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## Systematic and phylogeny of *Prodolichotis prisca* (Caviidae, Dolichotinae) from the Northwest of Argentina (late Miocene–early Pliocene): Advances in the knowledge of the evolutionary history of maras



### *Systématique et phylogénie de Prodolichotis prisca (Caviidae, Dolichotinae) du Nord-Ouest de l'Argentine (Miocène tardif–Pliocène inférieur) : avancées dans la connaissance de l'histoire évolutive des maras*

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## ABSTRACT

During the last decade, the taxonomic, phylogenetic, and evolutionary knowledge of the groups within Caviidae (i.e. Hydrochoerinae, Caviinae, and the stem eocardiids) has been improved and expanded. However, the evolutionary patterns of Dolichotinae are poorly known due to the lack of detailed taxonomic studies of their fossil forms. The subfamily Dolichotinae are known as patagonian mara (*Dolichotis patagonum*) and chacoan mara or “conejo de los palos” (*Dolichotis [Pediolagus] salinicola*) and, within Caviidae, are the second largest rodents after the capybaras. The subfamily presents its highest diversity in the late Miocene. *Prodolichotis* is represented by six species, but most of them have not been studied since their original description. An exhaustive description of the type species of *Prodolichotis* from the late Miocene–Pliocene of Northwest Argentina is here reported with the objective of filling the gaps and increasing the knowledge about the origin and diversification of the Dolichotinae. The phylogenetic analysis implemented here indicates that *Prodolichotis prisca* is one of the most basal species within Dolichotinae, suggesting that this group originated at least during the Miocene.

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## R É S U M É

Durant la dernière décennie, des progrès ont été accomplis quant à la taxonomie, la phylogénie et l'évolution des autres groupes au sein des Caviidae (c'est-à-dire Hydrochoerinae, Caviinae et la souche des Éocardiidés). À l'inverse, le patron évolutif des Dolichotinae est mal

## Mots clés :

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connu, en raison de l'absence d'études taxonomiques détaillées des formes fossiles. La sous-famille des Dolichotinae est connue en tant que mara de Patagonie (*Dolichotis patagonum*) et mara du Chaco ou « conejo de los Palos » (*Dolichotis [Pediolagus] salinicola*). Ce sont les deuxièmes plus grandes espèces de la famille des Caviidae après les capybaras. Cette sous-famille présente sa plus grande diversité de fossiles à la fin du Miocène en Amérique du Sud. *Prodolichotis* est représenté par six espèces au milieu du Miocène, mais la majorité d'entre elles n'ont pas été étudiées depuis leur description originelle. Avec comme objectif de combler les lacunes et d'accroître les connaissances sur l'origine et la diversification des Dolichotinae, on présente ici une description exhaustive des espèces de type *Prodolichotis* du Miocène supérieur–Pliocène du Nord-Ouest de l'Argentine. L'analyse phylogénétique mise en œuvre indique que *Prodolichotis prisca* est l'une des espèces les plus basales au sein des Dolichotinae, ce qui suggère que ce groupe est apparu au moins pendant le Miocène.

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## 1. Introduction

*Dolichotis patagonum* and *Dolichotis [Pediolagus] salinicola* inhabit in the lowland forests, shrubs, and grasslands of the Patagonia and Chaco ecoregions in the South of Bolivia and Paraguay and the North of Argentina, respectively. The distribution of both species overlaps in the center of Argentina (Cabrerá, 1953; Campos et al., 2001; Dunnun, 2015; Mares and Ojeda, 1982). They are known as Patagonian mara and chacoan mara or “conejo de los palos”, and they belong to the subfamily Dolichotinae. The average body size of *D. salinicola* is estimated at 2 kg, while for *D. patagonum* is 8 kg, thus they are the second largest rodents after the capybaras in the Family Caviidae (Álvarez et al., 2017).

Both species are terrestrial, with highly cursorial specializations such as clavicle reduction, elongated limbs, tibia, and fibula partly fused, digits reduced to three in hind limbs and four in forefeet (Campos et al., 2001; Dunnun, 2015; Ebensperger and Cofré, 2001; García-Esponda and Candela, 2016; Mares and Ojeda, 1982; Vaughan et al., 2013). The maras are diurnal and social, commonly taking shelter in vegetation, but can also occupy abandoned burrows of other mammals, or build simple burrows for breeding (Campos et al., 2001; Elissamburu and Vizcaíno, 2004; Rocha-Barbosa et al., 2015). The Patagonian maras are strongly monogamous, and breeding is communal but is not cooperative or solitary (Dunnun, 2015; Herrera, 2015; Taber and Macdonald, 1992).

The subfamily Dolichotinae is currently the least diverse within the family, but their diversity was higher in the past: fifteen extinct species in four genera (*Orthomyctera*, *Prodolichotis*, *Pliodolichotis*, and *Propediolagus*; Ameghino, 1888, 1889; Kraglievich, 1932; Ortega-Hinojosa, 1963) were described. The genera and species have complex taxonomic histories that must be clarified, with certain species considered to belong to other genus (Kraglievich, 1930; Quintana, 1996, 1997; Vucetich et al., 2015) or to other subfamily (Kraglievich, 1930; Madozzo-Jaén, 2017; Pérez and Pol, 2012; Quintana, 1998; Ubilla and Rinderknecht, 2003), but most have not been reviewed or studied since their original descriptions.

The oldest records of Dolichotinae come from the late Miocene of South America and are found in northern Brazil

(Kerber et al., 2017; Pérez et al., 2017: 17); Southeast of Uruguay (Ubilla and Rinderknecht, 2003) and central Argentina (Pascual, 1966; Vucetich and Pérez, 2011). Records of the late Miocene–early Pliocene (“Araucanense” and “Mesopotamian” faunas) come from the Northwest and Northeast of Argentina, and Neogene of La Rioja and Catamarca provinces (Kraglievich, 1932; Madozzo-Jaén et al., 2013; Powell et al., 1998; Rodríguez-Brizuela and Tauber, 2006; Rovereto, 1914). Many of these records belong to isolated teeth and fragmentary remains that have not been studied or specifically assigned to date. In addition, Dolichotinae species were recorded in the middle Miocene of Colombia (Fields, 1957; Walton, 1997), but their taxonomic assignment and phylogenetic position are currently under discussion (Pérez and Pol, 2012).

Divergence time estimates for Hydrochoerinae and Dolichotinae using a relaxed molecular clock yielded 13.2 Ma (Upham and Patterson, 2015) and 15.5 Ma (Opazo, 2005). The ghost lineage of Dolichotinae extends from the middle Miocene (13.5–11.8 Ma; Laventan, South American Land Mammal Age [SALMA]) to the middle Pliocene (3.7 Ma, Chapadmalan SALMA) according to the fossil remains considered in the phylogenetic hypothesis of Pérez and Pol (2012). One study with a wide taxon sampling retract the divergence to the Mayoan (approximately 12 Ma; Madozzo-Jaén and Pérez, 2017).

While in the last years progress has been made in the taxonomic, phylogenetic and evolutionary knowledge of other groups within Caviidae (Hydrochoerinae, Caviinae, and the stem eocardiids, Madozzo-Jaén, 2017; Madozzo-Jaén and Pérez, 2017; Madozzo-Jaén et al., 2018; Pérez, 2010a, 2010b; Pérez and Vucetich, 2011; Pérez et al., 2014, 2017; Vucetich and Pérez, 2011; Vucetich et al., 2014, 2015), the evolutionary pattern of Dolichotinae is practically unknown due to the lack of detailed taxonomic studies of their fossil forms. An exhaustive anatomical description of *Prodolichotis prisca* is here reported, aiming at filling such gaps and increasing the knowledge about the taxonomy, origin, and diversification of Dolichotinae. Further, the taxon is included in a phylogenetic analysis (modified from Madozzo-Jaén et al., 2018) to test its validity and its relationships with other Dolichotinae and Caviidae. In addition, the first analysis of the origin and time of diversification of Dolichotinae is carried out.

## 2. Materials and methods

### 2.1. Institutional abbreviations

FMNH-P or FMNH-PM: Paleontological Collection, Field Museum of Natural History, Chicago, USA; MACN-Pv: “Museo Argentino de Ciencias Naturales Bernardino Rivadavia”, “Colección Paleontología de Vertebrados, Ciudad Autónoma de Buenos Aires”, Argentina; MCH-P: “Museo Arqueológico Provincial Condor Huasi Sección Paleontología”; Catamarca, Argentina; PVL: “Colección de Paleontología de Vertebrados Lillo”, Tucumán, Argentina.

### 2.2. Anatomical and dental nomenclature

The cranial nomenclature follows [Cherem and Ferigolo \(2012\)](#) and the dental nomenclature follows [Pérez \(2010a, 2010b\)](#). The endocast nomenclature follows [Dozo \(1997a, 1997b\)](#) and [Campos and Welker \(1976\)](#).

### 2.3. Anatomical abbreviations

**Skull measurements.** aP4: alveolar protuberance of P4; app: paraoccipital apophysis; arf: anterior retroarticular foramen; av: auditory-visual sulcus; bc: crest of basioccipital; Be: basisphenoidal; Bo: basioccipital; cnd: nuchal dorsal crest; cnv: nuchal ventral crest; co: occipital condyle; cs: sagittal crest; ec: ectosylvian convolution; Ect: ectotympanic; fem: stylomastoid foramen; fit: infratympanic fenestra; fmg: magnum foramen; Fr: frontal; gc: glenoidea cavity; if: incisor foramen; ihs: interhemispheric sulcus; iv: intervisual sulcus; La: lacrimal; ls: lateral sulcus; mae: external auditory meatus; mc: marginal convolution; Mx: maxilla; Na: nasal; Pa: parietal; pce: caudal process of squamosal; pet: epitympanic sinus; Pl: palatine; pmp: mastoid of petrous; Pre: presphenoid; prf: posterior retroarticular foramen; Prmx: premaxilla; Pt: pterygoid; ptf: pterygoid fossa; pts: temporal of supraoccipital process; rdm: dorsal root of the zygomatic process; rvm: ventral root of the zygomatic process; Sq: squamosal; ss: sylvian or suprasylvian sulcus; ssc: suprasylvian convolution; to: temporal orifice of temporal meatus; vep?: sphenopalatine vacuities.

**Mandible measurements.** df: dorsal fossa; ias: incisive alveolar sheath; nMpi: masseter medialis pars infraorbitalis muscle.

**Dental abbreviations.** al: anterior lobe; ap4: anterior projection of anterior lobe of p4; c: cement; dc: dentine crest; e: enamel; FH<sub>y</sub>: longitudinal furrow opposite to hypoflexus; Hy: hypoflexus; M1/m1: upper/lower first molar; M2/m2: upper/lower second molar; M3/m3: upper/lower third molar; P4/p4: upper/lower fourth premolar; pl: posterior lobe; pp: posterior projection of M3.

