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Reappraisal of the giant caviomorph rodent *Phoberomys burmeisteri* (Ameghino, 1886) from the late Miocene of northeastern Argentina, and the phylogeny and diversity of Neopiblemidae

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ABSTRACT

Phoberomys is a giant caviomorph rodent included in the extinct Neopiblemidae. It is recorded in the late Miocene-Pliocene of South America (Argentina, Venezuela, Brazil and Peru), and is one of the largest rodents that have ever lived. In this contribution we study specimens of *Phoberomys* from the 'Mesopotamiense', late Miocene of Entre Ríos Province (Argentina), including several unpublished specimens and the holotypes of the five nominal species (*Ph. burmeisteri*, *Ph. praecursor*, *Ph. insolita*, *Ph. lozanoi* and *Ph. minima*) previously recognised for this unit. Our study indicates that all Mesopotamian specimens belong to *Phoberomys burmeisteri*, and that the differences among them reveal individual and ontogenetic variation. Our phylogenetic analysis indicates that Neopiblemidae is monophyletic and includes *Phoberomys*, *Neopiblema*, and *Perimys*. *Phoberomys* species are recovered as a clade, which is more closely related to *Neopiblema* than to the Patagonian *Perimys*. In addition, our study shows that *Eusigmomys* is not a Neopiblemidae, but a Dinomyidae.

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Introduction

Neopiblemidae is an extinct family of caviomorph rodents endemic of South America and recorded since the early Miocene to Pliocene (e.g. Ameghino 1887; Kraglievich 1926; Kramarz 2002; Carrillo & Sánchez Villagra 2015; Kerber et al. 2016). It includes at least four genera: *Perimys* from the early Miocene of Argentina and Chile (e.g. Ameghino 1887; Flynn et al. 2002; Kramarz 2002), *Doryperimys* from the early Miocene of Argentina (Kramarz et al. 2015), *Neopiblema* from the middle Miocene-Pliocene of Argentina, Brazil, Peru and Venezuela (e.g. Ameghino 1889; Negri & Ferigolo 1999; Vucetich et al. 2010; Antoine et al. 2015; Carrillo & Sánchez-Villagra 2015; Tejada-Lara et al. 2015), and *Phoberomys* from the late Miocene-Pliocene of Argentina, Brazil, Peru and Venezuela (e.g. Kraglievich 1926; Mones 1980; Horovitz et al. 2006; Kerber et al. 2016). In addition, two other genera are usually related with the Neopiblemidae: *Eusigmomys* and *Perumys*. *Eusigmomys oppositus* (see Ameghino 1904, 1905), from the middle Miocene of Argentina, was included in the Dinomyidae by Vucetich (1984), but is considered as a neopiblemid by several authors (e.g. Bondesio & Bocquentin-Villanueva 1988; Negri & Ferigolo 1999; Sanchez-Villagra et al. 2003). *Perumys gyulavarii* was described for the upper? Pliocene of Peru, and referred as closely related to the neopiblemid *Phoberomys* and the heptaxodontid *Amblyrhiza* (see Kretzoi & Vörös 1989), but recently Kerber et al. (2016) suggested that it could be assigned to *Phoberomys*.

The Neopiblemidae are characterised by euhipodont teeth, molars composed of two or more straight laminae with thick

interlaminar cement layers, among other features (see Bondesio et al. 1975). These rodents reached a wide range of sizes, with small (*Doryperimys*, and some species of *Perimys*), medium (some species of *Perimys*) and large (*Neopiblema*) forms. Moreover, some giant members of this family (*Phoberomys*) were among the largest rodents that have ever lived (e.g. Sanchez-Villagra et al. 2003; Millien & Bovy 2010; Geiger et al. 2013).

The phylogenetic relationships of Neopiblemidae with another caviomorph groups are not clear, but most studies support a close affinity with Chinchillidae (e.g. Kerber et al. 2016) or Dinomyidae (e.g. Horovitz et al. 2006; Kramarz et al. 2013); all of which are included within Chinchilloidea (e.g. Upham & Patterson 2015).

The genus *Phoberomys* has been recorded in several late Miocene-Pliocene units of South America. In the Urumaco Formation (late Miocene) of Venezuela (Figure 1), *Phoberomys pattersoni* have been reported (Mones 1980; Bondesio & Bocquentin-Villanueva 1988; Carrillo & Sánchez-Villagra 2015), and at least two other species of *Phoberomys* (see Carrillo & Sánchez-Villagra 2015). In the late Miocene of Brazil, '*Phoberomys bordasii*' (Patterson 1942) was considered as possibly belonging to *Neopiblema* (see Kerber et al. 2016). Other remains referred to *Phoberomys* sp. have been recovered from the Solimões Formation, in several sites of the Acre region of Brazil (Figure 1) (e.g. Kerber et al. 2016). From the Pliocene of Peru (Figure 1), was described the genus *Perumys* (Kretzoi & Vörös 1989) but later the material was assigned to *Phoberomys* (see Kerber et al. 2016).

In the 'Mesopotamiense' (late Miocene) of Entre Ríos Province (Argentina), neopiblemids reached a great taxonomic diversity



Figure 1. Map of South America showing localities with late Miocene-Pliocene records of Neopiblemidae.

and they constitute the only extinct family among Mesopotamian caviomorphs (e.g. Candela 2005; Nasif et al. 2013). Five nominal species of *Phoberomys* (*Ph. burmeisteri*, *Ph. praecursor*, *Ph. insolita*, *Ph. lozanoi*, and *Ph. minima*; Ameghino 1886; Kraglievich 1932, 1940) and two species of *Neopiblema* (*N. horridula* and *N. ambrosettianus*; Ameghino 1886, 1889; Negri & Ferigolo 1999) have been described from this unit, supposedly representing the highest specific diversity of the family during the late Miocene. It is noteworthy that none of the Mesopotamian species of *Phoberomys* have been revised since their descriptions (i.e. Ameghino 1886; Kraglievich 1932, 1940), although there are comments on the taxonomy of these species (Carrillo & Sánchez-Villagra 2010; Vucetich et al. 2010).

