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# More than 100 years of a mistake: on the anatomy of the atlas of the enigmatic *Macrauchenia patachonica*

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## Abstract

Ever since the discovery of the first remains of *Macrauchenia patachonica* by Charles Darwin in 1834, this taxon has puzzled researchers with its peculiar anatomy. Being the best-known member of the family Macraucheniidae and with fossil records in extensive areas of South America between the Middle to Late Pleistocene/earliest Holocene, *M. patachonica* has been extensively studied over decades, and recently even included in molecular studies. However, there are some elements of its skeleton that have been inadvertently unstudied. One of these elements is the atlas of *M. patachonica* that due to a misidentification made 159 years ago by the prominent zoologist Hermann Burmeister, was not examined or illustrated by later researchers even with access to excellent specimens. Here, we describe and illustrate the atlas of *M. patachonica* for the first time, correcting Burmeister's mistake. Overall, the anatomy of the atlas of *M. patachonica* is consistent with the anatomy of older macraucheniids. The atlas described by Burmeister as being *M. patachonica* probably corresponds to that of a bovid. It is noteworthy that most mounted skeletons of *M. patachonica* present today in museum exhibitions, display a correct atlas derived from a more complete specimen discovered ca. 1904 by the prominent palaeontologist Santiago Roth.

**Keywords** *Macrauchenia patachonica*, Macraucheniidae, Macraucheniinae, Atlas, Burmeister, Santiago Roth, SANUs, Bovidae, Late Pleistocene

## Resumen

Desde el descubrimiento de los primeros restos de *Macrauchenia patachonica* por Charles Darwin en 1834, este taxón ha intrigado a los investigadores por su peculiar anatomía. Siendo el miembro más conocido de la familia Macraucheniidae y con registros fósiles en extensas áreas de Sudamérica entre el Pleistoceno Medio y Tardío/Holoceno Temprano, *M. patachonica* ha sido ampliamente estudiada durante décadas, y recientemente incluso incluida en estudios moleculares. Sin embargo, hay algunos elementos de su esqueleto que inadvertidamente aún no han sido estudiados. Uno de estos elementos es el atlas de *M. patachonica*, que debido a una identificación errónea realizada hace 159 años por el destacado zoólogo Hermann Burmeister, no fue examinado ni ilustrado por investigadores posteriores aún con acceso a ejemplares excelentes. Aquí, describimos e ilustramos el atlas de *M. patachonica* por primera vez, corrigiendo el error de Burmeister. En general, la anatomía del atlas de *M. patachonica* es consistente con la anatomía de los macraucheniidos más antiguos. El atlas descrito por Burmeister como *M. patachonica* probablemente

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corresponde al de un bóvido. Cabe destacar que la mayoría de los esqueletos montados de *M. patachonica* presentes hoy en las exhibiciones de diferentes museos muestran el atlas correcto derivado de un espécimen más completo descubierto ca. 1904 por el destacado paleontólogo Santiago Roth.

**Palabras clave** *Macrauchenia patachonica*, Macraucheniidae, Macraucheniinae, atlas, Burmeister, Santiago Roth, SANUs, Bovidae, Pleistoceno Tardío