### 2.4. Phylogenetic analysis

To test the affinities of *P. prisca* within Caviidae, a cladistic analysis using a modified version of the combined dataset of [Madozzo-Jaén et al. \(2018\)](#) was performed. *P. prisca* and three characters were added to the dataset. The combined matrix ([Supplementary Online Material 1](#))

for this analysis resulted in 65 taxa, 143 morphological characters, and 4014 characters from DNA sequences ([Supplementary Online Material 2](#)). The equally weighted parsimony analysis was conducted using TNT 1.1 ([Goloboff and Catalano, 2016](#)), performing a heuristic search of 1000 Wagner tree replicates, followed by TBR branch swapping, collapsing zero-length branches under the strictest criterion. Support values were calculated using bootstrap and jackknife.

## 3. Systematic paleontology

Rodentia Bowdich, 1821  
 Hystricognathi Tullberg, 1899  
 Cavoidea Fischer, 1817  
 Caviidae Fischer, 1817  
 Dolichotinae Pocock, 1922  
***Prodolichotis* Kraglievich, 1932**  
*Type species.* *Dolichotis prisca* Rovereto, 1914  
*Prodolichotis prisca* (Rovereto, 1914)

1914 *Dolichotis prisca* Rovereto: 60, IV pl., fig. 4.

**Holotype.** MACN-Pv 8348, relatively complete skull; it lacks the anterior most part of the rostrum, the left zygomatic arch and a fragment of right maxilla with the complete dental series.

**Referred specimens.** MACN-Pv 8346, skull fragment with left P4–M1 and M3 and right P4–M3; MACN-Pv 8347, skull fragment with left P4 and anterior lobe of M1, and right P4–M2 and fragment of the anterior lobe of M3.

**Tentatively referred specimens.** FMNH-PM 1095, left mandible fragment with incisor, m2 and anterior lobe of m1 and m3; FMNH-P 14335, right mandible fragment with m1 or m2; FMNH-P 14336, right mandible fragment with incisor and p4–m2; MCH-P 96, left mandible fragment with p4–m2; PVL 3180, right mandible fragment with p4–m1; PVL 3302, left mandible fragment with p4–m2; PVL 4930, right mandible fragment with p4–m2; PVL 4931, left mandible fragment with m1–m3.

### 3.1. Geographic and stratigraphic distribution

*P. prisca* was described based on remains found in Andalhuala locality, Santa María Valley, Catamarca Province ([Fig. 1](#)) (see MACN sheet) with no accurate stratigraphic position (Araucanense, Rovereto, 1914). One dating (<sup>40</sup>Ar–<sup>39</sup>Ar) obtained in Santa María Valley, at the boundary between Las Arcas–Chiquimil formations (under the Andalhuala Formation) yielded an age of 6.88 Ma ± 0.06 ([Georgieff et al., 2014](#); [Spagnuolo et al., 2015](#)). The lower third of the Andalhuala Formation yielded an age of 6.02 ± 0.04 Ma ([Marshall et al., 1979](#)), and the upper limit was dated between 4.85 ± 0.70 Ma and 3.4 ± 0.6 Ma ([Strecker et al., 1989](#); see [Georgieff et al., 2017](#)).

Certain remains tentatively assigned to *P. prisca* in this study present more precise stratigraphic data ([Figs. 1 and 2](#)):

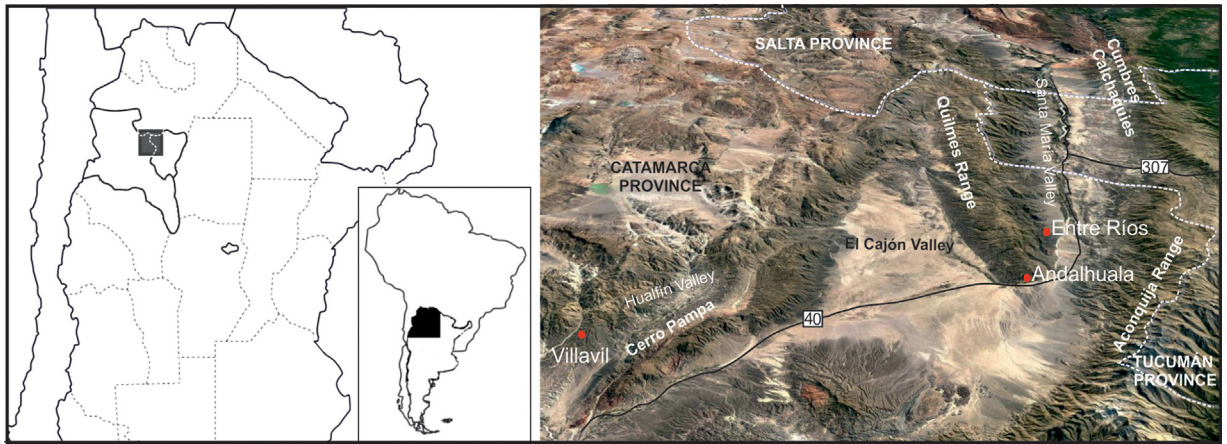


Fig. 1. Location map of the geographic distribution of *Prodolichotis prisca* in northwestern Argentina.

Fig. 1. Carte de localisation de la distribution géographique de *Prodolichotis prisca* dans le Nord-Ouest de l'Argentine.

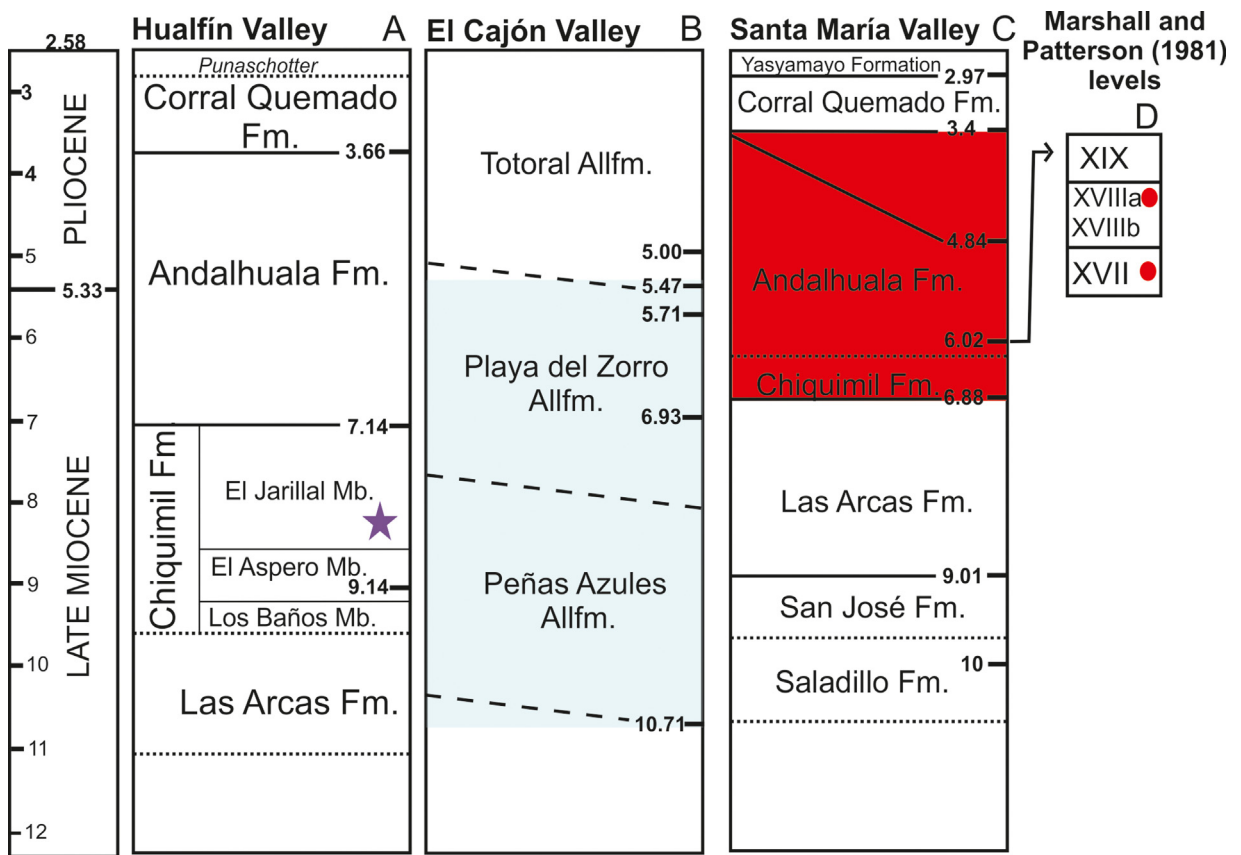


Fig. 2. Schematic synthesis of the lithostratigraphy and chronology of the late Miocene–Pliocene outcrops in Hualfín (A), El Cajón Valley (B), and Santa María Valley (C), Catamarca and Tucumán provinces, northwestern Argentina, and levels of Marshall and Patterson (1981) (D) modified from Armella et al. (2018). Stratigraphic provenances: star, PVL 4930, PVL 4931 and MCH-P 96; gray box (light blue box), PVL 3302; dark box (red box), MACN 8348 (holotype), MACN-Pv 8346 and MACN-Pv 8347; circle, FMNH-P 14335, FMNH-P 14336 and FMNH-PM 1095. Dotted lines indicate undefined stratigraphic boundaries. Fig. 2. Synthèse schématique de la lithostratigraphie et de la chronologie des affleurements Miocène tardif–Pliocène dans les vallées de Hualfín (A), El Cajón (B) et Santa María (C), Provinces de Catamarca et Tucumán, Nord-Ouest de l'Argentine et niveaux de Marshall et Patterson (1981) (D), modifié d'après Armella et al. (2018). Provenances stratigraphiques : étoile, PVL 4930, PVL 4931 et MCH-P 96 ; boîte grise (boîte bleu clair), PVL 3302 ; boîte sombre (boîte rouge), MACN-Pv 8348 (holotype), MACN-Pv 8346 et MACN-Pv 8347 ; cercle, FMNH-P 14335, FMNH-P 14336 et FMNH-PM 1095. Les lignes pointillées indiquent les limites stratigraphiques non définies.