In this contribution, we studied all the available material of *Phoberomys* from the 'Mesopotamiense', including the holotypes of the nominal species previously recognised and several unpublished specimens. We performed a phylogenetic analysis including the genus *Perimys* and all recognised species of *Neopiblema* and *Phoberomys*. We revised the inclusion of two taxa (*Eusigmomys* and *Perumys*) in the Neopiblemidae.

Material and methods

Studied material

We studied all the material of *Phoberomys* from the 'Mesopotamiense', including the holotypes of the five nominal species previously recognised, housed in the Museo Argentino de

Ciencias Naturales 'Bernardino Rivadavia' (MACN), in Buenos Aires, Argentina, and the Museo de La Plata (MLP), in La Plata, Argentina. The holotype of '*Dabbenea lozanoi*' (MLP 36) could not be found but it was studied through published illustrations (Kraglievich 1940).

Phylogenetic analysis

In order to test the phylogenetic relationships of recognised Mesopotamian species within Chinchilloidea, a cladistic analysis was conducted. We used the data matrix of Kramarz et al. (2013) with the modifications introduced by Kerber et al. (2016), who added both recognised species of *Neopiblema* (*N. horridula* and *N. ambrosettianus*), and the genus *Phoberomys* (based mainly on *Ph. pattersoni*).

We modified the data-set of Kramarz et al. (2013) and Kerber et al. (2016) including *Phoberomys burmeisteri* and the genus *Perimys*, and modifying four characters. The character 3 from Kramarz et al. (2013; i.e. *transverse penetration of hypoflexus/id in adult stages*) was replaced by *penetration degree of the hypoflexus in upper molars* (taken from Kramarz 2001). The character 7 from Kramarz et al. (2013; i.e. *very compressed valleys in adult stages*) was replaced by *width of the flexa/ids* (modified from Kramarz 2005). The character 28 from Kramarz et al. (2013; i.e. *external auditory meatus connected to accessory ventral opening*) was replaced by *presence/absence of tympanic fenestra* (modified from MacPhee 2011). The character 39 from Kramarz et al. (2013; i.e. *lateral fossa for mandibular insertion of masseter superficialis muscle*) was replaced by *fossa for the muscle masseter medialis pars posterior* (following Candela 2000).

We also added six characters: Character 40. Shape of the paracipital process: anteroposteriorly compressed (0); blunt or poorly developed (1); elongated (2). Character 41. Mastoid exposes on the occiput: present (0); absent (1). Taken from Kramarz (2001). Character 42. Location of the mandibular foramen: high in the mandibular ramus, opening dorso-medially (0); posterior to the retromolar fossa, opening dorsally (1); on the labial portion of the retromolar fossa, opening dorsally (2). Character 43. Interrupted enamel layer. absent (0); present (1). Character 44. Multilaminated M3 (six laminae or more): absent (0); present (1). Character 45. Calcaneus with secondary sustentacular facet: absent (0); present (1). Taken from Candela and Picasso (2008).

Six characters were treated as ordered: characters 1 (hypodonty), 3 (penetration degree of the hypoflexus in upper molars), 4 (number of transverse crests on M1-M2 in adult stages), 7 (width of the flexa/ids), 11 (posterior extension of the lower incisor), and 28 (presence/absence of tympanic fenestra).

The data matrix resulted in 45 characters and 17 taxa (see Supplementary Material). The phylogenetic analysis was performed following cladistic methodology (e.g. Hennig 1968; Farris 1983) using the program TNT 1.5 (Goloboff & Catalano 2016) available by the Willi Hennig Society. The heuristic search consisted on 200 Wagner trees replications, followed by a Tree Bisection Reconnection, saving 50 trees per replication. To calculate support values we used absolute Bremer index.

Neopiblemids of the 'Mesopotamiense'

The Ituzaingó Formation is a unit of fluvial origin mainly composed by sandstone, which crops out on the eastern margin of

