Nearctic Pleistocene ungulates from the Pampean region (Argentina) in the historical collections of Santiago Roth in Switzerland: an overview

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Abstract

Nearctic ungulates such as artiodactyls, perissodactyls, and proboscideans arrived in South America during the Great American Biotic Interchange. Among them are camelids, cervids, tayassuids, equids, tapirids and gomphotherids. A historical collection of Nearctic ungulates from Pleistocene deposits of the Pampean region in Argentina is here studied and described. The collection consists of specimens collected by Santiago Roth in the nineteenth century and brought to Europe, where they are housed in the paleontological collections of the University of Zurich and the Natural History Museum of Geneva. Among the taxa reported here are *Notiomastodon platensis, Lama guanicoe, Hemiauchenia paradoxa, Tayassu pecari, Morenelaphus* sp., *Hippidion* cf. *H. principale, Equus* cf. *E. neogeus*, and other indeterminate gomphotherids, camelids, tayassuids, cervids, and equids. The exact stratigraphic position of these fossils collected more than 130 years ago is in many cases uncertain. The historical collection is still relevant for taxonomic studies and for offering new insights into palaeobiogeography and palaeobiology of mammalian fauna of the region during the Pleistocene.

Keywords Cenozoic, South America, Fossils, Mammals, Great American biotic interchange

Resumen

Los ungulados neárticos como los artiodáctilos, perisodáctilos y los proboscídeos llegaron a América del Sur durante el Gran Intercambio Biótico Americano. Entre ellos se encuentran los camélidos, cérvidos, tayasuidos, équidos, tapíridos y gonfotéridos. Aquí se estudia y describe una colección histórica de ungulados neárticos procedentes de depósitos pleistocenos de la región pampeana en Argentina. La colección consta de especímenes que fueron recolectados por Santiago Roth durante el siglo XIX, llevándolos a Europa donde se encuentran depositados en las colecciones paleontológicas de la Universidad de Zúrich y el Museo de Historia Natural de Ginebra. Entre los taxones reportados aquí se encuentran *Notiomastodon platensis, Lama guanicoe, Hemiauchenia paradoxa, Tayassu pecari, Morenelaphus* sp., *Hippidion* cf. *H. principale, Equus* cf. *E. neogeus* y otros gonfotéridos, camélidos, tayasuidos, cérvidos y équidos

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indeterminados. La posición estratigráfica exacta de estos fósiles que fueron recolectados hace más de 130 años es en muchos casos incierta. La colección histórica sigue siendo relevante para los estudios taxonómicos y para ofrecer nuevos conocimientos sobre paleobiogeografía y paleobiología de la fauna de mamíferos de la región durante el Pleistoceno.

Palabras claves Cenozoico, América del Sur, Fósiles, Mamíferos, Gran Intercambio Biótico Americano

Introduction

Fossil Nearctic ungulates such as artiodactyls, perissodactyls, and proboscideans are well represented in the South American fossil record (see Alberdi & Prado, 2002; Cassini et al., 2016; Defler, 2019; Gasparini, 2013; Gasparini et al., 2011, 2014, 2017; González et al., 2014; Holanda & Ferrero, 2013; Mothé et al., 2012, 2013, 2017a, b, c; Scherer, 2013, and references therein). Their arrival in the Southern continent occurred during the Great American Biotic Interchange (GABI), a process triggered as a consequence of the establishment of a land bridge in Central America around ~10–7 Ma (e.g., Carrillo et al., 2015; Cione et al., 2015; Simpson, 1980; Webb, 1985, 2006). The GABI was characterized by a series of major migration "waves", mainly during the Pliocene–Pleistocene, that allowed a massive faunal exchange between North and South America (e.g., Woodburne, 2010); although there were early migrations for the late Miocene (Cione et al., 2015). The classic interpretation places the onset of the GABI by ~3.0 Ma, with some early migrations during the Late Miocene from South America to North America by ~9 Ma, and from North America to South America by ~7 Ma (e.g., Carrillo et al., 2015). Among the Nearctic ungulates that arrived in South America are camelids, cervids, tayassuids (artiodactyls), equids, tapirids (perissodactyls), and gomphotherids (proboscidean) (Webb, 2006). A peccary (Tayassuidae) from deposits of 3.7 Ma in Argentina (Chapadmalalan age according to Cione et al., 2007) has been referred to as one of the first artiodactyls to arrive in South America. Tayassuids, dromomerycine artiodactyls, tapirs, and gomphotheres, have been also claimed from Miocene deposits (~10 Ma) of the Amazon basin (Frailey & Campbell, 2012); although the taxonomy and age of some of these taxa have been questioned (Gasparini et al., 2021; Mothé & Avilla, 2015).

In this contribution, we review and describe the fossil Nearctic ungulates (gomphotherids, camelids, tayassuids, cervids, and equids) collected by Santiago Roth in Pleistocene deposits of the Pampean region in Argentina during the nineteenth century, currently housed in the paleontological collections of the University of Zurich (originally under Catalog 5, Roth, 1889), and the Natural History Museum of Geneva (unknown catalog; Voglino et al., 2023), Switzerland. The Pampean region of Argentina has been interpreted as an ecotonal area between arid zones of Patagonia and humid zones of Brazil (García-Morato et al., 2021).

The Roth contributions to Argentine geology and paleontology were conspicuous and numerous, and among them are the fossil collection and study of the pampean mammals associations. His field work was accompanied by a varied series of publications (Fernández, 1925; Giacchino & Gurovich, 2001; Sánchez-Villagra et al., 2023; Voglino, 2020; Voglino et al., 2023). Despite the fact that fossils brought by Roth to Switzerland were collected more than 130 years ago in the Pampas region of Argentina, the study of this historical collection is still relevant for taxonomic, paleobiological and paleobiogeographical purposes, and other studies aiming at insights into the paleodiversity of mammalian fauna of the region during the Pleistocene (see Lynch et al., 2020; Le Verger, 2023; Ruiz-Ramoni et al., 2023; Voglino et al., 2023).

Materials and methods

Referred specimens

The fossil collection studied here is represented by a total of 245 cranial and postcranial remains of gomphotherids, camelids, tayassuids, cervids, and equids (Additional file 1). The specimens are housed at the paleontological collections of the University of Zurich (PIMUZ A/V), and the Natural History Museum of Geneva, department of geology and paleontology (MHNG GEPI V-). Specimens from PIMUZ correspond to catalog 5, published by Roth (1889; see Additional file 1). The specimens housed at MHNG GEPI are not associated (if they were earlier, we do not know) with any of the catalogs published by Roth (Voglino et al., 2023).

Taxonomic identification involved an extensive bibliographic review and comparison with fossil and extant specimens housed at those two institutions in Switzerland as well as: CFA, Colección Mastozoológica, Fundación de Historia Natural 'Félix de Azara', Buenos Aires, Argentina; CIAAP, UNEFM-PF, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas de la Universidad Experimental Francisco de Miranda, Venezuela; IGM, Museo Geológico José Royo y Gómez, Servicio Geológico Colombiano, Bogotá, Colombia; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MBLUZ,
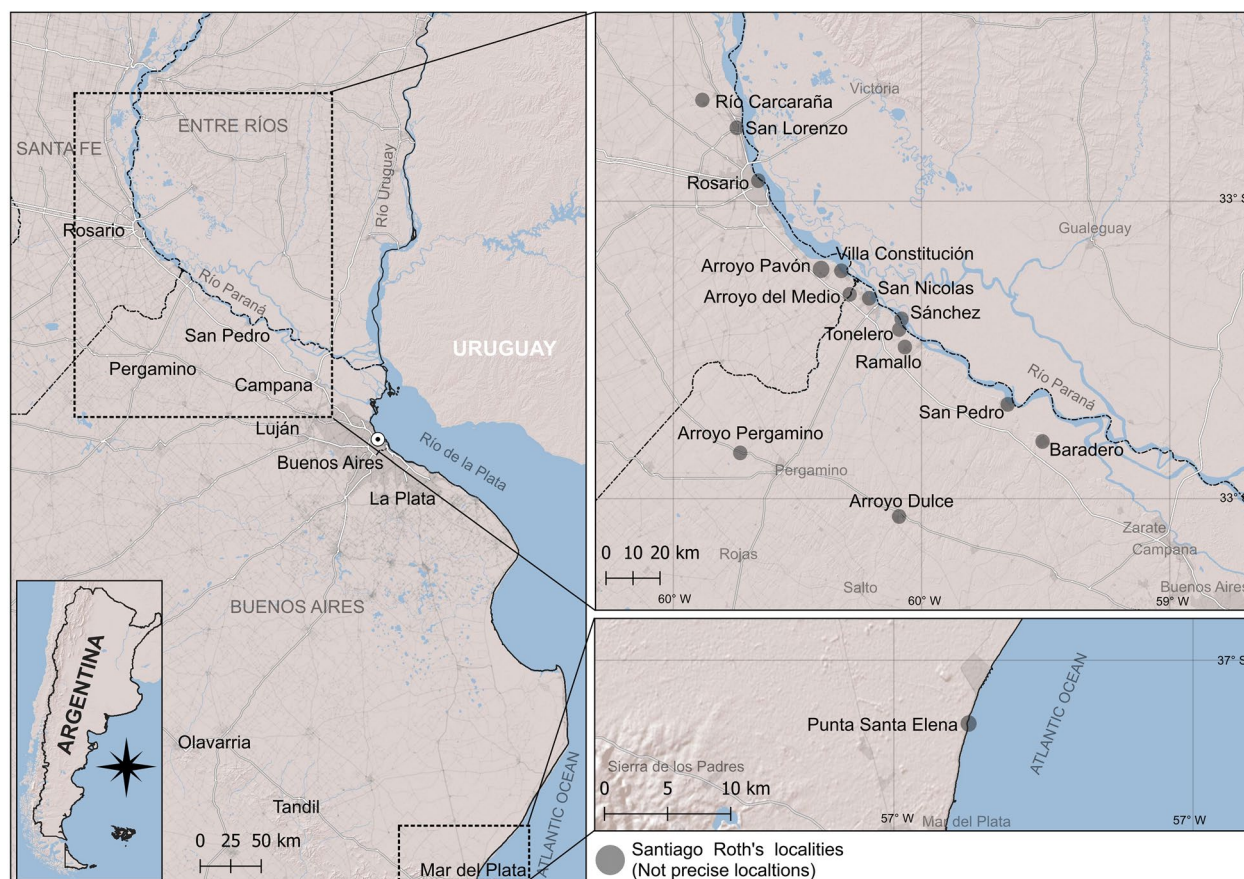
Fig. 1 Map of Pampean fossiliferous localities referred by Santiago Roth in Catalog 5 (Roth, 1889). Localities are not exact. The map was produced with QGIS V.3 3.22.0, with shape obtained from the Instituto Geográfico Nacional, Argentina (www.ign.gob.ar)

Museo de Biología de la Universidad del Zulia, Venezuela; MCNC, Museo de Ciencias de Caracas, Venezuela; MFA, Museo Provincial de Ciencias Naturales "Florentino Ameghino", Santa Fe; MUFYCA, Museo Universitario Florentino y Carlos Ameghino, Rosario, Santa Fe; MLP, Museo de La Plata, Argentina; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMB, Natural History Museum of Basel, Switzerland.

Anatomical abbreviations
Upper premolar (P), lower premolar (p), deciduous premolar (dP/dp), upper molar (M), lower molar (m), upper incisors (I), lower incisors (i), metacarpal (MC), metatarsal (MT).

Geographic context
The specimens studied here come from 19 fossiliferous sites (Additional file 1) located in the Buenos Aires Province and referred to by Roth (1889) as: Arroyo Dulce, Arroyo Pergamino, Ramallo, Baradero, Tolenero, Sánchez, San Nicolás, Punta Santa Elena, San Pedro, and indeterminate localities in the province, and Santa Fe: Arroyo Pavón, San Lorenzo, Villa Constitución, Río Carcarañá, and Rosario. Some of the localities mentioned above were generalized, their name was shortened to optimize space and place names on the map in Fig. 1 (see Additional file 1). The locality "Arroyo del Medio" lies at the border between the Buenos Aires and Santa Fe provinces, but the exact position is unknown. Few specimens do not have a specified locality in catalog 5 (see Additional file 1).

