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## The most ancient caviine rodent (Hystricognathi, Cavoidea) comes from the late Miocene of Northwest Argentina (South America)

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### ABSTRACT

The family Caviidae is one of the most diverse groups among South American hystricognath rodents and is represented by three main living lineages: Caviinae (cavies), Dolichotinae (maras) and Hydrochoerinae (capybaras). Caviinae includes the smaller forms of caviids represented by the extant *Microcavia*, *Cavia* and *Galea*. They are distributed in a wide range of environments throughout South America. In addition, three other genera from the late Miocene–Pliocene (*Dolicavia*, *Palaeocavia* and *Neocavia*) are recognised in high latitudes. In northwestern Argentina, the fossil forms of Caviinae have been poorly studied and for most of them there is no precise stratigraphic information. We describe and evaluate the phylogenetic affinities of the most ancient caviine from the Chiquimil Formation, Catamarca province, northwestern Argentina (9.14–7.14 ma). According to the morphological analysis of the mandibular and dental morphology and the results of the phylogenetic analysis, we assigned the new species tentatively to genus *Palaeocavia*. The phylogenetic position of the new species suggests an earlier origin for the lineage *Palaeocavia* + *Cavia* and for the entire clade Caviinae.

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Caviinae; *Palaeocavia*;  
phylogeny; late Miocene;  
north-western Argentina

### Introduction

Caviidae is one of the most striking groups within South American hystricognath rodents (Mares & Ojeda 1982; Wood 1985; Vucetich & Verzi 1995; Patton 2015) and is currently represented by three main lineages: Dolichotinae (maras), Caviinae (cuises) and Hydrochoerinae (capybaras), which encompass a wide ecomorphological disparity (Rowe & Honeycutt 2002; Woods & Kilpatrick 2005; Vucetich et al. 2011; Pérez & Pol 2012; Dunnum 2015; Patton 2015). The family is documented during the late middle to early late Miocene of Patagonia (during Mayoan SALMA; Vucetich & Pérez 2011), but its record is continuous and abundant during the later middle Miocene (Fields 1957; Patterson & Pascual 1972; Ubilla & Rinderknecht 2003; Pérez & Vucetich 2011; Pérez & Pol 2012; Vucetich et al. 2015).

Caviinae includes the smaller living forms of caviids, and includes a wide diversity of species, grouped in three genera (*Cavia*, *Microcavia* and *Galea*). This group inhabits a variety of environments, and presents the broadest geographical distribution of the family, covering much of South America, from northern Colombia, Venezuela, Guyana, Suriname and French Guayana to southern Argentina (Mares & Ojeda 1982; Woods & Kilpatrick 2005; Bezerra et al. 2007; Dunnum & Salazar-Bravo 2010; Ubilla & Rinderknecht 2014; Dunnum 2015). Although their diversity during the Cenozoic must have been higher than recent diversity, it is very poorly known. Fossil caviines are recognised

by *Microcavia* and *Cavia* (Pliocene), *Galea* (Quaternary) and other three completely extinct genera (*Palaeocavia*, *Neocavia* and *Dolicavia*). *Orthomyctera* and *Prodolichotis* have traditionally been associated with Dolichotinae (Ameghino 1889; Rovereto 1914; Kraglievich 1930; Fields 1957), while other authors consider that these genera are more related to Caviinae (Kraglievich 1932; Quintana 1998; Ubilla & Rinderknecht 2003). Thus, a more comprehensive taxonomic revision of *Orthomyctera* and *Prodolichotis* species and their incorporation in a phylogenetic framework is crucial to resolve the position of this genus within Caviidae.

Within the fossil forms of Caviinae, *Palaeocavia* (Ameghino 1889) is probably the most diverse genus, with four identified species in Argentina from the Pliocene of Buenos Aires Province: *Palaeocavia impar* (Ameghino 1888), *Palaeocavia avita* (Ameghino 1887), *Palaeocavia chapalmalense* (Ameghino 1908) and *Palaeocavia quequenense* (Kraglievich 1932); while other proposed taxon is *P. avita paranense* (Kraglievich 1940) from the late Miocene of Entre Ríos Province.

