Swiss Journal of Palaeontology

RESEARCH ARTICLE

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Carnivoran fossils from the Pampean region (Argentina): Santiago Roth collections in Switzerland

Damián Ruiz-Ramoni[1,2*], Jorge D. Carrillo-Briceno[3], Damian Voglino[4] and Francisco Juan Prevosti[1,2]

Abstract

Santiago Roth (1850–1924) was a naturalist that collected and sold fossils from the Pampean region (Argentina) in Europe. Much of the specimens collected by Roth are hosted at the Paläontologisches Institut und Museum, Universität Zürich and Muséun D'Histoire Naturelle of Geneva in Switzerland, but were never studied. In this article, we review the specimens of the order Carnivora under a taxonomical and temporal approach. We confirm the presence of 16 specimens of Carnivora collected by Roth between the provinces of Santa Fe and Buenos Aires. We identify felids (*Smilodon* sp., *Panthera onca*, and specimens related to these taxa), ursids (*Arctotherium* sp.), and canids (*Dusicyon avus* and specimens related, *Lycalopex* sp., and Caninae indet.). According to the information reported by S. Roth, all materials are from the Pleistocene of the Pampean Formation. However, given the scarcity of data, only the specific age of few specimens could be more accurately established.

Keywords *Arctotherium*, *Dusicyon*, *Lycalopex*, Pampean formation, *Panthera*, *Smilodon*

Resumen

Santiago Roth (1850–1924) fue un naturalista que recolectaba y vendía fósiles de la región de la Pampa (Argentina) en Europa. Gran parte de las muestras recolectadas por Roth se encuentran alojadas en el Paläontologisches Institut und Museum, Universität Zürich y en el Muséun D'Histoire Naturelle de Ginebra en Suiza, pero nunca fueron estudiadas. En este artículo, revisamos las muestras del orden Carnivora desde un enfoque taxonómico y temporal. Confirmamos la presencia de 16 muestras de Carnivora recolectadas por Roth entre las provincias de Santa Fe y Buenos Aires. Identificamos felinos (*Smilodon* sp., *Panthera onca* y muestras relacionadas con estos taxones), osos (*Arctotherium* sp.) y cánidos (*Dusicyon avus* y muestras relacionadas, *Lycalopex* sp. y Caninae indet.). Según la información reportada por S. Roth, todos los materiales provienen del Pleistoceno de la Formación Pampeana. Sin embargo, debido a la escasez de datos, solo se pudo establecer con mayor precisión la edad de algunas muestras específicas.

Palabras clave *Arctotherium*, *Dusicyon*, *Lycalopex*, formación Pampeana, *Panthera*, *Smilodon*

Handling editor: Gabriel Aguirre-Fernández

*Correspondence:
Damián Ruiz-Ramoni
drramoni@gmail.com
Full list of author information is available at the end of the article

Introduction

Carnivoran is the common name for the eutherian mammals of the order Carnivora (Bowdich, 1821). Their presence in South America (SA) is the result of the faunal exchange with North America that started at the end of the Neogene. Of the 23 carnivoran families (extinct and living), only seven are present in SA: procyonids, felids, canids, ursids, mustelids, mephitids, and pinnipeds. Although the richness and evolution of most of these groups are well-studied today (e.g., Marshall, 1985; Prevosti & Forasiepi, 2018; Ruiz-Ramoni, 2016; Soibelzon & Prevosti, 2012), during the nineteenth and middle of the twentieth century many of these were poorly known; their fossils were just being discovered.

The documentation of the paleontological finds of carnivorans in SA began in the nineteenth century with fossils discovered in Argentina and Brazil (e.g., Lund, 1837; d'Orbingy, 1837–1842; Muñiz, 1845; Ameghino, 1875, 1881; 1886; Gervais & Ameghino, 1880). In this region, early paleontological studies were significantly influenced by the contributions of earlier academics and naturalists such as Carl Hermann Conrad Burmeister, Pierre Joseph Auguste Bravard, Florentino Ameghino, among others (Podgorny, 2001). However, other least famous naturalists also contributed to the study of fossil animals in SA. This is the case of the Swiss-Argentine Kaspar Jakob Roth-Shuetz (1850–1924). Santiago Roth, as his name became adapted to Spanish, was born in Herisau, Switzerland, and later settled down with his family in the province of Buenos Aires in 1866. He worked as a saddler and, since 1870, collected and posteriorly sold fossils to Switzerland and other institutions around the world, including occasionally to private investors (e.g., Valdemar Lausen) (see Farro, 2009; Hansen, 2020), an activity promoted by the European Museums and frequent among some naturalists and explorers of the time (Podgorny, 2001).

Santiago Roth traveled to Switzerland to sell some of his collections (Roth Catalogs 4–6; Hansen, 2019) and took classes in Geneva with Carl Vogt (Laza, 2019; Hansen, 2020). The fossils sold to Lausen were finally donated to the Natural History Museum of Denmark and included the remains of Roth Catalogs 2 and 3 (Hansen, 2020; Catalog 1 could be part of the first large collection made by Roth and sold to Dr. Lausen, but is something that could not be certainly confirmed. Hansen pers. comm. to FJP) . In 1895 Francisco Pascasio Moreno hired Roth to take up the position of Head of the Paleontology Section at the "Museo de La Plata", the institution where he worked until his death (for biographical details see Torres, 1927; Weigelt, 1951; Bond, 1998; Laza, 2019; Sánchez-Villagra et al., in press).

Throughout his life, Roth explored different outcrops near the Paraná river, the Atlantic coast of Buenos Aires, Pampa, and Patagonia, where he made important paleontological and geological contributions (Roth, 1888, 1899, 1902, 1904a, 1904b; 1921; 1924), such as the descriptions of native SA ungulates, sloths, and other mammalian groups, and the Pampean sedimentary strata (Roth, 1898, 1903, 1911, 1927; Hauthal et al., 1899; see Bond, 1998; Laza, 2019; see also Carrillo-Briceño et al., in press).

Roth's collection and scientific contributions on carnivorans were limited in number and scope, but gave an interesting insight into the diversity and temporal distribution in the Pampean region. In his Pampean fossil catalogs Roth (1884, 1889, 1892) listed the presence of several carnivorans, including "*Machairodus*" (probably *Smilodon*), "*Ursus*" (probably *Arctotherium*), "*Canis*" (*Dusicyon*, *Lycalopex* or Canidae indet.), *Mephites* (*Conepatus*?), and indeterminate carnivorans. In his first monograph on the Pampean "Formation" Roth (1888) listed "*Machairodus*" and Caninae, gen. div. for his three Pampean "Formation" units, "*Ursus*" *bonaerensis* in middle Pampean, and "*Ursus Bernae*" in lower Pampean. He also listed *Arctotherium vetustum* and *Cyonasua argentina* for the "Mesopotamian" (Messinian?; Late Miocene) of the Entre Ríos Province (see Cione et al., 2000, 2015; Brandoni, 2013; del Río et al., 2018); currently accepted for the last taxa but not for the first one (see Cione & Tonni, 1999; Soibelzon, 2004; Prevosti & Forasiepi, 2018). In his last monograph on the geology of the Pampean plains he included observations relevant to the biogeographic event later named the Great American Biotic Interchange (Cione et al., 2015). Roth interpreted that during his "mesopampean horizon" ("horizonte Mesopampeano"; Ensanadan, Early–Middle Pleistocene; Cione & Tonni, 1999; Cione et al., 2015) the immigrants "*Machaerodus*" (=*Smilodon*) and *Arctotherium* appeared, among others, that lived with autochthonous taxa like *Mesotherium*. Later, in the younger "neopampean horizon" ("horizonte neopampeano"; Bonaerian?, Middle Pleistocene?; Cione & Tonni, 1995a, b, 2005; Cione et al., 2015) the living species *Canis azarae* (correspond to the living species *Lycalopex gymnocercus*) and *Felis concolor* (=*Puma concolor*) are first recorded.