Roth (1889) referred the fossils in catalog 5 as coming from the "Pampéen inférieur", "Interméd/Moyen", and "Supérieur", these being roughly equivalent to Pleistocene deposits of the mammalian stage/ages, upper Ensenadan–Bonaerian, and Lujanian, respectively, based on biozones defined by fossil mammals (Cione & Tonni, 2001; Cione et al., 2015). The locality and stratigraphic origin (according to Roth, 1889) are referred to for each specimen in Additional file 1. For more detailed information on the geology and stratigraphy of the localities mentioned here see Voglino et al. (2023).
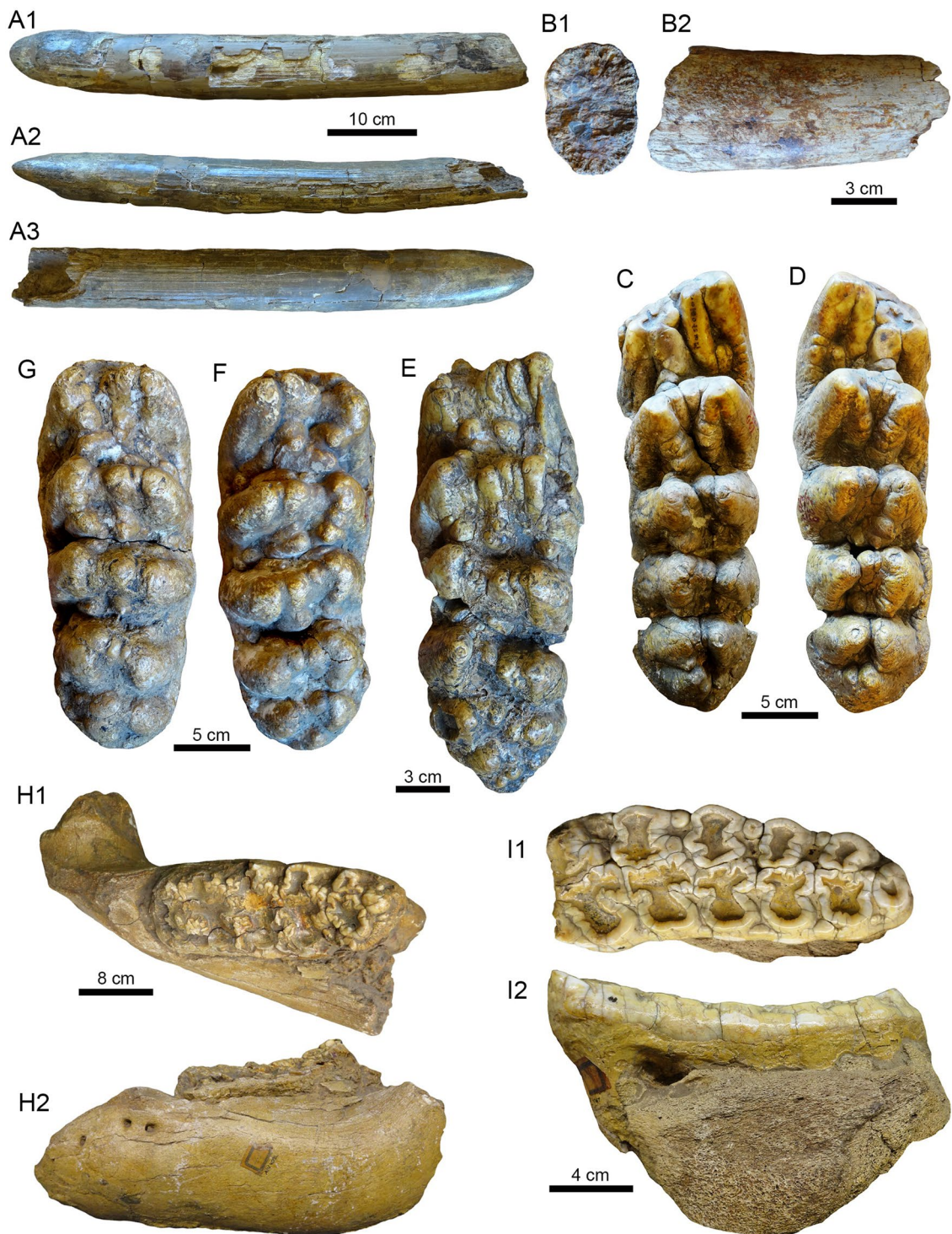
Fig. 2 Gomphotherids cranial remains from the Pampean region. **A1**–**B2**. *Notiomastodon platensis*. **A1**–**A3**. ?right upper task (MHNG GEPI V-3476). **B1**–**B2**. Upper tusk fragment (MHNG GEPI V-3504). **C**–**I2**. *Notiomastodon* cf. *N. platensis*. **C**–**D**. Left (**C**: MHNG GEPI V-3475) and right (**D**: MHNG GEPI V-3473) m3 from the same individual. **E**. Isolated left m3 (MHNG GEPI V-3478). **F**–**G**. Left (**G**) and right (**F**) M3 (MHNG GEPI V-3474) of the same individual. **H1**–**H2**. Left hemimandible fragment with m3 (PIMUZ A/V 4092). **I1**–**I2**. Left m3 (PIMUZ A/V 4161). Views: cross-section (**B1**), dorsal (**A2, H1**), labial (**I2**), left lateral (**H2**), lateral (**A1**, **A3**, **B2**), occlusal (**C**–**G**, **I1**)

Systematic paleontology

Proboscidea Illiger, 1811
Gomphotheriidae Hay, 1922
Notiomastodon Cabrera, 1929a
Notiomastodon platensis (Ameghino, 1888a).
(Fig. 2A1–B2).

Referred material

Two upper tusk fragments (MHNG GEPI V-3476 and MHNG GEPI V-3504). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons

MHNG GEPI V-3476 is a ?right, complete, short and straight not twisted upper tusk of 650 mm in length with and oval cross-section and a maximum diameter of 217 mm (Fig. 2A1–A3). No enamel layers or bands are observed, and superficial parallel folds-like are present along the tusk (Alberdi & Prado, 2022; Mothé et al., 2013). The distal tip of this specimen presents a remarkable wear, characteristic of proboscidean scratching trees and bushes (e.g., Semprebon et al., 2022). The smaller tusk fragment MHNG GEPI V-3504 is approximately 160 mm in length, also straight, oval in cross-section, and with a maximum diameter of 202 mm (Fig. 2B1–B2). This fragment belongs to the most distal part of the tusk, since no trace of roots is visible, and no enamel layers or bands are observed.

Remarks

For more than a century, the taxonomy of proboscideans in South America has been characterized by a long and controversial debate on the total number of genera and species (Alberdi et al., 2002; Alberdi & Prado, 2022; Campbell et al., 2009; Mothé et al., 2012, 2013, 2017a; Mothé & Avilla, 2015; Lucas, 2013; Prado et al., 2005, and references therein). In recent decades consensus has emerged suggesting the validity of only two genera of gomphothere in the southern continent, *Cuvieronius hyodon*, with a distribution restricted to the Andean countries, and *Notiomastodon platensis* (=*Stegomastodon platensis*), with a wide distribution in the continent that goes from the coast to mountainous areas (Alberdi & Prado, 2022; Mothé et al., 2013, 2017a; Mothé & Avilla, 2015). Mainly cranial features have been used to differentiate both genera, and tusks are valuable for these comparisons. In *Cuvieronius* upper tusks are elongated, sub-circular in cross-section, varying between straight to slightly upcurved and markedly twisted with a characteristic enamel band along the tusk body (Mothé et al., 2017a; Lucas, 2013; Mothé et al., 2016). In contrast,

Notiomastodon is characterized by upper tusks with a great morphological variation in length, curvature and robustness (circular to oval in cross-section), but these are never twisted, and the enamel may be absent or present as a single band or covering the entire tusk in juvenile and some adult individuals (Mothé et al., 2017a). According to Mothé et al. (2017a), in *Notiomastodon* the dentin cones that form the internal structure of the upper tusks have no torsion among themselves, a condition found in MHNG GEPI V-3476 and MHNG GEPI V-3504. The features of the tusks described here, including a straight shape with oval cross-section and lack of enamel band/layers, are in accordance with those features that characterized upper tusk of *N. platensis*.

Notiomastodon cf. *N. platensis.*
(Figs. 2C–I2, 3A–D).

Referred material

Lower third molars with fragmented roots and slight wear on first and second lophids that might belong to the same individual, since wear stages are very similar (MHNG GEPI V-3473 and MHNG GEPI V-3475, Fig. 2C–D), fragmented lower left third molar with no wear and no roots (MHNG GEPI V-3478, Fig. 2E), two upper third molars with fragmented roots and no wear that might belong to the same individual (MHNG GEPI V-3474, Fig. 2F–G), fragment of a left mandibular ramus with a third molar with advanced wear stage (PIMUZ A/V 4092, Fig. 2H1–H2), lower left third molar with advanced wear, roots and fragments of mandible (PIMUZ A/V 4161, Fig. 2 I1–I2), lower right third molar with intermediate wear and fragmented third pretrite (MHNG GEPI V-3479, Fig. 3A), lower left third molar with intermediate wear and fragmented at anterolingual border (MHNG GEPI V-3502, Fig. 3B), fragmented upper left first molar with intermediate wear (MHNG GEPI V-3491, Fig. 3C, and -3486), and fragmented lower right first molar missing part of the first lophid, with intermediate wear (MHNG GEPI V-3480). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons

All molars are bunodont with the characteristic double to simple trefoil wear pattern of *Notiomastodon platensis* (i.e., MHNG GEPI V-3502, -3491, -3486, and -3480). The third molars are pentalophodont and have a variable distal cingulum, and those teeth with no wear or intermediate wear show a range from 57 to 64 cups, which is within the *Notiomastodon*'s range of 35 to 82, as described in the literature (Mothé et al., 2017c). For total length of the complete molars see Additional file 1.

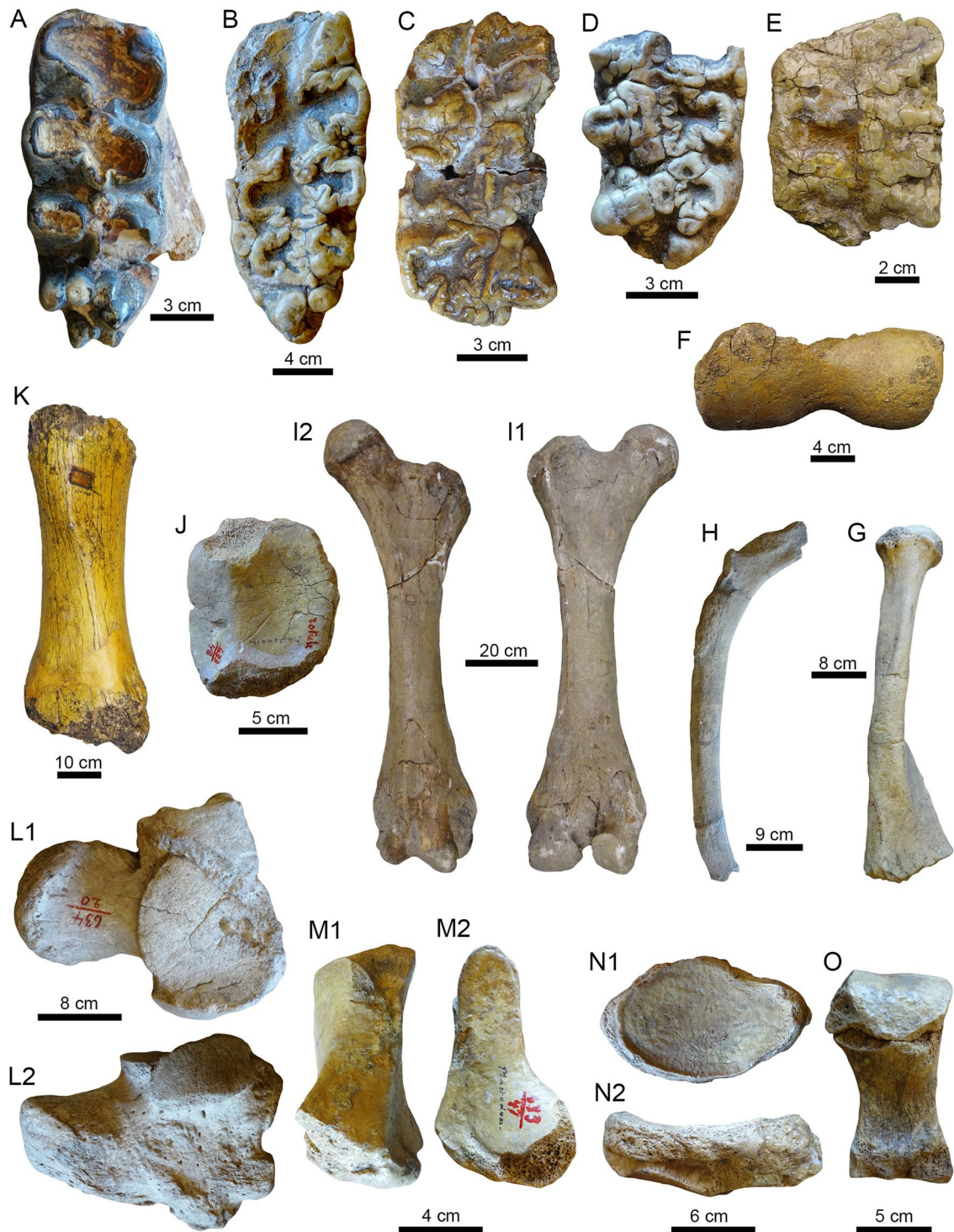**Fig. 3** Gomphotherids cranial and postcranial remains from the Pampean region. **A**–**D**. *Notiomastodon* cf. *N. platensis*; right m3 (**A**: MHNG GEPI V-3479), left m3 (**B**: MHNG GEPI V-3502), left M1 (**C**: MHNG GEPI V-3491), right m1 (**D**: MHNG GEPI V-3480). **E**–**O**. Gomphotheriidae indet. **E**. Molariform of indeterminate position (PIMUZ A/V 4136). **F**. Left distal humerus epiphysis (PIMUZ A/V 4159). **G**. Left radius (MHNG GEPI V-3477). **H**. Right rip fragment (MHNG GEPI V-3499). **I1**–**I2**. Left femur (PIMUZ A/V 4158). **J**. ?right patella (MHNG GEPI V-3490). **K**. Incomplete right tibia (PIMUZ A/V 4160). **L1**–**L2**. Right calcaneous (MHNG GEPI V-3505). **M1**–**O**. Right trapezoid (**M1**–**M2**), left navicular (**N1**–**N2**), and metatarsal III (**O**) (MHNG GEPI V-3494). Views: anterior (**K**, **I2**, **F–H**, **N2**), dorsal (**L1, N1**), right lateral (**L2**), lateral (**M1**), occlusal (**A–E**), plantar (**O**), posterior (**J**, **I1**), ventral (**M2**)