- Hualfin Valley (Villavil, Catamarca): PVL 4930, PVL 4931, and MCH-P 96 were found in El Jarillal, Member of the Chiquimil Formation. These sediments were dated with  $^{40}\text{Ar}-^{39}\text{Ar}$ , and yielded an age of  $9.14 \pm 0.09$  Ma (Sasso, 1997) for El Áspero Member (under El Jarillal Member) in Villavil locality. In the same valley, at Puerta de Corral Quemado locality, dating was performed at the limit between Andahuala and Chiquimil formations in  $7.14 \pm 0.02$  Ma (Esteban et al., 2014; Latorre et al., 1997; Sasso, 1997);
- Cajón Valley (El Molle, Catamarca): PVL 3302 comes from sediments with no stratigraphic data. In the northern area of this valley dating yielded ages of  $10.7 \pm 1.7$  Ma, while in the southern area it yielded ages of  $5.71 \pm 0.4$  Ma (Bossi et al., 2001; Strecker et al., 1989). Dating of the middle region yielded ages of  $6.93 \pm 0.08$  Ma and  $5.47 \text{ Ma} \pm 0.9$  (Schoenbohm et al., 2015; for stratigraphic position see Georgieff et al., 2017). However, the datings performed in this valley were not included in the profiles or mapped correctly. For further discussion about this, see Georgieff et al. (2017);
- Santa María Valley, (Entre Ríos, Catamarca): FMNH-P 14335 and FMNH-P 14336 come from the XVII level, and FMNH-PM 1095 comes from the XVIIIa level (Marshall and Patterson, 1981), both immediately located below the 6.02 Ma dating (XIX level in Marshall and Patterson, 1981). Therefore, a late Miocene-early Pliocene age is inferred for *P. prisca* (see § Discussion below).

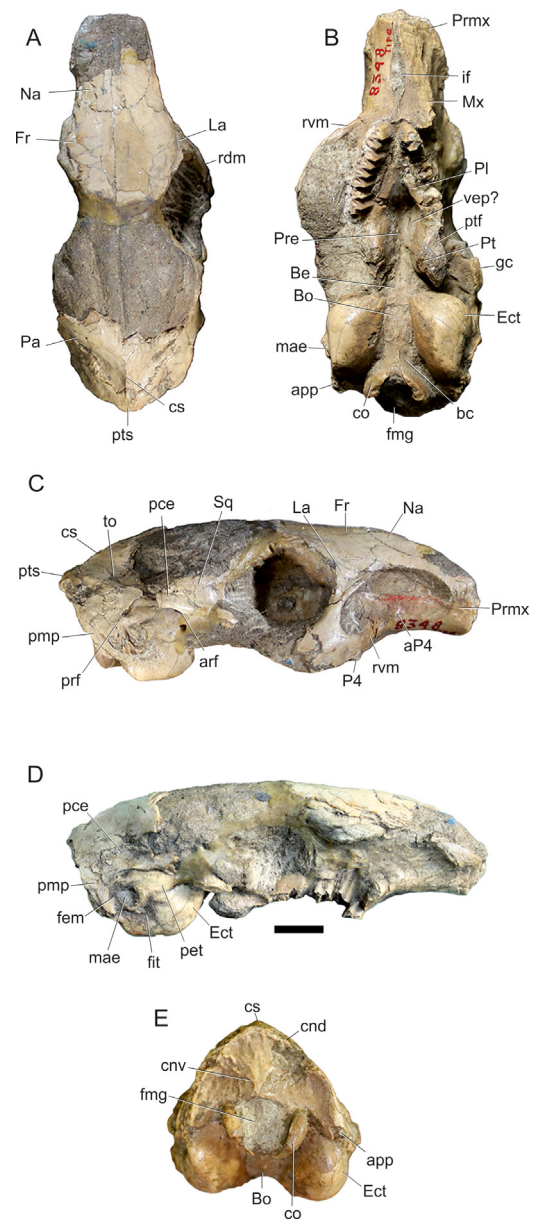
### 3.2. Extended diagnosis

*P. prisca* is characterized by a unique combination of characters (autapomorphies marked with an asterisk): molariforms with longitudinal furrow opposite to the hypoflexus; HSE and HPE absent, as in other Dolichotinae. \*P4 anteroposteriorly shorter than M1, M1 shorter than M2 and M2 shorter than M3; posterior projection of M3 posteriorly elongated, unlike *Dolichotis* and “*Orthomyctera*” *chapalmalense*. \*Upper masseteric fossa deeper than *Dolichotis* and “*Orthomyctera*” *chapalmalense*; nasolacrimal foramina closed in lateral view of the rostrum as in other Dolichotinae and unlike Caviinae. Dorsal projection of the premaxilla extending anteriorly to the level of P4; apex of mesopterygoid fossa extends up to M2 or slightly anteriorly; temporal fossa deeper than *Dolichotis* and “*Orthomyctera*” *chapalmalense*.

### 3.3. Description and comparison

Most of the anatomical knowledge about *P. prisca* is based on cranial remains (Figs. 3 and 4). The skull size is similar to *Dolichotis salinicola*, larger than *Cavia* and smaller than *D. patagonum* and “*Orthomyctera*” *chapalmalense*.

**Nasal.** Only the posterior most part of the nasal is preserved. This bone is relatively wider than in *Cavia apera*, *Microcavia australis*, *Galea musteloides*, and *D. salinicola*, and laterally contacts the premaxilla. Posteriorly, the nasal-frontal suture is anteriorly concave (U-shaped) and extends anteriorly to P4 at the same level of the root of the zygomatic arch (Fig. 3A). The suture differs from “*Orthomyctera*”

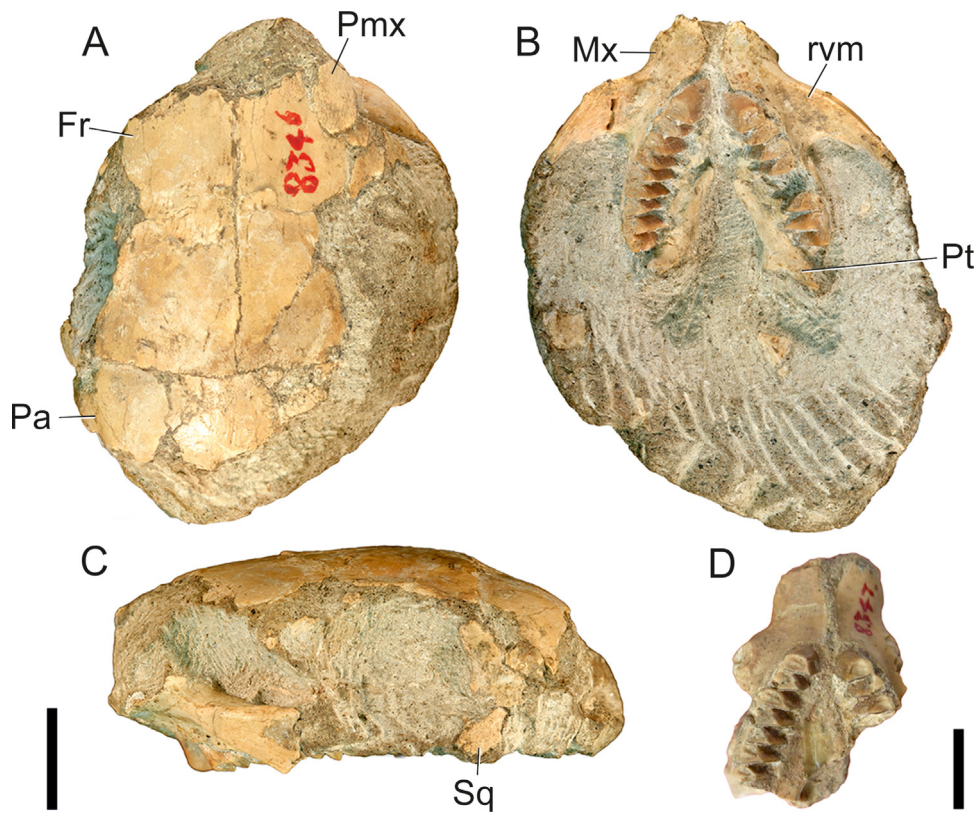


**Fig. 3.** *Prodolichotis prisca*, MACN-Pv 8348 (Holotype), dorsal view (A), ventral view (B), lateral view (C, D reflected), occipital view (E). Scale bar = 10 mm. See anatomical abbreviations.

**Fig. 3.** *Prodolichotis prisca*, MACN-Pv 8348 (Holotype), vue dorsale (A), vue ventrale (B), vue latérale (C, D réfléchi), vue occipitale (E). Barre d'échelle = 10 mm. Voir les abréviations anatomiques.

*chapalmalense* and *Dolichotis* in which it is straight, hexagonal or curved; and from *Cavia* in which it is quite variable (V-shaped, straight, hexagonal or curved).

**Premaxilla.** The dorsal process of the premaxilla is preserved, lacking most of the anterior part of the rostrum (Figs. 3A and 4A). In lateral view, the dorsal process does not exceed the level of P4, in contrast to *M. australis*, *Dolichotis* and “*Orthomyctera*” *chapalmalense*, in which the projection extends posteriorly to P4. The dorsal process of *P. prisca* is posteriorly wider than in *D. salinicola*, and differs from



**Fig. 4.** *Prodolichotis prisca*, MACN-Pv 8346 (A–C), MACN-Pv 8347 (D), dorsal view (A), ventral view (B, D), lateral view (C). Scale bar = 10 mm. See anatomical abbreviations.

**Fig. 4.** *Prodolichotis prisca*, MACN-Pv 8346 (A–C), MACN-Pv 8347 (D), vue dorsale (A), vue ventrale (B, D), vue latérale (C). Barre d'échelle = 10 mm. Voir les abréviations anatomiques.

*D. patagonum* in which it is not posteriorly expanded. The premaxilla-maxilla suture is V-shaped in the middle of the rostrum. The masseteric fossa for the insertion of the pars profunda of the masseter muscle (Fig. 3C) is deeper than in *Dolichotis*, “*Orthomyctera*” *chapalmalense*, and *cavies* are shallower than in *H. hydrochaeris*. In lateral view, the dorsal contour of the masseteric fossa is formed mostly by the premaxilla, unlike *Dolichotis*, in which this margin coincides with the premaxillary-maxillary suture.

In ventral view, the incisive foramen is sharp as in *C. aperea*, *G. musteloides*, *Dolichotis* and “*Orthomyctera*” *chapalmalense*. Sixty-four percent of this foramen extends inside the premaxilla in *P. prisca* (Fig. 3B), differing from “*O.*” *chapalmalense* and *Dolichotis*, in which this proportion is 74% and 83%, respectively.

**Maxilla.** The posterior portion of the rostrum, the anterior part of the zygomatic arch and a portion of palate are preserved. In lateral view, the masseteric fossa is widely extended in the rostrum and it is deeper than in *Dolichotis*, “*Orthomyctera*” *chapalmalense*, and *cavies*. The nasolacrimal foramen is not laterally open in the rostrum (Fig. 3C, D) as in *Dolichotis*, “*O.*” *chapalmalense*, and unlike *Caviinae* and *Hydrochoerinae*, in which it is open. The ventral margin of the posterior portion of the diastema is obliquely oriented, resembling that of *C. aperea*, *Dolichotis*, and “*O.*” *chapalmalense*.