Also, the genus has been mentioned in some recent faunistic lists of the Huayquerian (South American land-mammal Age; SALMA) from La Pampa, Mendoza and Entre Ríos Provinces (Montalvo et al. 1996; Candela 2005; Verzi & Montalvo 2008; Forasiepi et al. 2015). In northwestern Argentina, *Palaeocavia* has been cited for the Miocene–Pliocene limit in the Andalhuala

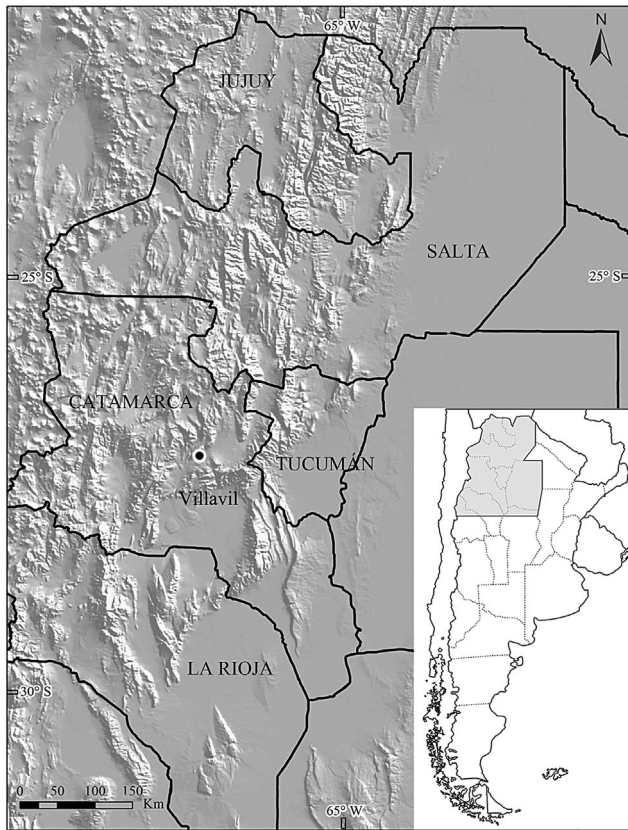


Figure 1. Location map of Villavil locality, Catamarca Province, Argentina.

Formation, Catamarca Province (Marshall & Patterson 1981; Cione et al. 2000) and the Maimará Formation in Jujuy Province (Candela et al. 2013).

*Neocavia lozanoi* (Kraglievich 1932) comes from the 'Araucanense' in the north-west of Argentina (late Miocene–Pliocene) (Bossi & Muruaga 2009), while *Neocavia depressidens* (Parodi & Kraglievich 1948) was described in the lower Pliocene of Buenos Aires Province (Cione & Tonni 1995). *Dolicavia minuscula* (Ameghino 1908) is the only species of this genus and was described for the Chapadmalalan SALMA of Buenos Aires Province.

In this study, new species assigned tentatively to *Palaeocavia* from the northwest of Argentina (Figure 1) is described, its phylogenetic position is analysed under the framework of Caviidae, and its taxonomic and biostratigraphic implications are discussed.

## Materials and methods

### Institutional abbreviations

MCH-P, Museo Arqueológico Provincial 'Condor Huasi', Sección Paleontología; Belén, Catamarca, Argentina.

### Anatomical and dental nomenclature

The mandibular nomenclature follows that of Woods and Howland (1979) and Pérez (2010), and the dental nomenclature follows Pérez (2010) (Figure 2). Dental measurements (Table 1) were taken with a 0.01 resolution digital gauge.