Remarks

Isolated molars are the most common fossils of the South American proboscideans, but unfortunately they are not fully diagnostic for *Notiomastodon* and *Cuvieronius* when isolated and/or fragmented, since most features are variable and overlapping (Mothé et al., 2017b). The total number of cusps in complete and well-preserved third molars has been successfully used to differentiate both genera (Mothé & Avilla, 2015; Mothé et al., 2017c). *Cuvieronius hyodon* presents third molars with a number of cusps ranging from 33 to 60, whereas in *Notiomastodon*, the number of cusps range between 35 and 82 (see Mothé et al., 2017c). As mentioned above, the complete third molars we are describing here show a range from 57 to 64 cusps, which is in the range of *Notiomastodon*. The fragmentary nature of some specimens does not allow access to the complete number of cusps but, since the wear pattern on pretrites and postrites is complex (double–trefoil), it suggests that the number of cusps of some specimens might be higher (e.g., PIMUZ A/V 4092, 4161, MHNG GEPI V-3502). The specimens reported herein are tentatively assigned to *Notiomastodon* cf. *N. platensis*.

Gomphotheriidae indet.
(Fig. 3E–O).

Referred material

Five broken and incomplete teeth with extreme wear (PIMUZ A/V 4105, 4136, 4185, 4279), left distal humerus epiphysis (PIMUZ A/V 4159), left radius (MHNG GEPI V-3477), left femur (PIMUZ A/V 4158), ?right patella (MHNG GEPI V-3490), right tibia (PIMUZ A/V 4160), right calcaneus (MHNG GEPI V-3505), navicular, right trapezoid, ?metatarsal III and ?metacarpal III (MHNG GEPI V-3494), and rib fragment (MHNG GEPI V-3499). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons

PIMUZ A/V 4105 is a fragment of hemimandible with incomplete and fragmented crown of a m2, and an indeterminate tooth fragment in a poor state of preservation. Number PIMUZ A/V 4279 corresponds to an incomplete and extremely worn molar, possibly M2 or m2, and two other molariform fragments of indeterminate position. PIMUZ A/V 4185 is represented by three fragmented and isolated lophs, possibly from the same individual. Specimen PIMUZ A/V 4136 is a broken molar with extreme wear of indeterminate position (Fig. 3E). Postcranial appendicular elements are represented by a left distal epiphysis of a humerus (PIMUZ A/V 4159, Fig. 3F), left radius of 567 mm in length missing the proximal epiphysis (MHNG GEPI V-3477, Fig. 3G), complete

left femur with a total length of 1045 mm (PIMUZ A/V 4158, Fig. 3I1–I2), diaphysis of a right tibia of 445 mm in length (PIMUZ A/V 4160, Fig. 3K), a ?right patella (MHNG GEPI V-3490, Fig. 3J), a complete right calcaneus (MHNG GEPI V-3505, Fig. 3L1–L2), navicular, right trapezoid, ?metatarsal III and ?metacarpal III (MHNG GEPI V-3494, Fig. 3M1–O). A fragmented right rib is the sole element from the axial skeleton (MHNG GEPI V-3499, Fig. 3H).

Remarks

The state of preservation of the dental remains and the lack of diagnostic characters on the postcranial bones (Mothé & Avilla, 2015), do not allow to classify these specimens beyond the family level. There are no detailed morphometric studies on postcranial elements of *Cuvieronius* and *Notiomastodon* that may demonstrate the taxonomic significance of postcranial features. Considering the known geographical distribution of *Notiomastodon* that includes the Pampean region (Alberdi & Prado, 2022; Lucas, 2013; Mothé & Avilla, 2015; Mothé et al., 2017a, b, c), the assignment to this taxon is ultimately likely.

Artiodactyla (Owen, 1848).
Camelidae Gray, 1821
Lama Cuvier, 1800
Lama guanicoe (Müller, 1776).
(Fig. 4A1–A3).

Referred material

An almost complete mandible with both incomplete lower molar series and without coronoid and angular processes and condyle (PIMUZ A/V 4089). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons

The mandible is gracile, broken at the level of both coronoid and angular processes. The dorsal and ventral margins of the horizontal ramus are almost parallel to each other. The lingual surface of the horizontal ramus is flat and the labial side is slightly convex. Both rostral and caudal mental foramina are not observed due to embedded sediment on the bone surface. There are five incisors. Caniniforms are not preserved. The dental formula shows the alveoli of premolars in the third and fourth positions as in *Lama guanicoe* and *Hemiauchenia paradoxa* (Lynch et al., 2020). The right hemimandible has m1–m3, while the left preserving m1–m2 series, being broken at level of the anterior root of the m3 (Fig. 4A2). Occlusal length and width, respectively, are 13 mm and 10 mm in m1, 18 mm and 11 mm in m2, and 23 mm and 10 mm in m3. The right m1–m3 series length is 54 mm. These
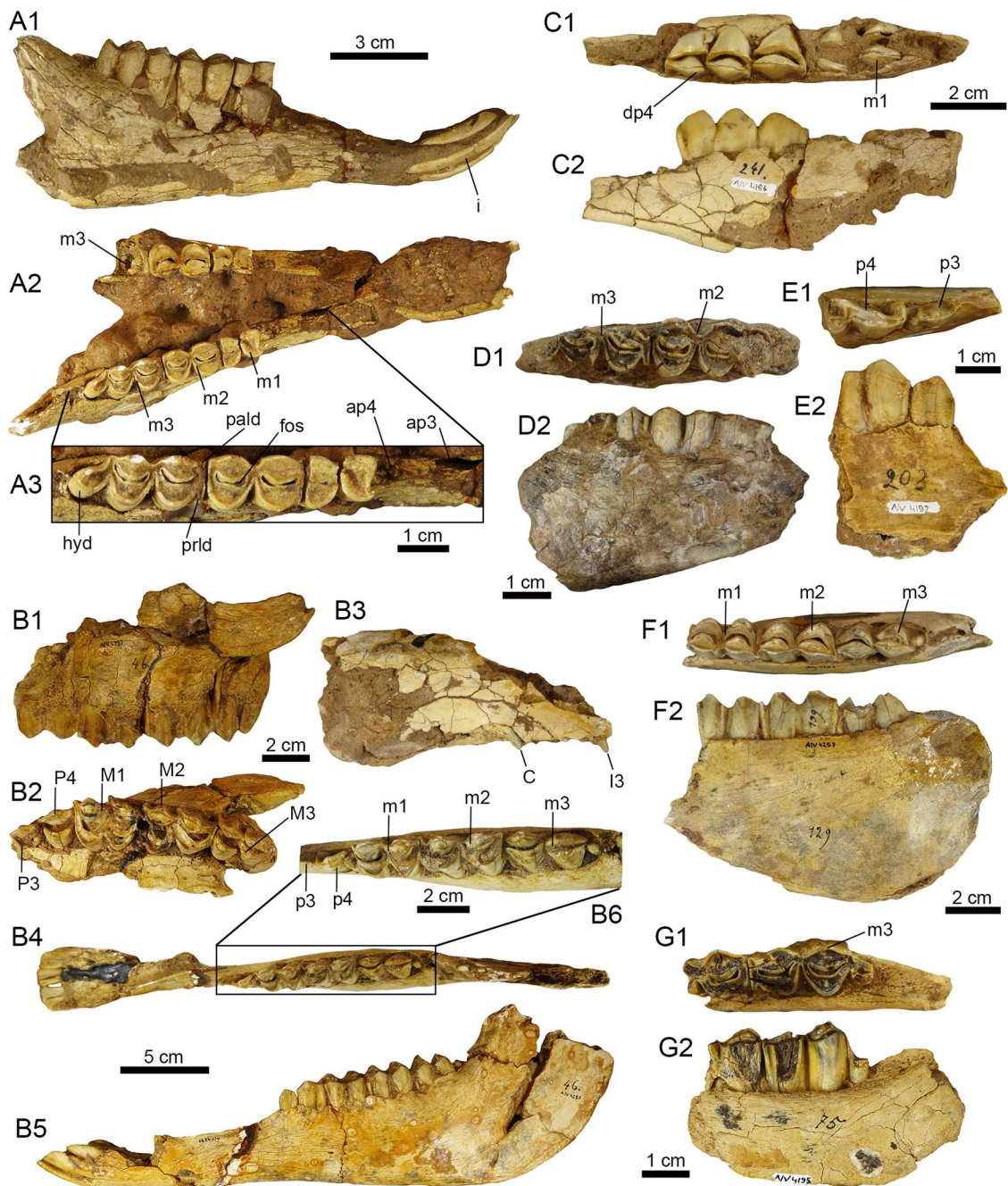
Fig. 4 Camelids cranial remains from the Pampean region. **A1**–**A3**. Mandible of *Lama guanicoe* (PIMUZ A/V 4089). **B1**–**B6**. Left maxilla (**B1**–**B2**), anterior region of the skull (**B3**), and left hemimandible of *Hemiauchenia paradoxa* (PIMUZ A/V 4287). **C1**–**G2**. Hemimandible fragments of *Hemiauchenia* cf. *H. paradoxa* (right: **C1**–**C2**: PIMUZ A/V 4186, **D1**–**D2**: PIMUZ A/V 4187, **E1**–**E2**: PIMUZ A/V 4192, **F1**–**F2**: PIMUZ A/V 4257; left: **G1**–**G2**: PIMUZ A/V 4195). Views: dorsal (**A2**, **B4**), left lateral (**B1**, **B5**, **G2**), lingual (**C2**, **F2**), right lateral (**A1**, **B3**, **D2**, **E2**), occlusal (**A3**, **B6**, **C1**, **D1**, **E1**, **F1**, **G1**), and ventral (**B2**). Canine (c), deciduous premolar (dp), fossa (fos), hypoconulid (hyd), incisors (i), lower molar (m), lower premolar (p), parastylid (pald), premolar alveolus (ap), protostylid (prld), upper molar (M), and upper premolar (P)

selenodont molars are characterized by having well-developed anterior stylids or "Llama buttresses" (protostylids and parastylids), although on m3 these are weakly prominent labio-lingually. The anterior fossa (trigonid

fossa, Scherer et al., 2007) on m1 is not seen due to the advanced wear, making this specimen to correspond to an adult with "wear stage 4" in the classification of Breyer (1977). All fossae are closed, which is more typical of

Camelidae than Cervidae (the latter group has the distal end of the anterior fossetid lingually opened) (Fig. 4A3). The labial lophids are U-shaped (e.g., Gasparini et al., 2017; Scherer et al., 2007), and the second lobe of each molar is set off from the anterior lobe by a pronounced vertical and deep labial flexid. The third lobe (hypoconulid) is smaller and oval in outline (Fig. 4A3).

Remarks
PIMUZ A/V 4089 displays many morphological characters consistent with South American Camelidae (see Lynch et al., 2020; Scherer, 2013). The morphological and morphometric features reported above allow us to assign PIMUZ A/V 4089 to *Lama guanicoe*. The fossil record of *Lama* is known since the Late Pleistocene deposits in Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Peru, and Uruguay (Scherer, 2013; Tonni & Politis, 1980, and references therein). However, according to Wheeler (1995), the records of *Lama* from Ecuador and Colombia need confirmation. *Lama* has been widely recorded from Holocene deposits in the southern region of Argentina, although its record at different sites from the middle and lower Paraná River basin during this time has been questioned (see Politis et al., 2011).