Santiago Roth (in Hauthal et al., 1899; Roth, 1904a, 1904b), also described material from Cueva del Milodón in Última Esperanza caves in Austral Patagonia (Chile), where he indicated the presence of *Canis* sp., *Canis avus* (now *Dusicyon avus*; Kraglievich in Oliver Schneider, 1926:145; see also Kraglievich, 1930; Berta & Marshall, 1978), *Canis familiaris*, *Mephitis suffocans* (an incomplete mandible that belongs to Mustelidae that could be *Galictis* sp., see Prevosti & Pardiñas, 2001), and bones of large felids. Although Roth first classified the felid material as *Iemish listai* gen. nov. (Hauthal et al., 1899), he later reassigned it to *Felis listai* (Roth, 1904a, 1904b), indicating that the "Iemish" (a mythical beast that was

believed to have survived until the present day) was a feline and not an edentate as F. Ameghino believed (Ameghino, 1899). However, as explained by Ángel Cabrera, this interpretation of Roth is not correct, and he considered that these felid remains belonged to a new subspecies of jaguar (*Panthera onca mesembrina* Cabrera, 1934; see also Martin 2013).

There is no compendium on all the carnivorans that Roth collected and delivered to European collections. Schulthess (1920) mentioned the carnivorans of Roth (1889) but did not study them. More recently, Hansen (2019) indicated that the material in the Natural History Museum of Denmark includes *Arctotherium bonarienseе*, *Canis*, *Galictis*, *Smilodon populator*, and Phocidae.

Here, we review the fossil carnivorans delivered by Roth to Swiss institutions under a taxonomic perspective and their geographic and chronological precedence. In his catalog "Fossiles de la Pampa, Amérique du Sud, N°5" (Roth, 1889), which the University of Zurich bought, he listed 286 fossils (284 numbered and two unnumbered) from the Buenos Aires and Santa Fe Provinces of Argentina, which include 9 carnivorans (some numbers have more than one specimen) (see also Voglino et al., in press). On the other hand, other fossils of carnivorans collected by Roth are also deposited in the collection of the Natural History Museum in Geneva, although there is no catalog from Roth associated with them and, like those of Zurich, they have not been studied yet.

Materials and methods

We present the description and comparison of the morphology of Roth's Pampean carnivorans housed in Switzerland. For comparison, we used data from bibliographic sources and materials stored in the collection of the "Museo Argentino de Ciencias Naturales Bernardino Rivadavia" and the "Museo de La Plata" in Argentina. The measurements were taken following and from Merriam and Stock (1932), Berta (1987), Kurtén and Werdelin (1990), Prieto et al. (2010), Rincón and Soibelzon (2007), Prevosti et al. (2015) and analyses of the material can be found in the Additional file.

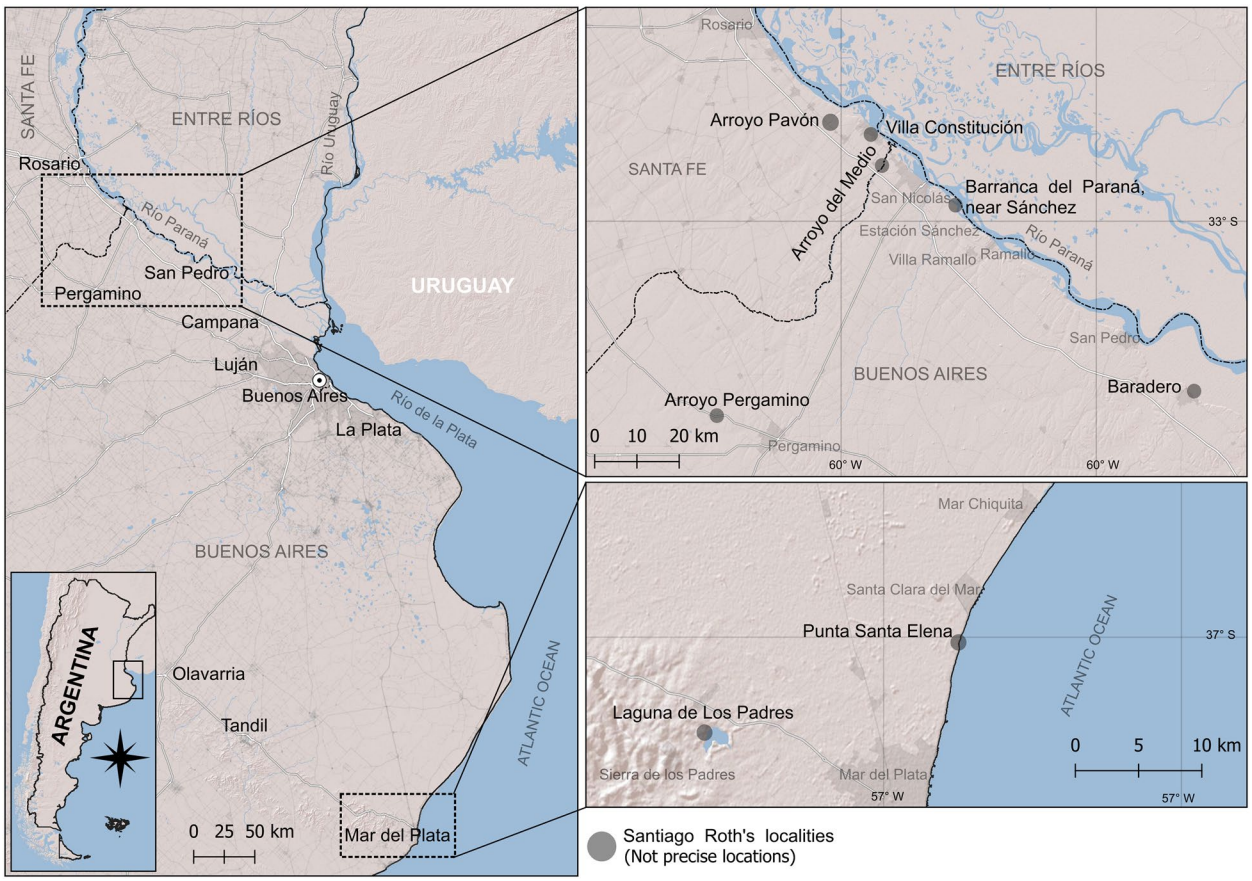

Fig. 1 Map of the Pampean localities of the provenance of the fossils carnivorans pieces collected and referred by Santiago Roth. Localities are not exact. Made with QGIS V.3 3.22.0

Additionally, we include a brief geological review of Roth's localities near the Paraná River to provide an approach to the temporality of the studied material.

Roth's localities and stratigraphic context

Information about the geographic provenance of the fossils in the fifth of Roth's catalogs (Roth, 1889), as well as in the Swiss institutions, is scarce. Due to some inconsistencies in the name of the localities observed between Roth (1889) and the collection labels made later, in the case of the material stored in Zurich we refer to the information in Roth's catalog.

The localities considered in this study cover two provinces of Argentina (Fig. 1): Santa Fe (Arroyo Pavón, Villa Constitución, and Arroyo del Medio) and Buenos Aires (Barranca del Paraná near to Estación Sanchéz, Arroyo Pergamino, Baradero, Punta Santa Elena, and Laguna de Los Padres). With the exception of Arroyo Pergamino, the localities are distributed in the vicinity of the Paraná river and the Atlantic coast. The localities presented by Roth are not precise, although most of them coincide with the places where he lived throughout his life, and the material probably comes from road cuts, canyons made by rivers, and eventual discoveries inside villages (Bond, 1998; Torres, 1927).