In lateral view, the dorsal root of the zygomatic arch is obliquely oriented as in *C. aperea* and *G. musteloides*, but differs from “*Orthomyctera*” *chapalmalense* and *Dolichotis* in which it is dorsoventrally oriented. The dorsal root of the zygomatic arch is complete (not interrupted by the lacrimal, Fig. 3C) similarly to “*O.*” *chapalmalense*, *D. salinicola*, and *C. aperea*, but differing from *G. musteloides*, in which the lacrimal extends up to the anterior margin of the dorsal root of the zygomatic process; in *D. patagonum* this character is variable, the lacrimal is exposed anteriorly to the dorsal root of the zygomatic arch, or it is not (Kraglievich, 1930). Anteriorly to the ventral root of the zygomatic arch, the alveolar protuberance of P4 is smaller than that of *D. patagonum*. The groove for the passage of the infraorbital nerve in the maxilla is absent, as in *Dolichotis* and “*O.*” *chapalmalense*, and in contrast to *Caviinae*, in which it is present.

The orbital portion is poorly preserved, the holotype presents only a fragment of the side wall corresponding to the alveolar protuberance of M3 (Fig. 3C). This protuberance posteriorly extends at least up to the interorbital constriction, differing from *Dolichotis* and “*Orthomyctera*” *chapalmalense*, in which it extends anteriorly to the interorbital constriction.

In ventral view (Figs. 3B and 4B, D) the posterior margin of the incisive foramen is sharpened, and in the holotype

a fragment of vomer can be seen in such margin of the incisive foramen. The intermaxillary suture forms a small flange as in “*Orthomyctera*” *chapalmalense* and *Dolichotis* and the ventral root of the zygomatic arch is at the level of P4. The maxillary portion of the palate (Figs. 3B and 4B, D) is small as in the other *Dolichotinae*, and differs from *cavies*, in which it is more posteriorly extended.

**Frontal.** In dorsal view, a fragment of frontal is preserved (Figs. 3A and 4A). The anterior margin of the nasal process is triangular in shape and slightly smaller than that of *D. patagonum*. The frontal is plane as in “*Orthomyctera*” *chapalmalense* and *Dolichotis*, but differs from *C. aperea* and *G. musteloides* in which the posterior portion of the frontal is convex. The interorbital constriction seems to be wider than in *cavies*, but the lateral margin of the frontal is broken. In lateral view, the orbital portion is concave, but it is poorly preserved in all specimens (Figs. 3A and 4A).

**Lacrimal.** This bone is not exposed anteriorly in the dorsal root of the zygomatic arch (Fig. 3C). Ventrally, it contacts the maxilla as in *D. salinicola*, “*Orthomyctera*” *chapalmalense*, and *cavies*; in some specimens of *D. patagonum*, the lacrimal contacts ventrally the jugal. The orbital portion is anteriorly concave, and the lacrimal-frontal suture and lacrimal foramen are not clearly preserved (Fig. 3C).

**Parietal.** The most anterior and posterior portions of this bone are preserved (Figs. 3A and 4A). The frontal-parietal suture is straight and in the posterior portion, the sagittal crest is well-developed and extends up to the supraoccipital. The temporal fossa is deeper than in *cavies*, *Dolichotis*, and “*Orthomyctera*” *chapalmalense*. At the level of the external auditory meatus, a temporal foramen (temporal orifice of the temporal meatus sensu Popesko et al., 1992) is immediately above the parietal-squamosal suture (Fig. 3C, D).

**Palatine.** A fragment of palatine is preserved in the palate. It is V-shaped and the maxilla-palatine suture is not clear, but two foramina are present in the anterior apex; the apex of the mesopterygoid fossa extends up to M2 or slightly anteriorly (Fig. 3B) as in *Dolichotis* and “*Orthomyctera*” *chapalmalense*, but in most *Caviinae* it extends posteriorly up to M3. The outline of the sphenopalatine vacuity is not clear, but it is likely to be at the level of M3, although this cannot be confirmed in the type specimen of *P. prisca* (Fig. 3B). In that case, it is more anterior than in *C. aperea*, *Dolichotis* and “*O.*” *chapalmalense*, in which it is at the level of the pterygoid fossa (or alar canal sensu Popesko et al., 1992). The pterygoid fossa is triangular in outline, with the anterior and lateral portion formed by the palatine, and the medial part formed by the pterygoid (Fig. 3B).

**Squamosal.** This bone preserves the zygomatic and auditive portions (Fig. 3C, D). The caudal process is dorsal to the tympanic bullae and it is anteroposteriorly straight, with the posterior portion slightly curved ventrally. The squamosal-supraoccipital suture extends posteriorly to the auditory meatus (Fig. 3C, D). The caudal process of the squamosal (pce) is large, similarly to *D. patagonum* and “*Orthomyctera*” *chapalmalense*, but differs from *D. salinicola* in that it is anteroposteriorly shorter; the posterior portion is more curved and expanded than in *P. prisca*. The pce of *cavies* is more curved and dorsoventrally shorter than

in *P. prisca*. Two retroarticular foramina between the pce and the ectotympanic are present in *P. prisca*. The anterior foramen is a fissure in the anterior portion of the tympanic bulla, and the posterior foramen is larger and oval-shaped as in *Dolichotis* (Fig. 3C, D).

**Ectotympanic.** The tympanic bullae are ovoid (Fig. 3B–E); in ventral view, the anteromedial-posterolateral axis of the tympanic bulla is approximately 33% of the length between the premaxillary-maxillary suture and the anterior border of the foramen magnum (Fig. 3B). This proportion is similar to *D. salinicola* and larger than *D. patagonum* and “*Orthomyctera*” *chapalmalense*. The *Caviinae* present the biggest tympanic bullae within *Caviidae*, except for *C. aperea*, in which such proportion is similar to that of *D. patagonum* (see Madozzo-Jaén et al., 2018).

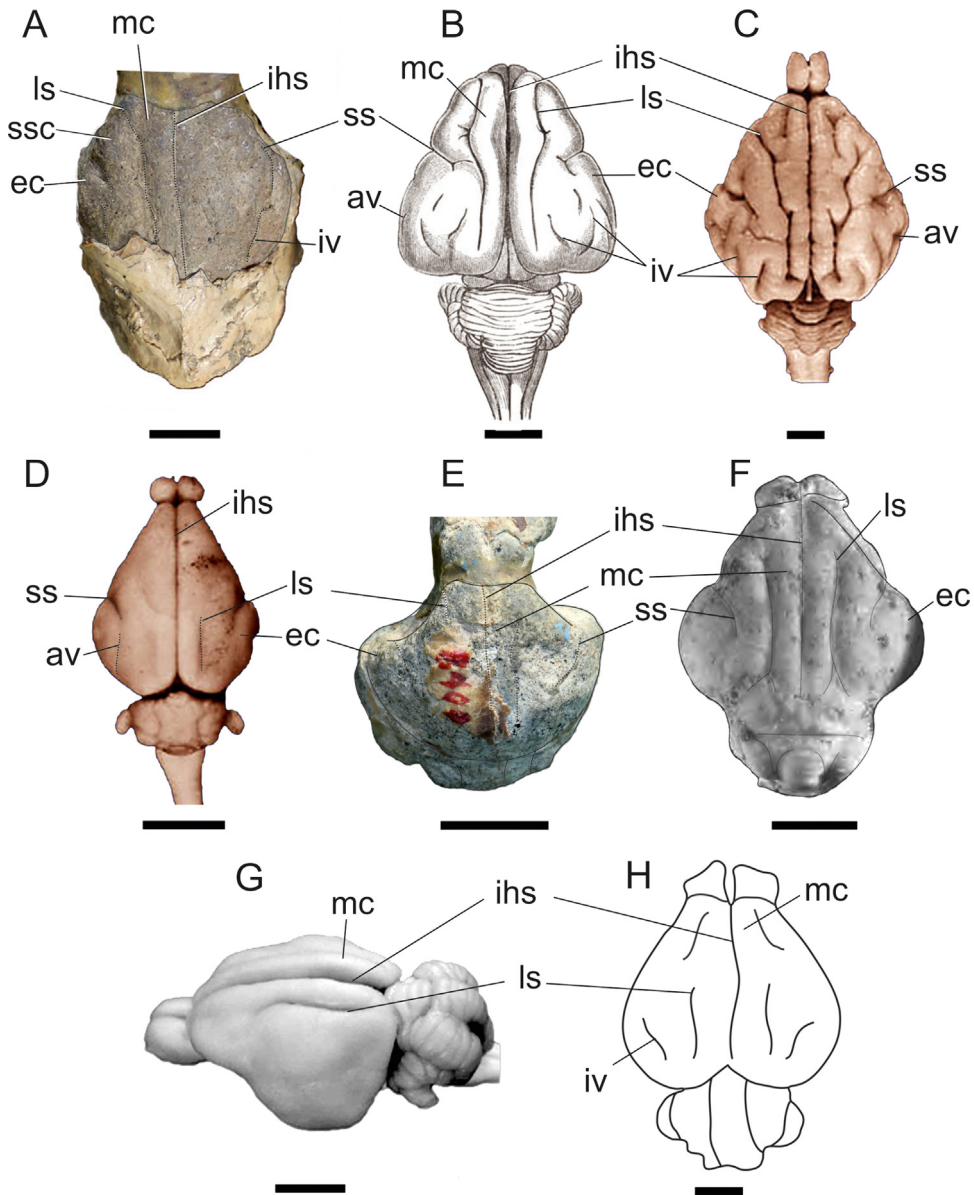
In lateral view (Fig. 3C, D), the epitympanic portion of the petrous or epitympanic sinus (pet) is bullet-shaped as in *Dolichotis* and “*Orthomyctera*” *chapalmalense*, but differs from *D. patagonum* in that the pet is more gracile and less convex. The external auditory meatus is at the level of the dental series as in *Dolichotis* and “*O.*” *chapalmalense*, but differs from *M. australis* in which it is below the dental series. The circular infratympanic fenestra is located anteroventrally to the mae, and it is smaller; both foramina appear to be completely separated as in *M. australis*, but differ from *Dolichotis* and *Cavia*, in which both foramina can be connected. The stylomastoid foramen is at the same level as the mae, posteriorly to them, and smaller (Fig. 3C, D). The mastoid portion of the petrous is exposed laterally, dorsoventrally oriented; and it is plane in all extension as in *Dolichotis* and “*O.*” *chapalmalense*, differing from *cavies* in that its ventral region is convex and exposed laterally and posteriorly.

**Presphenoid and basisphenoid.** These bones are completely fused; both are long and narrow, wider at their posterior end, and the basisphenoid contacts posteriorly the basioccipital (Fig. 3B). The basisphenoid is dorsoventrally flattened and has two small posterior ridges. The presphenoid and basisphenoid form the middle and posterior part of the roof of the mesopterygoid fossa.