Menegaz and Ortiz Jaureguizar (1995) reported the existence of a fossil *Lama* anatomically indistinguishable from *L. guanicoe* from Pleistocene deposits of the North Pampa (Buenos Aires Province), with dimensions similar to the range of *Hemiauchenia*. Lynch et al. (2020) reported a well-preserved South American Lamini partial skeleton from the Early Pleistocene of Argentina with a new cladistic analysis of the Camelinae subfamily. This specimen (PIMUZ A/V 4165) was also collected by Santiago Roth in the right cliff of the Paraná River, San Nicolás locality (Buenos Aires Province) (Roth, 1889). According to the hypothesized phylogenetic position by Lynch et al. (2020), PIMUZ A/V 4165 is more closely related to *L. guanicoe* and *Vicugna vicugna* than to *H. paradoxa*. On the other hand, some morphological, morphometric and few molecular considerations on *Lama* taxonomy recognize the extinct *Lama gracilis* as a valid Lamini taxon of a gracile vicuña from the Late Pleistocene–Early Holocene of Patagonia and Tierra del Fuego (Menegaz, 2000; Menegaz et al., 1989; Metcalf et al., 2016). Nevertheless, there is no consensus regarding the taxonomic status and phylogenetic context between the living and fossil camelids from South America (see Cajal et al., 2010; Cartajena et al., 2010; Miller, 1924; Stanley et al., 1994; Weinstock et al., 2009). Thus, these hypotheses must be tested by more molecular, morphological and morphometric studies.

At present, two living species of wild Lamini Camelidae have been recognized, *L. guanicoe* and *V. vicugna*, which are restricted to environments with arid to semi-arid conditions from the north-central area of the Andes and Patagonia (8° S to 55° S), and also between altitudes that range from sea level to 4000 m (Baldi et al., 2008; Franklin, 1982; Lichtenstein et al., 2008; Wheeler, 1995).

Hemiauchenia Gervais & Ameghino, 1880
Hemiauchenia paradoxa Gervais & Ameghino, 1880
(Fig. 4B1–B6).

Referred material
Anterior region of the skull and left maxilla with P3–M3, left hemimandible with three pair of lower incisors and p3–m3 from the same individual (PIMUZ A/V 4287). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
Cranial remains including fragmented premaxilla and part of the maxilla preserved up to the area of the infraorbital foramen, with right I3 and a caniniform (Fig. 4B3). The left maxilla shows the P3–M3 series with slight wear and M3 erupting. Both fossetids in M3 are opened (Fig. 4B2). The occlusal length of the molar series is 82 mm. PIMUZ A/V 4287 corresponds to a young-adult camelid (Breyer, 1977). The left hemimandible has three lower incisors (i1–i3) on both sides, a caniniform (that is separated from the incisors by a diastema), and p3–m3 series (Fig. 4B–B6). The occlusal length of the molar series is 105 mm. The lingual surface of the horizontal ramus is flat and the labial side is slightly convex (Fig. 4B4). Both rostral and caudal mental foramina are observed in labial view of the hemimandible. The former is located distally to the caniniform (Fig. 4B5). The left caniniform is preserved and both m3. The p3–m2 series has labial U-shaped lophids with closed fossae (Gasparini et al., 2017; Scherer et al., 2007). The second lobe of each cheek tooth is set off from the anterior lobe by a deep labial flexid. The third lobe (hypoconulid) is smaller and oval in outline. The anterior stylids (protostylids and parastylids) of lower molars are not observable because the teeth are partially inside their alveoli. All dental fossae are closed, with the exception of those in m3, showing both fossetids mesiodistally opened. PIMUZ A/V 4287 corresponds to a young-adult individual with permanent dentition already erupted but almost no wear ("wear stage 1" following Breyer, 1977).

Remarks
Hemiauchenia represents one of the largest Lamini camelids that inhabited South America during the Late Pliocene to Pleistocene (Gasparini et al., 2017; Scherer, 2013). It is known from outcrops mostly of Argentina and Uruguay (Cione & Tonni, 1999; Cione et al., 1999, 2015;

Gasparini et al., 2017; Menegaz & Ortiz-Jaureguizar, 1995; Ubilla, 2004; Ubilla & Perea, 1999). In contrast, *Palaeolama*, has been reported from Early Pleistocene deposits of Bolivia (MacFadden & Shockey, 1997; Marshall et al., 1984), and Late Pleistocene deposits of Bolivia, Brazil, Chile, Ecuador, Paraguay, Peru and Venezuela (Carrillo-Briceño, 2015; Cartelle et al., 1989; Marshall et al., 1984; Scherer, 2013).

López-Aranguren (1930) synonymized *H. paradoxa* to *Hemiauchenia major*, and Cabrera (1932, 1935) and Rusconi (1931) attributed the former taxon to *Palaeolama weddelli*. Later investigations revalidated *H. paradoxa*, although included in another genus: *Palaeolama* (see Hoffstetter, 1952). Webb (1974) and Scherer (2013) considered both *Hemiauchenia* and *Palaeolama* as valid taxa, but suggested that *H. paradoxa* is restricted to Argentina and *H. major* to northeastern Brazil. Nevertheless, some authors considered that the Brazilian forms correspond to *Palaeolama major* (Bergqvist, 1993; Cartelle et al., 1989; Guérin et al., 1990; Souza-Cunha, 1966). Some taxonomic studies suggested that morphological differences between *H. paradoxa* and *P. major* do not support a taxonomic separation, but rather indicate intraspecific variations (Cartelle, 1992, 1999). However, more recently Scherer (2009, 2013) supported the taxonomic validity of both genera for South America, with the recognition of at least three *Palaeolama* species: *P. weddelli*, *P. major*, and *P. hoffstetteri*. In contrast, *H. paradoxa* is considered the only valid species for this genus.

Hemiauchenia cf. *H. paradoxa.*
(Fig. 4C1–G2).

Referred material
Two fragments of right hemimandibles with deciduous dentitions (PIMUZ A/V 4186), right hemimandible body with m1–m3 partially preserved and left hemimandible body with dp4–m2 partially preserved (PIMUZ A/V 4187), right hemimandible with p3–p4 (PIMUZ A/V 4192), left hemimandible body with talonid of m2 and the entire m3 (PIMUZ A/V 4195), right hemimandible body with m2–m3 partially preserved (PIMUZ A/V 4201), two fragments of right and left hemimandibles with deciduous and permanent dentitions (PIMUZ A/V 4200), right hemimandible body with m1–m3 (PIMUZ A/V 4257), isolated m2 (PIMUZ A/V 4127, PIMUZ A/V 4179, A/V 4189), and isolated lower teeth (PIMUZ A/V 4196, PIMUZ A/V 4255). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
PIMUZ A/V 4186 corresponds to two rights hemimandibles with dp4 without wear and erupting m1. The dp4 is similar to teeth of the molariform series with three lobes.

The cusps are still separated and have no wear. The fossetids are mesiodistally opened (Fig. 4C1). PIMUZ A/V 4187 is represented by two fragments of a mandible probably from the same individual. The right hemimandible has the talonid of the m1–m3 partially preserved (Fig. 4D1–D2). The left hemimandible has a dp4 and both trigonids of m1–m2 fractured and cover by carbonate concretions. In this specimen the molars have all fossae closed and labial lophids with U-shaped. Left dp4 is similar to the molariform series, with three lobes. Right m3 shows the characteristic "Llama buttresses". PIMUZ A/V 4192 is a fragment of right hemimandible body with the p3–p4 series (Fig. 4E1–E2). The p3 is transversely compressed and formed by only one lobe; this tooth lacks wear. The p4, with slight wear, has a flexid on both, the labial and lingual sides, defining two lobes. The mesial lobe is mesiodistally elongated, and the distal one is transversely wide.

PIMUZ A/V 4195 is the left hemimandible body with the talonid of m2 and a m3 (Fig. 4G1–G2). The fossae of both molars are closed and the stylids on m3 are developed. The hypoconulid is smaller and oval and lack a fossa. PIMUZ A/V 4200 represents a right and left fragment of hemimandibles with teeth. The right series has the roots of m1 and complete m2–m3. The m3 lacks wear, lacks a hypoconulid, and has a small protostylid, and both fossetids are mesiodistally opened. The left series has dp4–m2. PIMUZ A/V 4201 is a fragment of the right hemimandible preserving the talonid of the m2 in advanced wear stage and the entire m3. No mesial stylids are observed in the m3, while the hypoconulid is smaller and oval in outline, lacking a fossa. PIMUZ A/V 4179, and PIMUZ A/V 4189, 4127, are isolated m2, the first is left, and the second and third are right. Teeth have different wear stages, closed fossae, and developed mesial stylids. PIMUZ A/V 4179 shows a "wear stage 1" with its fossetids lingually opened, suggesting this specimen to be of a young camelid (Breyer, 1977). PIMUZ A/V 4255 corresponds to m1, m2 and m3. Teeth do not preserve roots. PIMUZ A/V 4196 is represented by a left permanent p4 and probably a p3, m1 and m2. These teeth are similar to the molariform series previously mentioned in *H. paradoxa* (PIMUZ A/V 4287; see above). PIMUZ A/V 4257 is a right hemimandible with m1–m3 (Fig. 4F1–F2). The teeth have fossae closed, although fossetids on m3 are erupted and mesiodistally opened. Lingual stylid (protostylid) is presented in all molars and is lingually well developed, while the parastylid is only preserved on m1 and being more evident in the m2 (Fig. 4F1).

Remarks
No diagnostic characters have been observed in the lower deciduous teeth of South American camelids (e.g., Cabrera, 1932, 1935; Rusconi, 1931; Webb, 1974).
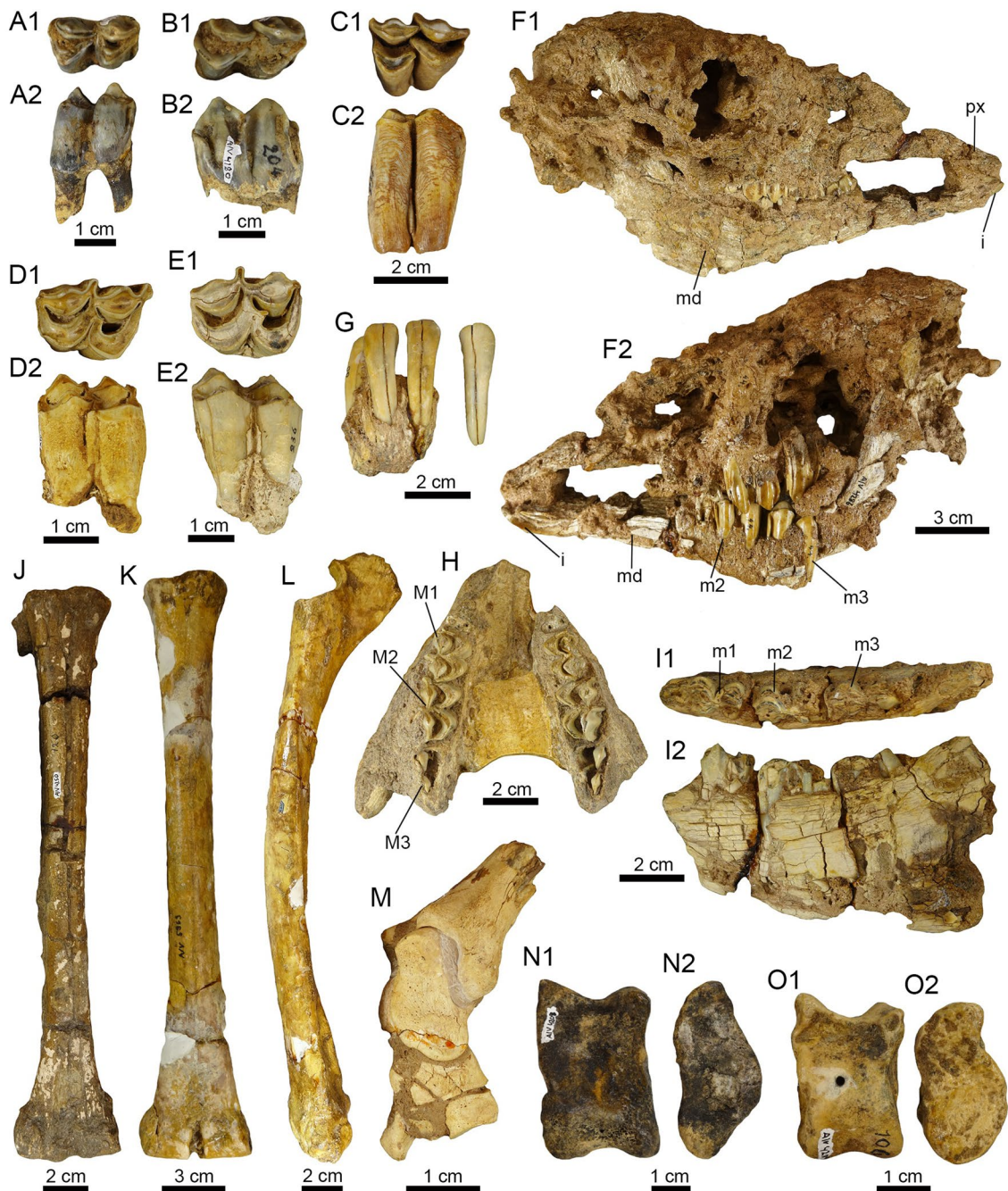
Fig. 5 Camelids cranial and postcranial remains from the Pampean region. **A1**–**E2**. Isolated upper teeth of cf. *Hemiauchenia* sp. (**A1**–**B2**: PIMUZ A/V 4205; **C1**–**C2**: PIMUZ A/V 4182; **D1**–**D2**: PIMUZ A/V 4098; **E1**–**E2**: PIMUZ A/V 4181). **F1**–**O2**. Camelidae Indeterminate. **F1**–**F2**. Skull and mandible with teeth of a young camelid (PIMUZ A/V 4286). **G**. Fragment of maxilla with four incisors (PIMUZ A/V 4253). **H**. Both premaxilla (PIMUZ A/V 4256). **I1**–**I2**. Fragment of maxilla with dentition (PIMUZ A/V 4253). **J**. left metacarpal (PIMUZ A/V 4250). **K**–**L**. Right metacarpal (**K**) and right radius-ulna (**L**) (PIMUZ A/V 5969). **M**. distal end of left tibia with astragalus, navicular and cuboid (PIMUZ A/V 4090). **N1**–**O2**. Left astragali (PIMUZ A/V 4208). Views: anterior (**G**), dorsal (**J**–**K**, **N1**, **O1**), labial (**A2**, **C2**), lingual (**B2**, **D2**, **E2**), medial (**L**, **N2**, **O2**), occlusal (**A1**, **B1**, **C1**, **D1**, **E1**, **I1**), left lateral (**F2**, **I2**, **M**), right lateral (**F1**), and ventral (**H**). Incisors (i), lower molar (m), mandible (md), premaxilla (px), and upper molar (M)