Roth based his stratigraphic scheme of the Pampean sediments on the classification of the levels of Ameghino (1881); lower, middle, upper, and lacustrine Pampean. Several authors have contributed to the understanding of the Pampean chronostratigraphy (see Toledo, 2011; Cione et al., 2015), but is F. Ameghino who provides an essential basis for the relationship of the Pampean strata to the presence and abundance of mammalian fossil remains (Ameghino, 1881, 1889). However, Roth interpretations differed in some aspects from Ameghino, being difficult to correlate between the geological interpretations of both naturalists. Roth (1921) presented a study about the geology of the Pampean plains, criticizing part of Ameghino's classification:

"*Ante todo hay que determinar con exactitud la fauna que contiene cada horizonte. Contamos con un gran material de mamíferos fósiles de la formación pampeana, que Ameghino ha distribuído en los pisos que él ha creado, pero, como he dicho, una gran parte de las piezas que menciona son de procedencia dudosa, lo que puede dar lugar a lamentables errores.* Author's translation: First of all, the fauna contained in each horizon must be accurately determined. We have a large amount of fossil mammal material from the Pampean Formation, which Ameghino has distributed in the levels that he has created, but, as I have said, a large part of the pieces he mentions are of dubious provenance, which can give rise to regrettable errors." (Roth, 1921:309–310).

Roth developed a stratigraphic profile (see Roth, 1888: p. 404) during the excavations carried out in 1882 for the construction of the first Cold Meat Store in SA (located in the present town of San Nicolás de Los Arroyos, near of the Paraná River; see ; Voglino, 2020;Voglino et al., in press). In this profile, he described different sedimentary units grouping them according to contemporary divisions of the Pampean Formation: "Obere Pampasformation" (upper Pampean); "Mittlere Pampasformation" (intermediate Pampean); "Untere Pampasformation" (lower Pampean). In Roth's catalog (Roth, 1889), he mentioned the levels as "Pamp. inf." (lower Pampean), "Pamp. Intermédiare" or "moyen" (middle Pampean), and "Pamp. sup." (upper Pampean).

For this division, he referred to its fossiliferous content (especially to the presence of *Typotherium*, now *Mesotherium*), and lithological descriptions with remarkable levels of greenish palustrine sediments (i.e., "Lacustrer Mergel") (see Fig. 2). These sediments, identified by Roth as the limits for the divisions of the Pampean Formation, have great chronostratigraphic value due to their broad extension within the study area and because of the fact that they present recent absolute or indirect dating.

In this sense, the boundary between the upper Pampean and the Intermediate Pampean would be defined in the upper part of the Paraná River canyon, by a level of greenish clayey silts, of wide regional development associated with the sedimentary unit US5 described by Voglino and Pardiñas (2005) (see also Voglino et al., in press). Its lateral continuity has been observed between Rosario and Baradero, although its extension is interrupted in many sections. A level of green pelites, described in the localities of Baradero and Zárate, was dated in 114.3 ± 7 ka BP and assigned to the last interglacial equivalent to the OIS 5 stage (Kemp et al., 2006; Tófalo et al., 2006), and corresponds to the base of the Upper Pampean of Roth (Fig. 2; Voglino et al., in press).

On the other hand, the boundary between the intermediate or middle Pampean and the lower Pampean would be clearly defined by the second level of greenish siltstones of great regional extension and frequently observed at the base of the Paraná River sediments. Voglino and Pardiñas (2005) recognized this level (US9b) as underlying a paleoedaphic level (US9) corresponding to the Hisisa geosol (Nabel et al., 1990, 1993). It is close to the Brunhes–Matuyama paleomagnetic boundary and therefore represents an excellent chronological indicator (ca. 0.78 Ma). The overlying sedimentary unit (US8) defined by Voglino and Pardiñas (2005), carries extinct mammal remains, among which *Mesotherium cristatum* and *Theriodictis platensis* stand out for their biostratigraphic significance. Prevosti and Palmqvist (2001) reviewed the findings of *T. platensis*, clearly restricting

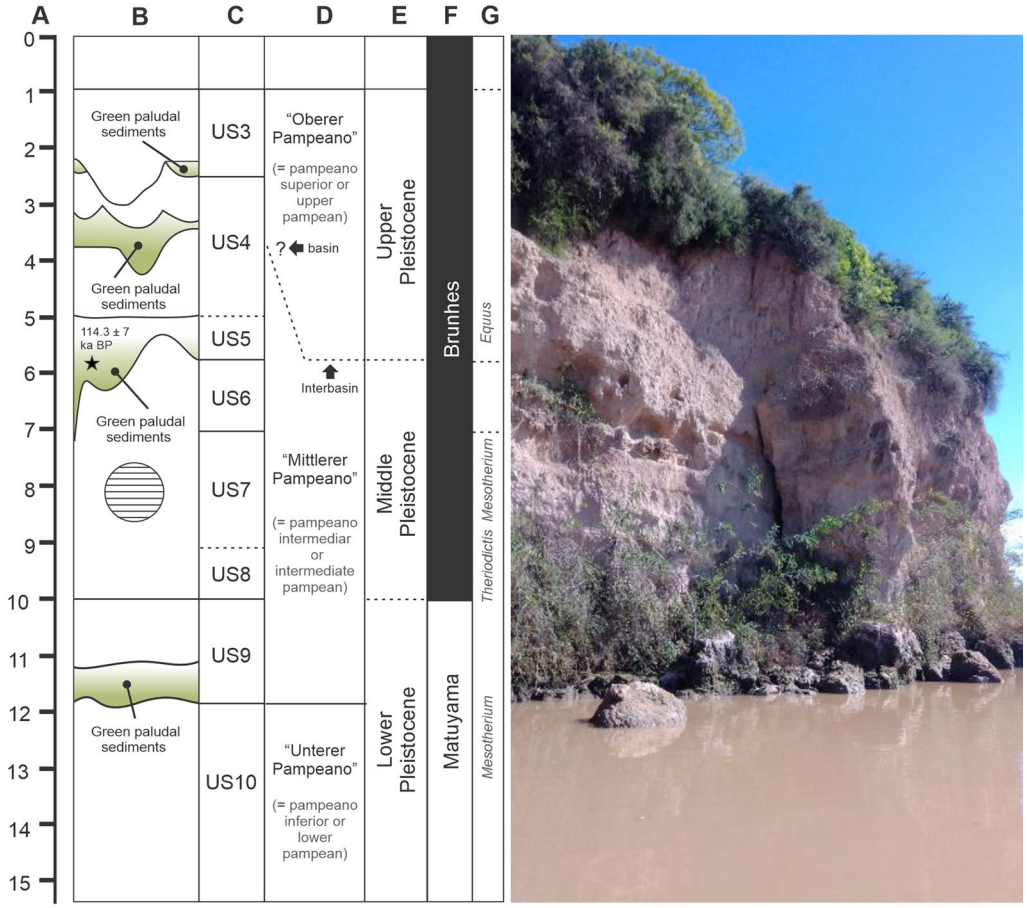

Fig. 2 Chronostratigraphic and biostratigraphic information of the region under study compared with the interpretation of Roth's stratigraphic scheme. **A**, Height (in m); **B**, lithology mentioned in the text; **C**, reference to the sedimentary units of Voglino and Pardiñas (2005); **D**, estimated position of the divisions of the Pampean Formation that Roth established for the area under study; **E**, series/epoch; **F**, magnetic polarity; **G**, biostratigraphy/guide taxa

the upper part of its biochron to the cuspidal Ensenadan. The age of the Ensenadan–Bonaerian boundary has been discussed by several authors (Cione & Tonni, 1999; Tonni et al., 1999), with an apparent consensus that this boundary is younger than 0.78 Ma and that the Ensenadan extends, in its cuspidal portion, into the Brunhes paleomagnetic epoch. Cione and Tonni (1999) have tentatively fixed the boundary between both floors (i.e., Ensenadan and Bonaerian) at around 0.5 Ma (Voglino & Pardiñas, 2005).