**Occipital complex.** The supraoccipital has a temporal process exposed dorsally, which contacts anteriorly the parietal, and lateroventrally with the caudal process of the squamosal as in *Dolichotis* (Fig. 3A,C). In posterior view, the dorsal nuchal and external occipital crests are small, but the ventral nuchal crest is developed with a triangle shape (Fig. 3E). The magnum foramen is straight in dorsal margin as some specimens of *D. salinicola*. There is a preserved portion of the paraoccipital process that is prolonged up to the level of the inferior border of the occipital condyle (Fig. 3D–E). Ventrally, the basioccipital is posteroventrally inclined and rectangular in section with a low ridge in the back half, and it is fused with the occipital condyles.

**Endocast.** MACN-PV 8348 preserves the neocortex (Fig. 5A). The endocast is giroencephalic with neocortical fissuration with the primary and secondary furrows. The telencephalic hemisphere is divided into three convolutions (marginal, suprasylvian, and ectosylvian) by the interhemispheric, lateral and sylvian or suprasylvian sulci (Dozo, 1997a) as in other *caviids*. The endocast of





**Fig. 5.** Endocast of Caviioidea, *Prodolichotis prisca* (A), *Dolichotis patagumun* (B), *Hydrochoerus hydrochaeris* (C), *Cavia porcellus* (D), *Neocavia lozanoi* (E), *Dolicavia minuscula* (F), *Dasyprocta primnolopha* (G), *Cuniculus paca* (H). Modified from Beddard (1891) (B), taken from <http://brainmuseum.org/> (C, D), modified from Madozzo-Jaén et al. (2018) (E), modified from Dozo (1997a, 1997b) (F, H), modified from Elston et al. (2006) (G). Scale bar = 10 mm.

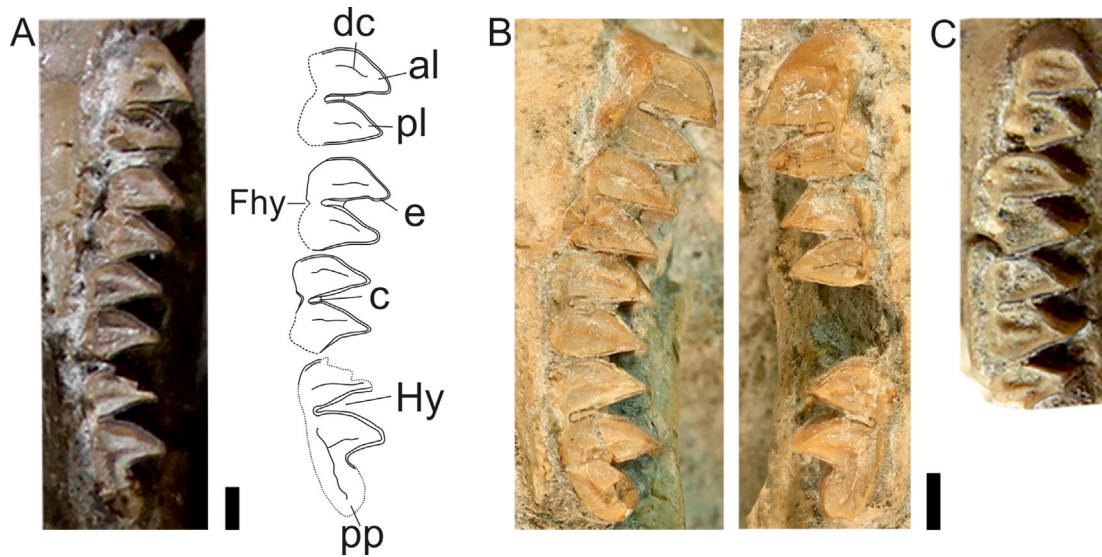
**Fig. 5.** Endocast of Caviioidea, *Prodolichotis prisca* (A), *Dolichotis patagumun* (B), *Hydrochoerus hydrochaeris* (C), *Cavia porcellus* (D), *Neocavia lozanoi* (E), *Dolicavia minuscula* (F), *Dasyprocta primnolopha* (G), *Cuniculus paca* (H). Modifié d'après Beddard (1891) (B), modifié d'après <http://brainmuseum.org/> (C, D), modifié d'après Madozzo-Jaén et al. (2018) (E), modifié d'après Dozo (1997a, 1997b) (F, H), modifié d'après Elston et al. (2006) (G). Barre d'échelle = 10 mm.

*P. prisca* is similar to that of *Dolichotis* but with less developed convolutions than that of *Hydrochoerus* (Fig. 5A–C, Campos and Welker, 1976; Dozo, 1997b). In *P. prisca*, it is rhomboid as in other Caviioidea; the ectosylvian convolution is similar to that of *Dolichotis*, less developed than in *Neocavia* and *Dolicavia* (Fig. 5E–F, Dozo, 1997a). The lateral sulcus extends anteriorly up to the telencephalic margin, as in *Dolichotis* and *Hydrochoerus*, but unlike *Cavia*, *Dolicavia*, and *Dasyprocta*, in which it does not reach the anterior margin (Fig. 5B–G). Further, it differs from *Dolicavia* and *Hydrochoerus* in that the lateral

sulcus is not caudally bifurcated. The suprasylvian sulcus (somatic-auditory sulcus sensu Campos and Welker, 1976) is anterolaterally-posteromedially oriented, and located between the somatic sensorial and auditory region, as in other caviids, differing from *Cuniculus* and *Dasyprocta* in which the suprasylvian sulcus is not present (Fig. 5G and H).

*P. prisca* has an intervisual sulcus between the lateral sulcus and the lateral margin of the endocast (Fig. 5A); this sulcus is present also in *Dolichotis*, *Hydrochoerus*, and *Cuniculus* but is absent in *Neocavia*, *Dolicavia*, and





**Fig. 6.** Upper dental series *Prodolichotis prisca*, MACN-Pv 8348 (Holotype) (A), MACN-Pv 8346 (B), MACN-Pv 8347 (C). Scale bar = 2 mm. See anatomical abbreviations.

**Fig. 6.** Série dentaire supérieure *Prodolichotis prisca*, MACN-Pv 8348 (Holotype) (A), MACN-Pv 8346 (B), MACN-Pv 8347 (C). Barre d'échelle = 2 mm. Voir les abréviations anatomiques.

*Dasyprocta* (Fig. 5B–C, E–H). The telencephalon of *Hydrochoerus* and *Dolichotis* is more complex than that of other Caviidae (Fig. 5B and C). The auditory-visual sulcus is located between the auditory and visual regions and the intersulci (iv2–iv3 sensu Campos and Welker, 1976: 253) in the visual region, more medially than the auditory-visual sulcus. In *Cavia*, the auditory-visual sulcus is present (Campos and Welker, 1976); nevertheless, certain authors do not differentiate it from the ectosylvian sulcus (Hatakeyama et al., 2017).

**Upper molariforms.** The dental series are anteriorly convergent (Fig. 6A–C). The upper molariforms are euhypsodont, with a constriction in the apex of each lobe and with a transverse dentine crest in the middle of the occlusal surface of each lobe, as in other Caviinae and Dolichotinae. The hypoflexus is funnel-shaped with cement; the enamel is continuous around the entire crown, but it is interrupted on the labial side, except in the furrow opposite to the hypoflexus, as in *Dolichotis* and “*Orthomyctera*” *chapalmalense* (Fig. 6A–C). The upper molariforms have a longitudinal furrow opposed to the hypoflexus, and the other flexi (HPE and HSE) are absent, as in *Dolichotis* and “*O.*” *chapalmalense*, differing from Caviinae in which the HSE (*Cavia*, *Microcavia*, *Palaeocavia*, *Neocavia*, *Dolicavia*) and HSE and HPE (*Galea*) are present.

The molariforms are double heart-shaped, but are less similar between each other than in *Dolichotis* and “*Orthomyctera*” *chapalmalense*. The anteroposterior length of P4 is larger than M1, M1 is lower than M2 (Table 1), unlike that of *C. aperea*, *Dolichotis*, and “*O.*” *chapalmalense*, in which M1 and M2 are approximately equal. The M3 is the largest tooth; and it presents an elongated posterior projection (Fig. 6A, B) similar to that of *Dolicavia* and *Neocavia*. It differs from *M. australis*, *Dolichotis* and “*O.*” *chapalmalense* in which the ppM3 is rounded as an incipient lobe, and from

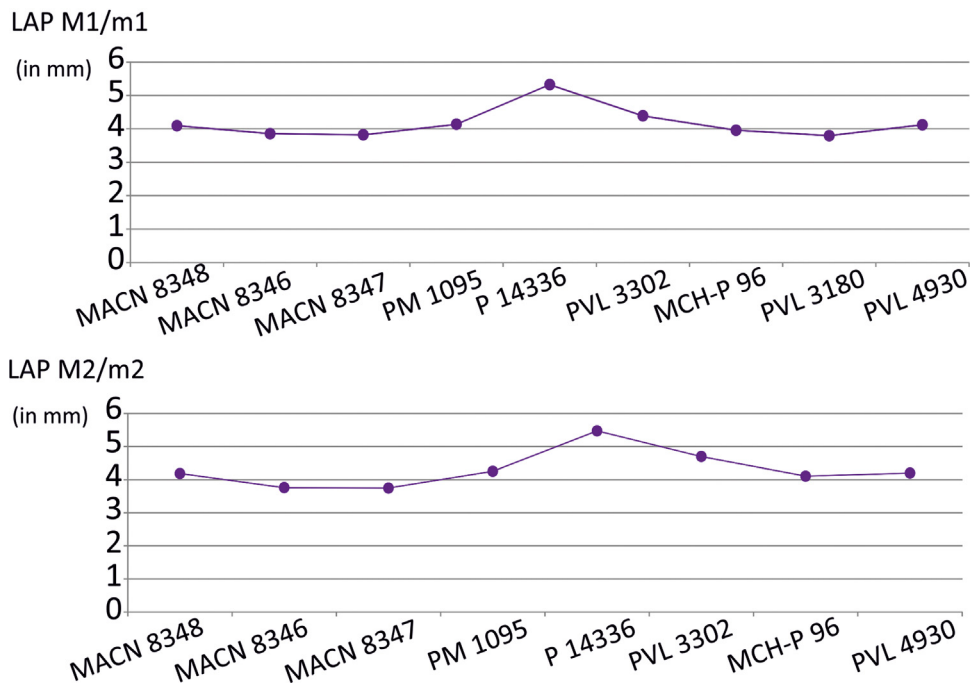
*C. aperea* in which the ppM3 is very short. The anteroposterior length of the anterior lobe of P4 is bigger than that of the posterior lobe, and the anteroposterior lengths of the posterior lobes of M1 and M2 are bigger than those of the anterior lobe (Table 1). It differs from *Dolichotis* and “*O.*” *chapalmalense* in which the lobes of M1–M2 are equal in size.