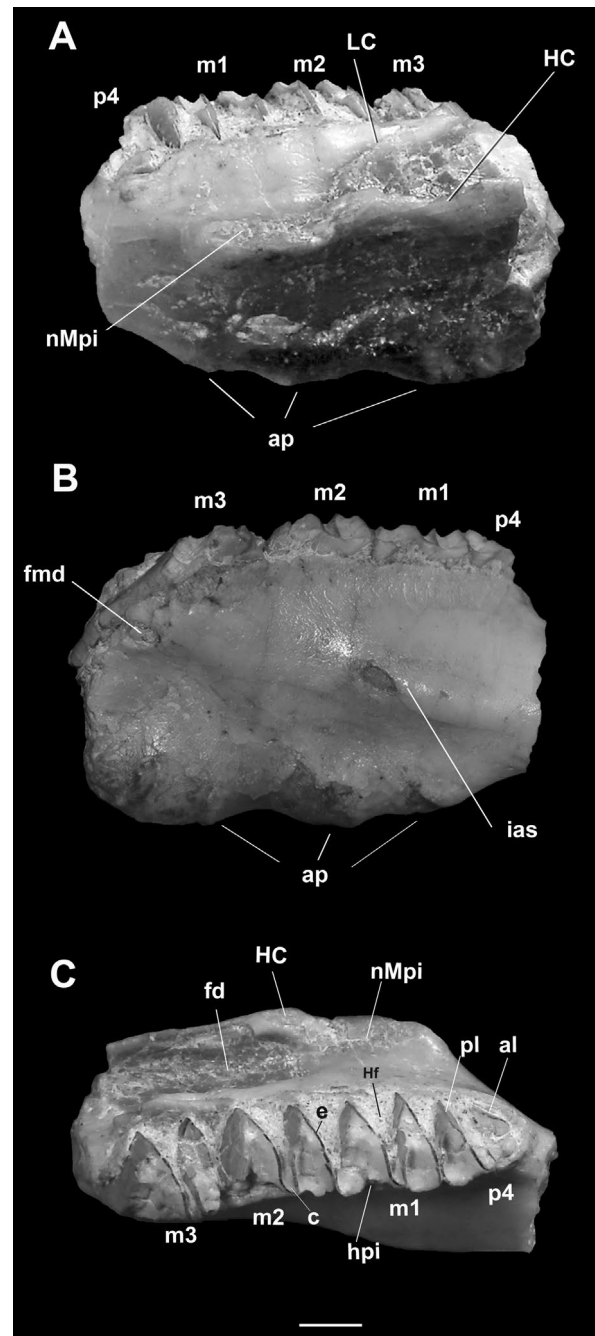


Figure 2. *Palaeocavia? mawka*, left mandible. (A) labial view; (B) lingual view; (C) occlusal view. Abbreviations: al, anterior lobe; ap, alveolar protuberances; c, cement; e, enamel; fd, dorsal fossa of horizontal crest; fmd, mandibular foramen; HC, horizontal crest; Hf, hypoflexid; hpi, primary internal flexid; ias, incisive alveolar sheath; LC, lateral crest; m1, lower first molar; m2, lower second molar; m3, lower third molar; nMpi, notch for the insertion of the tendon of the *masseter medialis pars infraorbitalis* muscle; p4, lower fourth premolar; pl, posterior lobe. Note: Scale bar = 5 mm.

### Anatomical and dental abbreviations

al, anterior lobe; ap, alveolar protuberances; c, cement; e, enamel; fd, dorsal fossa of horizontal crest; fmd, mandibular foramen; HC, horizontal crest; Hf, hypoflexid; hpi, primary internal flexid; ias, incisive alveolar sheath; LC, lateral crest; m1, lower first molar; m2, lower second molar; m3, lower third molar; nMpi, notch for the insertion of the tendon of the *masseter medialis pars infraorbitalis* muscle; p4, lower fourth premolar; pl, posterior lobe.

### Material for comparison

The new species was compared with extant and extinct species of Caviinae, Dolichotinae and Hydrochoerinae. The material fossil of the species used for comparison was mostly based on the type and/or referred material (e.g. *Neocavia*, *Dolicavia*, *Paleocavia impar*, *P. chapalmalense*). In case of the materials are lost (e.g. *Palaecocavia quequenense*, *P. avita*) we compared with the diagnosis and original drawings of these species.

### Phylogenetic analysis

For testing the affinities of the new species within Caviidae, a cladistic analysis was performed using a modified version of the combined data-set of Vucetich et al. (2015), which includes morphological characters and DNA sequences of four genes (12s, cytb, Ghr and Tth) from Genebank (Supplementary data 1). Twenty-two multistate characters of the morphological partition were considered as additive based on increasing degrees of similarity between the character states or in cases of interesting homologies. This combined data-set resulted in a concatenated matrix of 53 cavioid taxa (42 fossil and 11 extant), and one species of octodontoid for rooting more parsimonious topologies, 117 morphological characters and 4014 molecular data (Supplementary data 2). The equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff et al. 2008), performing an heuristic search of 1000 Wagner tree replicates followed by TBR branch swapping, collapsing zero-length branches under the strictest criterion. In order to test the robustness of the results, support values were calculated using Bremer index and bootstrap resampling techniques in TNT. Unstable taxa in the set of the most parsimonious trees (MPTs) were identified using IterPCR (Pol & Escapa 2009), in order to derive an informative reduced consensus.