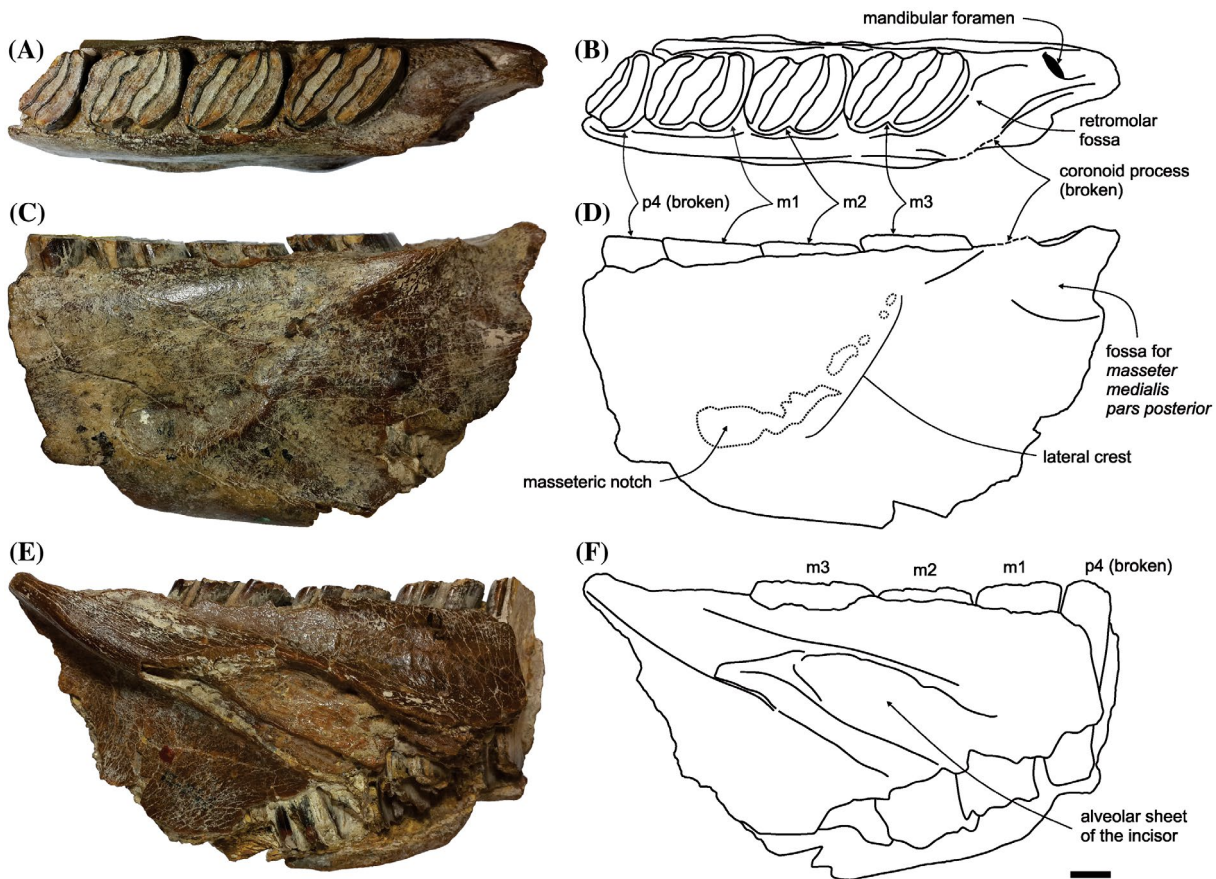


Figure 2. Holotype of *Phoberomys burmeisteri*. Left mandible (MLP 15-246) in dorsal (A), lateral (B) and medial (C) views, and schematic interpretation (D–F). Scale bar: 10 mm.

the Paraná River in the provinces of Corrientes and Entre Ríos, northeastern Argentina (e.g. Herbst 2000; Brunetto et al. 2013).

The fossil vertebrates recorded in the Ituzaingó Formation came from the Lower Member of the unit (Brunetto et al. 2013), which is commonly referred to as ‘Mesopotamiense’ (*sensu* Frenguelli 1920) or ‘Conglomerado osífero’ (see Cione et al. 2000; Herbst 2000; Brandoni 2013; Brunetto et al. 2013). Based on the vertebrate fossil record, the ‘Mesopotamiense’ have been referred to the Huayquerian Stage/Age of the South American chronologic continental scale (Cione et al. 2000). Moreover, a dating of the upper levels of the underlying Paraná Formation on c. 9.5 Ma (see Pérez 2013) suggest a middle late Miocene (Tortonian) age for the ‘Mesopotamiense’ (Brandoni 2013).

The Neopiblemidae reached a great diversity in the ‘Mesopotamiense’, where they constitute the only extinct family among caviomorph rodents, but it has been considered that the systematics of the clade must be revised and that this diversity could be lesser than previously proposed (e.g. Candela 2005; Nasif et al. 2013).

Three genera of neopiblemids (*Neopiblema*, *Phoberomys*, and *Perimys*) were identified in the ‘Mesopotamiense’ (e.g. Ameghino 1886, 1889; Kraglievich 1926). Two species of *Neopiblema* are currently recognised for this unit: *Neopiblema horridula* and *Neopiblema ambrosettianus* (the latter including ‘*Euphilus kurtzii*’, see Negri & Ferigolo 1999). Moreover, five species of *Phoberomys* were also described for this unit: *Ph.*

burmeisteri, *Ph. praecursor*, *Ph. insolita*, *Ph. lozanoi*, and *Ph. minima* (Ameghino 1886; Kraglievich 1932, 1940).

Perimys scalabrinianus (Ameghino 1889) was the only species of the early Miocene genus *Perimys* described for the ‘Mesopotamiense’. The holotype of this species is currently lost (Candela 2005), and specimens from the ‘Mesopotamiense’ previously referred to *Perimys* (MACN-Pv 9067, 9068) correspond actually to isolated cheek teeth of *Lagostomus* (pers. obs.). Therefore, only two genera are recognised among Mesopotamian Neopiblemidae: *Neopiblema* and *Phoberomys*.

Systematic paleontology

RODENTIA Bowdich, 1821

HYSTRICOGNATHI Tullberg, 1899

CAVIOMORPHA Wood and Patterson (in Wood, 1955)

CHINCHILLOIDEA Kraglievich, 1940

NEOPIBLEMIDAE Kraglievich, 1926

Genus *Phoberomys* Kraglievich, 1926

1886. *Megamys* Laurillard in D’Orbigny 1842, p. 110. Ameghino, p. 39. part.

1891. *Euphilus* Ameghino 1889, p. 903–904. Ameghino, p. 246. part.

1926. *Phoberomys* Kraglievich, p. 127.

1988. *Dabbenea* Kraglievich 1926, p. 127–128. Bondesio and Bocquentin-Villanueva, p. 33.