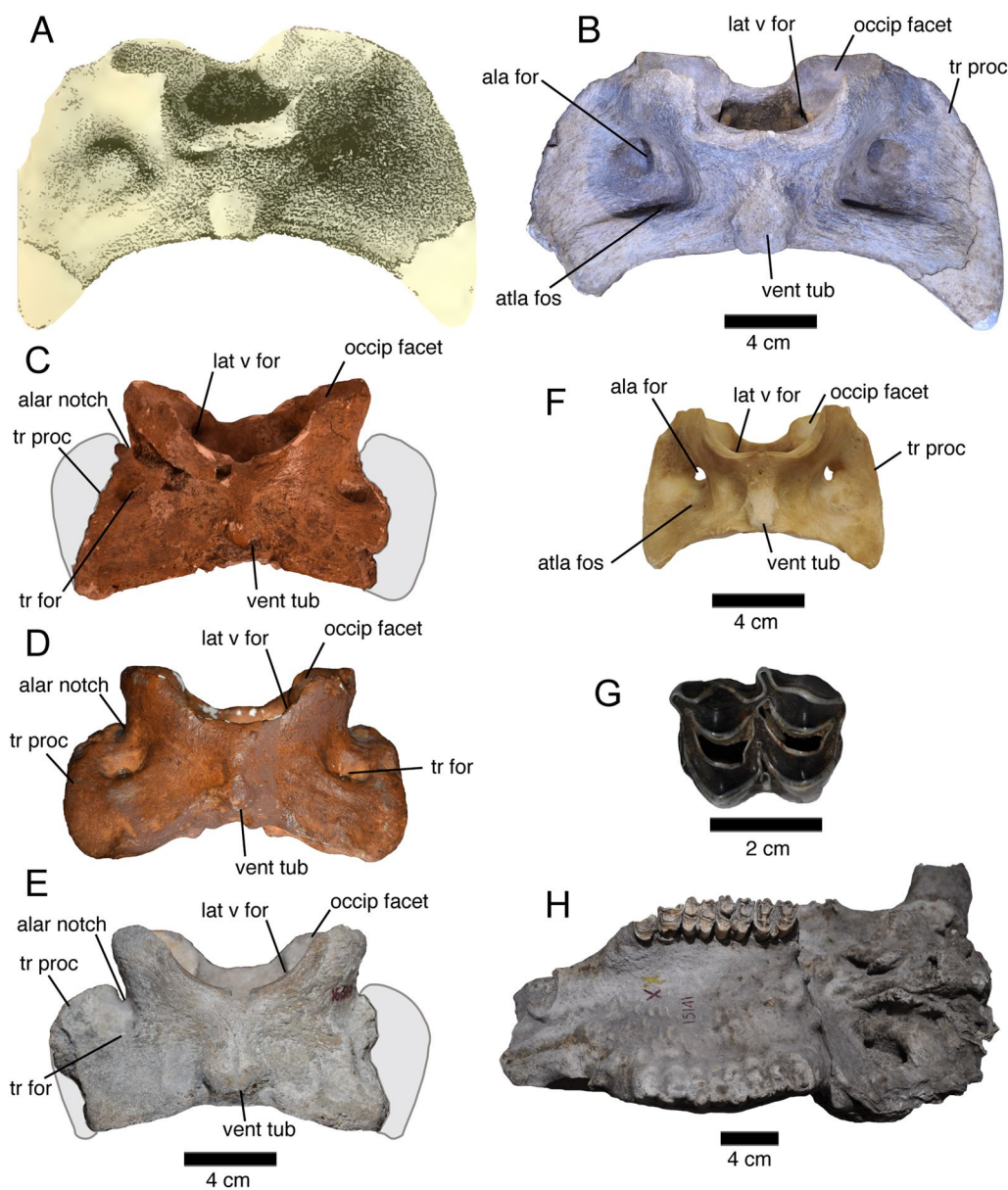
## Introduction

South American native ungulates (SANUs) were a key component of the South American fauna during most of the Cenozoic, displaying an enormous taxonomic diversity and disparity in terms of morphology and body size (Simpson, 1980). Their anatomical uniqueness was probably related to an endemic evolution in an almost completely isolated South America, which was interrupted by the appearance of the Isthmus of Panama, a terrestrial bridge that fully connected both continents likely by 2.8 Ma (O’Dea et al., 2016; but see Montes et al., 2015 for an alternative view). SANUs are traditionally classified into five orders: Astrapotheria, Litopterna, Notoungulata, Pyrotheria and Xenungulata (McKenna & Bell, 1997). Among SANUs, litopterns are the most similar to extant ungulates in terms of dental, cranial, and postcranial proportions, presenting cursorial postcranial adaptations early in their evolutionary history (Scott, 1910; Croft et al., 2020). Although most Paleogene litopterns have uncertain affinities with one another (Cifelli, 1993), Neogene litopterns are generally classified into three well-defined families: Macraucheniidae, Protherotheriidae and Adianthidae (Cifelli, 1983; Soria, 2001; Gelfo et al., 2016). Macraucheniids were small to large-sized litopterns (i.e., 53–1200 kg), presenting three-toed feet, elongated necks, and a trend towards retraction of the nasals (Bond, 1999; Püschel et al., 2023; Vizcaíno et al., 2012). The family Macraucheniidae was traditionally subdivided into two subfamilies: “Cramaucheniinae” (Eocene to Middle Miocene) and Macraucheniinae (Late Miocene to Late Pleistocene/Early Holocene; Soria, 1981), but only the latter has been consistently shown to be monophyletic in recent phylogenetic analyses (Forasiepi et al., 2016; McGrath et al., 2018; Schmidt & Ferrero, 2014; Püschel et al., 2023). The most distinctive common feature of macraucheniines is having a retracted nasal aperture that suggests the presence of a proboscis (Bond, 1999; Burmeister, 1864–1869a; Scott, 1910; Rusconi, 1957). Macraucheniines also share some postcranial features, including characteristics in the atlas, such as a posterior border of the transverse process posterior to the articular facet for the axis (Püschel et al., 2023).

Among macraucheniids, the macraucheniine *Macrauchenia patachonica* stands out as the last and best-known member of this family, with a fossil record

between the Ensenadan South American Land Mammal Age (SALMA; Middle Pleistocene) to the Lujanian SALMA (Late Pleistocene-Holocene) in Argentina, Brazil, Bolivia, Chile, Paraguay, Peru, and Uruguay (Bond, 1999; Scherer et al. 2009). With body mass estimations that vary from 830 kg (Fariña et al. 1998) to 1100 kg (Fariña, 1996), *M. patachonica* is one of the largest SANUs that ever existed and also an important member of the South American megafauna during the Pleistocene. In terms of *M. patachonica* phylogenetic affinities, recent molecular analyses suggested that this taxon and its closest relatives (i.e., other litopterns) form a monophyletic group with notoungulates, and that this group is closely related to Perissodactyla (Buckley, 2015; Welker et al. 2015; Westbury et al. 2017). In contrast to the recent molecular interest in *M. patachonica*, the anatomy of this taxon has not been frequently revisited in recent years in spite of recent fossil discoveries (e.g., Martínez Rivera & Rojas Mondaca 2020), morphofunctional studies (e.g., Blanco et al. 2021), and numerous specimens available in museum collections.