### Taxonomical background

The genus *Palaecocavia* was described into the subfamily Caviinae for Ameghino (1889). This author describes two species within the Pliocene, in Monte Hermoso locality, Buenos Aires Province, Argentina: *P. avita* (Ameghino 1887; Ameghino 1889) based on mandibular remains and *P. impar* (Ameghino 1888; Ameghino 1889) defined from material cranio-mandibular. Both species were originally named as *Cavia* and posteriorly synonymised to *Palaecocavia* (Ameghino 1889). In 1908, Ameghino named new specie, *P. chapalmalense* of Chapadmalalan wildlife (SALMA) without providing a formally description, but posteriorly this species was figurate by Rovertto (1914) and recognised for Mones (1986). From the bank of the river Quequén Salado in Buenos Aires Province in sediment of Pliocene, *P. quequenense* (Kraglievich 1932) was described based on a fragment of right maxillary. The oldest species is *Palaecocavia paranense* (Kraglievich 1932), which is described within the *Piso Mesopotamiense* in Entre Ríos Province (Huayqueriense, SALMA). This species is described based on a fragment of mandibular. Moreover, the author refers skull fragment in La Plata City (Buenos Aires Province) but not described (Kraglievich 1932). Posteriorly, this taxon was subsumed under *P. avita* enduring as the subspecies *P. avita paranensis* (Kraglievich 1940).

### Systematic paleontology

Order RODENTIA (Bowdich 1821)  
 Infraorder HYSTRICOGNATHI (Tullberg 1899)  
 Superfamily CAVIOIDEA (Fischer 1817)  
 Family CAVIIDAE (Fischer 1817)  
 Subfamily CAVIINAE (Fischer 1817)  
*Palaecocavia? mawka* sp. nov.

### Holotype

MCH-P 164: left mandibular fragment with p4–m3 (Figure 2).

### Derivation of name

The specific epithet refers to old or ancient in the language Quechua.

### Geographic and stratigraphic provenance

The new species comes from the Jarillal Member, which is the upper member of the Chiquimil Formation (Galván & Ruiz Huidobro 1965; Marshall & Patterson 1981; Muruaga 1998, 2001a, 2001b; Bossi & Muruaga 2009) that crops out in Villavil locality, Catamarca Province, Argentina (Figure 1). The tuff in the limit between the Chiquimil Formation and the overlying Andalhuala Formation was dated 7.14 + 0.02 Ma (Latorre et al. 1997). The lower dating was performed in the El Áspero Member (sediment underlying the Jarillal Member) and gave an age of 9.14 + 0.09 Ma (Sasso 1997). These dates coincide with the later Tortonian–early Messinian age (Esteban et al. 2014).

### Diagnosis

Caviinae diagnosed by following unique combination of characters: the small size species and lacks the anterior–posterior projection of first lobule of p4 and the position oblique to the same on axis of the mandible. The shape of anterior lobe of molariforms is lanceolate (leaf-shaped) and the posterior lobe is heart-shaped. The lingual edge of hypoflexid is forming a bezel contour. Differs of *P. chapalmalensis* and *P. impar* for absent of the mylohyoid shelf; wide and shallow depth and the lacks of cement of primary flexid (hpi) in molariforms. In comparison with *P. avita* shared the shallow depth of primary flexid in molariforms, but differs from this in that anterior lobe in the new species seems slightly larger than *P. avita*.

### Description and comparison

#### Mandible

The new species of *Palaecocavia? mawka* consists of a left mandibular fragment that lacks anterior and posterior portions of the dentary, but preserves p4–m3 (Figure 2). The preserved mandibular body presents the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (nMpi), the lateral crest (sensu Woods 1972) and the anterior portion of the horizontal crest (Figure 2(A)), which jointly with the morphology of the molariforms, provide important phylogenetic information within Caviidae.



In labial view, the nMpi is placed between p4 and m1 and is bordered by a lateral edge (Figure 2(A)), resembling the condition of *P. impar*, *P. chapalmalense*, *Cavia tschudii*, *Cavia aperea* and *Galea musteloides*. The notch is posteriorly continuous with the horizontal crest, which presents a well-developed ridge and anteriorly begins at the level of the anterior lobe of m2, like in other Caviidae. The dorsal fossa is located dorsal to the horizontal crest, for insertion of the *masseter medialis* muscle and in *P. mawka* this crest differs in depth from the dorsal concavity formed by nMpi, as in all the Caviinae. The lateral crest in *P. mawka* originates at the level of the anterior lobe of m2, and is dorsally convex, differing from *Microcavia australis* and *G. musteloides*, which have a straight lateral crest, but similar to *C. aperea*, *C. tschudii*, *N. lozanoi*, *P. impar* and *P. chapalmalense*. *Palaeocavia? mawka* exhibits conspicuous alveolar protuberances which correspond to p4–m2, on the ventral margin of the dentary (Figure 2(A) and (B)) like *P. impar* and *P. chapalmalense*.