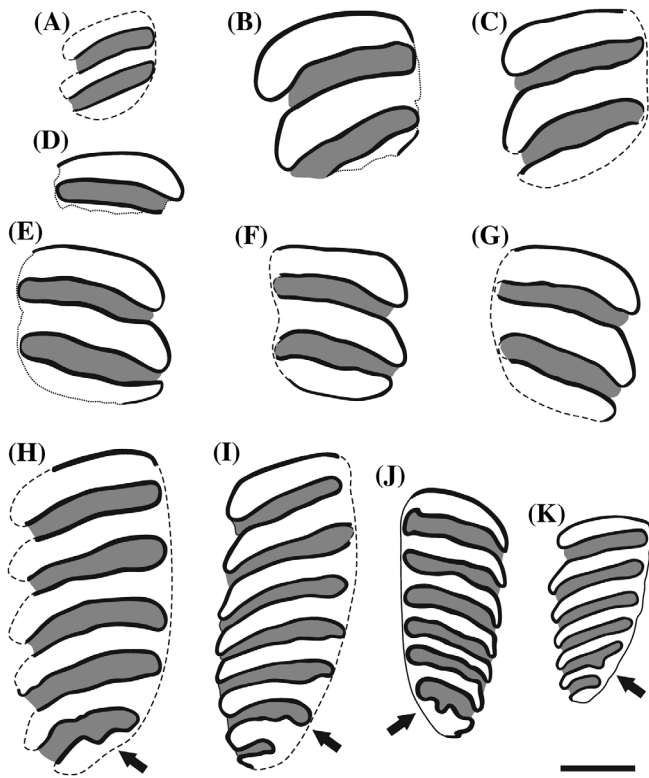


Figure 3. Upper dentition of *Phoberomys burmeisteri*. (A) MACN-Pv 3461 (holotype of ‘*Dabbenea minima*’), left P4?; (B) MACN-Pv 4068, left M1 or M2; (C) MLP 41-XII-13-149, left M1 or M2; (D) MACN-Pv 2542, fragment of right M1 or M2; (E) MACN-Pv 3290, right M1 or M2; (F) MLP 15-261, right M1 or M2; (G) MLP 15-249, right M1 or M2; (H) MLP 15-256, left M3; (I) MLP 15-251 (holotype of ‘*Dabbenea insolita*’), left M3; (J) MLP 36 (holotype of ‘*Dabbenea lozanoi*’), right M3; (K) MLP 52-X-5-80, left M3. J is modified from Kraglievich (1940). Scale bar: 10 mm.

2016. *Perumys* Kretzoi & Vörös 1989, p. 111. Kerber, Negri, Ribeiro, Nasif, Souza-Filho, Ferigolo, p. 7.

Type species: ‘*Megamys*’ *burmeisteri* Ameghino 1886.

Geographic and stratigraphic distribution: late Miocene-Pliocene of Argentina, Brazil, Peru and Venezuela.

Included species: *Phoberomys burmeisteri* and *Phoberomys pattersoni*.

Phoberomys burmeisteri (Ameghino 1886)

(Figures 2–4)

1886. *Megamys burmeisteri* Ameghino, p. 41.

1891. *Euphilus burmeisteri* (Ameghino). Ameghino, p. 246.

1926. *Phoberomys burmeisteri* (Ameghino). Kraglievich, p. 127, lam. 5.

Phoberomys praecursor Kraglievich 1932, p. 136. **new**

synonymy

Dabbenea insolita Kraglievich 1940, p. 750–754. **new**

synonymy

Dabbenea lozanoi Kraglievich 1940, p. 750, 754–755. **new**

synonymy

Dabbenea (Prodabbenea?) minima Kraglievich 1940, p. 750, 755–756. **new synonymy**

Holotype: MLP 15-246, left mandibular fragment with broken p4 and complete m1-m3 (Figure 2).

Referred material: MACN-Pv 2446, left p4; MACN-Pv 2494, right m3; MACN-Pv 2645, right m1 or m2; MACN-Pv 3288, right m3; MACN-Pv 3470, fragment of right m3; MACN-Pv

3475, right m1 or m2; MACN-Pv 4729, fragment of right mandible with p4; MACN-Pv 6620, left m1 or m2; MACN-Pv 9026 (holotype of ‘*Phoberomys praecursor*’), left p4; MACN-Pv 15304 (plaster cast of the holotype) left mandibular fragment with broken p4 and complete m1-m3; MLP 15-257, right p4; MLP 15-254, right m3; MACN-Pv 6612, upper incisor fragment; MACN-Pv 3290, right P4, M1 or M2; MACN-Pv 3448, fragment of left P4, M1 or M2; MACN-Pv 3461 (holotype of ‘*Dabbenea minima*’), left P4, M1 or M2; MACN-Pv 4068, left P4, M1 or M2; MACN-Pv 2542, fragment of right P4, M1 or M2; MACN-Pv 13480, left P4, M1 or M2; MACN-Pv 15306 (plaster cast of the type of ‘*Dabbenea insolita*’), left M3; MACN-A 5831, left P4, M1 or M2; MLP 15-249, right P4, M1 or M2; MLP 15-251 (holotype of ‘*Dabbenea insolita*’), left M3; MLP 15-256, left M3; MLP 15-261, right P4, M1 or M2; MLP 41-XII-13-149, left P4, M1 or M2; MLP 52-X-5-80, left M3; MLP 36 (holotype of ‘*Dabbenea lozanoi*’), right M3 (not found, studied through published illustrations).

Geographic and stratigraphic provenance: All the material came from the eastern margin of the Paraná River, between the town of Brugo and Paraná City, in Entre Ríos Province, Argentina (Figure 2). The material was recovered from the Lower Member (=‘Mesopotamiense’ *sensu* Frenguelli 1920; =‘Conglomerado osífero’) of the Ituzaingó Formation, late Miocene (e.g. Cione et al. 2000; Herbst 2000; Brandoni 2013; Brunetto et al. 2013).

Emended diagnosis: Species of *Phoberomys* with M3 with six to eight laminae, less straight than in *Ph. pattersoni*; the sixth or seventh laminae of the M3 with deep anterior indentations, differing from *Ph. pattersoni*; p4 with four laminae, the first two or three united labially, and the last one or two free from other laminae; m1-m3 with three laminae that can be all separated or the first two united labially.