The specimens referred above are tentatively attributed to *Hemiauchenia* cf. *H. paradoxa*, because they have a similar size and similar dental morphology as shown by *H. paradoxa* from Pleistocene deposits of Argentina and Brazil (Scherer et al., 2007; Vezzosi et al., 2019).

cf. *Hemiauchenia* sp.
(Fig. 5A1–E2).

Referred material
Isolated molars likely M1? or M2? (PIMUZ A/V 4098, 4103, 4180, 4181, 4182). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
The material is represented by four left (PIMUZ A/V 4103, 4180, 4182), and one right (PIMUZ A/V 4181) likely M1 or M2, characterized by different wear stages (Fig. 5A1–E2). The mesial lobe is larger than the distal one, with very large stylids (metastyle, parastyle and mesostyle), and with a deeper fossa of the trigon.

Remarks
These molars have a size similar to those of *Hemiauchenia* (Cabrera, 1935; Scherer et al., 2007) and with U-shaped lingual lophs differing from those in the teeth of *Palaeolama major* which are V-shaped (see Scherer et al., 2007; Webb, 1974). According to a study based on North American specimens, the shape of the lophs is a generic difference between *Hemiauchenia* and *Palaeolama* (Webb, 1974). Larger samples of South American camelids are needed to test this generic difference among others dental characteristics observed in the upper dentitions.

Camelidae indet.
(Fig. 5F1–O2).

Referred material
The remains include four lower incisors, fragment of maxilla and right hemimandible, both with dentition (PIMUZ A/V 4253), badly preserved skull, mandible and dentition of a young camelid (PIMUZ A/V 4286), fragment of a mandible and both premaxilla (PIMUZ A/V 4256), 75 isolated molariforms (PIMUZ A/V 4254), and isolated and fragmentary hemimandible, symphysial bone and six incisors and molariform teeth (PIMUZ A/V s/n and no geographic context; see Additional file 1). Postcranial remains include a left eroded metacarpal (PIMUZ A/V 4250), distal end of left tibia with astragalus, navicular and cuboid (PIMUZ A/V 4090), right radius-ulna and right metacarpal, probably from the same individual (PIMUZ A/V 5969), three eroded astragali, a navicular and a podial phalanx (PIMUZ A/V 4208).

Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
The left fragment of maxilla of PIMUZ A/V 4253 has the M1–M3 series with the M1 completely covered by carbonate concretions. The lower dentition has right i1–i2 and left i1–i2 (this last incisor is isolated) (Fig. 5G). The right hemimandible body has the distal root of p4 and m1–m2 out of their sockets, while m3 is in eruption (Fig. 5I1–I2). All molars have similar size to that of a large camelid, although the occlusal surfaces are fractured or covered by carbonates that make them inaccessible for comparisons. The skull PIMUZ A/V 4286 presents a morphology and dimensions of a small camelid as *Lama*. However, the carbonates adhered to this specimen make impossible to recognize diagnostic features. The maxilla and the mandible in this specimen do not present diagnostic elements for a generic assignment. PIMUZ A/V 4254 is represented by numerous upper and lower teeth (N° 75) of different sizes attributed to Camelidae, and its state of preservation does not allow more accurate determinations. The left metacarpals III and IV under the number PIMUZ A/V 4250 (Fig. 5J) are fused to each other, except at the distal end, as is seen in camelids. PIMUZ A/V 4090 is represented by a distal end of left tibia articulated with astragalus, navicular, and cuboid; the covering by carbonates (Fig. 5M) impedes an assignment beyond the family level. PIMUZ A/V 5969 is a partially damaged right radius-ulna (Fig. 5L), and right metacarpal (Fig. 5K). PIMUZ A/V 4208 is represented by three eroded astragali (Fig. 5N1–O2), a navicular and a podial phalanx. Two of three astragali resemble in size that of a small camelid, such as *Lama guanicoe*, while the larger has a morphology and size that resembles *Hemiauchenia* (Scherer et al., 2007). Both navicular and podial phalanx do not allow a more precise determination.

Remarks
A specific assignation of the above specimen is not possible due to its poor preservation and/or lack of diagnostic characters.

Tayassuidae Palmer, 1897
Tayassu Fischer von Waldheim, 1814
Tayassu pecari (Link, 1795).
(Fig. 6A1–A2).

Referred material
Left hemimandible fragment with the root of m2 and m3 mostly complete (PIMUZ A/V 4188). Geographic data of the specimens are provided in Additional file 1.
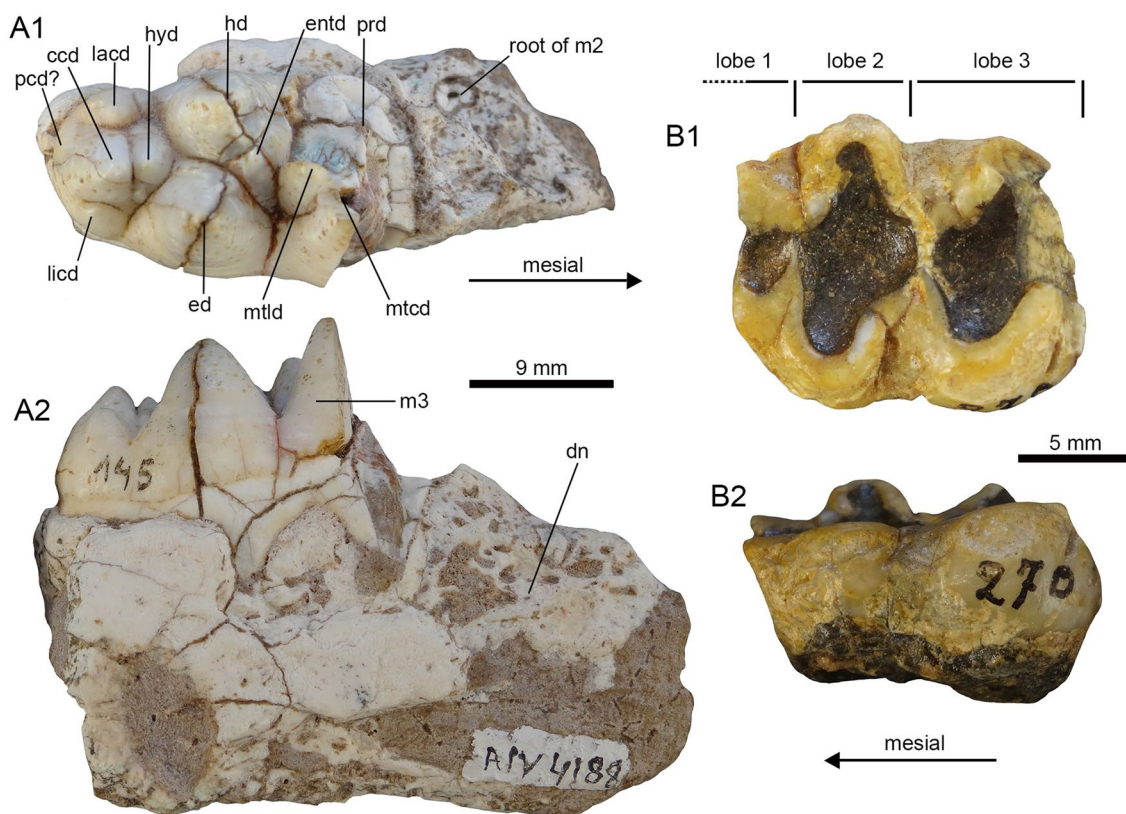
Fig. 6 Tayassuidae remains from the Pampean region. **A1**–**A2**. Left hemimandible fragment with root of m2 and m3 mostly complete (PIMUZ A/V 4188). **B1**–**B2**. Left/right? deciduous p4 (PIMUZ A/V 5258). Views: labial/lingual (**B2**), lingual (**A2**), occlusal (**A1**, **B1**). Central conulid (ccd), dentary (dn), entoconid (ec), entoconulid (entd), hypoconid (hd), hypoconulid (hyd), lateral conulid (lacd), lingual conulid (licd), metaconid (mtcd), metaconulid (mtld), posterior conulid (pcd), and protoconid (prd)

Description and comparisons

PIMUZ A/V 4188 is a fragment of the left hemimandible with the last root of m2 and a m3 mostly complete. The tooth is brachydont and bunodont, preserving three main sharp cusps with slight wear: metaconid mesially, separated by a valley from the hypoconid, and entoconid distally (Fig. 6A1). The molar is broken at the level of the protoconid and consequently we were unable to check the presence of a crenulated cingulid (e.g., Gasparini, 2007). The first pair of anterior cusps (metaconid and protoconid) are partially broken, although both together are slightly wider than the posterior pair (hypoconid and entoconid), which is well preserved (Fig. 6A1). Behind both lobes, there is a third lobe with complex configuration in which four cusps with different size are seen, as in *Tayassu pecari* (see Gasparini, 2007; Parisi Dutra et al., 2017). Following Gasparini (2007) and Parisi Dutra et al. (2017), PIMUZ A/V 4188 falls in the size range of *T. pecari*, with a mesio-distal length of 22 mm and a linguo-labial width of 12 mm. This m3 is elongated mesiodistally, with subrectangular outline due to the presence of the third cuspidate lobe that forms distally a complex hypoconulid (Frailey & Campbell, 2012).

Remarks

Following Gasparini (2007) and Parisi Dutra et al. (2017), the configuration of the m3 reported here is clearly different from that of *Brasilochoerus* spp., *Parachoerus wagneri*, *Tayassu tajacu*, and *Platygonus* spp. (with the exception of *Platygonus chapadmalensis*), because these tayassuids have a simple third lobe (with an unique dominant cusp; see Gasparini, 2007), sometimes accompanied by a pair of smaller cusps (Frailey & Campbell, 2012; Gasparini & Ferrero, 2010).

Tayassuidae is among the earliest groups of mammals that entered South America during the GABI (Woodburne, 2010). Their extensive fossil record is associated with Late Cenozoic deposits in Argentina, Brazil, Uruguay, Bolivia, Colombia, Peru and Venezuela (Gasparini, 2013; Montellano-Ballesteros et al., 2014; Parisi Dutra et al., 2017, and references therein). The exact moment of its first arrival is controversial, with estimated dates ranging between about 3.7 and 3.1 Ma (see Cione et al., 2007, 2015; Woodburne, 2010). According to the fossil record, the diversity and abundance of tayassuids in South America are greater during the Pleistocene than Pliocene and Holocene (Gasparini, 2013). Moreover, the larger diversity and

abundance of fossil species of tayassuids in South America is concentrated in Argentina (Gasparini, 2013), where, according to Gasparini (2007), three genera with twelve species of Tayassuidae were recognized. Peccaries experienced a remarkable decrease in diversity near the Pleistocene–Holocene boundary (Gasparini, 2013), and only two genera (*Parachoerus* and *Tayassu*) and three species are living today (Gasparini, 2013; Parisi Dutra et al., 2017). Among these, the white-lipped peccary *Tayassu pecari* is widely distributed across the Neotropical region, from northern Argentina to southeastern Mexico (Bustos et al., 2019; Gasparini et al., 2014). Despite its large range of distribution and fossil record in South America (Gasparini, 2013; Montellano-Ballesteros et al., 2014), its past occurrence is scarce and restricted to the Middle Pleistocene–Holocene of the Buenos Aires, Corrientes, Misiones, Santa Fe, and Santiago del Estero (Gasparini, 2013; Gasparini et al., 2014). Some morphological features in *T. pecari* are likely associated with the humid climate conditions and woodland environments that they inhabited (Gasparini et al., 2014). However, *Tayassu pecari* occupied an extensive geographic range and must have had wide ecological tolerances, making it difficult to predict the habitats where it lived (Parisi Dutra et al., 2017; Bustos et al., 2019).