In lingual view (Figure 2(B)), the root of the lower incisor extends to the level of the posterior lobe of m1, similar to the condition in *D. minuscula*, *Microcavia chapalmalensis*, *N. lozanoi* and *P. impar*, but differently from *G. musteloides*, *Galea spixii* and *P. chapalmalense*, in which the root of the lower incisor reaches the anterior lobe of m2. The mylohyoid crest is absent in *Palaeocavia? mawka*, resembling the condition of *M. australis* and *M. chapalmalensis*. The mandibular foramen is located below the m3, similar to the condition of other caviids.

### Lower teeth

The molariforms of the new specimen are euhyposodont and bilobed, with a constriction in the apex of each lobe and cement in the hypoflexid (Figure 2(C)). The hypoflexid is funnel-shaped and its lingual apex is bevelled. The enamel is continuous around the entire crown but is interrupted on the lingual side of the anterior lobe and on the posterior-lingual corner of the posterior lobe of molariforms.

The p4 is anteroposteriorly and transversely smaller than m1–m3 (Figure 2(C); Table 1). The anterior lobe of p4 is oblique:

it lacks the anterior projection and reaches the anteroposterior axis of the mandible (Figure 2(C)). The posterior lobe is heart-shaped but is more narrow and shorter than the posterior lobe of the molars.

The new species shares the presence of a p4 with two well-developed lobes but without the anterior projection of the anterior lobe with *Palaeocavia*, *Cavia* and *Neocavia*, whereas in other caviines (*Microcavia*, *Galea*, *Dolicavia*), the p4 has an anterior projection differently developed. In addition, *Palaeocavia? mawka* resembles the species of *Palaeocavia* in the markedly oblique orientation of the anterior lobe of p4, and in the lanceolate (leaf-shaped) anterior lobe of the molars, unlike the condition of other caviines in which the anterior lobe of the molars is heart-shaped (*Dolicavia*, *Neocavia*, *Microcavia*, and *Galea*), whereas in *Cavia*, it is laminar.

In the molars, the anterior lobe is smaller and more lanceolate (leaf-shaped) than the posterior lobe (Figure 2(C)). The hypoflexid is wide and funnel-shaped, with parallel edges in its inner portion. The lingual edge of this flexid is anteriorly deeper, forming a bezel contour (Figure 2(C)).

The molariforms present a wide and shallow primary internal flexid (hpi) which lacks of cement in *Palaeocavia? mawka*, but in the other caviines (e.g. *Cavia*, *Neocavia*, *Palaeocavia*), the hpi is deeper and has cement. The *Palaeocavia? mawka* and other species of *Palaeocavia* share the funnel-shaped and bevelled hypoflexid. However, this condition is different in other caviines (e.g. *M. australis* and *M. chapalmalensis*, *D. minuscula*, *N. lozanoi* and *G. musteloides*), in which the hypoflexid is funnel-shaped, narrower and transversally shorter, with a rounded lingual apex. On the other hand, the hypoflexid in *Cavia* is narrow and very long.

The materials of *Palaeocavia avita* and *P. quequenense* are lost, for this reason the comparison with *P. mawka* has been based on the original diagnosis and drawings of these species. Although *P. quequenense* was described on a maxillary fragment, the measurements and morphology are differentiable of the new species. *P. mawka* has slightly smaller teeth than *P. avita* and *P. quequenense* (Table 1). In addition, *P. avita* has narrower the anterior lobe of p4 and *P. quequenense* has a deeper external flexus than the hpi. of *P. mawka*.