Description and comparisons

Upper teeth: The upper dentition of *Phoberomys burmeisteri* is only known by isolated teeth. Beyond size, the P4-M2 of *Ph. burmeisteri* are similar to those of *Neoepiblema* and *Ph. pattersoni*, with three laminae of dentine and enamel united labially, with interlaminal cement as thick as the laminae (Figure 3(A)–(G)). The enamel layer of the cheek teeth is continuous and does not vary in its thickness on the leading edge or the trailing edge, unlike Dinomyidae (Candela et al. 2013). The second lamina has a larger transverse diameter and is slightly curved posterolingually at the lingual end.

There are usually seven or eight laminae united labially in the M3, but in some specimens there are six laminae (Figure 3(H)). The M3 has less straight laminae than in *Ph. pattersoni*, what was already noted by Mones (1980). The sixth or seventh laminae have anterior indentations or inflections near their labial end (Figure 3(H)–(K)), being even less straight than the other laminae, clearly differing from *Ph. pattersoni* which have straight laminae (see Mones 1980).

There is a middle fragment of an isolated upper incisor (MACN-Pv 6612) that was referred to *Phoberomys burmeisteri* (see Kraglievich 1940), but it was not associated with any other material. It is a very large tooth (see Table 1), even larger than that of the largest fossil rodent *Josephoartigasia monesi* (Rinderknecht & Blanco 2008). The labial face of the incisor is smooth and slightly curved, and the enamel reaches further in the medial face.

Table 1. Dental measurements in mm of *Phoberomys burmeisteri*.

Material number	Tooth	APD	TD
MACN-Pv 6612	I	37.68	35.62
MACN-Pv 13480 ^a	P4/M1/M2	17	21.4
MACN-Pv 4068 ^a	P4/M1/M2	21.5	22.2
MACN-Pv 3290 ^a	P4/M1/M2	22.2	22.7
MLP 15-249	P4/M1/M2	21.7	20.82
MLP 15-261	P4/M1/M2	20.57	19.04
MACN-Pv 3461 ^a	P4/M1/M2	13.7	15.7
MACN-A 5831 ^a	P4/M1/M2	21	31.4
MLP 15-251	M3	33.96	19.33
MLP 36 ^b	M3	34	14.5
MLP 15-256	M3		
MACN-Pv 9026 ^a	p4	28.7	22.2
MACN-Pv 2446	p4	36.98	16.45
MLP 15-257 ^a	p4	32.8	24.5
MACN-Pv 4729 ^a	p4	30.8	20.2
MACN-Pv 2645	m1/m2	12.34	7.59
MACN-Pv 3475	m1/m2	25.23	19.91
MACN-Pv 6620	m1/m2	24.52	21.13
MLP 12-246	m1	18.24	16.03
MLP 12-246	m2	21.82	15.74
MLP 12-246	m3	25.93	17.14
MACN-Pv 3288	m3	26.74	19.02
MACN-Pv 2494	m3	38.77	20.09
MLP 15-254 ^a	m3	33.3	24.2

Notes: APD, anteroposterior diameter; TD, transverse diameter.

^aCarrillo and Sánchez-Villagra (2015).

^bKraglievich (1940).

Lower teeth: The lower dentition is mostly known by isolated teeth, as the upper one, but also is known an almost complete dentition, corresponding to the holotype of *Phoberomys burmeisteri* (MLP 15-246; Figure 2(A),(B)).

As occur in all members of the family, the lower cheek teeth are composed by laminae of dentine and enamel, separated by thick cement layers. The enamel layer do not vary in its thickness on the leading edge or the trailing edge (Figure 4).

The p4 is composed of four laminae, being the first two (rarely the first three) united labially (Figure 4(B)–(E)). Different degrees

of union of the second and third laminae can be observed among the studied material (see Figure 4(B)–(D)).

In an m1 or m2 of a juvenile specimen (MACN-Pv 2645; see Figure 4(F)–(G)) can be observed that a pentalophodont pattern in occlusal view, became tetralophodont towards the base of the tooth, after the first and second laminae became fused. It is likely that with more wear the teeth would acquire a trilophodont pattern. The first lophid of the trilophodont pattern would be the result of the union of the three most anterior lophids of the pentalophodont juvenile teeth.

Adult m1-m3 have three laminae usually completely separated, but in some specimens the first and second laminae can be united labially (see Figure 4(M)), like in the m1-m3 of *Neoepiblema*. The m3 is more anteroposteriorly elongated, and with more obliquely oriented laminae, than the m1 and m2.

Mandible: The mandible is only known by the holotype (MLP 15-246). The masseteric notch for the tendon of the *M. masseter medialis pars anterior* (*sensu* Woods 1972; = *pars infraorbitalis*, *sensu* Woods & Howland 1979) is located low in the mandible body, and at level of the m1 (Figure 2(C),(D)), like in *Neoepiblema*.

The coronoid process is broken at its tip, and the base is located at the level of the posterior part of the m3. This differs from *Neoepiblema*, in which the coronoid process starts in the posterior portion of the m2.

The retromolar fossa is well developed, as in Chinchillidae and other *Neoepiblemidae* like *Perimys* and *Neoepiblema*. The mandibular foramen is large and located posterolingually to the retromolar fossa, in the dorsal part of the mandible (Figure 2(A),(B)), like in *Neoepiblema*. In Chinchillidae the mandibular foramen is located in the medial portion of the retromolar fossa, and in *Dinomyidae* it is posterior to the retromolar fossa, like in *Phoberomys*, but located in the medial face of the mandible (see Nasif 2010).

