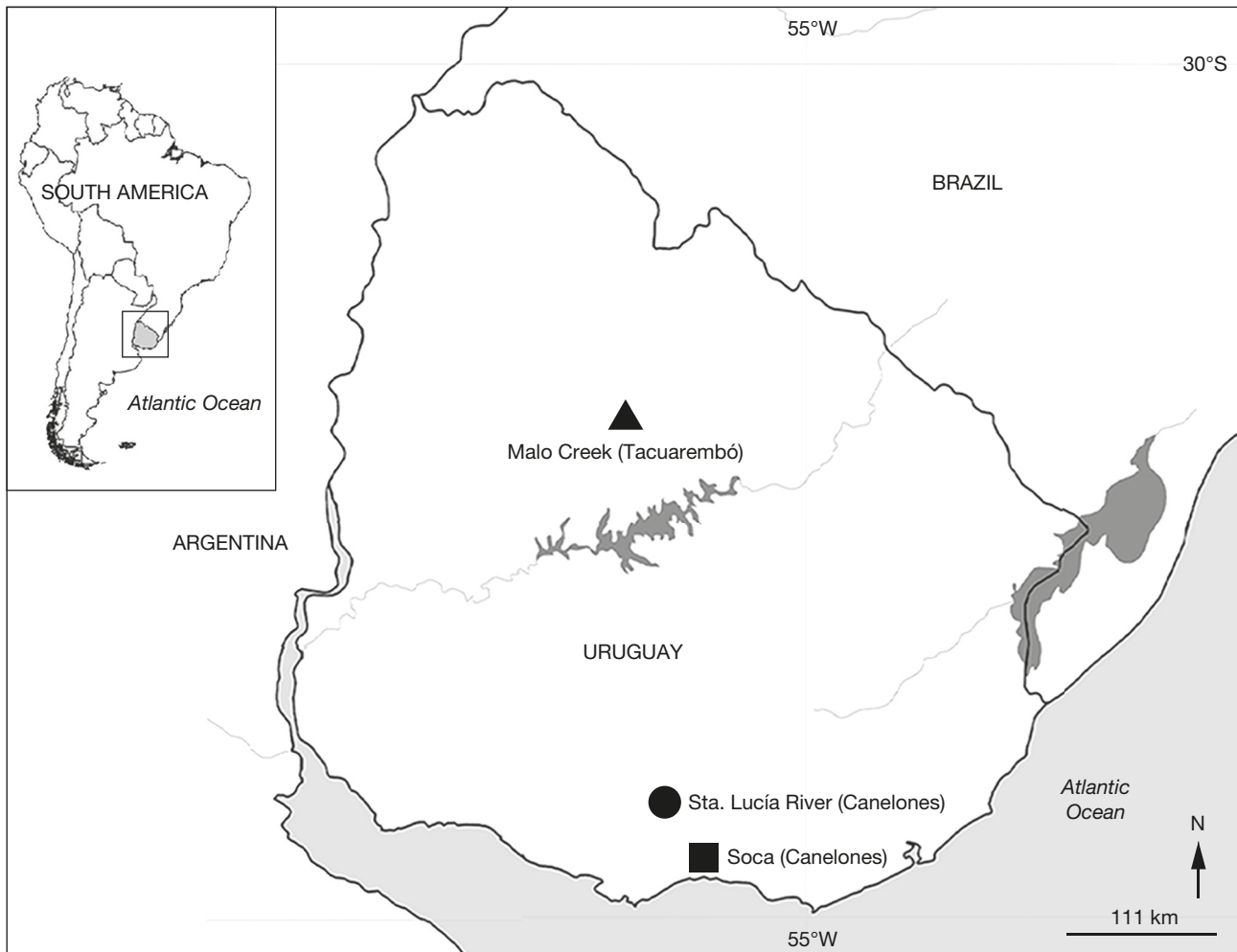
Fɪɢ. 1. — Map showing the location of the findings.

The Dolores Formation, which is mainly located in western and southern Uruguay, in the Santa Lucia River Basin (Ubilla *et al.* 2011; Ubilla & Martínez 2016), is comprised of silty claystones and siltstones, clay deposits, sandstones, and gravel (mudstone). It is generally brownish, with shades of gray-green locally, and a maximum thickness of 10 m. It was deposited in semiarid and cold climatic conditions (Martínez & Ubilla 2004; Corona *et al.* 2013). Several absolute dates based on radiocarbon and OSL/TL methods were obtained for the Dolores Formation, with ages ranging from 30-27 to 11.1-10.5 ka BP (Ubilla *et al.* 2011 and references therein; Ubilla *et al.* 2018). Based on the mammalian assemblage, this unit is correlated with the Lujanian Stage/Age (Upper Pleistocene-Groenlandian) (Ubilla *et al.* 2011 and references therein).