Tayassuidae indet.
(Fig. 6B1–B2).

Referred material
Left/right? dp4 with at least two lobes (PIMUZ A/V 5258). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
PIMUZ A/V 5258 is a deciduous bunodont and brachydont dp4, with advanced wear of the occlusal surfaces of their lobes, indicating that the specimen belongs to a young adult individual. Molarization in PIMUZ A/V 5258 is evident as occurs in the deciduous premolars of fossil and living Tayassuidae (Frailey & Campbell, 2012; Gasparini, 2007; Gasparini et al., 2011). Because of wear, it is rather difficult to describe in detail the tooth morphology (e.g., principal and accessory cusps) of PIMUZ A/V 5258.

Remarks
A systematic allocation for this isolated tooth (PIMUZ A/V 5258) is doubtful due to its incomplete preservation.

Cervidae Goldfuss, 1820
Morenelaphus Carette, 1922
Morenelaphus sp.
(Fig. 7A1–A3).

Referred material
An incomplete left antler (PIMUZ A/V 4162). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
PIMUZ A/V 4162 consists of a long and complex incomplete left antler (Fig. 7A1–A3). The preserved portion of antler shows the mean beam, fragmented anteriorly near the second ramification and with a rounded cross-section (Carette, 1922; Kraglievich, 1932). Additionally, the second and third ramifications are directed forward, while the mean beam is backward. The second and third ramifications form an angle of approximately 45 degrees at the intersection of their axes. The antler is twisted on its own axis and has longitudinal grooves slightly marked along the external surface, following the torsion of the antler.

Remarks
According to Ameghino (1888b) and Alcaraz (2010), the mean beam in *Morenelaphus* is clearly curved backwards after the third ramification, as it is observed in PIMUZ A/V 4162. Traditionally, antlers have been used as diagnostic structures for different taxonomic levels within fossil Cervidae from South America (Alcaraz, 2010; Ameghino, 1888b; Kraglievich, 1932). Some other studies have used other structures for taxonomical purposes (Orcesi et al., 2019; Pêgo, 2014; Vezzosi, 2015; Vezzosi & Chimento, 2021). PIMUZ A/V 4162 is a fragment of antler without any other structure associated, which does not allow an assignment beyond *Morenelaphus* sp.

Morenelaphus is recognized by its long and huge antlers (e.g., Ameghino, 1888b; Cabrera, 1929b; Carette, 1922). Two species were described from Pleistocene deposits of Pampean region of Argentina: *Morenelaphus brachyceros* and *Morenelaphus lujanensis*. The systematic distinction of both species is supported solely by the morphology of its antlers (Alcaraz, 2010; Ameghino, 1888b; Cabrera, 1929b; Gervais & Ameghino, 1880; Menegaz, 2000); although some cranial and dental features help to differentiate these fossil forms (Chimento et al., 2019; Rotti et al., 2021; Vezzosi & Chimento, 2021; Vezzosi et al., 2020). The fossil record suggests that both *Morenelaphus* species belong to different biochronologic intervals within the Pleistocene (Alcaraz, 2010; Cassini et al., 2016). *Morenelaphus* was considered a typical extinct deer from Pampean lowlands of Argentina, Uruguay, and southern to northern Brazil (Cassini et al., 2016; Chimento et al., 2019; Ferrero et al., 2007; Kraglievich, 1932; Rotti et al., 2021; Ubilla & Martínez, 2016; Vezzosi et al., 2019). Some studies suggest grasses were the most frequent element in the diet of *Morenelaphus* (Rotti
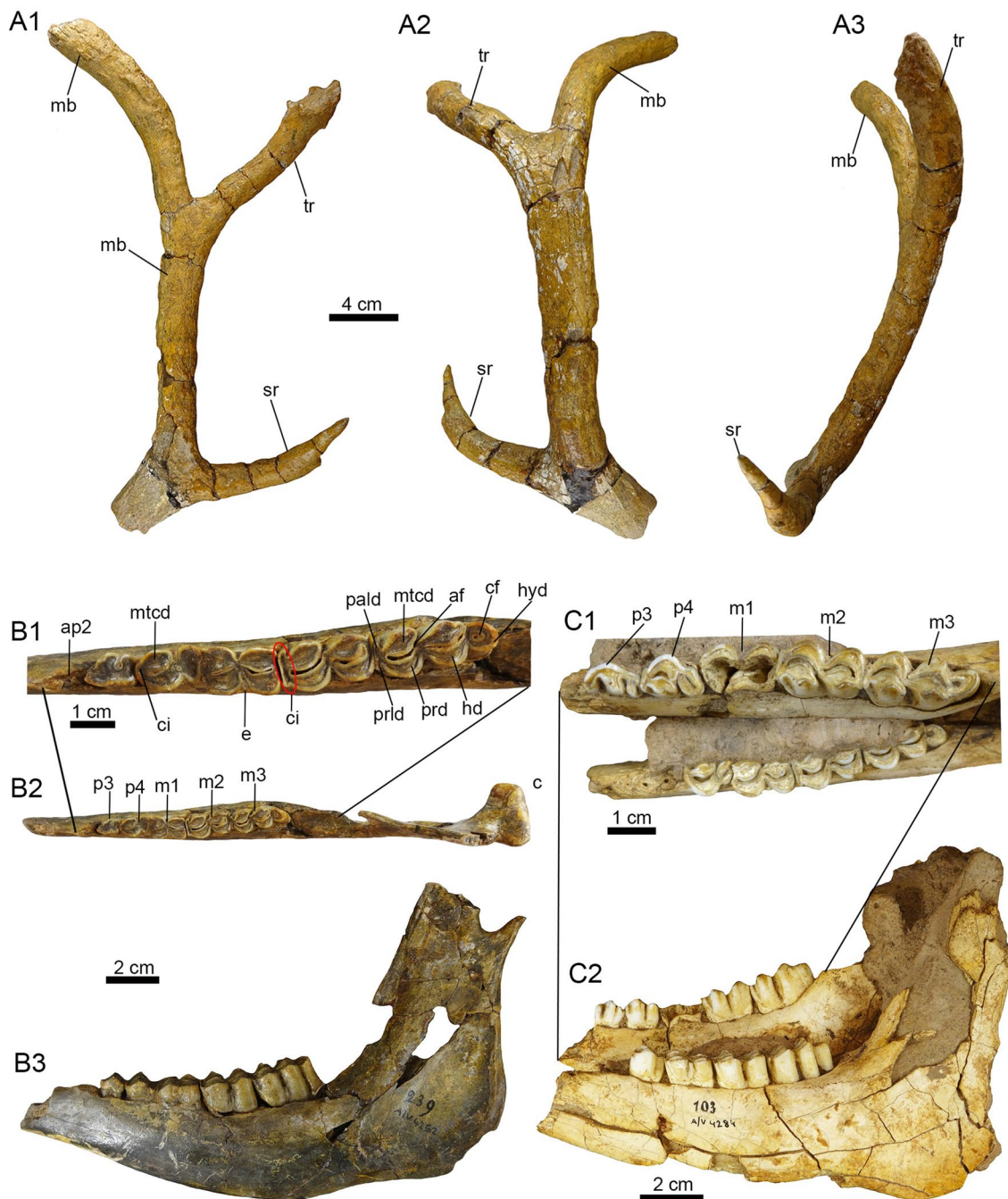
Fig. 7 Cervid remains from the Pampean region. **A1**–**A3**. Incomplete left antler of *Morenelaphus* sp. (PIMUZ A/V 4162). **B1**–**C2**. A left hemimandible (**B1**–**B3**: PIMUZ A/V 4252), and a mandible (**C1**–**C2**: PIMUZ A/V 4284) of Cervidae indeterminate. Views: anterior (**A3**), dorsal (**B2**), lateral (**A2**), left lateral (**B3**, **C2**) medial (**A1**), occlusal (**B1**, **C1**). Anterior fossetid (af), cingulid (ci), circular fossa (cf), ectostylid (e), hypoconid (hd), hypoconulid (hyd), (lower molar (m), lower premolar (p), mean beam (mb), metaconid (mtcd), parastylid (pald), premolar alveolus (ap), protoconid (prd), protostylid (prld), second ramification (sr), and third ramification (tr)

et al., 2018), although Tomassini et al. (2020), suggested more browser feeding preferences.

Cervidae indet.
(Fig. 7B1–C2).

Referred material
Left hemimandible with alveoli of p2 and p3–m3 series (PIMUZ A/V 4252), and mandible with left p4–m3 series and root of p2–p3, and right dentition with p3–m3 series (PIMUZ A/V 4284). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
PIMUZ A/V 4252 is a left hemimandible partially preserved with p3–m3 series and the alveoli of a p2 (Fig. 7B1–B3). Teeth do not show an advanced wear stage (Fig. 7B1). The occlusal length of the molar series is 61 mm. PIMUZ A/V 4284 preserves both hemimandibles (Fig. 7C1–C2). The left dentition has the p4–m3 series and root of both p2–p3, while the right dentition preserves the p3–m3 series, but its m1 is lingually broken. The length of the right m1–m3 series is 51 mm, and the left one is 52 mm. Teeth are bunoselenodont; most of cusps are differentiated, although well-developed cristids are present. Both mandibles are robust with a diastema shorter than that of any living South American deer.

Remarks
The dentition of PIMUZ A/V 4252 and PIMUZ A/V 4284 have a premolar–molar series with six teeth as in Cervidae (Heckeberg, 2020), in contrast to five present in Camelidae (Lynch et al., 2020). The presence of a short diastema is a morphological character that has been considered diagnostic of *Morenelaphus* (Alcaraz, 2010; Chimento et al., 2019; Menegaz, 2000; Pêgo, 2014). Pêgo (2014) reported, in the molars of *Morenelaphus*, a U-shaped morphology in the labial section where the protoconid and hypoconid are present; while living Odocoileini (*Blastocerus*, *Odocoileus*, *Ozotoceros*, *Subulo*, *Pudu*, and *Hippocamelus*) have a V-shaped section. The U-shape form is observed in the dentitions of both specimens PIMUZ A/V 4252 and PIMUZ A/V 4284 (Fig. 7B1, C1). However, mandibular remains with teeth associated to skulls with dentitions and/or antlers in *Morenelaphus* are unknown (Vezzosi, 2015; Vezzosi & Chimento, 2021). Moreover, a short diastema is not possible to be recognized in PIMUZ A/V 4252 and PIMUZ A/V 4284, and other specimens of the genus as suggested by Chimento et al. (2019). In fact, the length of the diastema is highly variable during ontogeny in living deer and must be tested in a large comparative framework between South American species. In PIMUZ A/V 4252 and PIMUZ A/V

4284, the dentition, in occlusal view, is subparallel and positioned at the level of the m2–m3 with a more lingual projection in the hemimandible, while in the Camelidae (*Hemiauchenia paradoxa*, *Lama guanicoe*, and *Palaeolama major*) the cheek molars are positioned parallel with a labio-lingual direction to the hemimandible (Lynch et al., 2020; Scherer et al., 2007). The anterior fossetid opens at the mid-lingual portion of the trigonid in p4–m3 (e.g., Fig. 7B1). There is no vestige of a back fossetid in m1 and m2; however, in m3 this fossetid opens lingually. The hypoconulid is large and with a rounded-shape. There is a circular fossa (Fig. 7B1). In South American Camelidae molariforms are smaller with an oval/suboval shape and without a fossa. An anterior cingulid is recognized in p4, although weakly developed. We do not see an anterior cingulid in m1, due to preservation and wear stage. The metaconid is the largest cups of the p4 trigonid. The m3 has the metaconid with pronounced protostylid and parastylid, an uncommon feature among Pleistocene South American Camelidae (Scherer et al., 2007). According to Heckeberg (2020), ectostylids are variably present from one to three in the lower molars of Cervidae. Those are never high, and are affected by advanced wear in aged individuals. Here an ectostylid in the m1 is observed (Fig. 7B1). We do not rule out that PIMUZ A/V 4252 and PIMUZ A/V 4284 could belong to either *Morenelaphus* or another American deer, since our comparisons do not allow to offer a more specific determination. It is necessary that these characteristics could be revised and tested in a broader comparative and phylogenetic framework to establish affinities with extant or extinct South American deer.

Perissodactyla Owen, 1848
Equidae Gray, 1821
Hippidion Owen, 1869
Hippidion principale (Lund, 1846).
Hippidion cf. *H. principale*
(Fig. 8A1–B2).