**Table 1.** Measurements of teeth in mm.

Measurement		<i>P. mawka</i>	<i>P. impar</i> <sup>a</sup>	<i>P. avita</i> <sup>a</sup>	<i>P. avita paranense</i> <sup>b</sup>	<i>P. quequenense</i> <sup>b</sup>	<i>P. chapalmalense</i>
P4	W	–	–	–	3'	–	–
M1	W	–	–	–	–	2.8'	–
M2	W	–	–	–	–	2.8'	–
M3	W	–	–	–	–	2.8'	–
P4–M3 length		–	–	–	14.5	15	–
p4	APL	2	3.5	3	–	–	2.93
	W	al:1.8 pl:2.2	2.8'	2.5'	2.2'	–	al:2.01 pl:2.58
m1	APL	3.1	4.5	3.7	–	–	3.68
	W	al:2.7 pl:2.8	3.2'	2.5'	–	–	al:2.97 pl:3.09
m2	APL	3.1	4.5	3.7	–	–	3.36
	W	a1:2.2 pl:2.5	3.2'	2.5'	2.8'	–	al:2.98 pl:2.86
m3	APL	3.9	4.5	3.7	–	–	–
	W	al:2.5 pl:2.3	3.2'	2.5'	–	–	al:3.01
p4–m3 length		12.1	17	–	–	–	–
Lower diastem length		–	15	11	–	–	12.81

Note: APL, anteroposterior length; W, width; al, anterior lobe; pl, posterior lobe; ', maximum width.

<sup>a</sup>From Ameghino (1889).

<sup>b</sup>From Kraglievich (1932).