Finally, the Libertad Formation, which extends south of the country, contains wavy surfaces and is characterized by lodolites, loess, and sandstones; it has a reddish-brown coloration, incorporates multiform calcium carbonate, and has a thickness of approximately 30 m. It is assumed that this unit was deposited during the early to middle Pleistocene, mainly by stratigraphic criteria (Martínez & Ubilla 2004), although recent dates are approximately 20-17 ka BP

(Gutiérrez *et al.* 2005; Cid *et al.* 2014). According to the mammalian fossil assemblage, this unit is correlated with the Bonaerian Stage/Age (middle to late Chibanian, 400-126 ka, see Cione *et al.* 2015) and Lujanian Stage/Age (upper Pleistocene-Groenlandian) and was deposited in a savannah-like environment or arid to semiarid conditions (Corona *et al.* 2012).

MATERIAL AND METHODS

For comparative analysis, skeletal material of *Panthera onca* and *Puma concolor* Linnaeus, 1771 housed in the FC-DPV were used. Published literature of the aforementioned felids and *Panthera atrox* (Leidy, 1853) from Merriam & Stock (1932); Méndez-Alzola (1941); Currier (1983); Seymour (1989); Ferrero (2008); Christiansen & Harris (2009); Montellano-Ballesteros & Carbot-Chanona (2009); Morales-Mejía *et al.* (2010); Carbot-Chanona & Gómez-Pérez (2014); Chimento & Agnolín (2017); Chimento & Dondas (2017); Rodriguez *et al.* (2018); Ruiz-Ramoni *et al.* (2020) were also used. Dental nomenclature follows Berta (1987).

TABLE 1. — Measurements (in mm) of the fossil material studied (CGF 104, FC-DPV 501, FC-DPV 1890) compared with *Puma concolor* Linnaeus, 1771, *Panthera atrox* (Leidy, 1853) and *Panthera onca* (Linnaeus, 1758) (extant and extinct) specimens. Abbreviations: **N**, number of individuals (for other abbreviations see Material and methods); **OR**, observed range. Data according to Merriam & Stock (1932), Seymour (1989), Chimento & Agnolín (2017), and Chimento & Dondas (2017).

	CGF 104	FC-DPV 501	FC-DPV 1890	*Puma concolor*		*Panthera atrox*		*P. onca* SA (fossil)		*P. onca* (extant)	
				OR	N	OR	N	OR	N	OR	N
TL	191.6	–	186	113.5-154.8	15	206-318	16	–	–	161-198	11
Hm1	45.3	–	39.5	24.6-33.9	12	46-67.1	16	26-39.5	6	28.9-42.4	12
Bm1	18.4	–	17.1	10.4-14.5	12	20-36.9	16	–	–	12-17.6	12
TRLc–m1	107.6	–	103.9	65-78	12	116.4-156.7	14	–	–	77.3-98.3	12
cAP	–	–	17.4	10.6-15.2	15	21.4-33	40	18-21.4	3	13.2-23.5	112
cML	–	–	18.2	8.2-12.2	15	13.9-21.5	17	14.5-16.4	3	9-17	11
p3AP	17.8	–	–	12-16.6	15	17-21.6	17	17-18.2	2	11.8-16.9	11
p3ML	9.1	–	–	5.5-8.3	15	8.9-13.2	17	8.1	1	4.3-9.2	11
p4AP	24.8	–	–	14.4-17.4	15	25.8-32.3	17	22-24.2	3	15.5-22.2	11
p4ML	11.1	–	–	7.11-9.6	15	12-16.9	17	10-11.2	3	8.2-11.7	12
m1AP	26.6	23.2	23.9	15.7-20.4	15	25.1-34	51	22.4-23.5	6	16.5-24.8	112
m1ML	13.1	10.8	11.6	7-9.5	15	12.5-17.9	50	11-12.5	6	6.7-11.4	11

Body mass estimates were made based on allometric equations formulated for extant felids (Van Valkenburgh 1990; Thackeray & Kieser 1992) using measurements of the first lower molar (Appendix 1). To reduce the bias between the geometric mean and arithmetic mean, a correction factor (the ratio estimator [RE], that is the ratio between the average observed body masses of the sample and the average estimated body masses from the allometric equation) was used to correct this underestimation (see Smith 1993 and references therein). Body mass estimates of the typical prey species available to *P. onca* and the maximum prey size were calculated using equations formulated for extant felids by Prevosti & Vizcaíno (2006), Hemmer (2007), and Prevosti & Martin (2013) (Appendix 1). To infer the prey size, the average body mass estimate of the carnivore was used. According to data availability, the mean absolute value of the percent prediction error (%PE) and the coefficient of correlation (r) were used as comparative indicators of the accuracy of the prediction of the study variables.