Referred material
A fragmented skull, ?right talus articulated with the central tarsal bone, and a left first phalanx from the same individual (PIMUZ A/V 4100). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
PIMUZ A/V 4100 is an incomplete skull preserved only in its ventral side (Fig. 8A1). The premaxilla bears the left I3, and both maxillae have canines and the complete right and left dental series P1–P4 and M1–M3. With the exception of P1, premolars and molars are robust and square-like in shape; premolars being larger than molars
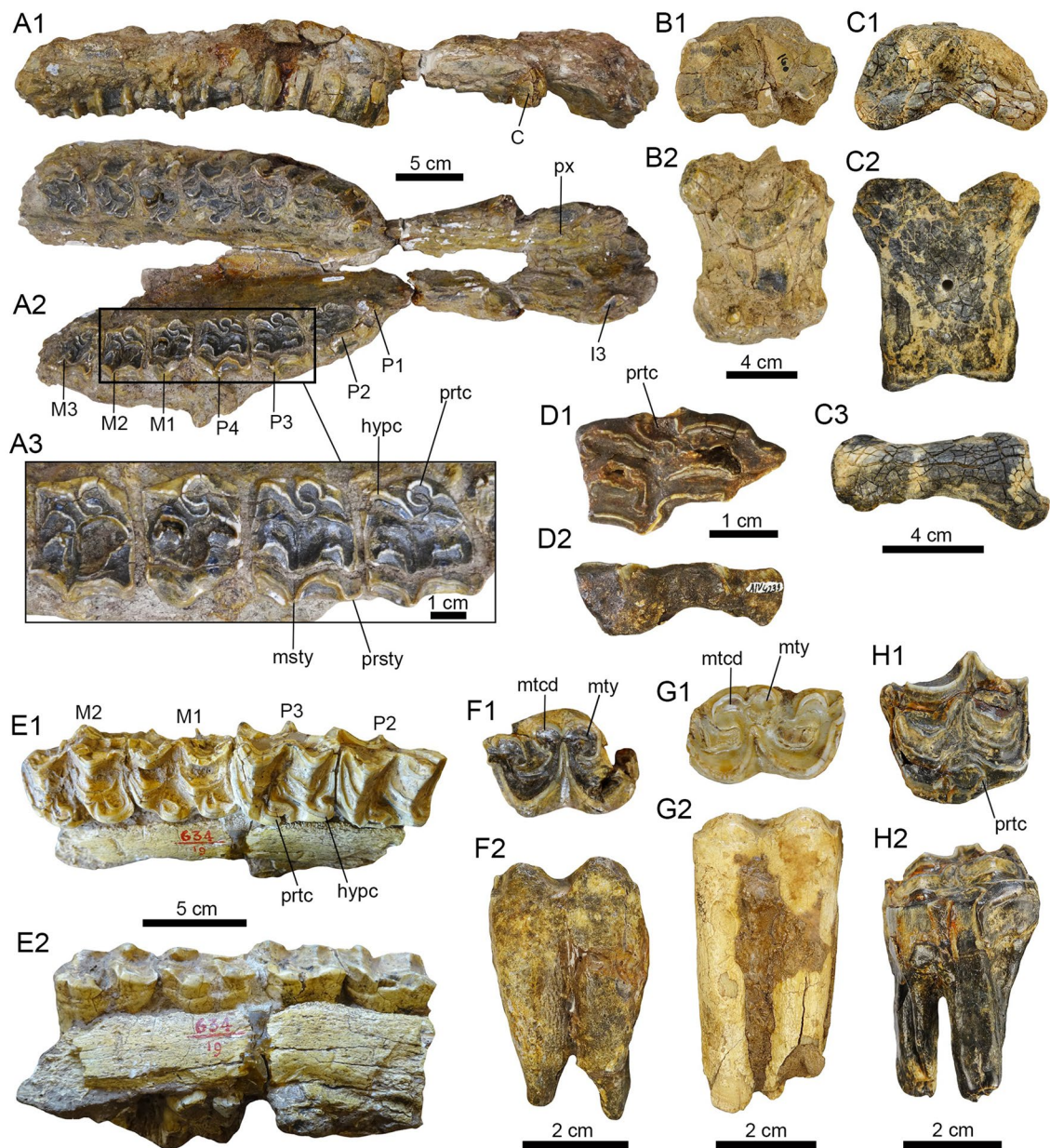
Fig. 8 Equids from the Pampean region. **A1**–**B2**. *Hippidion* cf. *H. principale* (PIMUZ A/V 4100); fragmented skull in ventral view (**A1**–**A3**), and left first phalanx (**B1**–**B3**). **C1**–**H2**. *Hippidion* sp.; left first phalange (**C1**–**C3**: PIMUZ A/V 4205), deciduous left P2 (**D1**–**D2**: PIMUZ A/V 4239), left maxillary fragment with molariforms (**E1**–**E2**: MHNG GEPI V-3779), and isolated lower right p3 or p4 (**F1**–**F2**: PIMUZ A/V 4220), lower left p3 or p4 and (**G1**–**G2**: PIMUZ A/V 4197), and left ?M2 (**H1**–**H2**: PIMUZ A/V 4198). Views: labial (**D2**, **F2**, **G2**), lateral (**C3**), lingual (**E2**, **H2**), palmar/plantar (**B2**, **C2**), right lateral (**A1**), occlusal (**A3**, **D1**, **E1**, **H1**, **G1**), proximal (**B1**, **C1**), and ventral (**A2**). Canine (c), hypocone (hypc), incisors (i), mesostyle (msty), metaconid (mtcd), metastylid (mty), parastyle (prsty), premaxilla (px), protocone (prtc), upper molar (M), and upper premolar (P)

(Fig. 8A2–A3). Occlusal length ranges approximately between 45 and 33 mm in premolars, and between 29 and 33 mm in molars. The right M1–M3 series length is 92 mm, and the left is 94 mm. The total length of the right series P1–M3 is 216 mm, and the left is 217 mm. The wear on the premolars and molars is not advanced,

allowing a clear observation of the dental morphology, which is characterized by oval to rounded protocone, a hypocone with angular/subtriangular shape, and a more pronounced parastyle than the mesostyle. The pre/postfossettes are visible only in the M1. Other cranial/postcranial elements of presumably the same individual

include two skull fragments in a poor state of preservation, a ?right talus in fragmentary condition and articulated with the central tarsal bone, and a first left phalanx of the third digit of 85 mm in length (Fig. 8B1–B2).

Remarks

According to Alberdi et al., (2005, 2006) the dentition of *Hippidion* is characterized by an oval to rounded protocone, character that is present in PIMUZ A/V 4100. *Hippidion* is considered an endemic genus from South America with a biochron spanning from the Pliocene to the Late Pleistocene (Prado & Alberdi, 1996). Three species have been recognized, (1) *Hippidion principale*, being the most robust species and the best known from the Argentinian Pampa, and with possible reports from Peru and Ecuador; (2) *Hippidion devillei*, which is an intermediate size species, with a fossil record throughout the central Andes of Peru and the Argentinian Pampa (although it may have reached as far north as Venezuela, see Labarca et al., 2021); and (3) *Hippidion saldiasi*, which is the smallest species, restricted to Late Pleistocene deposits from the Patagonian region and some localities further north in Chile (see Alberdi & Prado, 1993; Labarca et al., 2021; Prado & Alberdi, 2017). *Hippidion saldiasi* is a species named by Roth, 1899 (original nomination *Onohippidium saldiasi* Roth, 1899). The differentiation between the *Hippidion* species combines an analysis of the skull and metapodial characters, with emphasis in the size and proportions of the appendicular bones (Alberdi & Prado, 1993; Alberdi et al., 1995; Prado & Alberdi, 2017). PIMUZ A/V 4100 has dental characters similar to those of *H. principale* referred from Argentina, Brazil, and Tarija in Bolivia (e.g., Alberdi et al., 2001b, 2003, 2006; MacFadden, 1997; Prado et al., 2012, 2013). The dimension of the M1–M3 series and total length of the P1–M3 series in PIMUZ A/V 4100 fit the range of length variability of *H. principale*. An assignment of PIMUZ A/V 4100 to the largest *Hippidion* species, *H. principale*, seems likely.

Hippidion sp.
(Fig. 8C1–H2).

Referred material

Left maxilla with four molariforms and two ?right isolated molariforms (MHNG GEPI V-3779), two right M3 (PIMUZ A/V 4115, 4238), left dP2 (PIMUZ A/V 4239), left ?M2 (PIMUZ A/V 4198) and left M3 (PIMUZ A/V 4222), right p3 or p4 (PIMUZ A/V 4220), left p3 or p4 and (PIMUZ A/V 4197), and p2 or p3 (PIMUZ A/V 4219), right m3 (PIMUZ A/V 4240), and left first phalanges (PIMUZ A/V 4205). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons

The left maxilla MHNG GEPI V-3779 (Fig. 8E1–E2) preserves four molariforms (P3–M2) in addition to two isolated right P3 or P4, and M1 or M3, likely from the same individual. Occlusal length in the maxillary molariforms ranges approximately between 32 and 33 mm in premolars, and between 30 and 31 mm in molars. The premolars exhibit fossettes and a prominent sub-elliptical protocone (Fig. 8E1). The other isolated upper premolars and molars (PIMUZ A/V 4115, 4198, 4222, 4238–39; see Fig. 8D1–D2, H1–H2) are robust and characterized by oval/elliptical to rounded protocone. These molariforms have occlusal length ranging approximately between 27 and 45 mm. The isolated lower premolars/molars (PIMUZ A/V 4197, 4219, 4220, 4240; Fig. 8F1–G2) are characterized by a rounded and small metaconid and metastylid, and a rounded protoconid and hypoconid, a typical dental pattern of *Hippidion* (Alberdi & Frassinetti, 2000; Alberdi & Prado, 2004; Alberdi et al., 2001b, 2003, 2005, 2006, 2007; Cerdeño et al., 2008; MacFadden, 1997; Prado et al., 2012, 2013; Scherer & Da Rosa, 2003). These occlusal length of the lower isolated molariforms range approximately between 30 and 37 mm. The first phalanx of the third digit (PIMUZ A/V 4205, Fig. 8C1–C3) is not in a good state of preservation, and it is 80 mm in maximum length and a 64 mm in width.

Remarks

The molariforms MHNG GEPI V-3779 exhibit fossettes and a prominent sub-elliptical protocone that differs from the oval to rounded protocone present in the molariforms of PIMUZ A/V 4100 assigned here to *Hippidion* cf. *H. principale* (see Fig. 8A3). We cannot rule out that molariforms MHNG GEPI V-3779 from the Pampean region could belong to either *H. principale* or *H. devillei*. *Hippidion saldiasi* is smaller in size and to date is restricted to the Late Pleistocene of the Patagonian region and some localities in Chile (Labarca et al., 2021; Prado & Alberdi, 2017). Our comparisons do not allow to offer a more precise determination of these specimens because their fragmentary nature and advanced tooth wear (e.g., PIMUZ A/V 4115, 4198, 4219-20, 4222, 4238-40). In reference to the left first phalange PIMUZ A/V 4205, its broad shape suggests an attribution to *Hippidion* sp. (see Alberdi et al., 2001a).