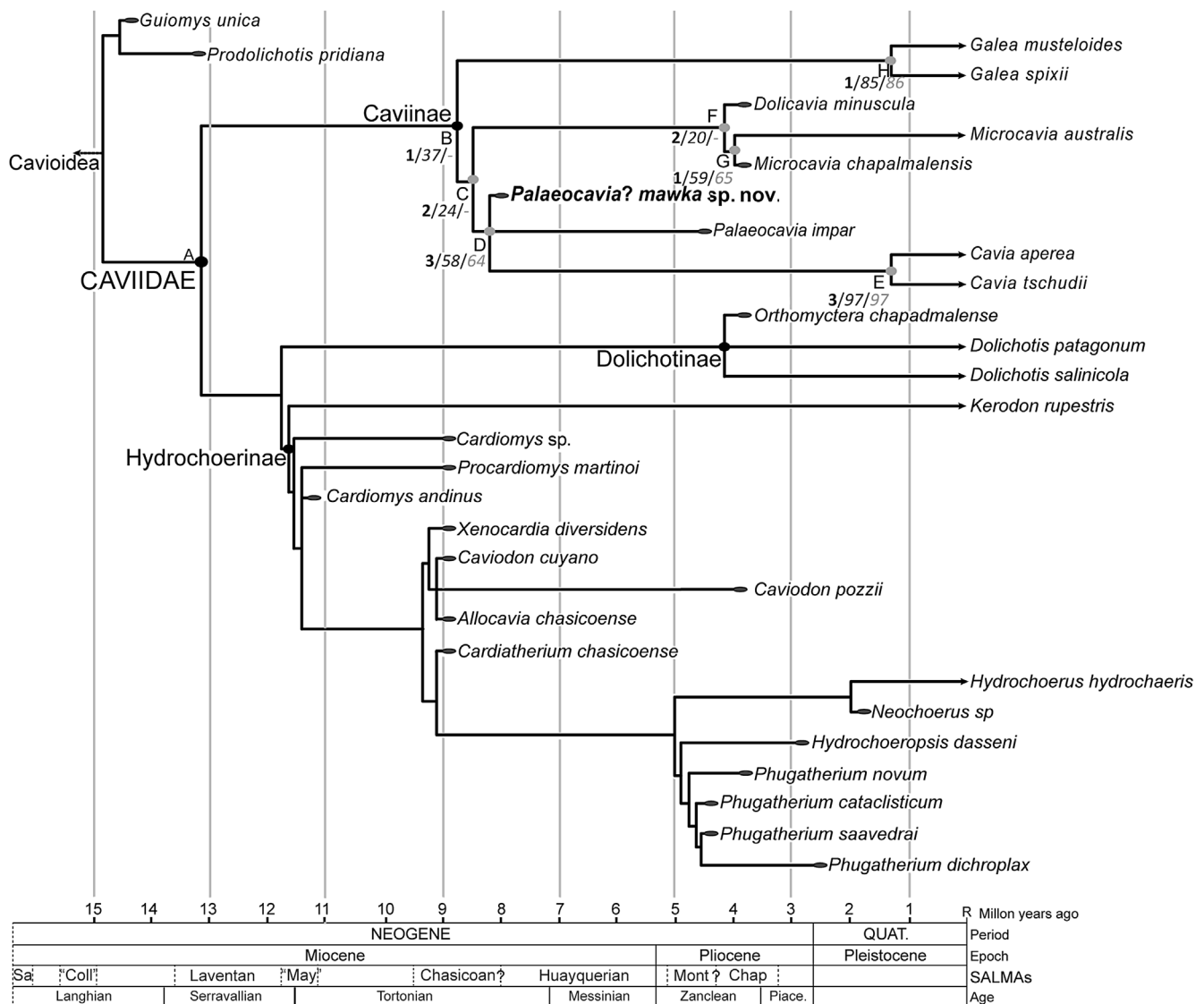
## Phylogenetic analysis

The parsimony analysis resulted in a total of 136 MPTs, of 3244 steps (CI = 0.609; RI = 0.471), in which the three main living lineages of Caviidae (Caviinae, Dolichotinae and Hydrochoerinae) are recovered. In the strict consensus, the crown-group Caviidae shows a basal polytomy with the euhyposodont eocardiids because the fragmentary *Microcardiodon huemulensis* takes different positions within this clade in the MPTs. However, when the alternative positions taken by this unstable taxon are ignored, the monophyly of Caviidae is recovered in the reduced consensus (Figure 3, node A).

*Palaeocavia? mawka* is nested within Caviinae (Figure 3, node B) and is more closely related to *P. impar* and *Cavia* (Figure 3, node D) than to the other caviines. However, *Palaeocavia? mawka* collapses in a polytomy with *P. impar* and the node of *Cavia* (*C. apera* + *C. tschudii*). The different possible resolutions of this polytomy are: (1) *Palaeocavia? mawka* is the sister group of *P. impar* + *Cavia*, (2) *Palaeocavia? mawka* is the sister group of

*Cavia*, whereas *P. impar* is the most basal species in this node, or (3) *Palaeocavia? mawka* and *P. impar* form a monophyletic group, which is the sister group of *Cavia*. However, there are no synapomorphies that support these three topologies in particular.

The unambiguous synapomorphies that support the position of *Palaeocavia? mawka* in all MPTs (Figure 3, node D) are: nMpi located between p4 and m1 (character 21 [0]), lateral crest curved, deflecting anteroventrally from the base of the coronoid process (c. 28[1]), well-developed bulge of the alveolar protuberance of m1 on the ventral margin of the dentary (c. 34[1]), and p4 with two well-developed lobes, but lacking of an anterior projection (c. 75[1]). In addition, three unambiguous synapomorphies support the position of *Palaeocavia? mawka* in some of the MPTs: well-developed posteroventral projection of the posterior end of the mandibular symphysis (chin, in lateral view), forming an elongate peg, exposed in lateral view (c. 6[0]); short anteroposterior length of incisive foramina (c. 45[1]); and laminar-shaped anterior lobe of m1–m2 (c. 86[2]). This node has moderate



**Figure 3.** The node Caviidae in the reduced consensus ignoring the fossil taxon *Microcardiodon huemulensis*.

Notes: The capital letters indicate the node, numbers in bold indicate Bremer indices, numbers in italics represent absolute bootstrap values and numbers in grey represent GC bootstrap values. Abbreviations: Chap, Chapadmalalan; 'Coll', 'Colloncuran'; QUAT., Quaternary; 'May', 'Mayoan'; Mont?, Montehermosan; 'Piace.', 'Piacenzian'; Sa, Santacrucian; SALMAs, South American Land Mammal ages.

support values in the phylogenetic analysis (Bremer = 3; bootstrap absolute/GC frequency = 64/58; see Figure 3, node D).

Caviinae (Figure 3, node B) is supported by four morphological unambiguous synapomorphies: labial edge of the condyle (the insertion point of *m. masseter posterior*) in posterior view projecting laterally with respect to the wall of the dentary, forming a small knob (c. 7[0]); developed pterygoid shelf (c. 18[0]); interorbital width shorter than the braincase (c. 44[1]); and strongly convex anterior portion of the parietals (c. 48[2]). *Galea* is the most basal among caviines (Figure 3, node H) and the clade *D. minuscula* + *Microcavia* (Figure 3, nodes F–G) is the sister group of *Palaeocavia? mawka* + *P. impar* + *Cavia* (Figure 3, nodes D–E). The synapomorphies list of the phylogenetic analysis is detailed for each node within Caviinae in the Supplementary data 3.