All measurements were performed with digital calipers accurate to 0.1 mm and expressed in millimeters, following von den Driesch (1976) (Appendix 2).

ABBREVIATIONS
Mandible and dental measurements
Bm1   breadth of the mandible at the posterior border of the m1;
cAP   antero-posterior diameter of the canine;
cML   transverse diameter of the canine;
Hm1   height of the mandible at the posterior border of the m1;
m1 AP   antero-posterior diameter of the m1;
m1 ML   transverse diameter of the m1;
p3AP   antero-posterior diameter of the p3;
p3ML   transverse diameter of the p3;
p4AP   antero-posterior diameter of the p4;
p4ML   transverse diameter of the p4;
TL   total length;
TRL c-m1   tooth row length canine-m1.

Institutions
CGF   Colección particular Gonzalo Fierro, Montevideo;
FC-DPV   Facultad de Ciencias-Colección Paleontológica (Vertebrados fósiles), Montevideo, Uruguay.

Other abbreviations
GABI   Great American Biotic Interchange;
OSL   optically stimulated luminescence;
RE   ratio estimator.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family FELIDAE Fischer von Waldheim, 1817
Subfamily PANTHERINAE Pocock, 1917
Genus *Panthera* Oken, 1816

Panthera onca (Linnaeus, 1758)

[*Felis*] *onca* Linnaeus, 1758: 42. — Type locality: "America meridionali" restricted to Pernambuco, Brazil by Thomas (1911).

Felis nigra Erxleben, 1777: 512. — Type locality: "Brasilia et Guiania."

Felis panthera Schreber, 1778: 384; pl. 99. — No type locality given.

F. [*Felis*] *jaguar* Link, 1795: 90. Renaming of *F. onca* Linnaeus, 1758.

Leopardus hernandesii Gray, 1857: 278. — Type locality: "Mazatlan."

Panthera onca – Fitzinger 1869: 211. First use of current name combination.

Felis jaguarete Liais, 1872: 451. Renaming of *F. onca* Linnaeus, 1758.

Felis jaguapara Liais, 1872: 451. Renaming of *F. onca* Linnaeus, 1758.

Felis jaguatyrica Liais, 1872: 459. Renaming of *Felis nigra* Erxleben, 1777.

Felis centralis Mearns, 1901: 139. — Type locality: "Talamanca, Costa Rica."

Felis paraguensis Hollister, 1914: 169. — Type locality: "Paraguay."

Felis notialis Hollister, 1914: 170. — Type locality: "San Jose, Entre Rios, Argentina."

Felis ramsayi Miller, 1930: 14. Replacement name for *Felis paraguensis* Hollister, 1914.

REFERRED MATERIAL. — CGF 104 (Fig. 2; Table 1), right mandible; FC-DPV 1890 (Fig. 3; Table 1), left mandible; FC-DPV 501 (Fig. 4; Table 1), right m1.

Fɪɢ. 2. — **A**, **B**, CGF 104; right hemimandible. **A**, right lateral view; **B**, occlusal view. Scale bar: 10 cm.

Gᴇᴏɢʀᴀᴘʜɪᴄ ᴀɴᴅ sᴛʀᴀᴛɪɢʀᴀᴘʜɪᴄ ʟᴏᴄᴀᴛɪᴏɴ. — CGF 104, Santa Lucia River near San Ramon town (Department of Canelones), Dolores Formation, late Pleistocene-early Holocene; FC-DPV 1890, Malo Creek (Department of Tacuarembo), Sopas Formation, late Pleistocene; FC-DPV 501, Soca locality (Department of Canelones), Libertad Formation, Pleistocene.