Equus Linnaeus, 1758
Equus neogeus Lund, 1840
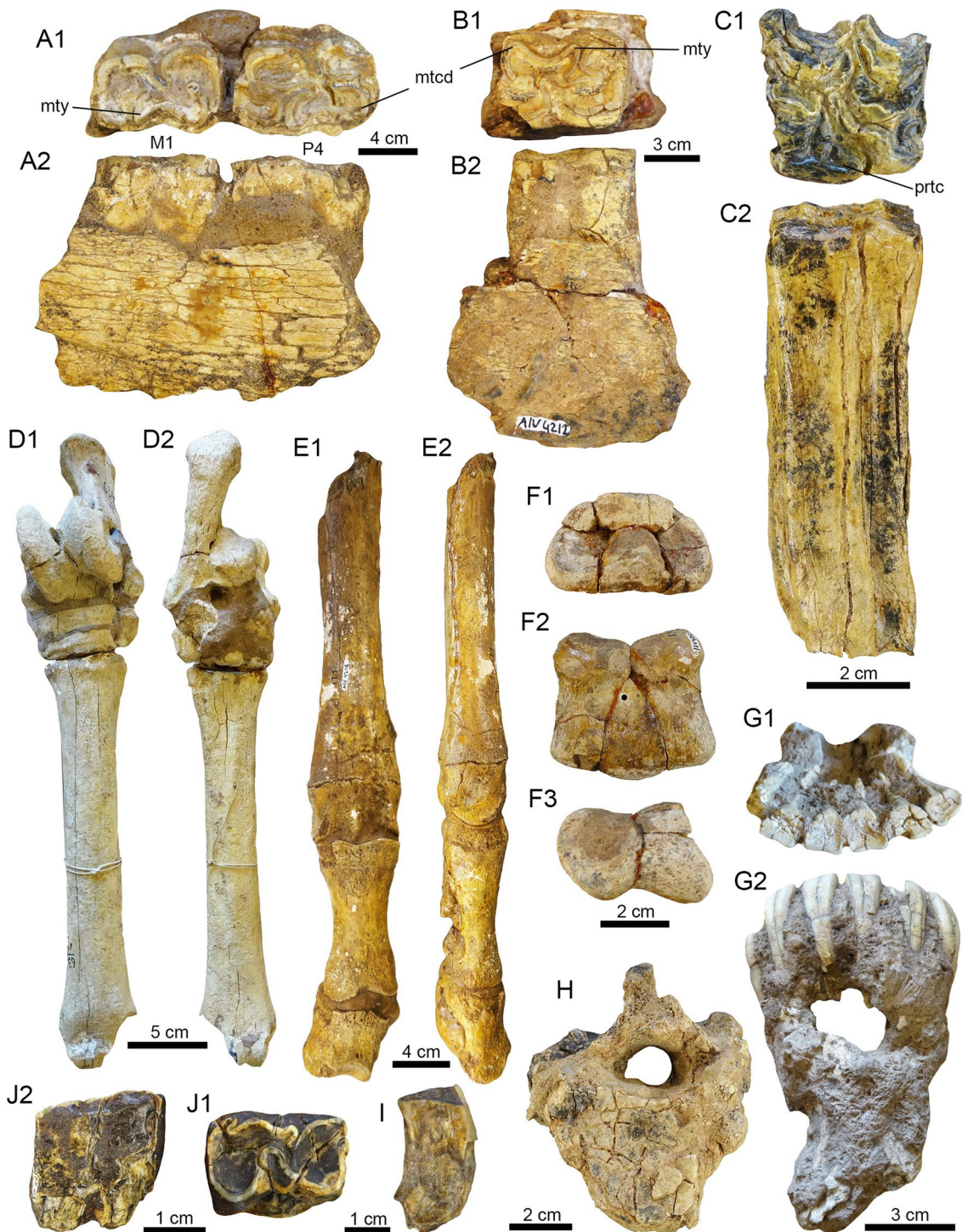*Equus* cf. *E. neogeus*
(Fig. 9A1–E2).

Fig. 9 Equids from the Pampean region. **A1**–**E2**. *Equus* cf. *E. neogeus*. **A1**–**A2**. Hemimandible fragment with left? p4-m1 (PIMUZ A/V 4183). **B1**–**B2**. Hemimandible fragment with m1 (PIMUZ A/V 4212). **C1**–**C2**. Left M1 (PIMUZ A/V 4236). **D1**–**D2**. Left metatarsal (MTIII) with articulate tarsal bones (MHNG GEPI V-3778). **E1**–**E2**. Right metacarpal (MCIII) with first and second phalanges (PIMUZ A/V 4248). **F1**–**J2**. Equidae indeterminate. **F1**–**F3**. Second phalange of the III digit (PIMUZ A/V 4242). **G1**–**G2**. Lower symphyseal bone with incisor teeth (MHNG GEPI V-3780). **H**. Thoracic vertebra (PIMUZ A/V 4132). **I**. incisor (PIMUZ A/V 4241). **J1**–**J2**. indeterminate lower molar (PIMUZ A/V 4244). Views: dorsal (**D1**, **E1**, **G1**), right lateral (**E2**), labial (**B2**), lateral (**F3**), lingual (**A2**, **C2**, **J2**), occlusal (**A1**, **B1**, **C1**), palmar/plantar (**D2**, **F2**), posterior (**H**), proximal (**F1**), ventral (**G2**), Indet. (**I**). Metaconid (mtcd), metastylid (mty), and protocone (prtc)

Referred material
Left M1 (PIMUZ A/V 4236), left p4–m1 (PIMUZ A/V 4183) and left m1 (PIMUZ A/V 4212), incomplete right metacarpal (MCIII) with first and second phalanges associated (PIMUZ A/V 4248), and incomplete left metatarsal (MTIII) with articulate tarsal bones (MHNG GEPI V-3778). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
PIMUZ A/V 4236 is a relatively complete left M1 (Fig. 9C1–C2), missing the cementum of the mesial part and with an occlusal length of approximately 30 mm. The occlusal surface is well preserved and it is possible to observe the pli caballin and a well-defined and triangular protocone that is longer at its distal part than in the mesial part. The lower left p4–m1 (PIMUZ A/V 4183, Fig. 9A1–A2) have an occlusal length of 26 mm and 24 mm, respectively. Left m1 (PIMUZ A/V 4212, Fig. 9B1–B2) has an occlusal length of 23 mm. The occlusal surface of the specimens is well-preserved, showing a double knot characterized by a rounded metaconid and a relatively angular metastylid, an elongated ectoflexid, and a protoconid and hypoconid with slightly straight labial edges (see Alberdi et al., 2002; Prado & Alberdi, 2017).

The specimen PIMUZ A/V 4248 is an incomplete right MCIII, missing its proximal part and articulated with first and second phalanges (Fig. 9E1–E2). Because the bones are preserved in physical connection, we have not been able to take precise measurements, but its maximal length is approximately 83 mm. An evident epiphyseal line shows an incomplete fusion between the diaphysis and epiphysis, which suggests that PIMUZ A/V 4248 could belong to a subadult individual. MHNG GEPI V-3778 is represented by a left MTIII, missing the left section of the distal epiphysis, for this reason a total length of 240 mm is estimated; all the tarsal bones are still articulated, including the talus and calcaneus (Fig. 9D1–D2).

Remarks
The dental occlusal pattern and characters present in PIMUZ A/V 4183, 4212, and 4236 (e.g., protocone, metaconid, pli caballin), as described above, can likely be associated more with *Equus* than *Hippidion* (see Prado & Alberdi, 2017, and references therein). The first phalanx articulated to the right MCIII (PIMUZ A/V 4248) is slender and more elongated than those present in *Hippidion*; its maximal length of approximately 83 mm is similar to those reported for *Equus* (see Prado et al., 2012). Similarly, the rather slender morphology of the left MTIII

(MHNG GEPI V-3778) is characteristic of the genus *Equus*, with values of a maximal length (240 mm) similar to estimates for *E. neogeus* (see Prado et al., 2012, table 1).

The taxonomic validity of the South American fossil *Equus* species have been under debate in the last decades (see Alberdi & Prado, 2004; Prado & Alberdi, 1994, 2017). Hoffstetter (1950) included all different species of *Equus* from South America in the subgenus *Amerhippus*, based only in the lack of infundibular marks in the lower incisor surface and consequent loss of surface enamel; nevertheless, the validity and use of *Amerhippus* have been questioned by Orlando et al. (2008) and Prado & Alberdi (2017). Traditionally five species of *Equus* were recognized in the fossil record of South America (e.g., Prado & Alberdi, 1994), but Prado & Alberdi (2017) based on both extensive revision of the morphological and morphometric characters of cranial and postcranial elements recognized as valid only three species (1) *E. andium* (?Middle–Late Pleistocene), (2) *E. insulatus* (Middle–Late Pleistocene), and (3) *E. neogeus* (Late Pleistocene). Recently, Machado & Avilla (2019) questioned the diagnosis and taxonomic validity of the three *Equus* species suggesting the possibility of only a single species of native *Equus* in South America, namely *E. neogeus*. We do not rule out that the specimens described herein from the Pampas region could belong to *E. neogeus* due to their morphology.

Equidae indet.
(Fig. 9F1–J2).

Referred material
A lower symphyseal bone with six incisors (MHNG GEPI V-3780), right m1 or m2 (PIMUZ A/V 4203), and indeterminate lower molar (PIMUZ A/V 4244), two isolated fragmented molariforms and an isolated incisor (PIMUZ A/V 4241), thoracic vertebra (PIMUZ A/V 4132), and second phalange of the III digit (PIMUZ A/V 4242). Geographic data of the specimens are provided in Additional file 1.

Description and comparisons
The lower symphyseal bone with six incisors MHNG GEPI V-3780 (Fig. 9G1–G2) shows a dental occlusal surface with advanced wear, likely suggesting an old individual. This specimen, together with the other isolated molariforms (PIMUZ A/V 4203, 4241, 4244, Fig. 9I–J2), the thoracic vertebra (PIMUZ A/V 4132, Fig. 9H), a second phalange of the III digit (PIMUZ A/V 4242, Fig. F1–F3), are fragmented or in poor preservation state.

Remarks

The fragmentary and/or poor preserved condition of the above-mentioned specimens makes it difficult to determine diagnostic characters for more precise identifications.

Concluding remarks

Santiago Roth collected several fossils remains of Nearctic ungulates from Pleistocene beds of the Pampean region that are now stored in the University of Zurich (PIMUZ A/V) and the Natural History Museum of Geneva (MHNG GEPI V-). Other important fossil collections were also sold by Roth to Dr. Valdemar Lausen and are currently housed in the Natural History Museum of Denmark (Hansen, 2019, 2020). According to Fernández (1925), fossils in the Roth catalogs 4 to 6 were sold to Swiss Museums. Of the collections studied here and deposited in Geneva and Zurich, we have only been able to correlate the fossils deposited in Zurich with Catalog No. 5. So far, we have not been able to relate the fossils deposited in Geneva with any of the other catalogs published by Roth (see Voglino et al., 2023) and mentioned by Fernández (1925) and Hansen (2020). All the fossil specimens studied here come from Pleistocene deposits of Pampean region, collected by Roth in the Buenos Aires and Santa Fe provinces. The stratigraphic position is referred to in this contribution as the Inferior, Intermediate and Superior Pampean (Additional file 1) as in Roth, 1889 (Voglino et al., 2023); however, precise correlation with the current stratigraphic scheme for Pampean Region is largely imprecise or uncertain.

The Nearctic ungulates from the Roth collections studied here include gomphotherids, camelids, tayassuids, cervids, and equids (Additional file 1). Gomphotherids and equids remains widely recorded in Pleistocene deposits of South America, with abundant and well-known material from Argentina (Alberdi & Prado, 2022; Mothé et al., 2012, 2013, 2017c; Prado & Alberdi, 2017). *Notiomastodon platensis* is the only gomphothere reported in the fossil record of Argentina, while *Cuvieronius* is not known in the region (Alberdi & Prado, 2022; Mothé et al., 2013, 2017c, and references therein). Stratigraphic studies of the Roth localities (e.g., Voglino et al., 2023) could offer a more detailed and relevant overview of the stratigraphy of gomphotheres and equids in the Pampas region during the Pleistocene. Integration on space and time and revisionary work of specimens could allow the investigation of taxon cycles, evolutionary and biogeographical dynamics of species that experience successive range expansions and contractions over time (Ricklefs & Bermingham, 2002; Wilson, 1961).

Camelids is the most diverse and abundant group in the studied sample, including the specimen reported by Lynch et al. (2020). The Camelidae are abundant in South America and are recorded in several Pliocene–Pleistocene deposits of the Pampean region of Argentina (Gasparini et al., 2017; Scherer, 2013). At end of the Pleistocene, like most of the Pleistocene megafauna, some camelid forms became extinct in South America, and the smaller taxa became restricted to dried and colder regions of the southern continent including Patagonia (Menegaz & Ortiz Jaureguizar, 1995; Tonni & Politis, 1980). This condition has been attributed to the climatic changes that took place at the end of the Pleistocene (e.g., Last Glacial Maximum; Iriondo, 1999; Iriondo & García, 1993), making the lowland as pampas not favorable for camelids and other mammals such as tropical tayassuids.

Deer are the most diverse lineage of medium-to-large herbivores in South America since the beginning of the Pleistocene (Cassini et al., 2016). Regardless of the great extant diversity spanning six living genera, which survived the extinctions of the end of the Pleistocene, the taxonomic diversity during that period might have been as high as the extant one (Cassini et al., 2016). Although all of the fossil deer are only known by their fossil antlers, *Morenelaphus* records also include few cranial remains associated with antlers (Chimento et al., 2019; Rotti et al., 2021; Vezzosi & Chimento, 2021; Vezzosi et al., 2020). Some of the specimens described here (hemimandibles) do not allow more accurate taxonomic determinations. Nevertheless, they offer new insights into the morphology of large deer cranial elements in extinct species. *Morenelaphu*s is considered a typical megamammal of Argentina with occurrence in open lowlands from the Pampean region to the southern part of the Chaco and Mesopotamia (Cassini et al., 2016; Chimento et al., 2019; Ferrero et al., 2007; Tomassini et al., 2020; Vezzosi et al., 2019).

The fossil record of tayassuids in South America is abundant (Gasparini, 2013). In contrast, the fossil record from Argentina is scarce and restricted to the end of the Quaternary, with abundant remains of *Tayassu pecari* mostly reported in the Pampean region and Mesopotamia (Gasparini & Ferrero, 2010; Gasparini et al., 2011, 2014).

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-023-00273-7.

> **Additional file 1.** Fossil specimens and localities of provenance.

Declarations

Competing interests
The authors declare that they have no competing interest.

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