Ever since the discovery of the first remains of *M. patachonica* by Charles Darwin in 1834 in the vicinity of Puerto San Julián in the Argentinean Patagonia, the peculiar anatomy of this taxon has puzzled researchers. Darwin sent the remains of this taxon to England, where Richard Owen (1838) named and described *M. patachonica*, classifying it within the order “Pachydermata” (i.e., a now obsolete order that grouped rhinoceroses, elephants, tapirs, and hippopotamuses together), but with affinities with ruminants, and in particular to the Camelidae. The remains found by Darwin were extremely fragmentary and consisted of different postcranial elements including two cervical vertebrae, seven lumbar vertebrae, and elements of the fore and hindlimbs. Over the following years, more elements of *M. patachonica* were reported (e.g., Gervais 1855), but it was only with the publications of Burmeister (1864, 1864–1869a, 1864–1869b) that the skull and dentition of this animal were described alongside other, previously unknown parts of this taxon such as the atlas. Burmeister (1864, 1864–1869a) described the atlas of *M. patachonica* as being extremely similar to the atlas of ruminants such as the ox (Fig. 1A–B). However, a recent revision of the atlas of macraucheniids (Püschel et al. 2023), put into question the association



**Fig. 1** Atlas of Burmeister (1864, 1864–1869a) in comparison with atlases of *Macrauchenia patachonica* and bovid material. **A, B** The bovid atlas of Burmeister as a drawing in Burmeister (1864–1869a; Plate IV) in ventral view (**A**), and photographed in ventral view (**B**). **C–E** Atlases of *Macrauchenia patachonica* in ventral view: PIMUZ A/V 5700 (**C**), cast in the MACN of MLP 12-14244 (**D**), and MACN-PV 16618 (**E**). **F** Atlas of *Bos taurus* (Chillingham cattle; NMS.Z.2023.49) in ventral view. **G** Left upper molar of a bovid, probably *Bos*, from the Bravard collection (MACN-PV 2379), found in the “Pampean Formation”, Entre Ríos, Argentina, and classified by Florentino Ameghino as *Platatherium pampeanus*. **H** Bovid skull, probably *Bos* (MACN-PV 15141), showing some diagenetic alteration affecting its colour and texture. Notice in **A** and **B** the absence of the transverse foramen and the alar notch, and also the great development of the dorsal tubercle. These features are clearly different from an atlas of *Macrauchenia* (**C, D**) and are consistent with an atlas of *Bos*, particularly with *Bos primigenius* (personal observation [HPP]; not illustrated). The considerable size difference between the bovid atlas of Burmeister (**A**) and the specimen of *Bos taurus* (**B**) can be explained by the fact that the latter is a Chillingham cattle, which is a relatively small-sized cattle breed, and potentially by sexual dimorphism (Grigson, 1974). The silhouettes in grey are reconstructions of the missing portions of the atlases. Abbreviations: *ala for*, alar foramen; *atla fos*, atlantic fossa; *lat v for*, lateral vertebral foramen; *occip*, occipital; *tr for*, transverse foramen; *tr proc*, transverse process; *vent tub*, ventral tubercle

of the atlas described by Burmeister (1864, 1864–1869a) with *M. patachonica*. In light of the examination of an undescribed specimen of *M. patachonica* with an

associated atlas, Püschel et al. (2023) suggested that Burmeister’s (1864, 1864–1869a) atlas corresponds to a ruminant, and likely, a bovid (possibly *Bos* or *Bison*). This

means that currently there is no valid description or illustration in the literature of the atlas of *M. patachonica*.

Here, we describe and illustrate the atlas of *M. patachonica* correcting this mistake made by Burmeister 159 years ago. The description is based on three different atlases of this taxon, two of them associated with other elements that are unequivocally from *M. patachonica* (Fig. 1C–E). Importantly, these two more complete specimens (PIMUZ A/V 5700 and MLP 12-1424; Fig. 1C–D) were collected by the Swiss-Argentine palaeontologist Santiago Roth in the 19<sup>th</sup> century. The former is currently deposited in the Paleontological Institute and Museum, University of Zurich, Switzerland, as a part of the Roth collection (Catalogue No. 5; Roth, 1889); the latter is currently on exhibition at the Museo de La Plata, Argentina. In addition, we conducted a historical revision of how Burmeister in 1864 may have made this mistake in assigning a bovid atlas to *M. patachonica*, and why his description was never amended.

## Methods

Descriptions were based on direct observation/images from museum collections of relevant specimens. Measurements were taken in centimetres digitally using Fiji (ImageJ v2.1.0; Schindelin et al., 2012), to the nearest two decimal places. We followed the Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, 2017) for the anatomical terminology.