Cᴏᴍᴘᴀʀᴀᴛɪᴠᴇ ᴅᴇsᴄʀɪᴘᴛɪᴏɴ
The hemimandibles are very robust and the horizontal ramus is high; a marked angle is formed towards the symphysial region. Mandible FC-DPV 1890, when placed on a flat surface, rests on the symphysis region and angular process, while material CGF 104 has a third point of contact configured by the slightly convex inferior border of the horizontal ramus, which shows great variation in this regard among pantherines (Merriam & Stock 1932; Christiansen & Harris 2009). The angular process in both materials does not project conspicuously backward compared with *Puma concolor* (Merriam & Stock 1932) but is ventrally deflected, as in *Panthera onca* and *Panthera atrox* (Christiansen & Harris 2009); the condyles are markedly transverse. In CGF 104, the coronoid process is robust and, in lateral view, does not sweep backward behind the condyle, as observed mainly in *P. onca* and *P. concolor*, and it differs from *P. atrox*, which often clearly does (Merriam & Stock 1932; Christiansen & Harris 2009). The masseteric fossa in both materials is deep and barely reaches the posterior border of the m1, as observed in *P. onca* and *P. concolor*, while in *P. atrox* it reaches at most the middle part of the m1 (Merriam & Stock 1932). In the labial face of each mandibular ramus, the characteristic foramina of the large extant felids are observed (Méndez-Alzola 1941). The dentition is markedly hypercarnivore. In CGF 104, the canine is not preserved, although, based on the size of the alveolus, it is inferred to be a large tooth; in FC-DPV 1890, the canine is very robust. In occlusal view, it shows a rounded shape, as observed in *P. onca*, but it differs from *P. concolor*, which is more oval (Morales-Mejía *et al.* 2010). Unfortunately, due to its preservation, it is very difficult to identify some diagnostic characteristics, such as the lateral crest. The premolars of the CGF 104 material are

Fig. 3. — **A**, **B**, FC-DPV 1890; left hemimandible: **A**, left lateral view; **B**, occlusal view. Scale bar: 10 cm.

similar in form but with a remarkable difference in size. The principal cusp in each premolar (the protoconid) is directed upwards with a slight inclination in a posterior way. In the m1 of both materials (CGF 104 and FC-DPV 1890) and in the FC-DPV 501 specimen, both cusps are nearly equal in size in a similar way as observed in *P. onca* or *P. concolor* (Méndez-Alzola 1941); moreover, in *P. atrox*, the protoconid is larger, almost twice the length in some cases, than the paraconid (Montellano-Ballesteros & Carbot-Chanona 2009; Carbot-Chanona & Gómez-Pérez 2014; Chimento & Agnolín 2017). Additionally, the protoconid is higher than the paraconid; in its distal portion, the development of a tiny talonid is observed.

REMARKS

According to the absolute size, the material studied here is quite larger than those of *Puma concolor* and in general is smaller than *Panthera atrox*, being within the expected range of values observed for *Panthera onca* (Table 1; see Merriam & Stock 1932; Méndez-Alzola 1941; Seymour 1989; Ferrero 2008; Morales-Mejía *et al.* 2010; Chimento & Agnolín 2017; Chimento & Dondas 2017). However, for CGF 104, some of these measurements (p3 and m1) are in the lower values reported for *P. atrox* (Merriam & Stock 1932; Montellano-Ballesteros & Carbot-Chanona 2009; Carbot-Chanona & Gómez-Pérez 2014; Chimento & Agnolín 2017 among others).

Body mass estimates for the CGF 104 material show that this animal weighed up to 173 kg (Table 2) according to the equation from Thackeray & Kieser (1992), which has a smaller % PE and thus would have a better prediction range (see Supplementary Material 1). For material FC-DPV 1890 and FC-DPV 501, the body mass estimates were clearly over 100 kg (Table 2).

On the other hand, the body mass of the potential prey for material CGF 104 is over 250 kg and up to 360 kg, and the largest prey size is over 800 kg (Table 3). For the other two materials, the typical prey mass is less than 200 kg, and the maximum prey body mass is between 500-600 kg (Table 3). In any case, it is worth noting that all estimations of body mass made for extinct taxa should be considered with caution and taken as a relative approach rather than absolute values (Prevosti & Vizcaíno 2006; Losey *et al.* 2017, see also Manzuetti *et al.* 2020).

DISCUSSION

ANATOMICAL COMMENTS AND PALEONTOLOGICAL RECORD
Mandibular and dental morphology is, in general, quite similar in most pantherines and, according to the reported variation, has many shared characteristics among the species of the genus

TABLE 2. — Body mass estimation (in kg) based on antero-posterior diameter of the m1 (m1AP). Mean body mass: CGF 104, 168.7; FC-DPV 1890, 119.6; FC–DPV 501, 108.7.