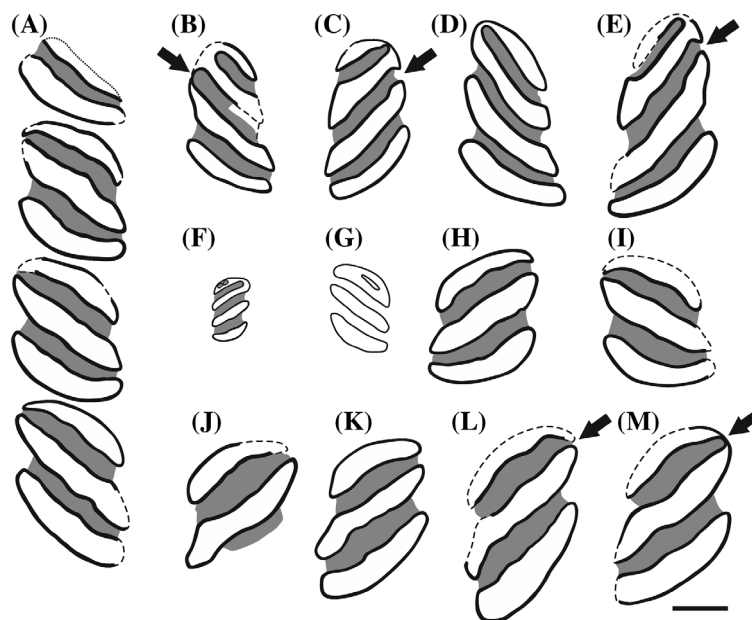


Figure 4. Lower dentition of *Phoberomys burmeisteri*. (A) MLP 15-246, holotype, portion of p4 and m1-m3; (B) MACN-Pv 9026 (holotype of *Ph. praecursor*) left p4; (C) MACN-Pv 4729, right p4; (D) MACN-Pv 2446, left p4; (E) MLP 15-257, right p4; (F) MACN-Pv 2645, right lower molar; (G) MACN-Pv 2645, contour pattern of the base; (H) MACN-Pv 3475, right m1 or m2; (I) MACN-Pv 6620, left m1 or m2; (J) MACN-Pv 3470, portion of right m3; (K) MACN-Pv 3288, right m3; (L) MACN-Pv 2494, right m3; (M) MLP 15-254, right m3. Scale bar: 10 mm.

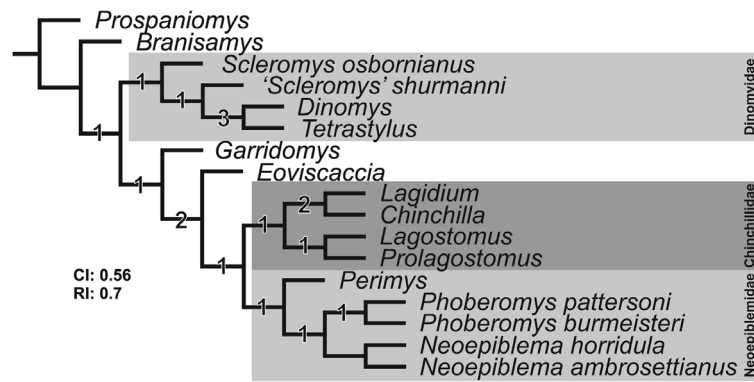


Figure 5. Most parsimonious tree, with a length of 102 steps, showing phylogenetic relationships of selected Chinchilloidea.

Notes: Numbers indicate absolute Bremer support index; CI, consistency index; RI, retention index.

There is a fossa for the muscle *masseter medialis pars posterior* (lateral fossa for mandibular insertion of *masseter superficialis* muscle *sensu* Kramarz et al. 2013) like in *Neoepilema* and Chinchillidae. Only the anterior portion of the fossa and the crest of the fossa for the *M. masseter medialis* (*sensu* Candela 2000) are preserved (Figure 2(B),(C)).

The alveolar sheet of the incisor reaches the posterior part of the m3 (Figure 2(D),(E)), like in *Neoepilema*.

Phylogenetic analysis

In our analysis, only one most parsimonious tree of 102 steps was obtained (see Figure 5).

Neoepilemidae is recovered as a monophyletic group supported by five unambiguous synapomorphies (characters 7[width of the flexa/ids-very thick], 8[leading edges wider than trailing edges-absent], 22[frontals longer than parietals-absent], 24[anterior margin of internal nares-at M3 or posterior] and 27[sagittal crest-present]), including the genera *Perimys*, *Neoepilema*, and *Phoberomys*. *Neoepilema* and *Phoberomys* conform also a monophyletic group (supported by one synapomorphy: character 43[0]). *Phoberomys* is supported by one unambiguous synapomorphy (character 44[multilaminated M3-present]).

The family Neoepilemidae is more closely related to Chinchillidae than to Dinomyidae, in agreement with cladistics analyses (e.g. Kerber et al. 2016) and with traditional studies (e.g. Kraglievich 1926, 1940; Bondesio et al. 1975). The position of *Eoviscaccia*, as sister group of Chinchillidae + Neoepilemidae, could respond to the high number of missing data due to the fragmentary nature of the material referred to this taxa. Nevertheless, Chinchillidae, Neoepilemidae and the chinchilloids *Garridomys* and *Eoviscaccia* conform a clade supported by three unambiguous synapomorphies (characters 3 [penetration degree of the hypoflexus in upper molars-hypoflexus extends more than half-way across the crowns], 5 [cement-present], and 8 [leading edges wider than trailing edges-present]).

Discussion

Mesopotamian diversity of *Phoberomys*

Two nominal species of *Phoberomys* from the 'Mesopotamiense' were based upon lower cheek teeth (*Ph. burmeisteri* and *Ph.*

praecursor), and three species were based upon upper cheek teeth (*Ph. insolita*, *Ph. lozanoi* and *Ph. minima*). Likely, the fragmentary nature of the material referred to *Phoberomys* from this unit, represented by isolated teeth which in some cases show marked size variation, have led to previous authors (i.e. Ameghino 1886; Kraglievich 1932, 1940) to identifying these specimens as pertaining to different species. Accordingly, most of the upper cheek teeth were identified as *Ph. insolita*, but also as *Ph. lozanoi* and *Ph. minima*, and most of the lower cheek teeth as *Ph. burmeisteri*, but also as *Ph. praecursor*.