**Institutional Abbreviations.** AMNH, American Museum of Natural History, New York, USA; NMS, National Museums Scotland, Edinburgh, United Kingdom; MACN-PV, Museo Argentino Ciencias Naturales “Bernardino Rivadavia”, Colección Nacional de Paleontología Vertebrados, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; PIMUZ, Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland; ROM, Royal Ontario Museum, Toronto, Canada.

## Systematic palaeontology

Mammalia Linnaeus, 1758

Eutheria Huxley, 1880

Panperissodactyla Welker et al. 2015

Litopterna Ameghino, 1889

Macraucheniiidae Gervais, 1855

Macraucheniiinae Gervais, 1855

Macrauchenia patachonica Owen, 1838

= *Macrauchenia patagonica* Lydekker, 1893

**Holotype and type locality.** NHMUK PV M 43402, astragalus, femur, tibia-fibula, ulna-radius proximal fragment, two cervical vertebrae, seven lumbar vertebrae, metapodials, among other postcranial fragments described by

Owen (1838), collected on the south side of San Julián Port, Santa Cruz Province, Argentina.

**Specimens here compared and described.** PIMUZ A/V 5700 (Fig. 1C), posterior portion of the cranium, complete series of seven cervical vertebrae (atlas, axis, C3–C7), five thoracic vertebrae (T1–T5), right scapula, right humerus, right ulna-radius, carpals (scaphoid, lunate, cuneiform, pisiform, trapezium, trapezoid, magnum, unciform), metacarpals (Mc II, Mc II, and Mc IV), and phalanges (proximal, intermediate, and distal), from Arroyo del Medio, Santa Fe Province, Argentina (Catalogue No. 5, specimen 223; Roth, 1889); MLP 12-1424 (Fig. 1D), partially complete skeleton that includes cranium and many postcranial elements including the atlas, from Arrecifes, Buenos Aires Province, Argentina (Sefve, 1925); MACN-PV 16618 (Fig. 1E), isolated atlas from Río Carcarañá, under the highway bridge, Santa Fe Province, Argentina.

**Known distribution.** Argentina, Brazil, Bolivia, Chile, Paraguay, Peru, and Uruguay Pleistocene to Holocene/Ensenadan to Lujanian (2–0.08 Ma; Bond, 1999; Scherer et al. 2009).

## Description of the atlas of *Macrauchenia patachonica*

A detailed description of the atlas of the macraucheniid *Micrauchenia saladensis* that includes comparisons with other macraucheniiids (including *Macrauchenia patachonica*) was conducted in a previous work (Püschel et al., 2023). However, the atlas *Macrauchenia patachonica* was not formally described, so what follows is a brief description of the atlas of this species.

The atlas of *M. patachonica* is wider than it is tall, and wider than it is long (Table 1). Anteriorly, the atlas presents articular facets for the occipital condyles of the cranium or occipital facets, which are closer to each other ventrally than they are dorsally (Fig. 2A). The occipital facets are overall strongly concave, except by their ventralmost portion in which they are slightly convex. Posteriorly, the atlas of *M. patachonica* exhibits almost flat and oval articular facets for the axis, and medial to these facets, in the ventral portion of the neural arch, there is a concave facet for the odontoid (Fig. 2B). Lateral to each articular facet for the axis, there is a small oval posterior opening of the transverse foramen (*foramen transversarium*), which is located in the medialmost portion of the transverse process of the atlas. The dorsal and ventral tubercles (*tuberculum dorsale* and *tuberculum ventrale*) are visible in both anterior and posterior views. Both tubercles have a similar degree of development (i.e.,



**Table 1** Measurements of the atlas of Burmeister (1864–1869a, 1864), a *Bos taurus* atlas, and atlases of *Macrauchenia patachonica*

| Species  | Specimen                 | Maximum antero posterior length | Maximum width in the proximal end at occipital facets | Maximum width between distal facets for axis | Maximum width over transverse process | Transverse process length | Maximum dorso ventral height | Maximum mediolateral width of vertebral foramen | Maximum dorsoventral height of vertebral foramen |
|--|--------------------------|---------------------------------|---|--|---------------------------------------|---------------------------|------------------------------|---|--|
| <i>Bos?</i>  | MACN-PV 2 <sup>a</sup>   | 9.41                            | 13.65   | 12.10  | 21.14                                 | 9.41 <sup>b</sup>         | 8.61                         | 4.13  | 2.56   |
| <i>Bos taurus</i> (Chillingham cattle <sup>f</sup> ) | NMS.Z.2023.49            | 6.10                            | 7.48  | 6.48   | 10.26                                 | 6.01                      | 5.18                         | 3.68  | 1.98   |
| <i>Macrauchenia patachonica</i>                      | PIMUZ A/V 5700           | 8.96                            | 10.66   | 11.33  | 15.09 <sup>c</sup>                    | 6.96 <sup>b</sup>         | 7.60                         | 5.50  | 4.43   |
| <i>Macrauchenia patachonica</i>                      | MLP 12-1424 <sup>d</sup> | 8.35                            | 11.79   | 11.68  | 15.01 <sup>e</sup>                    | 5.99 <sup>d</sup>         | 7.36                         | 5.45  | 3.92   |
| <i>Macrauchenia patachonica</i>                      | MACN-PV 16618            | 8.84                            | 12.76   | 13.57  | 15.46 <sup>c</sup>                    | 6.33 <sup>b</sup>         | 8.28                         | 5.37  | 3.97   |