	According to equation from Van Valkenburgh (1990)	According to equation from Thackeray & Kieser (1992)
CGF 104	164.1	173.2
FC–DPV 1890	118.4	120.7
FC–DPV 501	108.1	109.2

(Christiansen & Harris 2009). In particular, the combination of some morphological characteristics, along with measurements, of the material studied here are congruent with the variability recognized in *Panthera onca*. The most important anatomical characteristics of fossils useful to differentiate them from other large conical toothed cats, such as *Puma concolor* and *Panthera atrox*, are as follows: the angular process does not project conspicuously backward, the coronoid process does not extend posteriorly to the condyle, the masseteric fossa reaches the posterior end of m1, the general shape of the canine, and m1 cusps (paraconid and protoconid) of similar size. Moreover, this material correspond to large specimens for the species (in particular the material CGF 104). In addition, the proportions of the p3 and p4 are used as diagnostic characteristics to discriminate among some pantherines (see Hemmer *et al.* 2010). In this way, the size of the p3 is in the measurement range for *P. onca* and *P. atrox*; moreover, the p4 length is intermediate between these two taxa (smaller than *P. atrox* and slightly larger than *P. onca*), but its thickness is clearly jaguar-sized (see Table 1).

The fossil record of *P. onca* in the Americas is quite scarce (Diaz 2010; Chahud & Okumura 2020). The oldest remains assigned to the species come from early to middle Pleistocene sediments from North America (Seymour 1989; Diaz 2010; Rodriguez *et al.* 2018; Ruiz-Ramoni *et al.* 2020). However, there is no agreement about the oldest record in South America (see, among others, Ferrero 2008; Diaz 2010; Cruz *et al.* 2012; Labarca 2015; Rodriguez *et al.* 2018). For instance, according to Van Valkenburgh (1991) and Berman (1994), *P. onca* has been recorded since the Ensenadan Stage/Age (Gelasian-Early Chibanian, 2.58-0.4 Ma, see Cohen *et al.* 2013, 2020), including the Pampean Region of Argentina, but according to Seymour (1989) and Arroyo-Cabrales (2002), *P. onca* entered the late Pleistocene. During the late Pleistocene-early Holocene, it was also recorded in Argentina, Bolivia, Brazil, Chile, Ecuador, Peru, Uruguay, and Venezuela (Ubilla *et al.* 2004; Labarca & López 2006; Ferrero 2008; Shockey *et al.* 2009; Cruz *et al.* 2012; Rodrigues *et al.* 2014; Rodriguez *et al.* 2018; Chahud & Okumura 2020 among others). On the other hand, two extinct subspecies, larger than modern jaguars, are recognized: the North American *P. o. augusta* (Leidy, 1872) (see Seymour 1989; Ruiz-Ramoni *et al.* 2020; Chahud & Okumura 2020) and the southern South American *P. o. mesembrina* Cabrera, 1934, the so-called Patagonian Jaguar (see Labarca 2015; Martin 2016; Prevosti & Forasiepi 2018 among others); however, the taxonomic status
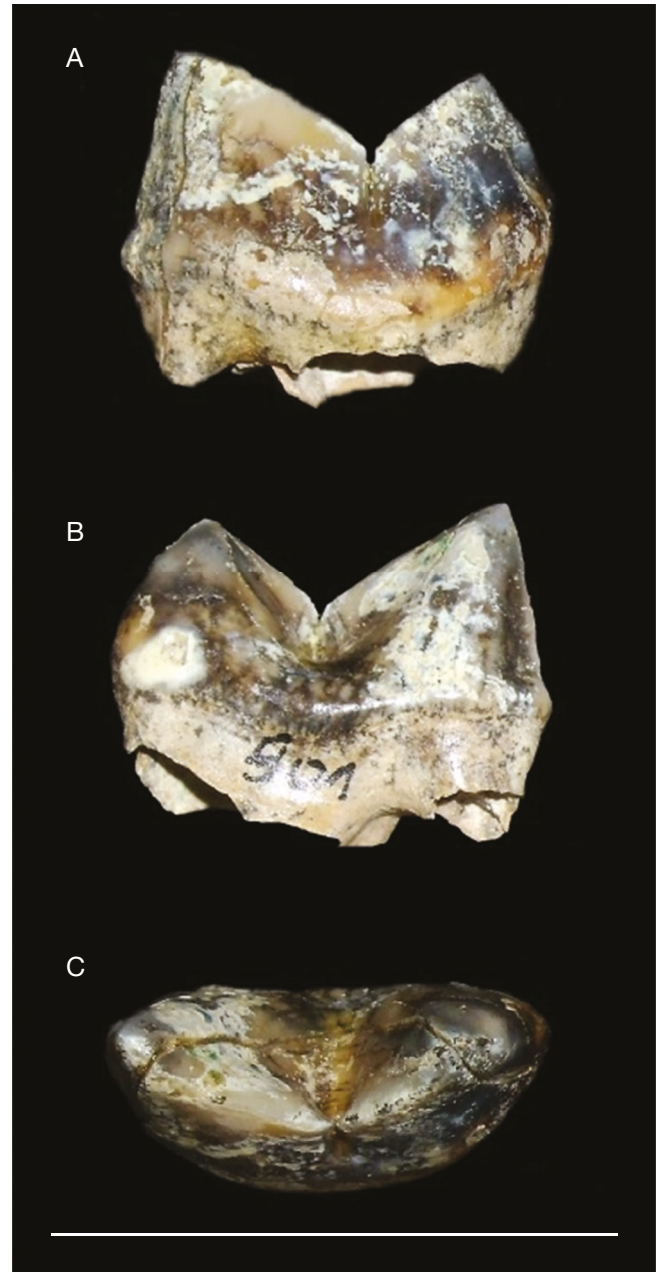
FIG. 4. — **A-C**, FC-DPV 501; right m1: **A**, external view; **B**, inner view; **C**, occlusal view. Scale bar: 3 cm.