**Mandible.** So far, only cranial material has been described for *P. prisca* (see below, Remarks section). However, certain mandibles have been previously assigned to this species (FMNH-P 14335 and FMNH-PM 1095, Marshall and Patterson, 1981), or to *Palaeocavia* sp. (FMNH-P 14336, Marshall and Patterson, 1981), or to cf. *Dolichotis* (MCH-P 96, Esteban et al., 2014) and to Caviidae indet. (PVL 3302, included in the PVL collection donated by Peirano in 1939; PVL 4930, PVL, 4931, Powell et al., 1998) as well as to other specimens found in the revised collections that are restudied here, and that can be tentatively assigned to *P. prisca* due to the morphology and size of their molariforms (Table 1, (Figs. 7 and 8). It is similar in size to that of *D. salinicola* and more robust than that of caviids. In lateral view, the dorsal margin of the diastema (Fig. 8A) is similar to that of *M. australis* and more oblique than that of *Dolichotis*. The mental foramen is located anteriorly to p4 at half the dorsoventral height of the lateral surface of the dentary, as in other caviids. The notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle is located between m1–m2, as in *M. australis*, *Dolichotis* and “*Orthomyctera*” *chapalmalense*, but it differs from *C. aperea* and *G. musteloides* in which the nMpi is between P4–m1. The horizontal crest (only preserved in PVL 3302 and PVL 4931; Fig. 8B–C) is well-developed, forming a laterally projected shelf that connects to the nMpi (Fig. 9B, C). The dorsal fossa of the horizontal crest is deeper than the nMpi (Fig. 8C and 9B).

**Table 1**Measurements (in mm) of the upper and lower molariforms of *Prodolichotis prisca* and *P. cf. prisca*.**Tableau 1**Mesures (en mm) des molariformes supérieures et inférieures de *Prodolichotis prisca* et de *P. cf. prisca*.

			MCAN 8348	MACN 8346	MACN 8347	PM 1095	P 14336	PVL 3302	MCH-P 96	PVL 3180	PVL 4930
	LAP dental series	Right		16.31							
		Left		15.94							
P4/p4	LAP	Right	4.30	4.15	4.39					3.94	
		Left	4.48	4.16	4.05			4.38	3.69		
	LLA	Right	2.21	2.22	2.03		2.44		1.72	2.06	
		Left	2.25	2.26	2.00			2.46			
	LLP	Right	2.05	1.66	2.08					1.70	
		Left	2.08	1.69	1.82			1.64	1.73		
	WAL	Right	3.45		3.28						
		Left		3.63	3.25			2.75	2.52		
	WPL	Right	3.45		3.23						
		Left		3.71	3.43			3.34	3.09		
M1/m1	LAP	Right	4.02	3.90	3.99		5.32			3.79	4.12
		Left	4.17	3.71	3.66	4.14		4.39	3.96		
	LLA	Right	1.97	2.00	1.80		2.48			1.79	1.81
		Left	2.00	1.79	1.78	1.74		1.98	1.66		
	LLP	Right	1.99	1.76	2.11		2.51			1.79	2.02
		Left	2.08	1.74	1.78	1.97		2.14	2.02		
	WAL	Right	3.42	3.64	3.73						3.77
		Left		3.30	3.72	4.27		3.65	3.79		
	WPL	Right	3.19	3.47	3.53						3.80
		Left		3.34	3.29			3.61	3.60		
M2/m2	LAP	Right	4.12	3.76	3.75		5.47				4.20
		Left	4.25			4.25		4.70	4.11		
	LLA	Right	1.86		1.63		2.61				
		Left	1.97			1.84		2.11	1.84		
	LLP	Right	2.16	1.72	1.97		2.66				
		Left	2.26			2.16		2.22	2.02		2.04
	WAL	Right	3.26		3.10						3.76
		Left				4.35		3.99			
	WPL	Right	3.45	3.22	3.12			4.05			3.76
		Left				3.57					
M3/m3	LAP	Right	6.36	5.39							
		Left	6.38	4.95							
	LLA	Right	2.05	1.64							
		Left	2.26	1.79		2.07					
	LLP	Right	3.97	3.16							
		Left	4.03	3.69							
	WAL	Right	3.01								
		Left		3.02		3.29					
	WPL	Right	2.93								
		Left		3.06							

LAP: anteroposterior length of molariforms; LLA: anteroposterior length of anterior lobe of molariforms; LLP: anteroposterior length of posterior lobe of molariforms; MACN: "Museo Argentino de Ciencias Naturales Bernardino Rivadavia"; M/m1: upper/lower first molar; M/m2: upper/lower second molar; M/m3: upper/lower third molar; P/p4: upper/lower fourth premolar; WAL: mediolateral length of anterior lobe of molariforms; WPL: mediolateral length of posterior lobe of molariforms.



**Fig. 7.** Graphic measurements of molars (LAP) of *Prodolichotis prisca* and of materials tentatively assigned to *Prodolichotis prisca* (in mm). Measurements of anteroposterior length of M1/m1 (top), measurements of anteroposterior length of M2/m2 (bottom).

**Fig. 7.** Mesures graphiques des molaires (LAP) de *Prodolichotis prisca* et des matériaux provisoirement attribués à *Prodolichotis prisca* (en mm). Mesures de la longueur antéropostérieure de M1/m1 (en haut), mesures de la longueur antéropostérieure de M2/m2 (en bas).

In lingual view (Fig. 8D–F, K–N), the incisor extends backwards to the level of the anterior lobe of m2, as in *C. aperea*, *Dolichotis*, and “*Orthomyctera*” *chapalmalense*. The pterygoid fossa is well-developed, and the mylohyoid crest is not present (Fig. 8E–F, L) as in *Dolichotis* and “*O.*” *chapalmalense*. Alveolar protuberances are present on the ventral margin (Fig. 8G).

**Lower molariforms.** The lobes are more meso-lingually elongated (Table 1, Fig. 9) than in *Dolichotis*, “*Orthomyctera*” *chapalmalense* and other species of *Orthomyctera*, in which the lobes are more rounded, and similar in shape. In addition, m1 is anteroposteriorly shorter than m2, differing from *Dolichotis* and “*O.*” *chapalmalense*, in which the anteroposterior length of m1 and m2 is similar. The anterior lobe of p4 of FMNH-P 14336, MCH-P 96 and PVL 4930 (Fig. 9E–G) presents a rounded and elongated anterior projection (app4), similarly to *D. salinicola*. The PVL 3180 and PVL 3302 (Fig. 9) present a well-developed app4 separated from the anterior lobe by a well-marked flexid, and differs from *D. patagonum*, which has an incipient lobe-shaped projection in the app4, and from *C. aperea*, which has no app4. The m3 is the largest molar, as in *Dolichotis*, “*O.*” *chapalmalense* and other species of *Orthomyctera*.

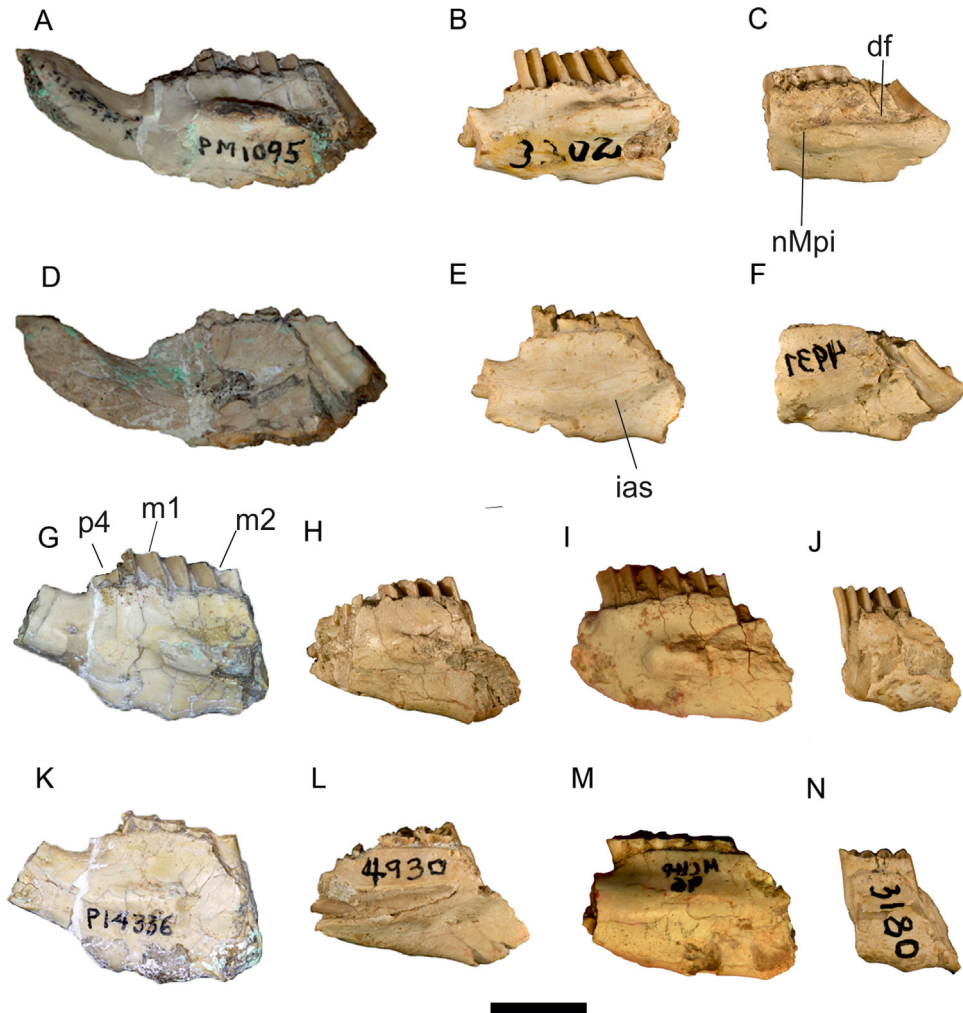
**Remarks.** *P. prisca* was described by Rovereto (1914) on the basis of a skull (MACN 8348) from the Araucanense of Santa María Valley. Kraglievich (1932) referred a mandibular fragment (MACN 8519) from Huayquerías de San Carlos, south of Mendoza Province to *P. prisca*, but this material is currently missing and such collection number corresponds to a left mandible with p2–p4, and a right mandible with p4–m3 of the Notoungulate *Pachyrukhos*.

In this revision, I do not agree with certain assignments of materials to *P. prisca* (e.g., Marshall and Patterson, 1981; Ubilla and Rinderknecht, 2003), detailed below.