<sup>a</sup> The same specimen number is used for the associated remains of *Macrauchenia patachonica* found by Bravard

<sup>b</sup> The transverse processes are broken so they were probably slightly longer

<sup>c</sup> It was estimated from the most complete half

<sup>d</sup> The measurements were taken in a cast of MLP 12-1424, currently exhibited in a mounted skeleton in the MACN

<sup>e</sup> The transverse processes are broken in this specimen, but preparators added the missing areas which were included in the measurements.

<sup>f</sup> The Chillingham cattle is a relatively small-sized *Bos taurus* breed (Grigson, 1974).

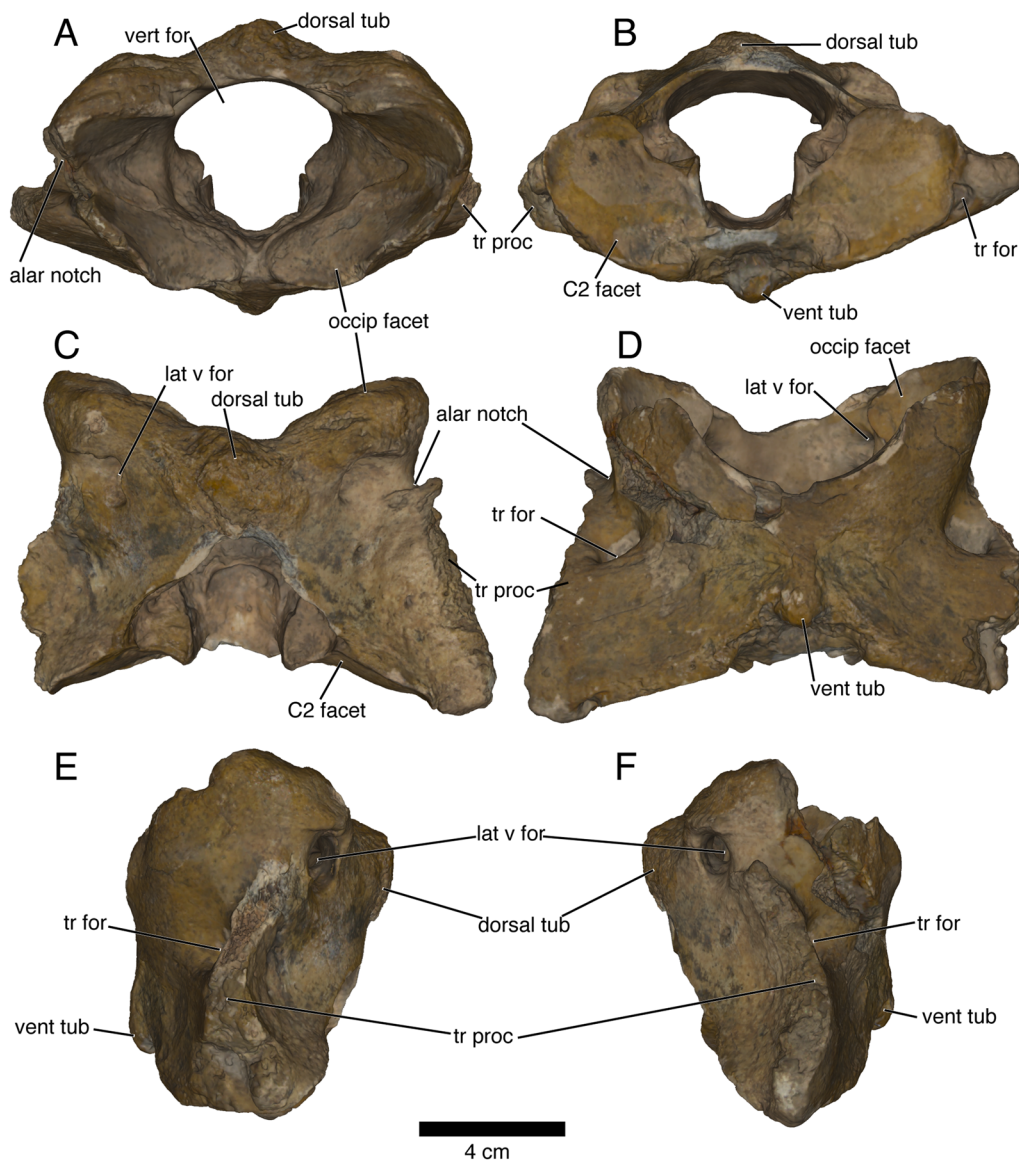
similar height), although the ventral tubercle is mediolaterally narrower and is located more posteriorly in comparison to the dorsal tubercle.