of the latter is under debate. In this way, Cione *et al.* (2009) considered *P. o. mesembrina* indistinguishable from extant jaguars. Moreover, Metcalf *et al.* (2016) found, based on mitochondrial sequences, that the *P. onca* of the Pleistocene of South American Patagonia was genetically different from the modern jaguar but more closely related to it than to Old World pantherines; thus, it represents the extinct subspecies *P. onca mesembrina*. However, according to Chimento & Agnolín (2017), these remains, based on anatomy and its size, correspond to the American lion *P. atrox*, so its taxonomic status is far from resolved.

Although fossil remains of these felids have been previously listed on Uruguayan faunal lists (see Ubilla & Perea 1999;

TABLE 3. — Body mass estimation (in kg) of the typical prey (**TPM**) and maximum prey (**MPM**) for the studied material.

	According to equation from Prevosti & Vizcaíno (2006)		According to equation from Prevosti & Martin (2013)		According to equation from Hemmer (2007)
	TPM	**MPM**	**TPM**	**MPM**	**TPM**
CGF 104	252.6	887.1	323.4	826.3	362.6
FC-DPV 501	111.5	503.2	164.4	532.4	156.1
FC-DPV 1890	133.2	569.2	190.4	585.8	187.5

Ubilla *et al.* 2004), to date, no material of such species have been reliably described. Thus, the present remains are the first properly documented fossil records of this taxon for the country. Moreover, the material studied here along with some remains from Buenos Aires Province (Argentina) (see Seymour 1989; Ferrero 2008; Cruz *et al.* 2012; Moreno & Lima-Ribeiro 2015; Rodriguez *et al.* 2018), considering that the *P. o. mesembrina* remains could correspond to *P. atrox* (see above), would be at the southernmost limit of the distribution of the representative fossils of the species.

PALEOECOLOGICAL ASPECTS AND BODY MASS
Currently, *Panthera onca* lives mainly in tropical conditions within dense vegetation near water sources (rivers, creeks, etc.) or swampy areas, although they show wide environmental tolerance (Seymour 1989; Swank & Teer 1989; Ferrero 2008; Diaz 2010; Rodrigues *et al.* 2014; Moreno & Lima-Ribeiro 2015; Chahud & Okumura 2020). In its distribution range, the species compete for food with another large felid, namely, *Puma concolor*, although their interactions are minimal, and they seem to mutually avoid each other (Seymour 1989 and references therein; Harmsen *et al.* 2009; Romero-Muñoz *et al.* 2010; Rueda *et al.* 2013; Ávila-Nájera *et al.* 2020). However, when both felids are sympatric, *P. concolor* is more abundant in dry areas, while *P. onca* prefers more humid areas (Seymour 1989 and references therein). Additionally, temporal separation has been reported between these two felids (Harmsen *et al.* 2009; Romero-Muñoz *et al.* 2010; Ávila-Nájera *et al.* 2020), and in addition to the aforementioned, jaguars generally show a greater dependence on larger prey than pumas (Romero-Muñoz *et al.* 2010; Payán Garrido & Soto Vargas 2012; Rueda *et al.* 2013; Ávila-Nájera *et al.* 2020). Therefore, it is expected that a segregation pattern based on spatiotemporal distribution and prey preference has probably occurred in the past.