FMNH-P 15288 is a mandible fragment with m1–m3 from Puerta de Corral Quemado, Catamarca without precise stratigraphic horizon (Marshall and Patterson, 1981). The anteroposterior length of m1 is similar to m2, and m3 is longer than m1 and m2, the lobes of molars are more rounded than those of *Dolichotis*, “*Orthomyctera*” *chapalmalense* and other species of *Orthomyctera*. It differs from *P. prisca*, in which the molar lobes are more elongated meso-lingually and the m1 is anteroposteriorly shorter than m2. For these reasons, I suggest that FMNH-P 15288 does not correspond to *P. prisca*.

MACN-Pv 12335 is a skull fragment with complete molariform series, coming from sediments of Río V, San Luis Province (Ubilla and Rinderknecht, 2003). This specimen shows anatomical differences with *P. prisca*. In MACN-Pv 12335, the nasolacrimal foramen is open in the lateral portion of the rostrum, unlike *P. prisca*, which has no foramen. The dorsal projection of the premaxilla extends behind the level of P4, unlike *P. prisca* in which this extension is anterior to the P4; the dorsal root of the zygomatic process of the maxilla is interrupted by the lacrimal, whereas in *P. prisca*, the lacrimal is allocated posteriorly to the maxilla. The palate is extended up to the anterior lobe of M3, and the apex of the mesopterygoid fossa is blunt and different from *P. prisca* in which the mesopterygoid fossa is V-shaped and the apex is at the level of M2. The dental series is shorter than in *P. prisca*. Based on these morphological characters and based on the diagnostic characters





**Fig. 8.** Specimens tentatively referred to *Prodolichotis prisca*, FMNH-PM 1095 (A, D reflected), PVL 3302 (B, E reflected), PVL 4931 (C, F reflected), FMNH-P 14336 (G reflected, K), PVL 4930 (H reflected, L), MCH-P 96 (I, M reflected), PVL 3180 (J reflected, N). Labial view (A–C, G–J), lingual view (D–F, K–N). Scale bar = 10 mm. See anatomical abbreviations.

**Fig. 8.** Spécimens provisoirement attribués à *Prodolichotis prisca*, FMNH-PM 1095 (A, D réfléchie), PVL 3302 (B, E réfléchie), PVL 4931 (C, F réfléchie), FMNH-P 14336 (G réfléchie, K), PVL 4930 (H réfléchie, L), MCH-P 96 (I, M réfléchie), PVL 3180 (J réfléchie, N). Vue labiale (A–C, G–J), vue linguale (D–F, K–N). Barre d'échelle = 10 mm. Voir les abréviations anatomiques.

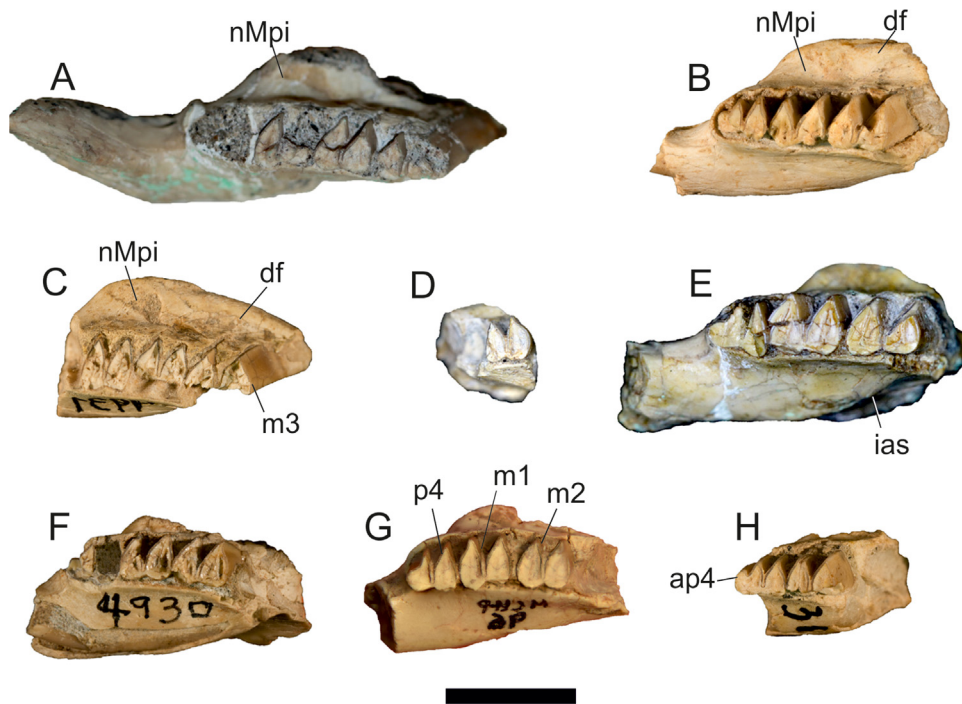
of *P. prisca* (see above) MACN-Pv 12335 does not belong to *P. prisca*.

#### 4. Phylogenetic analysis

The combined analysis resulted in a total of 2058 most parsimonious trees (MPTs), of 3351 steps. The strict consensus of all trees was calculated (Fig. 10). The synapomorphies of the phylogenetic analysis are detailed in the [Supplementary Online Material 3](#). In this analysis, the subfamily Dolichotinae (node B) was recovered as a monophyletic group, and supported by three unambiguous synapomorphies in MPT: plane palatal surface (C. 58.0); longitudinal furrow opposite to hypoflexus present (C. 80.0), and absent nasolacrimal foramina (C. 48.1). The internal relationships of Dolichotinae are resolved: *P. prisca* is the most basal Dolichotinae and

*“Orthomyctera” chapalmalense* is closely related to *Dolichotis*. The node C (“*O.*” *chapalmalense* + *Dolichotis*) is supported by two unambiguous synapomorphies in MPT: posterior projection of the posterior lobe in M3 is an incipient lobe-shaped structure (C.140.3) and the dorsal process of the premaxilla is extended posteriorly to P4 (C.38.2). The monophyly of *Dolichotis* (node D) is supported by one unambiguous synapomorphy in MPT: the dorsal end of the coronoid process is pointed and posterodorsally projected (C. 13.0).

*P. prisca* has three unambiguous apomorphies: development of the temporal fossae, deep (C. 45.2); maximum width of the anterior half of the basioccipital, 20% respect to the width of the basicranium (C. 64.0); relative size of the upper molars,  $P4 > M1 < M2$  (C. 135.1), and the upper masseteric fossa, deep (C. 49.1). Further, in agreement with previous studies (Kraglievich, 1930; Quintana, 1996, 1997;



**Fig. 9.** Molariforms of referred specimens. Lower molariforms series, FMNH-PM 1095 (A, reflected), PVL 3302 (B, reflected), PVL 4931 (C, reflected), FMNH-P 14335 (D), FMNH-P 14336 (E), PVL 4930 (F), MCH-P 96 (G reflected), PVL 3180 (H). Scale bar = 10 mm. See anatomical abbreviations.

**Fig. 9.** Molariformes des spécimens auxquels il est fait référence. Série des molariformes inférieurs, FMNH-PM 1095 (A, réfléchi), PVL 3302 (B, réfléchi), PVL 4931 (C, réfléchi), FMNH-P 14335 (D), FMNH-P 14336 (E), PVL 4930 (F), MCH-P 96 (G réfléchi), PVL 3180 (H). Barre d'échelle = 10 mm. Voir les abréviations anatomiques.

Vucetich et al., 2015), I also suggest the use of quotation marks for the name “*Orthomyctera*” *chapalmalense*, pending further studies that will transfer it to *Dolichotis*.

## 5. Discussion

### 5.1. Systematic affinities of *P. prisca*

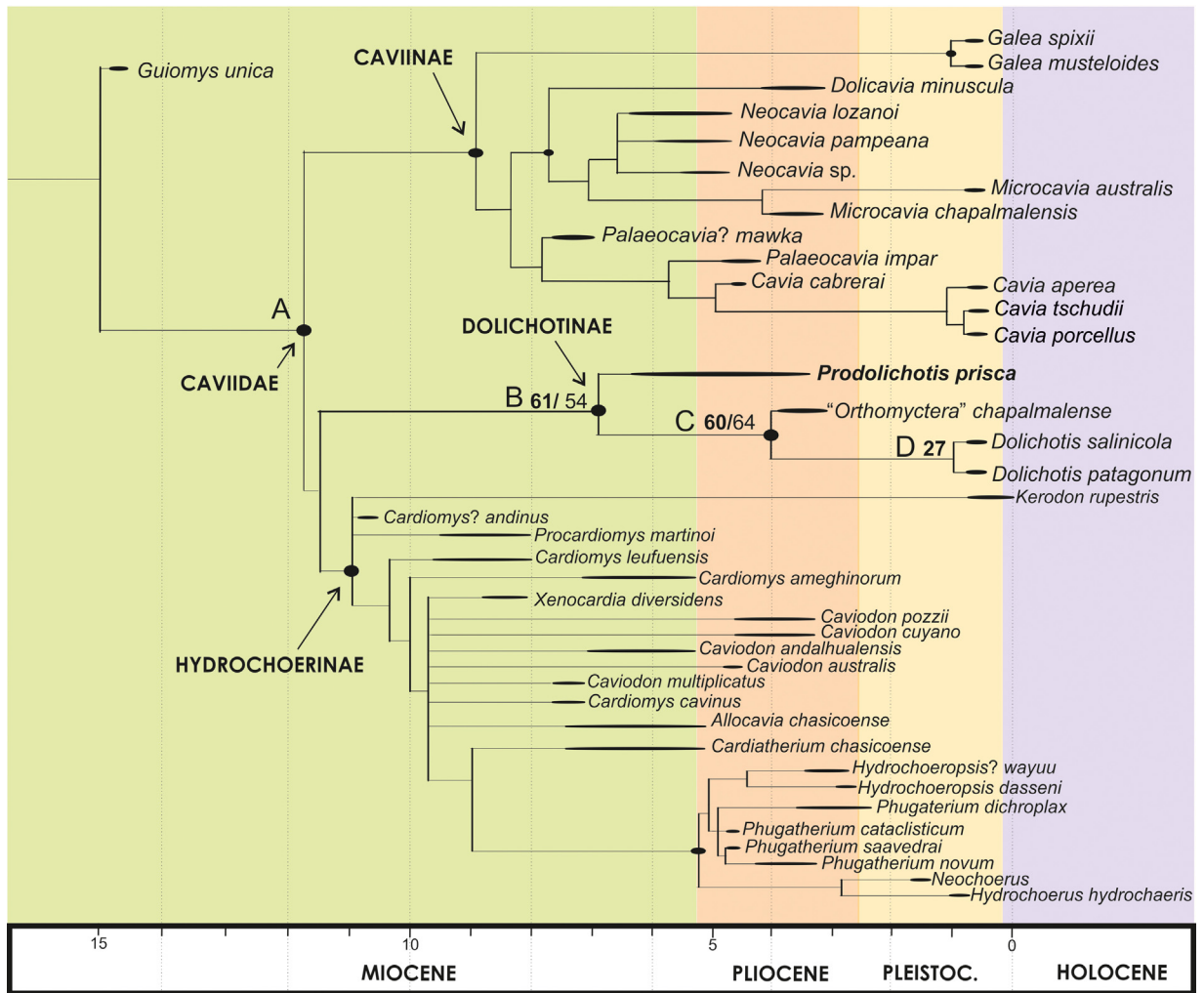
On the basis of morphological and phylogenetic studies, the validity of *P. prisca*, and its basal position in relation to *Dolichotis* are corroborated (node B, Fig. 10). *P. prisca* is undoubtedly a Dolichotinae because it shares two synapomorphies with this clade. The absence of the nasolacrimal foramen opening laterally in the rostrum differs from Caviinae and Hydrochoerinae, in which the nasolacrimal foramen opens laterally in the rostrum. Another character shared with Dolichotinae is the presence of a longitudinal furrow opposite to the hypoflexus, a plesiomorphic character present in certain “eocardiids” (e.g., *Eocardia robertoi*, *Schistomys erro*).