Dorsally and posterior to the occipital facets, the atlas of *M. patachonica* presents anteroposteriorly elongate lateral vertebral foramina (*foramen vertebrale laterale*) for the first cervical spinal nerve and vertebral artery (Evans & Lahunta, 2012; Fig 2C). Lateral from each lateral vertebral foramen, there is an alar notch (*incisura alaris*) for the vertebral artery. The transverse processes of the atlas are developed laterally and posteriorly from the alar notch, being anteroposteriorly elongated. The posterior end of the transverse processes of the atlas covers the articular facets for the axis, terminating in a posteriorly projecting rounded lobe. The latter feature is shared with other macraucheniiines and is present in earlier members of this subfamily such as *Micrauchenia saladensis* (Püschel et al. 2023). It was not possible to measure the exact mediolateral width of the transverse processes as this is incomplete in all the specimens examined in this work (Fig. 1C–E). However, considering that MACN-PV 16618 has the anterior portion of the right transverse process preserved (Fig. 1E), and PIMUZ A/V 5700 has the posteriormost portion of the same element preserved (Fig. 1C), it is possible to say that overall the transverse processes are moderately mediolaterally broad, and proportionally very similar to the transverse processes of *Micrauchenia saladensis* (Püschel et al. 2023).

Ventrally, the atlas of *M. patachonica* presents the anterior opening of the transverse foramen, which is

mediolaterally wide and very close to the alar notch (Figs. 1C–E and 2D). In lateral view, the lateral vertebral foramen is more exposed than the transverse foramen, as the latter is partially covered by the curvature of the transverse process (Fig. 1E–F). The three atlases examined (PIMUZ A/V 5700, MLP 12-1424, MACN-PV 16618) of *M. patachonica* have similar sizes and proportions (Table 1).

Overall, the anatomy of the atlas of *M. patachonica* is consistent with the anatomy of other macraucheniiines, in particular, with macraucheniiines, being very different from the anatomy of *Bos* (Fig. 1F) and Burmeister's (1864, 1864–1869a) atlas (Püschel et al. 2023). The atlas described by Burmeister (1864, 1864–1869a) is consistently bigger than the atlases of *M. patachonica* here examined in all dimensions (Fig. 1), except the size of the vertebral foramen, which is slightly smaller in the former (Table 1). In addition, Burmeister's (1864–1869a, 1864) atlas has the following distinctive features (Fig. 1B): (a) absence of a transverse foramen, (b) presence of marked atlantic fossa (*fossa atlantis*), (c) transverse process extended anteriorly to the occipital facet of the atlas (i.e., absence of an alar notch), (d) very strong dorsal tubercle, (e) closely appressed articular facets for the axis and (d) dorsoventrally compressed ovoid vertebral foramen (Püschel et al. 2023). All these features are consistent with a bovid atlas possibly of the genus *Bos* (Fig. 1F) or *Bison*, and are absent in *M. patachonica*. The domestic *Bos taurus* exhibits an important sexual dimorphism and size variation within and among different breeds (Grigson,



**Fig. 2** Atlas of *Macrauchenia patachonica* (PIMUZ A/V 5700). **A** anterior view; **B** posterior view; **C** dorsal view; **D** ventral view; **E** left lateral view; **F** right lateral view. Note that this specimen has both transverse processes broken, although the distalmost portion of the right transverse process is complete. The different views of the atlas are based on images of a 3D model obtained by a surface scanner. Abbreviations: *dor tub*, dorsal tubercle; *lat v for*, lateral vertebral foramen; *occip*, occipital; *tr for*, transverse foramen; *tr proc*, transverse process; *vent tub*, ventral tubercle; *vert for*, vertebral foramen

1974). Considering the maximum width in the proximal end at occipital facets (Table 1), if the atlas described by Burmeister (1864, 1864–1869a) is effectively a *Bos taurus* specimen, this would be a relatively large specimen of domesticated cattle (close to the upper size limit; Grigson, 1974), being potentially a large bull.

Considering all the evidence available and the important morphological gap between the atlas described by Burmeister (1864, 1864–1869a) as pertaining to

*Macrauchenia patachonica*, and the *M. patachonica* specimens here examined (PIMUZ A/V 5700, MLP 12-1424, and MACN-PV 16618), it can be established with certainty that Burmeister's (1864, 1864–1869a) atlas (grouped with MACN-PV 2 in the MACN collections) does not correspond to *M. patachonica*. The same applies to the atlas MACN-PV 3, not mentioned by Burmeister (1864, 1864–1869a) but probably from the same collection of Burmeister's (1864, 1864–1869a) atlas. However,

how a prominent zoologist such as Hermann Burmeister made this mistake, and how only 159 years later this mistake has been amended, are still open questions.