Moreover, these felids coexisted during the late Pleistocene in South America, in addition to *P. concolor*, with other large carnivorous mammals, such as saber-toothed cats (*Smilodon fatalis* Leidy, 1868; *S. populator* Lund, 1842), short face bears (*Arctotherium* Burmeister, 1879), and large canids (*Aenocyon* (synonym of *Canis) dirus* (Leidy, 1858), see Perri *et al.* 2021; *Protocyon troglodytes* (Lund, 1838) (see Prevosti *et al.* 2009; Prevosti & Forasiepi 2018; Manzuetti *et al.* 2018, 2020). However, according to differences in body mass, trophic segregation could be inferred between *P. onca* and the cited carnivores, so the competition among them would be limited (see Prevosti & Martin 2013; Bocherens *et al.* 2016).

The diet of *P. onca* includes medium to large mammals, up to 600 kg, but they also show a marked preference for reptiles, particularly caimans, lizards, turtles, boas, and anacondas (Seymour 1989; Swank & Teer 1989; Prevosti & Vizcaíno 2006; Payán Garrido & Soto Vargas 2012). In this context, and according to our results of typical prey mass, *Tayassu pecari* (Link, 1795), *Hydrochoerus* Brisson, 1762, *Tapirus terrestris* (Linnaeus, 1758), *Lama* (*Vicugna*) Molina, 1782, *Equus neogeus* Lund, 1840, *Hippidion* Roth, 1899 and *Mazama* Rafinesque, 1817, among others, are recorded in late Pleistocene strata in the territory of current Uruguay (Prevosti *et al.* 2009 and references therein; Ubilla & Martínez 2016), so the possibility that some of these species could have been potential prey of *P. onca* cannot be ruled out.

Finally, body mass estimates for the CGF 104 material greatly surpass the known body mass for most extant individuals of the species (for males, 37-121 kg; for females, 31-100 kg; see Sunquist & Sunquist 2009 and references therein; however, individuals of 130 kg to 158 kg are occasionally reported; see Seymour 1989 and references therein) and are more congruent with fossil remains assigned to this taxon (Prevosti & Martin 2013). For the remaining materials, those values are above the range of females of the species but within the known body mass range for this taxon (Sunquist & Sunquist 2009), particularly towards the larger sizes of the species.

Based on the larger size and body mass of the members of the populations living in the Pleistocene, these felids could potentially hunt larger prey than extant individuals, including juvenile mega mammals (Prevosti & Vizcaíno 2006, see also Prevosti & Martin 2013). The estimation of the body mass of the maximum prey reported here (particularly for material CGF 104) could, to some extent, be indicative of such predatory behavior, but prey preferences of an apex predator are conditioned by a complex combination of factors, such as the size of prey, availability, prey density, and scavenging activities (Schaller 2009). Compared with other solitary felid predators, extant jaguars show an unusually low predator-to-prey body mass ratio, which means that they tend to kill prey slightly smaller than themselves (Hayward *et al.* 2016). In this way, the predation of jaguars over megafauna species could be unusual, and they most likely focused their efforts on smaller animals available within the late Pleistocene herbivore assemblage. This condition, along with the effect of megafaunal extinction and reduction of jaguar body mass at the end of the Pleistocene, suggests that the predatory jaguar ecology has been substantially altered since then (Hayward *et al.* 2016). Additionally,

it was observed that jaguars can use both medium- and large-sized prey that are available and behaviorally vulnerable (González & Miller 2002). Thus, the prey plasticity displayed by *P. onca* may have contributed to their survival to the present (see Hayward *et al.* 2016).

CONCLUSIONS

The material described here, based on morphology and measurements, are assigned to large individuals of *Panthera onca*. These remains are the first fossil materials of this taxon reliably determined for Uruguay and additionally represent the southern limit of its distribution during the Pleistocene in South America. Currently, *P. onca* is the apex predator in South America, inhabiting mainly environments with vegetative cover. During the late Pleistocene in the territory of Uruguay, a large carnivore guild was integrated, potentially hunting upon medium-size mammals.

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APPENDICES. — Supplementary materials.

APPENDIX 1. — Body mass equations used in this article.