Based on these observations, Roth's middle Pampean would include all the Middle Pleistocene in the Paraná River canyons and in the tributary stream in the vicinity of their mouths. It is associated with loess deposits deeply modified by pedogenesis and with numerous hiatuses, marked by discontinuity surfaces (Tófalo et al., 2008; Voglino, 2017; Voglino & Pardiñas, 2005). But it would also include the Upper Pleistocene's basal part and the Lower Pleistocene's final part. Some findings assigned by Roth to the intermediate Pampean in the sections distant from the Paraná River ravines (inter-basin areas) may correspond to much more recent sediments, which lithologically can be confused with Upper Pleistocene–Holocene deposits (see discussion in Toledo, 2011).

Institutional abbreviations. **MACN-Pv**, Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales, Bernardino Rivadavia. **MHNG GEPI V**, Natural History Museum of Geneva, Department of Geology and Paleontology. **MLP**, Museo de La Plata. MZSP, Museo of Zoology, University of São Paulo. **-M** and **-S**, Museo Municipal de Mar del Plata, Buenos Aires. **PIMUZ**, Paläontologisches Institut und Museum, Universität Zürich.

Other abbreviations. **C**/**c**, upper/lower canine. **P**/**p**, upper/lower premolar. **M**/**m**, upper/lower molar. The

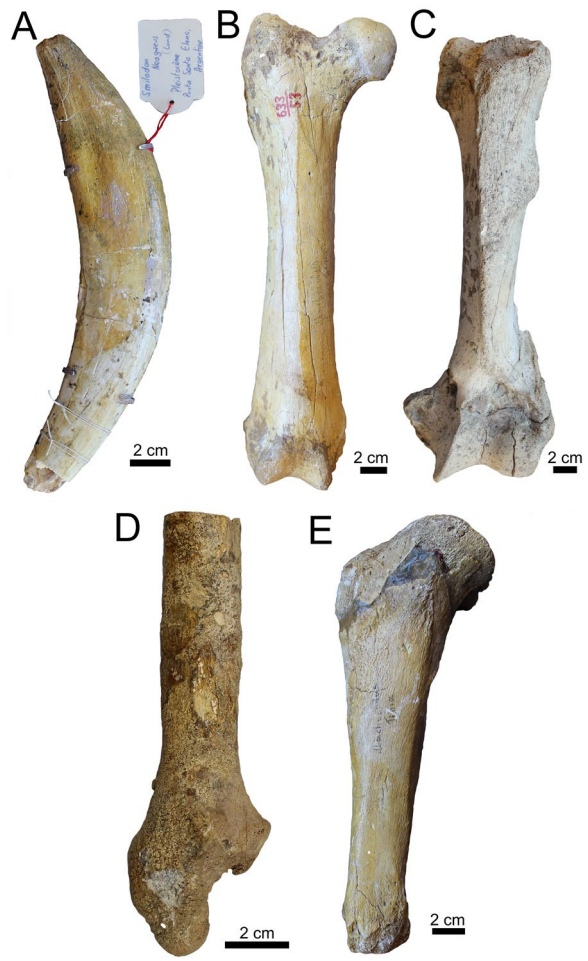

Fig. 3 *Smilodon* sp. **A**, MHNG GEPI V-3211(633/52), upper right canine. **B**, MHNG GEPI V-3213(633/53), right femur in frontal view. **C**, MHNG GEPI V-3215(634.18), left humerus in frontal view. cf. *Smilodon* sp. **D**, PIMUZ A/V 4213, right ulna in frontal view. **E**, MHNG GEPI V-3214(633/52), left tibia in lateral view

numbers that accompany dental abbreviations mean the position of the tooth in the dental series.

Systematic paleontology

Carnivora Bowdich, 1821
Felidae Fischer de Waldheim, 1817
Machairodontinae Gill, 1872
Smilodon Lund, 1842
Smilodon sp.
(Fig. 3A–D)

Referred material. MHNG GEPI V-3211(633/52) (Fig. 3A): upper right canine with the crown fragmented and the broken distal section. MHNG GEPI V-3213(633/53) (Fig. 3B): right femur. MHNG GEPI V-3215(634.18) (Fig. 3C): left humerus.

Description and comparison. The upper canine MHNG GEPI V-3211(633/52) has the crown hypertrophied (length approx. 115 mm) and laterally compressed. During the Pleistocene in SA, the only mammals that presented this morphology were the machairodontine felines (subfamily Machairodontinae). MHNG GEPI V-3211(633/52) has a sagittal fissure that divides the tooth into two parts. The sagittal crest of the crown lacks an apparent crenulation, which is a feature discriminant between members of the tribe Smilodontini (sabretooth without obvious crenulation) and Homotheriini (scimitar-tooth with evident crenulation) (Ruiz-Ramoni et al., 2020; Wallace et al., 2013). The only genus of Smilodontini recognized in SA is *Smilodon*, with three species: *S. fatalis*, *S. gracilis*, and *S. populator* (Berta, 1987; Kurtén & Werdelin, 1990; Prevosti & Forasiepi, 2018). The morphology of the upper canines is not diagnostic to separate these three species and it is not possible to assign the specimen to species level. In a morphometric approach, MHNG GEPI V-3211(633/52) matches the size of the larger *S. fatalis* and the smaller *S. populator* (see Additional file 1: Fig. S1).

MHNG GEPI V-3213(633/53) is a femur of a large feline, with a morphology similar to the femur of *S. populator* of MACN-Pv 46 from Luján and 5-M from Mar del Plata, in the province of Buenos Aires, Argentina (Churcher, 1967), and MZSP-Pv 01 from São Paulo State, Brazil (de Castro & Langer, 2008).

The femoral head of MHNG GEPI V-3213(633/53) has a distal prominence at the base that has been pointed out as a feature to distinguish this feline from the members of Felinae clade (Prevosti & Pomi, 2007). In addition, the shaft is robust, similar to some machairodontines, while in *Panthera* and *Puma* the femur is more gracile. The greater trochanter rises above the femoral head, as seen in MACN-Pv 46, 5-M, and MZSP-PV 01; in *S. gracilis* and some Homotherini this structure is not as projected above the femoral head (Berta, 1987; Martin et al., 2000). In MHNG GEPI V-3213(633/53), the minor trochanter is not as developed as in *Smilodon*; however, it may be due to taphonomic effects.

MHNG GEPI V-3215(633.18) is a robust humerus that corresponds to a large mammal. Merriam and Stock (1932) used the morphology of this bone to differentiate between *Smilodon* and other large felines. In ventral view, the contour of the front end of the greater tuberosity is strongly projected in other felines more than in *Smilodon*. In MHNG GEPI V-3215(633.18), this tuberosity is projected, not as in *Panthera* but more than in the descriptions of Merriam and Stock (1932) for *S. fatalis*. On the other hand, in MHNG GEPI V-3215(633.18), the insertion of the muscle deltoideus is well developed, as in machairodontines felines, and differing from *Panthera*.

In MHNG GEPI V-3215(633.18), the bicipital and deltoid crests fuse in a V-shape, as occurs in machairodontines; in *Panthera* this fusion is U-shaped. In MHNG GEPI V-3215(633.18), the medial epicondyle is highly projected laterally, as in *Smilodon*, while in scimitar-tooth felines this projection is prominent. Despite this, MHNG GEPI V-3215(633.18) has the medial epicondyle more projected than the humerus 652-S of *S. populator* from the Mar del Plata, Argentina (Churcher, 1967). On the other hand, the measurements of MHNG GEPI V-3215(633.18) do not coincide with the data reported by Merriam and Stock (1932) for *S. fatalis* from the Late Pleistocene of Rancho La Brea in California, USA, which could suggest a different species. Despite this, morphometric approximations are unreliable because MHNG GEPI V-3215(633.18) presents bone alterations at the level of insertion of the muscle extensor carpi radialis longus and brevi.

cf. *Smilodon* sp.
(Fig. 3D–E)

Referred material. PIMUZ A/V 4213, distal fragment of a right ulna (Fig. 3D). MHNG GEPI V-3214(633/52) (Fig. 3E): left tibia, with the proximal epiphysis, somewhat deteriorated.