## Discussion

The new species *Palaeocavia? mawka* provides enough information to corroborate its nested position as a Caviinae more closely related to *P. impar* and *Cavia* than to the other Caviidae (see Phylogenetic analysis above).

The general morphology of *P.? mawka* closely resembles Caviinae. It is mainly because of small size, presence of the primary internal flexid (hpi) and lack of secondary internal flexids. The p4 has two well-developed lobes, in contrast to Hydrochoerinae (Figure 3) that exhibits three lobes in p4. Furthermore, the molars of Hydrochoerinae have secondary and tertiary internal flexids (hsi and hti). Dolichotinae (Figure) and Caviinae differ, among other features, in the longitudinal furrow, which is opposed to the hypoflexid in Dolichotinae and absent in Caviinae, and the primary internal flexid (hpi) is present in Caviinae and absent in Dolichotinae as in *P.? mawka*. In addition, in Dolichotinae and Hydrochoerinae, the dorsal fossa of the horizontal crest is as deep as the nMpi, whereas in Caviinae, their depths are different.

According to the analysis of the mandibular and dental morphology, the new species is closely related with *Palaeocavia* and *Cavia* since shares the position of the nMpi between p4 and m1 (Figure 2(A)), the presence of two well-developed lobes in p4 and the anterior lobe obliquely oriented (Figure 2(C)). The configuration of p4 is shared with *Cavia*, but in this genus, the anterior lobe of p4–m3 is laminar and the hpi is much deeper than in *Palaeocavia*. Moreover, in *Palaeocavia? mawka*, the anterior lobe of m1–m3 is leaf-shaped and the posterior lobe is heart-shaped, with the hpi resembling the m1–m3 of *Palaeocavia*. However, the hpi of *P.? mawka* is shallower, and the teeth are smaller those that of *P. impar*, *P. chapalmalense*, *P. avita* (Table 1).

Although the taxonomic identity of the new specimen *P.? mawka* is quite clearly differentiable from the other species of Caviinae. The assignment to the genera *Palaeocavia* is doubtful because the phylogenetic position is not resolved. *P.? mawka* forms a polytomy with *P. impar* and *Cavia*. However, the new species is not part of the clade *C. aperea* + *C. tschudii*, since synapomorphies of these species (Supplementary data 3) are not shared with *Palaeocavia? mawka* or *P. impar*.

In this context, *Palaeocavia? mawka* increases the high diversity of caviines during the Miocene–Pliocene, up-to-date

fossil caviines are recognised by at least seven species distributed in three genera (*Dolicavia*, *Neocavia* and *Palaeocavia*). It is the single specimen with precise stratigraphic provenance, so far the Caviinae from northwestern Argentina has no precise stratigraphic information, because most of them were found in the ‘Araucanense’ (Rovereto 1914; Kraglievich 1932), and these ‘levels’ encompass the entire stratigraphic column of Chiquimil and Andalhuala formations (Bossi & Muruaga 2009; Nasif 2009). Moreover, in the northwest of Argentina, *Palaeocavia* has only been described at generic level (Marshall & Patterson 1981; Cione et al. 2000; Candela et al. 2013), with no species having been cited.

Finally, *Palaeocavia? mawka* relocates the first appearance of the *Palaeocavia* + *Cavia* and the first occurrence of the Subfamily Caviinae to the Tortonian – Messinian (9.14–7.14 ma). This result would confirm the hypothesis of Pérez and Pol (2012) about the presence of *Palaeocavia* in sediments older than the Monterhermosan SALMA, indicating an earlier origin of the genus *Palaeocavia* and Caviinae.

It is worth remarking that the oldest fossil record of *Cavia* is from the late Pliocene (Verzi & Quintana 2005), and recent studies of molecular phylogenies estimate the origin of this genus in the early Pliocene (4.1 mya; Opazo 2005) or late Miocene–early Pliocene (Dunnum & Salazar-Bravo 2010). The new species confirmed the origin of the lineage that led *Cavia* would have been at least 3 million years earlier.

The fossil forms of Caviinae have been poorly studied, both from taxonomic and phylogenetic standpoints; thus, better knowledge of the alpha taxonomy of the fossil forms of this subfamily is crucial. This would shed light on the diversity, the evolutionary history and the significance of the acquisition of morphological characters, both in this group and in the entire Caviidae.

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