The basal position of *P. prisca* is justified, since it lacks certain characters present in “*Orthomyctera*” *chapalmalense* and *Dolichotis*. The dorsal process of the premaxilla is extended posteriorly to the level of P4 in “*O.*” *chapalmalense* and *Dolichotis*; this character is shared with some Caviinae (e.g., *M. australis*, *Dolicavia*) and some Hydrochoerinae (e.g., *Caviodon andalhualensis*, *Hydrochoerus hydrochaeris*). As discussed in previous papers (Quintana, 1998; Ubilla and Rinderknecht, 2003), the presence of an

incipient lobe-shaped posterior projection in M3 could be a character independently acquired in the other lineages (*M. australis*), and the condition of *P. prisca* (posteriorly extended ppM3) would be a plesiomorphic state shared with the eocardiids (e.g., *Eocardia robusta*, *Guiomys unica*).

### 5.2. Completing the ghost lineage of maras

Since the late Neogene, the Dolichotinae were already diversified in South America, with records in the North of Brazil, Southeast of Uruguay, and in the North and center of Argentina (Kerber et al., 2017; Madozzo-Jaén et al., 2013; Pascual, 1966; Pérez et al., 2017; Powell et al., 1998; Rodríguez-Brizuela and Tauber, 2006; Rovereto, 1914; Ubilla and Rinderknecht, 2003; Vucetich and Pérez, 2011). Their record occurs up to the present in Argentina (Ameghino, 1889; Kerber et al., 2011; Lema et al., 2009; Ubilla et al., 2009; Verzi and Quintana, 2005). Although the fossil diversity of Dolichotinae is greater than the present one, the actual number of species could be overestimated. These nominal species have been described on the basis of fragmentary material, and until now, none of them had been restudied, since only a few of their original descriptions were included in the phylogenetic analysis (Madozzo-Jaén, 2017; Pérez, 2010a; Pérez and Pol, 2012). For this reason, the diversity of Dolichotinae in the fossil record could be less than currently known, but certainly greater than the current diversity. The knowledge of the fossil Dolichotinae and the alpha taxonomy is crucial for



**Fig. 10.** Strict consensus from the 2058 most parsimonious trees phylogeny adjusted in time shows Caviidae node. Caviidae (node A), Dolichotinae (node B), "*Orthomyctera*" *chapalmalense* (node C)+ *Dolichotis* (node D). Numbers in bold indicate jackknife support values, numbers in italics represent bootstrap values.

**Fig. 10.** La phylogénie de consensus strict des 2058 arbres les plus parcimonieux ajustés dans le temps montre le nœud de Caviidae. Caviidae (nœud A), Dolichotinae (nœud B), "*Orthomyctera*" *chapalmalense* (nœud C)+ *Dolichotis* (nœud D). Les chiffres en gras indiquent les valeurs *jackknife*, les chiffres en italique représentent les valeurs *bootstrap*.

the understanding of the evolutionary history and significance of the acquisition of morphological characters of this group.

As mentioned above, molecular studies estimated the divergence time of the split of Hydrochoerinae and Dolichotinae between 15.5–11.8 Ma (Opazo, 2005; Upham and Patterson, 2015). Phylogenetic analyses based on molecular and anatomical characters of Caviodea estimated a ghost lineage in the early evolution of Dolichotinae of approximately 9 Ma, from the middle Miocene (11.8–13.5 Ma) to the middle Pliocene (3.7 Ma; Madozzo-Jaén and Pérez, 2017; Pérez and Pol, 2012; Vucetich and Pérez, 2011). However, due to the presence of remains (currently under study) of Dolichotinae in the middle Miocene of Colombia (Fields, 1957; Walton, 1997), an earlier origin cannot be discarded. The revision of the alpha taxonomy of *P. prisca* and its incorporation in a

phylogenetic analysis help completing a portion of the lineage of Dolichotinae, and sheds light on the evolution of living maras (Fig. 10B, Madozzo-Jaén and Pérez, 2017; Pérez and Pol, 2012). The presence of *P. prisca* in the late Miocene–early Pliocene is based on records of the holotype in Santa María Valley (6–3.5 Ma) and referred cranial materials, and not from the ages assigned to the carrier level of the mandibular remains found in nearby intermontane valleys (5 to 10 Ma), because their assignment to *P. prisca* is still preliminary, and the diversity of maras of those times is currently under revision.

### 5.3. Approach to the relationship between body size and the fissurization pattern of the telencephalon

In rodents, certain studies of the endocast were performed on extant species (e.g., Campos and Welker, 1976;



**Table 2**

Presence (p) and absence (–) of neocortical sulcus and estimated body size (in grams) according to different authors.

**Tableau 2**

Présence (p) et absence (–) du sulcus néocortical et taille du corps estimée (en g), selon différents auteurs.

	Interhemispheric sulcus (ihs)	Lateral sulcus (ls)	Suprasylvian sulcus (ss)	Intervisual sulcus (iv)	Auditory-visual sulcus (av)	Dozo (1997a, 1997b) Body size	Weisbecker and Schmid (2007) Body size	Bertrand and Silcox (2016) Body size	Main size	Álvarez et al. (2017) Body size
<i>Dasyprocta</i>	p	p	–	–	–	–	2983 <sup>a</sup>	2555	19.40	3746 <sup>a</sup>
<i>Cuniculus paca</i>	p	p	–	p	–	–	7500	5373	33.68	8554
<i>Dolicavia minuscula</i>	p	p	p	–	–	–	–	–	–	–
<i>Cavia porcellus</i>	p	p	p	–	p	534.52	800	525	4.50	704
<i>Prodolichotis prisca</i>	p	p	p	p	–	–	–	–	–	–
<i>Dolichotis salinicola</i>						–	2000	–	–	1836
<i>Dolichotis patagonum</i>	p	p	p	p	p	–	8500	6412	26.84	8018
<i>Hydrochoerus hydrochaeris</i>	p	p	p	p	p	–	60,000	26,824	67.36	51,899

<sup>a</sup> Average body size of all the species of *Dasyprocta* in Álvarez et al. (2017).

Pilleri et al., 1984 and references therein), but up to date, only a few studies on fossil forms of caviomorphs have been accomplished (Dozo, 1997a, 1997b; Dozo et al., 2004), and the existent studies focused mainly on basal forms of the Order Rodentia (Bertrand and Silcox, 2016; Bertrand et al., 2016, 2018).

The patterns of the neuroanatomical sulcus in rodents are broad; from neocortex smooth with no sulcus or convolutions (lissencephalic) to fold into numerous convolutions (giroencephalic). Based on quantitative data, Pilleri et al. (1984) proposed a correlation between the development of the neocortical sulcus and body size. From descriptions and comparisons among the giroencephalic endocast of certain fossil and living members of Caviioidea, it can be observed that the Caviidae present well-defined body size patterns, which correlate with the complexity of the neocortical sulcus patterns. However, when such patterns are analyzed at the level of Caviioidea, exceptions can be found (Table 2).

Body and brain size of Dolichotinae are intermediate among Caviidae, as is their complexity in the neocortical sulcus patterns (Table 2). I estimate that *P. prisca* is smaller than *D. salinicola*, which is smaller than *D. patagonum*. In *P. prisca*, the pattern of development of the neocortical sulcus is less complex than that of *Dolichotis*; in turn, the pattern of the latter is less developed than that of *Hydrochoerus*, which presents the most developed neocortical sulcus and the largest body within Caviidae (Table 2).

Among Caviidae, cavies have the smallest body size and simplest neocortical sulcus pattern. *Cavia* and *Dolicavia* have a similar body size (Dozo, 1997a, 1997b) but the endocast of *Cavia* exhibits a greater number of neocortical sulcus than *Dolicavia*, although it is less defined than the latter (Table 2). For this reason, certain authors have classified the brain of *Cavia* as lissencephalic (Musa et al., 2016; Silva et al., 2016). Quantitative studies suggest that current mammals whose brain mass is less than five grams are lissencephalic (Macrini et al., 2007); however, *Cavia* has a brain mass of 4.5 grams and a giroencephalic telencephalon (Table 2; Bertrand and Silcox, 2016).

When analyzing the variability within Caviioidea, medium body size has a complex relation with the fissurization pattern of the telencephalon (Table 2). I estimated that the body size of *Dasyprocta* is slightly larger than *P. prisca*, and *Cuniculus* and *Dolichotis* are similar to each other and larger than *Dasyprocta* and *P. prisca*. However, the development of neocortical sulcus in *Dasyprocta* and *Cuniculus* is much smaller than *P. prisca* and *Dolichotis*. Descriptive data of the telencephalon of Caviidae are here reported. However, future studies should be carried out in order to explore the potentially large amount of unexplored phylogenetic data (Macrini et al., 2007).

## 6. Conclusions

The first fossil remains of Dolichotinae were described by Ameghino in 1888, and subsequently, several species were described (Ameghino, 1889, 1908; Fields, 1957; Kraglievich, 1932; Rovereto, 1914). Nevertheless, details of their diversification, biogeographical history and character acquisition remain scarcely known, despite their extensive fossil record (Vucetich et al., 2015). I suggest that the

diversity of Dolichotinae in the past was much higher than that of the present, although the number of fossil species would be less than that currently described. The validity of *P. prisca*, and its basal position with respect to *Dolichotis* is corroborated. The transference of “*Orthomyctera chapalmalense*” to the genus *Dolichotis* related to the other Dolichotinae records is currently in study. The geographical and temporal distribution shows that Dolichotinae are recorded at least since the late Miocene-early Pliocene, in lower and middle latitudes. The study of the alpha taxonomy of fossil forms and their inclusion in phylogenetic analyzes increase the knowledge of the diversity of Dolichotinae, and sheds light to complete the patterns of distribution and ghost lineages, to evaluate evolutionary changes in this subfamily.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2018.07.003>.

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