Description and comparison. The ulna PIMUZ A/V 4213 has few characteristics that would not allow a precise classification; the transverse diameter of the shaft (31.5 mm) is robust, which indicates that it could belong to a large feline such as *Panthera* or a Machairodontinae. The styloid process is pronounced distally as in *Panthera* or *Smilodon*, while it is shorter in Homotherini. In some *Panthera* specimens, the styloid process draws a continuous curve on the posterior side after the insertion of the pronator quadratus muscle. In contrast, *Smilodon* is slightly squarer, like PIMUZ A/V 4213. The genus *Panthera* has a notch on the inner side of this process. In PIMUZ A/V 4213, this notch is not evident.

The tibia MHNG GEPI V-3214(633/52) is similar to that of 796-S of *S. populator* from Mar del Plata (Churcher, 1967) but it slightly differs from the MACN-Pv 46 of the same species from Luján. Since the distal articulation is less projected vertically than in MACN-Pv 46.

Remarks. PIMUZ A/V 4213 was originally undetermined by Roth (Catalog 5 N° 272; Roth, 1889); it was classified as *Incertae sedis* by Schulthess (1920) and later as *Smilodon neogeus* and *S. populator* in the PIMUZ collection labels. Because the material is not diagnostic, its assignment to a *Smilodon* could not be confirmed either.

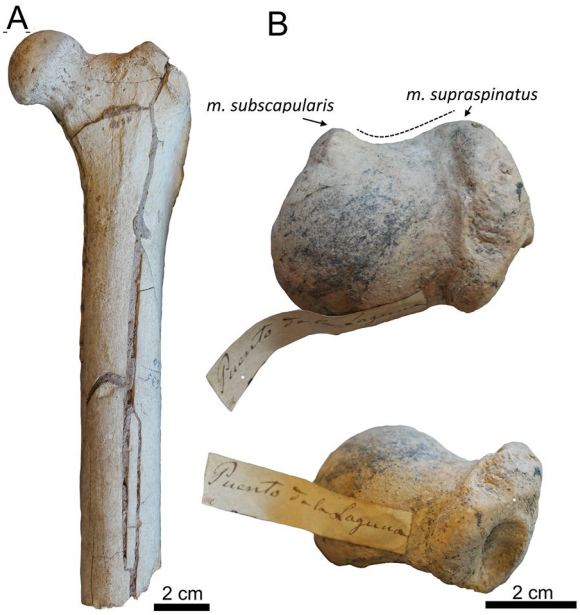

Fig. 4 *Panthera* sp. **A**, MHNG GEPI V-3205(635/20), right femur in frontal view. cf. *Panthera*. **B**, MHNG GEPI V-3202, right humerus epiphysis. The open U-shaped morphology between the insertion of the m. subscapularis and m. supraspinatus is highlighted

Similarly, MHNG GEPI V-3214(633/52) was classified as *Smilodon* in the Geneva collection, but based on the arguments presented above, we cannot be conclusive on the determination.

Pantherinae Pocock, 1917
Panthera Oken, 1816
Panthera onca (Linnaeus, 1758).
(Fig. 4A)

Referred material. MHNG GEPI V-3205(635/20): right femur without the distal epiphysis (Fig. 4A). *Description and comparison***.** MHNG GEPI V-3205(635/20) is a femur with a morphology similar to that of a large feline. It have a gracile appearance, as opposed to MHNG GEPI V-3213(633/53). There is no prominent tuberosity near to the femoral head, which makes it possible to identify within the Felinae (Berta, 1987; Prevosti & Pomi, 2007). Although it is fragmented, the greater trochanter does not overlap with the femoral head. The angle between the femoral head and the greater trochanter is obtuse, as occurs in *Panthera onca*, and different from other felines such as *Puma concolor*. The minor trochanter is small. The diaphysis is straight but cracked with sediment filling the fissures.

cf. *Panthera* sp.
(Fig. 4B)

Referred material: MHNG GEPI V-3202: proximal head of a right humerus (Fig. 4B).

Description and comparison. MHNG GEPI V-3202 corresponds to the proximal epiphysis of a right humerus of a large mammal. The humeral head is slightly below the level of the greater tubercle, as in some carnivorans (i.e., large canids, felids, and ursids). In proximal view, the insertion of the muscle subscapularis projects posteriorly and reaches the same level as the insertion of the muscle supraspinatus. In ursids, these insertions project further and draw a closed U between them, similar to canids and felids like *Panthera*, but the U is more open in the latter. In MHNG GEPI V-3202, this morphology is observed but with a very open non-symmetrical U (see Fig. 4B). In some machairodontines, the insertion of the muscle supraspinatus projects posteriorly much more than the muscle subscapularis, differing from MHNG GEPI V-3202 belongs to some group of felids. Other large SA felines, like *P. concolor*, present a strongly developed insertion of the muscle supraspinatus, which differs from MHNG GEPI V-3202.

MHNG GEPI V-3202 was referred to *P. onca* in the MDNG catalog, but the observed morphology is inconclusive for this assignment.

Fig. 5 *Arctotherium* sp., PIMUZ A/V 4215. **A**, right mandible in labial view and occlusal view of the molars. **B**, right radius in frontal view. **C**, phalanges in upper view. **D**, thoracic vertebra. **E,** cf. Ursidae. PIMUZ A/V 4266, metatarsus III

Ursidae Fischer de Waldheim, 1817
Tremarctinae Merriam & Stock, 1925
Arctotherium
Arctotherium sp.
(Fig. 5)

Referred material. PIMUZ A/V 4215: a right mandible with the c1, m1–m3 (Fig. 5A); a right radius (Fig. 5B); two phalanges (Fig. 5C); thoracic vertebra (Fig. 5D).

Description and comparison. The mandible of PIMUZ A/V 4215 corresponds to a short-faced bear (*Arctotherium*) with teeth size of an intermediate specie as *A. vetustum*, *A. bonariense*, or *A. tarijense*; it is not as small as an *A. wingei*, but not large as an *A. angustidens* (see Additional file 1: Fig. S2). Following the characters defined by Soibelzon (2004), this specimen has some features which relate it to *A. vetustum*. The hypoconid of the m2 is low and semi-flat; in *A. tarijense* it is tall and conical. An internal low cuspid is fused to the hypoconid, whereas in *A. bonariense* this cuspid is high and independent. The entoconid is formed by three cuspids, while in *A. tarijense* there are only two. However, the m3 of PIMUZ A/V 4215 does not match to the description given by Soibelzon (2004) for *A. vetustum*. The m3 is slightly elongated, while in *A. vetustum* it was described as subcircular. For us, the morphology of this character is variable among individuals of this species; MACN-Pv 1201 (from the Middle Pleistocene of Buenos Aires, Argentina) has circular m3, while in MACN-Pv 1277 (type of *A. vetustum*, from the middle to Late Pleistocene of Entre Rios, Argentina) this molar is elongated, as in PIMUZ A/V 4215. A similar situation occurs with a narrowing that arises between this molar's protoconid and hypoconid. This morphology is marked in PIMUZ A/V 4215, as in MACN-Pv 1277, but in other specimens of *A. vetustum* is weak.

In addition to the variability of the shape of the m3 indicated above, the angular process is more distally projected than other specimens of this species (e.g., MACN-Pv 1201). But, in MACN-Pv 17486 (*A. vetustum*, from the Middle to Late Pleistocene of Entre Ríos, Argentina), this process is projected as in PIMUZ A/V 4215(45), indicating marked variability within this species. For this reason, our assignment is not conclusive at the species level, and we consider that a revision of the morphological variability of *A. vetustum* and *A. bonariense* is needed.