A qualitative analysis of all the available material of *Phoberomys* from the 'Mesopotamiense', and a comparison with the better known *Ph. pattersoni*, from the late Miocene of Venezuela, indicate that actually all the specimens collected in the 'Mesopotamiense' belong to a single species, *Ph. burmeisteri*, and that the observed differences can be explained as individual and ontogenetic variation.

Almost all the lower cheek teeth have been previously assigned to *Phoberomys burmeisteri*, except for a p4, holotype of '*Ph. praecursor*', because it has the first three laminae united labially instead of the first two, like *Ph. burmeisteri*. In the available sample of isolated p4 there is a variable degree of union between the second and third laminae, so we consider that '*Ph. praecursor*' is a junior synonym of *Ph. burmeisteri*. In addition, Carrillo and Sánchez-Villagra (2015) stated that the labial connections of the laminae in the m1-m3 are variable in *Phoberomys pattersoni*, what is also observed in *Ph. burmeisteri*.

Kraglievich (1940) used the number of laminae of the M3 to distinguish species of '*Dabbenea*' (= *Phoberomys*), with eight laminae for '*Dabbenea insolita*', and seven laminae for '*Dabbenea lozanoi*'. But he also stated (Kraglievich 1940) that the multilaminar M3 of '*Dabbenea*' was analogous to that of the living *Hydrochoerus hydrochaeris*, for which twelve to thirteen laminae are present, but also fourteen or eleven laminae can be found (but see Aeschbach et al. 2016). Therefore, a variable number of laminae of the M3 could be considered within the intraspecific variability of *Phoberomys*, and it would not be a definitive character to separate species of *Phoberomys*. Moreover, the number of laminae present in the M3 of *Phoberomys* have been traditionally considered as seven or eight (e.g. Bondesio & Bocquentin-Villanueva 1988), but M3 referred to *Phoberomys* with six laminae were reported by Kraglievich (1940) and Carrillo and

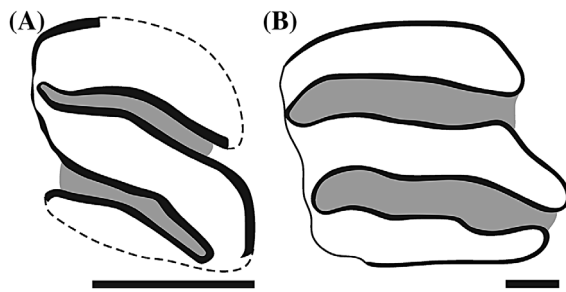


Figure 6. (A) *Eusigmomys oppositus*, MACN-A 11189, right upper cheek tooth; (B) *Peromys gyulavarii* (holotype), right upper cheek tooth, possibly a P4 (modified from Kretzoi & Vörös 1989). Scale bar: 5 mm.

Sánchez-Villagra (2015), suggesting a higher variability than previously considered for the morphology of this tooth.

Almost all the isolated P4, M1 or M2 were previously referred to '*Dabbenaea insolita*', except for the holotype of '*D. minima*', a P4, M1, or M2 that was considered a different species because of its small size (see Table 1), but the material likely correspond to a juvenile individual and the differences are considered here as intraspecific ontogenetic variation. Note that protohypsodont and euhypsodont cheek teeth of different groups of caviomorphs (e.g. Hydrocheriidae, Dinomyidae) grow in all its dimensions (width and length, not only crown height) throughout the life of the individuals (Vucetich et al. 2005; Candela & Nasif 2006). Neopiblemidae shows a similar ontogenetic tooth growth than that detected in other hypsodont caviomorphs. Moreover, it was traditionally considered (e.g. Mones 1980; Bondesio & Bocquentin-Villanueva 1988) that there is a significant size difference between *Phoberomys* species, but according to Carrillo and Sánchez-Villagra (2015) the interspecific differences, including size, could be difficult to assess.

Therefore, all upper cheek teeth can be referred to the same species than the lower cheek teeth, *Phoberomys burmeisteri*, despite there are no associated upper and lower dentition. On this basis, the synonymy of *Ph. praecursor*, *Ph. insolita*, *Ph. lozanoi* and *Ph. minima* with *Ph. burmeisteri* is justified.

Phylogeny of Chinchilloidea

The phylogenetic relationships within Chinchilloidea are not fully understood, and there are few studies (e.g. Kramarz 2002, 2005; Kramarz et al. 2013; Kerber et al. 2016) that includes living and fossil taxa of several families (i.e. Chinchillidae, Dinomyidae, Neopiblemidae, and Cephalomyidae).

Despite our study was not an exhaustive analysis of the phylogenetic relationship of all Chinchilloidea, it is noteworthy that it support the traditional view (e.g. Kraglievich 1926; Bondesio et al. 1975) that Neopiblemidae and Chinchillidae are more closely related to each other than to Dinomyidae. Moreover, our analysis showed that Neopiblemidae is a clade including *Perimys*, *Neopiblema*, and *Phoberomys*, supporting previous studies (e.g. Bondesio et al. 1975), and that *Phoberomys* is more closely related to *Neopiblema* than to *Perimys*.

A future, more exhaustive analysis, including more taxa of Neopiblemidae (i.e. species of *Perimys* and the genus *Doryperimys*), other chinchilloids (e.g. Cephalomyidae,

Loncolicu, *Incamys*) and more characters, could give a better understanding of the phylogenetic relationship within the Chinchilloidea.

Revised diversity of the Neopiblemidae

A comprehensive history of changes in the family concept and included genera was given by several authors (e.g. Mones 1980; Negri & Ferigolo 1999). Here we present major changes in the inclusion of different genera within Neopiblemidae.