### The bovid atlas of Burmeister, a chronology of a historical mistake

After the first description of *M. patachonica* based on a very fragmentary specimen (Owen, 1838), Gervais (1855) included more details of the postcranial anatomy of *M. patachonica*, in particular of the forelimb, but the atlas and also the skull of this taxon were still unknown at that time. In 1856 Auguste Bravard (1803–1861), a French naturalist, geographer and geologist based in Argentina, collected near the city of Salto, Buenos Aires Province, an almost complete skull and a large part of the skeleton of *M. patachonica*. In 1857 Bravard named this fossil *Opistorhinus falconeri*, alluding to the strange position of the nasal openings at the back of the snout (Bravard, 1857). However, this was an invalid name as *Macrauchenia patachonica*, the name given by Owen (1838), took precedence. Unfortunately, Bravard met his death before he could complete the description of the new material of *M. patachonica* in the strong earthquake that occurred on March 20th, 1861, which almost completely destroyed the old city of Mendoza (Burmeister, 1885). However, he made some excellent graphic plates of the elements of this material.

In 1864, Hermann Burmeister (Germán Burmeister in Spanish; 1807–1892), then director of the Museo Público in Buenos Aires (currently MACN “Bernardino Rivadavia”), described in detail the material discovered by Bravard using his unpublished graphic plates kept in the museum, publishing two separate descriptions of *M. patachonica*, one version in Spanish and another in German (Burmeister, 1864, 1864–1869a). In these descriptions, Burmeister mentioned the addition of an atlas of *M. patachonica* that was unknown to Owen and Bravard, and that was already housed in collections of the Museo Público of Buenos Aires (Burmeister, 1864, 1864–1869a). This atlas is presented in Plate IV of Burmeister (1864–1869a; Fig. 1A), which is the last plate in that work with figured elements of *M. patachonica*. Burmeister (1864) mentioned that among the remains collected by Bravard, there were only five cervical vertebrae, which included the vertebrae from the second to the sixth. Therefore, the atlas mentioned by Burmeister (1864, 1864–1869a) was not among the original remains of *M. patachonica* found by Bravard and included in his original drawings. The origin of the atlas described by Burmeister (1864, 1864–1869a) is currently unknown and omitted in his descriptions, which obscures the reasoning of Burmeister in the assignment of this atlas to *M. patachonica*. It is possible that Burmeister based this assignment on the

size of this element, as it broadly fits with an animal of the size of *M. patachonica*.

Burmeister (1864) observed that the anatomy of this atlas was consistent with the anatomy of ruminants, and after comparing it with the ox, sheep and deer, he concluded that among them, this atlas was more similar to that of the ox, but, almost twice as large. Burmeister’s description of this atlas is consistent with recent observations (Püschel et al. 2023) and our interpretation of this atlas pertaining to a bovid (possibly *Bos* or *Bison*). Although there are a few accounts of native bovids to South America, such as *Platatherium magnum* from Argentina (Gervais & Ameghino, 1880) and *Colombibos atactodontus* from Colombia (Hernández & De Porta, 1960), these taxonomic assignments have been dismissed by later authors who considered these remains pertaining most likely to domestic cattle of the genus *Bos* (Hoffstetter, 1971; Thomas, 1984; Fig. 1G). Indeed, historical accounts place the introduction of domestic cattle in the Americas specifically during the second voyage of Christopher Columbus to the Antilles in 1493 (Rodero et al. 1992). In the following years, with the aid of Spaniards, domestic cattle expanded from the Caribbean to other regions of the Americas, reaching Argentina before the end of the 16th century (Rouse, 1977). Therefore, if Burmeister’s (1864, 1864–1869a) atlas was effectively found in Argentina, it most likely belongs to domesticated cattle remains. It is possible that bovid remains were buried in colonial times, which led to the confusion of researchers such as Burmeister, particularly because their colour and state of preservation visually suggest that they are old. For instance, in the MACN collection, there is *Bos* cranium (MACN PV 15141) which considering its colour and preservation, it looks like a Pleistocene fossil skull (Fig. 1H). The exact provenance of this specimen is unknown but likely it came from the Pampean region; it was catalogued on 27 April 1944 and belonged to the old collections of the MACN.

At the time of Burmeister’s descriptions, the Auguste Bravard collection was on sale (Burmeister, 1864), so it is likely that the material was inaccessible to him. The Bravard collection was finally acquired by the National Government in 1866 (Burmeister, 1885), and although it was intended for the Academia Nacional de Ciencias of Córdoba, it ended up deposited in the Museo Público of Buenos Aires. Over the years and decades that passed since Burmeister’s (1864, 1864–1869a, 1864–1869b) descriptions, the specimen of *Macrauchenia patachonica* MACN-PV 2, which includes Bravard’s original specimen and Burmeister’s atlas, has been a reference specimen for studying this taxon. However, no author corrected Burmeister’s taxonomic assignment mistake until recently (Püschel et al. 2023). This is curious considering the fact





**Fig. 3** Skeletal reconstructions of *Macrauchenia patachonica*. **A** Burmeister's (1864–1869a) reconstruction. **B** Mounted skeleton (based on casts of MLP 12-14244) in the MACN exhibition ca. 1940. **C** Mounted skeleton (MLP 12-14244) in the MLP exhibition 2022. **D** Mounted skeleton (based on casts of MLP 12-14244) in the MACN exhibition 2020. **E** Mounted skeleton (AMNH 14489) in the AMNH exhibition 2019. **F** Mounted skeleton (ROMVP00410, based on casts of MLP 12-14244) in the ROM exhibition 2022. Note in **A** that the atlas fits the shape of the bovid atlas of Burmeister (1864–1869a, 1864), although it was represented much smaller than its real size. AMNH 14489 in **c** presents Burmeister's (1864–1869a, 1864) atlas, which suggests that other elements could be casts of MACN material.