The postcranial material of PIMUZ A/V 4215(45) is not very diagnostic. However, the radius and phalanges are shorter than the largest *Arctotherium* species, which makes it possible to discriminate it from *A. angustidens* (e.g., MLP 35-IC-26–4 from the Middle Pleistocene of La Plata, Buenos Aires) (Soibelzon & Schubert, 2011). This is consistent with size observations made on dental material.

cf. *Ursidae*
(Fig. 5E)

Referred material. PIMUZ A/V 4266 metatarsal III, with the posterior end deteriorated (Fig. 5E).

Description and comparison. PIMUZ A/V 4266 is a left metatarsal III that was assigned to a bear. In felines such as Pantherines, the metatarsals are elongated and with a straight diaphysis. In machairodontines, the metatarsals are slightly more curved and robust. A similar morphology is observed in ursids; however, the data are inconclusive to confidently support this assignment.

Canidae Fischer de Waldheim, 1817
Caninae Fischer de Waldheim, 1817
Dusicyon Hamilton-Smith 1839.
Dusicyon avus (Burmeister, 1866).
(Fig. 6A–D)

Referred material. PIMUZ A/V 4211 dental series with left P4–M2, a posterior fragment of P3; left mandible fragment with p4–m2 (Fig. 6A and B). PIMUZ A/V 4232: right isolated m1, m2, and p? (Fig. 6C). PIMUZ A/V 4228, portion of left maxilla with P4, partial M1, and the roots of M2 (Fig. 6D).

Description and comparison. The protocone of the P4 of the PIMUZ A/V 4211 is broken but apparently was directed mesiolingually. This carnassial is long in comparison to M1 and m2 lengths (see Additional file 1: Table S3). The p4 has a second accessory distal cusp, and the distal cingulum is acute. The size of the m1 and the described characters allow for identifying this specimen as *Dusicyon avus* (Berman & Tonni, 1987; Prevosti et al., 2011; 2015). The m1 of the PIMUZ A/V 4232 is large, and albeit it is strongly worn, the hypoconulid is apparently well-developed hipoconulid since it is expanded distally. The size of the m1 and its proportions to the length of the m2 agree with *D. avus*, but it also overlaps with the largest specimens of *L. culpaeus*. The apparently well-developed hypoconulid and the mentioned metric characters suggest that this specimen belongs to *D. avus*. Associated with these specimens is an incomplete canine that does not belong to a carnivoran, and a right p3? that has a blunt and low principal cusp and a tiny distal accessory cusp that could belong to *Canis*. Beyond its morphological pattern, its color and other taphonomic features (i.e., the presence of root marks)

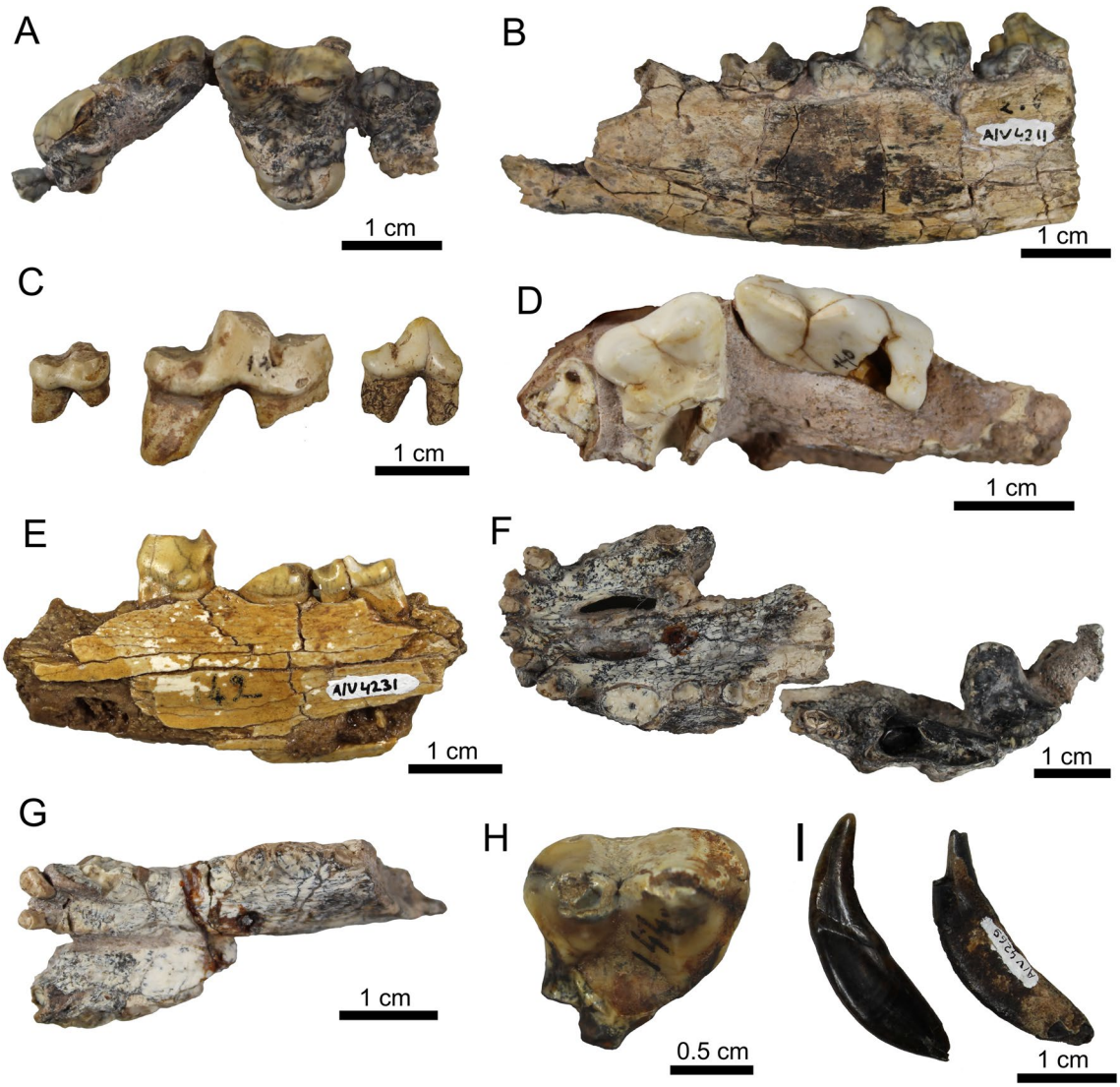

Fig. 6 *Dusicyon avus*. PIMUZ A/V 4211, **A**, upper denture (part P3, P4–M2) in occlusal view. **B**, left mandible fragment in buccal view. PIMUZ A/V 4232, **C**, m2, m1, and p?, in buccal view. **D**, PIMUZ A/V 4228, portion of left maxilla in occlusal view. cf. *Dusicyon avus*. **E**, PIMUZ A/V 4231, right mandible fragment in lingual view. PIMUZ A/V 4226, **F**, skull fragment in ventral view and dental segment (part of P3, P4–M1). **G**, distal fragment of both mandibles in occlusal view. Caninae indet. **H**, PIMUZ A/V 4268, M1 fragment in occlusal view. **I**. PIMUZ A/V 4269, isolated canines

suggest that it does not belong to the same individual represented by the m1–2. The protocone of the P4 of the PIMUZ A/V 4228 is reduced and directed mesiolingually but end close to the mesial border of the tooth. The P4–M1 measurements are in the range of *Dusicyon* (see Additional file 1: Fig. S3). These morphometric features allow discarding its assignation to other canid taxa (see Berman & Tonni, 1987; Prevosti et al. 2011; 2015).

cf. *Dusicyon avus*
(Fig. 6E)

Referred material. PIMUZ A/V 4231 fragment of right mandible with roots of p4, deteriorated m1, and m2 (Fig. 6E).