Body mass equations (in kg) for felids according to Van Valkenburgh (1990). Measurements in mm. %PE, percent prediction error:
– based on antero-posterior diameter of the m1 (m1AP)
log body mass = 3.05 × log m1AP − 2.15; %PE 29.72

Body mass equations (in kg) for felids according to Thackeray & Kieser (1992). Measurements in mm. %PE, percent prediction error:
– based on antero-posterior diameter of the m1 (m1AP)
log body mass = 3.37 × log m1AP − 2.57; %PE 27.73

Body mass equations (in kg) of the typical prey (TPM) and the maximum prey (MPM) for extant felids following Prevosti & Vizcaíno (2006). M is the body mass (in kg) of the carnivorous mammal. %PE, percent prediction error; r, coefficient of correlation:
log body mass TPM = 1.86 × log M − 1.74; %PE, 77.73; r, 0.9
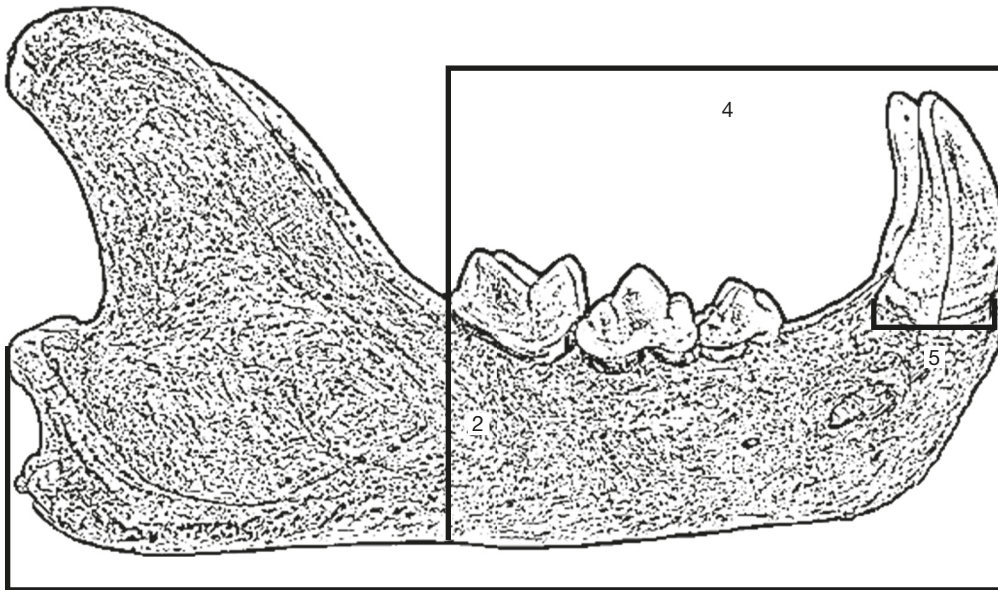log body mass MPM = 1.29 × log M + 0.075; %PE, 15.23; r, 0.88

Body mass equations (in kg) of the typical prey (TPM) and the maximum prey (MPM) for extant felids following Prevosti & Martin (2013). M is the body mass (in kg) of the carnivorous mammal. %PE, percent prediction error; r, coefficient of correlation:
log body mass TPM = 1.54 × log M − 0.92; %PE 54.55; r, 0.9
log body mass MPM = 1.00 × log M + 0.69; %PE 35.02; r, 0.88

Body mass equation (in kg) of the typical prey (TPM) for extant felids following Hemmer (2007). M is the body mass (in kg) of the carnivorous mammal:
log body mass TPM = 1.917 × log M − 1.710

APPENDIX 2. — Measurements used in this article: **1**, TL; **2**, Hm1; **3**, Bm1; **4**, TRLc-m1; **5**, cAP; **6**, cML; 7, p3AP; **8**, p3ML; **9**, p4AP; **10**, p4ML; **11**, m1AP; **12**, m1ML. Abbreviations: **Bm1**, breadth of the mandible at the posterior border of the m1; **cAP**, antero-posterior diameter of the canine; **cML**, transverse diameter of the canine; **Hm1**, height of the mandible at the posterior border of the m1; **m1 AP**, antero-posterior diameter of the m1; **m1 ML**, transverse diameter of the m1; **p3AP**, antero-posterior diameter of the p3; **p3ML**, transverse diameter of the p3; **p4AP**, antero-posterior diameter of the p4; **p4ML**, transverse diameter of the p4; **TL**, total length; **TRL c-m1**, tooth row length canine-m1.