that a specimen more complete of *M. patachonica* MLP 12-1424 found in ca. 1904 by Santiago Roth and later mounted in the MLP exhibition (Fig. 3C), preserves an associated atlas with an anatomy consistent with that of

macraucheniiids instead of ruminants. Sefve (1925) mentioned this specimen and compared it with a different specimen of *M. patachonica* from Ayacucho in a revision of this species. However, Sefve (1925) focused his



description only on certain elements, such as the forelimb, without mention of the cervical vertebrae of MLP 12-1424.

In his publication, Burmeister (1864–1869a) included the first reconstruction of the articulated skeleton of *M. patachonica* with a silhouette of his putative body displaying a conspicuous trunk (Fig. 3A), a representation of this taxon that he also reproduced in later publications (Burmeister, 1864–1869b, 1889). This representation of *M. patachonica* was a hallmark for the artistic reconstruction of this species (Forasiepi et al. 2021). It is interesting to mention that despite the atlas described by Burmeister being too large for Bravard's skull (MACN-PV 2), in the reconstruction of the skeleton of *M. patachonica*, the atlas is a relatively small element, in accordance with the size of the skull and following vertebrae (Burmeister, 1864–1869a), which support the hypothesis that Burmeister may have not examined directly Bravard's skull and the controversial atlas at the same time. Bravard's fossils (MACN-PV 2) were reproduced and interchanged with other institutions (e.g., cast at the AMNH). However, the mounted skeleton of *M. patachonica* in the exhibition of the MACN is not based on the specimen MACN-PV 2, being instead a cast of the MLP material (MLP 12-1424; Fig. 3B, D), obtained by the MACN through an interchange of cast specimens at the beginning of the 20<sup>th</sup> century.

It is interesting to note that the mostly casted specimen AMNH 14489, currently on exhibition at the AMNH, has an atlas with a ruminant morphology, which is extremely similar to Burmeister's atlas (Fig. 3E). The original specimen AMNH 14489 is from Salto, Buenos Aires Province, Argentina, and consists of some ribs, caudal vertebrae, and manus/pes elements, whereas the rest of the skeleton, including the atlas, are casts. The only information that the AMNH records have on the acquisition of the specimen is that it was obtained in an exchange from Buenos Aires, Argentina around 1908. Considering the morphology and size of the atlas of AMNH 14489, it is likely that this is a cast of the atlas described by Burmeister (1864–1869a, 1864), which suggests that the exchange was arranged with the MACN. This also means that the staff of the MACN had not noticed Burmeister's mistake. Unlike MACN-PV 2 and MLP 12-1424, the dentition in the skull and mandible of AMNH 14489 is complete, although the missing teeth could have been restored by the AMNH staff. Another very complete cast of the skeleton of *M. patachonica* is present in the ROM exhibition (ROMVP00410) in Canada (Fig. 3F), which was exchanged with the MLP in the early to mid-1930s. Considering its features, ROMVP00410 is probably an exact copy of MLP 12-1424.

## Conclusions

We describe and illustrate the atlas of *Macrauchenia patachonica* for the first time, correcting a mistake made 159 years ago by Burmeister (1864, 1864–1869a). The anatomy of the atlas of *M. patachonica* is consistent with the anatomy of other members of the subfamily Macraucheniniinae. The atlas assigned by Burmeister (1864, 1864–1869a) does not belong to *M. patachonica*, belonging probably to a bovid as previously suggested (Püschel et al., 2023). The mounted skeletons based on the cast of MLP 12-1424 have the correct atlas of *Macrauchenia*, whereas those based on Bravard's material maintained Burmeister's mistake (e.g., AMNH 14489). Key specimens for amending this mistake (MLP 12-1424 and PIMUZ A/V 5700) were discovered by Santiago Roth more than a century ago.

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## Author contributions

HPP conceived and designed the study. HPP and AGM took pictures of the specimens of interest. HPP prepared the figures. HPP and AGM gathered historical information on the specimens of interest. HPP examined the anatomy of the specimens, took measurements of the specimens, and wrote an initial manuscript. HPP and AGM contributed to the writing of the submitted version of the manuscript.

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## Availability of data and materials

The 3D model of the atlas of the *Macrauchenia patachonica* specimen PIMUZ A/V 5700 is available in Morphosource (<https://www.morphosource.org>) as media 000526226, and also in Sketchfab in the Palaeontological Museum UZH digital collection (<https://skfb.ly/oJNTG>). Scanning and 3D models of the atlas of the *Macrauchenia patachonica* (PIMUZ A/V 5700) are contributions to the project SWISSCOLLNET, SCN133-ZH to Gabriel Aguirre Fernández.

## Declarations

### Competing interests

The authors declare no competing interests.

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