Description and comparison. The length of the m1 of PIMUZ A/V 4231, and its proportions compared to the m2 length agree with *D. avus* but overlap with the largest *L. culpaeus* (see Additional file 1: Fig. S4).

Lycalopex Burmeister, 1854
Lycalopex sp.
(Fig. 6F–G)

Referred material. PIMUZ A/V 4246, maxilla divided into two portions, (1) distal end with all the incisors, roots of the canines the and p1, and the alveolus of the right p2, and (2) dental series from P3 to partial M2 (Fig. 6F); distal mandibular fragment with left i3 and canine (without crown), and right i2, i3 and canine (without crown), p1, p2 and part of p3 (without crown) (Fig. 6G), in addition to unidentifiable fragments.

Description and comparison. PIMUZ A/V 4246 has the protocone of the P4 well developed and strongly oriented mesioligually beyond the mesial border of the tooth. The size and morphometry of the dentition resembles specimes of *Lycalopex culpaeus* (see Additional file 1: Fig. S5). The protocone of the P4 is well developed, while in *L. culpaeus* this structure is normally reduced. Due to this difference, it is not assigned to this living species.

Caninae indet.
(Fig. 6H, I)

Referred material. PIMUZ A/V 4268, right incomplete M1 without talond (Fig. 6H). PIMUZ A/V 4269, isolated canines, plus unidentifiable tooth fragments (Fig. 6I).

Description and comparison. PIMUZ A/V 4268 is a medium to large-sized canid. It is observed that it does not have a well-developed labial cingulum, unlike *Aenocyon dirus*. PIMUZ A/V 4268 was previously classified in the collection label as *Paleocyon troglodytes*, or confrontable with this species. Due to its incomplete nature, it is impossible to discard other large hypercarnivore canids recorded in SA (i.e., *Theriodictis*, *Protocyon*). Reduction of the labial cingulum of the M1 differs from *Aenocyon* and most *Canis* species. PIMUZ A/V 4268 presents a morphology seen in others SA large canids (Berta, 1988; Ruiz-Ramoni et al., 2022). The size of this molar is smaller than in "*Canis*" *gezi*. PIMUZ A/V 4269 are canines of a small canid, but do not present diagnostic features that permit to assign them to any species.

Discussion

We confirmed the assignment to the order Carnivora for 10 of the 11 specimens mentioned in Roth's Catalog 5 (1889) (see Table 1). The number 144 (Catalog 5; now PIMUZ A/V 4267) corresponds to a carnivoran tooth from Barranca del Paraná, Sánchez, Buenos Aires. This tooth is a robust incisor (see Additional file 1: Fig. S6), more than those observed in *Panthera* or *Puma*, with a very curved root, unlike *Smilodon*, and with a crown very fragmented, but somewhat compressed mesiodistally so that it does not appear to be a carnivoran. PIMUZ A/V 4267 was recognized as a Carnivora by Roth (1889) and Schulthess (1920). Later, it was referred to *Smilodon* sp. indet. in PIMUZ collection catalog. For the above reasons we consider PIMUZ A/V 4267 as a Mammalia indet.

Of the confirmed carnivorans, one specimen is probably the felid *Smilodon*, from Arroyo del Medio; one specimen is referred to the short face bear *Arctotherium* from Arroyo Pergamino, and six are canids, of which five belong to small and medium taxa such as *Dusicyon avus* and *Lycalopex* sp. from Villa Constitución, Arroyo

Table 1 Geographical and stratigraphic provenance of the fossil carnivorans material housed in the Roth collections in Switzerland

Systematics	Taxa	Collection number	Roth catalog	Material	Locality	Pampean level
Felidae	cf. *Smilodon*	PIMUZ A/V 4213	272	Postcranial	Arroyo del Medio, SF–BA	MPamp/MPlei
Ursidae	*Arctotherium* sp.	PIMUZ A/V 4215	45	Cranial + postcranial	Arroyo Pergamino, BA	MPamp/LPlei?
Ursidae	cf. Ursidae	PIMUZ A/V 4266	104	Postcranial	Arroyo del Medio, SF–BA	MPamp/MPlei?
Canidae	*Dusicyon avus*	PIMUZ A/V 4232	143	Dental	Villa Constitución, SF	UPamp/LPlei
Canidae	*Dusicyon avus*	PIMUZ A/V 4211	246	Cranial + dental	Villa Constitución, SF	MPamp/LPlei
Canidae	*Dusicyon avus*	PIMUZ A/V 4228	140	Cranial + dental	Arroyo del Medio, SF–BA	MPamp/MPlei?
Canidae	cf. *Dusicyon avus*	PIMUZ A/V 4231	142	Cranial + dental	Baradero, BA	UPamp/LPlei
Canidae	*Lycalopex* sp.	PIMUZ A/V 4246	141	Cranial + dental	Arroyo Pavon, SF	MPamp/MPlei?
Canidae	Caninae indet	PIMUZ A/V 4269	144	Dental	Sanchez, BA	MPamp/MPlei?
Canidae	Caninae indet	PIMUZ A/V 4268	144	Dental	Sanchez, BA	MPamp/MPlei?
Felidae	*Smilodon* sp.	MHNG GEPI V-3211(633/52)	?	Dental	Punta Santa Elena, BA	MPlei-LPlei?
Felidae	*Smilodon* sp.	MHNG GEPI V-3215(633/18)	?	Postcranial	Pampa of Argentina, BA?	Pleistocene
Felidae	*Smilodon* sp.	MHNG GEPI V-3213(633/53)	?	Postcranial	BA	Pleistocene
Felidae	*Smilodon* sp.	MHNG GEPI V-3214(633/52)	?	Postcranial	BA	Pleistocene
Felidae	*Panthera onca*	MHNG GEPI V-3205(635/20)	?	Postcranial	Punta Santa Elena, BA	MPlei-LPlei?
Felidae	cf. *Panthera*	MHNG GEPI V-3202	?	Postcranial	Laguna de los Padres, BA	Pampean/Pleistocene

BA Buenos Aires; *LPlei* Late Pleistocene; *MPamp* middle Pampean; *MPlei* Middle Pleistocene; *SF* Santa Fe; *UPamp* upper Pampean

del Medio, Baradero, and Arroyo Pavón, and two were not possible to identify from Sánchez. As commented by Schulthess (1920) and Weigelt (1951), the history of the acquisition of this collection is clear and was bought to Zurich at the end of the nineteenth century (in 1889 sensu Schulthess, 1920, or 1891 sensu Weigelt, 1951) with the combination of donations of different organizations and people (Schulthess, 1920).

The material stored in the Natural History Museum in Geneva (see Table 1) consists of six fossils of felines corresponding to *Smilodon* and *Panthera*. The origin of this material is mainly the Pampean Atlantic coast. Some elements come from Punta Santa Elena and Laguna de Los Padres, and there is not much information on the origin of the remaining specimens. The history of this collection is less clear and could correspond to one of the first large collections made by Roth, the one that he sent to Geneva, where he needed to repair most of the specimens to finally sell them in 1880 (Schulthess, 1920). This collection was received and revised by Professor C. Vogt, with whom Roth could get some studies in an academic space (Schulthess, 1920). Finally, it is not clear where the collection of Catalog 6 (Roth, 1892) was deposited. This catalog was printed in Zurich and included several specimens of "*Canis*" (numbers 34 93, 34 94, 34 95, and 34 101) and one "*Mephites*" (number 34 96). This collection was held by Roth's wife (Elizabeth Schütz) in Zurich when he traveled back to Argentina in 1891 (Weigelt, 1951; see also Hansen, 2019).

Without considering the time between species descriptions and taxonomic rearrangements that have occurred up to the present day, all Pampean carnivorans in Switzerland collected by Roth have recognized morphology. All taxa had been identified previously in the Pampean region (Prevosti & Forasiepi, 2018). However, one of the main problems with Roth's material collected by is the stratigraphic provenance (see Roth's localities and stratigraphic context).

All carnivorans deposited in Zurich (Catalog 5; Roth, 1889) come from levels between intermediate Pampean and upper Pampean. All upper Pampean materials are referred to the Upper Pleistocene, ca. 41.5–114.3 ± 7 ka BP ka BP (Alberdi & Prado, 2012; Kemp et al., 2006; Tófalo et al., 2006) (Fig. 2 and Table 1; Voglino et al., in press). For those from the middle Pampean, origin determination is more uncertain because this level encompasses the lower limit of the Upper Pleistocene, the entire Middle Pleistocene, and the upper part of the Lower Pleistocene (see Fig. 2). Nevertheless, we highlight the case of Arroyo Pergamino and Villa Constitución cases because of their biostratigraphic implications.

In Arroyo Pergamino (Buenos Aires Province), Roth indicated the presence of an ursid (PIMUZ A/V 4215) from the middle Pampean, here recognized as *Arctotherium* sp. However, our observations make us consider two species: *A. vetustum* and *A. bonariense*. The middle Pampean in the outlying areas of the Paraná River (interbasin areas) could be confused with the Late Pleistocene sediments of the Lujanense (see Toledo, 2011). In addition, in this same level Roth described remains of *Equus* sp. (PIMUZ A/V 4183 and 4242; pers. obs.), which can be interpreted within the *Equus* biozone (Cione et al., 2015) that corresponds to the Lujanian (Late Pleistocene to Early Holocene). Based on this, PIMUZ A/V 4215 is expected to come from the Late Pleistocene. If PIMUZ A/V 4215 is an *A. vestustum*, it may be one of the most modern records for the species (Soibelzon et al., 2005). In case it belongs to *A. bonariense*, it would fit with other chronological records for this species (Soibelzon et al., 2005).

In Villa Constitución (Santa Fe Province), Roth refered that the materials of canids (*D. avus*) come from the upper Pampean (PIMUZ A/V 4232) and middle Pampean (PIMUZ A/V 4211) levels. In the middle Pampean levels of this locality, *Equus* remains were identifed (PIMUZ A/V 4236; pers. obs.), which generates, for PIMUZ A/V 4211, the same situation described above for Arroyo Pergamino. The *Equus* biozone is associated with the record of *D. avus*, which is recognized from the Late Pleistocene to the Holocene (Prevosti et al., 2015). This is also supported by the coloration of the fossil. A dark coloration is characteristic of the fossils from the local stratigraphic levels assigned to the cuspidal Ensenadan (Voglino, pers. obs.). Because PIMUZ A/V 4211 does not present this characteristic, we consider a Late Pleistocene age.

On the other hand, the data are even scarcer for material stored in Geneva (Table 1). Some materials are assigned to the Pleistocene, with the exception of the *Panthera onca* femur, MHNG GEPI V-3205 (635.20), which says it comes from "Pampéen Ensenadéen" (Ensenadan Pampean) of Punta Santa Elena (Buenos Aires Province). This locality has a late Ensenandan (0.78–ca. 0.5 Ma) in the base with ensenadan fossils like *Mesotherium* and *Theriodictis*, and sediments with normal polarity of the Brunhes chron in the base of the profile, and younger ages above it (see discussion in Prevosti, 2006 and Prevosti et al., 2009; Cione et al. 2002; Bidegain et al. 2005). This indicates that MHNG GEPI V-3205(635.20) and probably 3211(3211), assigned to *Smilodon* sp., could have a late Ensenadan to Lujanian age.

In conclusion, all specimens that Roth sold to Switzerland contribute to the paleontological record of the Pampean region, but given that there is no precise stratigraphic control in the present context, it is not possible to recognize the scope of his discoveries about carnivorans.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-023-00274-6.

Additional file 1: Table S1. Measurementsof the fossil material of felines collected by S. Roth and deposited in Swiss collections. * Not exact measurement. **Table S2.** Measurementsof the fossil material of ursids collected by S. Roth and deposited in Swiss collections. * Not exact measurement. **Table S3.** Measurementsof the fossil material of canids collected by S. Roth and deposited in Swiss collections. * Not exact measurement. **Fig. S1.** Scatter plot of upper canine measurementsof MHNG GEPI V-3211with respect to Smilodon species. Comparative data were obtained from Merriam and Stock, Berta, Kurtén and Werdelin, and Prieto et al.. **Fig. S2.** Scatter plot of dental measurementsof PIMUZ A/V 4215with respect to fossil ursid species from South America. Comparative data were obtained from the personal databaseand Rincón and Soibelzón. **Fig. S3.** Principal ComponentAnalysis based on dental measurements, showing the position of PIMUZ A/V 4246with respect to other South American canids. **Fig. S4.** Scatter plot showing the location of PIMUZ A/V 4231, PIMUZ A/V 4211, and PIMUZ A/V 4232with respect to the relationship between the length of m1 and m2 of some South American canids. Cerdocyon thous, Dusicyon australis, Dusicyon avus, Lycalopex culpaeus, Lycalopex gymnocercus + Lycalopex griseus + Lycalopex sechurae. **Fig. S5.** Principal ComponentAnalysis based on dental measurements, showing the position of the M1–P4 of PIMUZ A/V 4246with respect to other South American canids. **Fig. S6.** PIMUZ A/V 4267, incisor in lateral view.

Acknowledgements
We thank M. Sanchez-Villagra and G. Aguirre-Fernández of the Paläontologisches Institut und Museum of the Universität Zürich, and L. Cavin of the Muséun D'Histoire Naturelle of Geneva for support and access to the collections with Roth material. DRR and JC are grateful to the Lateinamerika-Zentrum Zürich for financial support for the visit to the Swiss collections. We thank L. Cruz of the MACN-Pv for access to comparison material, M. Farro (Archivo Histórico of the MLP) and Álvaro Mones for useful comments, J.L. Aguilar of the Museo de San Pedro, Buenos Aires, and K. Hansen of the University of Copenhagen for providing us with information on the historical context of Santiago Roth. Thanks to M. Sánchez Villagra, M. Bond, M. Reguero, and A. Forasiepi to share their in press work. SwissCollNet (SCN133-ZH), CONICET and the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2019-2874) provided partial finantial support. The shape for the map was obtained from Instituto Geografico Nacional, Argentina (www.ign.gob.ar). We thank the editors A. Forasiepi and G. Aguirre-Fernandez for their comments on the manuscript.

Author contributions
DRR participated in the conceptualization, data collection, analysis, and writing of the manuscript. JDCB participated in the conceptualization, data collection, and writing of the manuscript. DV described fundamental aspects of the biostratigraphic context. FJP participated in data analysis, conceptualization, writing of the manuscript. All authors read and approved the final manuscript.

Funding
This work was partially supported by the Lateinamerika-Zentrum Zürich.

Availability of data and materials
The data generated and analyzed in this study are included in the Additional files. The materials studied are deposited in the Paläontologisches Institut und Museum of the Universität Zürich and Muséun D'Histoire Naturelle of Geneva. The databases used for morphometric analysis belong to DRR and FJP; contact these authors to request further information.

Author details
[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina. [2]Museo de Ciencias Antropológicas y Naturales, Universidad Nacional de La Rioja (UNLaR). Av. Luis M. de la Fuente s/n, 5300 La Rioja, Argentina. [3]Universität Zürich, Paläontologisches Institut und Museum, Karl-Schmid-Strase 4, 8006 Zurich, Switzerland. [4]Museo de Ciencias Naturales A. Scasso. Observatorio del Patrimonio Arqueológico y Paleontológico (OPAP; CRePAP, Dirección Provincial de Patrimonio Cultural), Calle Don Bosco 580. San Nicolás de los Arroyos, Buenos Aires, Argentina.

Received: 20 January 2023 Accepted: 17 April 2023
Published online: 05 July 2023

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