The family Neopiblemidae was erected by Kraglievich (1926) to include two genera: *Neopiblema* and *Dabbenaea*. Later, the family was re-characterised and new species were described (Kraglievich 1940). Bondesio et al. (1975) included *Perimys* and *Scotaeumys* in Neopiblemidae and studied the relationships of the Neopiblemidae with Chinchillidae.

Bondesio and Bocquentin-Villanueva (1988) realised that *Dabbenaea* was a synonym of *Phoberomys*, a genus that was considered until then as a Dinomyidae (e.g. Kraglievich 1926, 1932). Two other genera included in the same subfamily of *Phoberomys* were then considered as possible neopiblemids, *Euphilus* and *Eusigmomys*. Later, Bocquentin-Villanueva et al. (1990) synonymized *Euphilus* with *Neopiblema*.

Scotaeumys was later considered as juvenile *Prologostomus* (Vucetich & Verzi 1993; Kramarz 2002).

Perimys was first considered a Chinchillidae (e.g. Ameghino 1887, 1889; Scott 1905), and later a Neopiblemidae (Bondesio et al. 1975) and a Cephalomyidae (e.g. Vucetich 1985). More recently, it was again included in the Neopiblemidae (e.g. McKenna & Bell 1997; Kramarz 2002).

The recently described *Doryperimys* is closely related to *Perimys* and was included in the Neopiblemidae (Kramarz et al. 2015).

Therefore, there are currently four undisputed genera included in the Neopiblemidae: *Perimys*, *Doryperimys*, *Neopiblema* and *Phoberomys*, which share a series of characters: euhypsodont cheek teeth with two or more laminae of dentine surrounded by enamel united labially in the upper molars, thick interlaminal cement layers (ch.7[2]), leading edges not wider than the trailing edges (ch. 8[1]), frontals not longer than the parietals (ch. 22[0]), anterior margin of internal nares at M3 or posterior (ch.24[1]), and presence of sagittal crest (ch.27[0]).

In addition, there are two genera usually associated with this family, *Eusigmomys* and *Peromys*. *Eusigmomys oppositus* was described by Ameghino (1904, 1905) for the middle Miocene ('Friasian') of Santa Cruz Province, Argentina (see Vucetich 1984) as a Chinchillidae (= 'Viscaccidae'; Ameghino 1904). Later, Vucetich (1984) considered this taxon as a Dinomyidae. Several authors (e.g. Bondesio & Bocquentin-Villanueva 1988; Negri & Ferigolo 1999; Carrillo & Sánchez-Villagra 2015) have considered *Eusigmomys* as a neopiblemid.

The holotype of *Eusigmomys oppositus* is currently lost (see Vucetich 1984), but our analysis of an upper molar (MACN-A 11189) referred to this species that match the description of Ameghino (1904) reveals that it clearly does not belong to Neopiblemidae because it has three laminae, the first and second united labially and the second and third united lingually, forming an 'S' pattern (see Figure 6(A)). This morphology is

similar to some Dinomyidae like *Simplimus* and *Scleromys*, supporting the statement of Vucetich (1984).

On the other hand, *Perumys gyulavarii* was described for the upper? Pliocene of Peru as a caviomorph closely related to *Phoberomys* and *Amblyrhiza* (Kretzoi & Vörös 1989). The holotype, and only known material, was originally described as a lower molar (m2), but Kerber et al. (2016) noted that it is actually an upper cheek tooth, probably pertaining to *Phoberomys*. The holotype of *Perumys gyulavarii* can be assigned with certainty to *Phoberomys* by the presence of three laminae united labially, with thick interlaminal cement layers (see Figure 6(B)), and its size, much larger than *Neopiblema*, so *Perumys* is a junior synonym of *Phoberomys* as suggested by Kerber et al. (2016). The validity of *Phoberomys gyulavarii* (new combination) needs to be evaluated in a broader context, comparing with more material, but as the holotype and only known material consist of an isolated tooth it is difficult to make a thorough comparison.

Biogeographic remarks

The presence of the same genera of Neopiblemidae in the 'Mesopotamiense', in the Urumaco Formation (late Miocene of Venezuela; e.g. Mones 1980; Bondesio & Bocquentin-Villanueva 1988), and in the Solimões Formation (late Miocene of Brazil; e.g. Negri & Ferigolo 1999; Kerber et al. 2016) suggest a biogeographic connection of the 'Mesopotamiense' with the Brazilian subregion (*sensu* Hershkovitz 1958; see Candela 2005). Also, this family (along with other vertebrate groups; see Cione et al. 2000; Candela & Morrone 2003) permits to differentiate the Mesopotamian area from northwestern and central Argentina, the last two without records of neopiblemids, during the late Miocene (Candela 2005).

The fossil record of the Neopiblemidae suggests two different biogeographic stories for the family, the first one includes the small to medium sized *Perimys* and *Doryperimys*, restricted to the early Miocene of Argentinian Patagonia and Chile (e.g. Ameghino 1887; Flynn et al. 2002; Kramarz 2002; Kramarz et al. 2015), and the second one includes the large to giant *Neopiblema* and *Phoberomys*, recorded from the middle Miocene to the Pliocene in Northern South America (e.g. Ameghino 1889; Kraglievich 1926; Mones 1980; Negri & Ferigolo 1999; Horovitz et al. 2006; Vucetich et al. 2010; Antoine et al. 2015; Carrillo & Sánchez-Villagra 2015; Tejada-Lara et al. 2015; Kerber et al. 2016).

Conclusions

During the late Miocene, Neopiblemidae is represented by *Neopiblema* and *Phoberomys*. *Phoberomys* includes at least two species: *Ph. burmeisteri*, recorded exclusively in the 'Mesopotamiense' of Argentina, and *Ph. pattersoni*, distributed in lower latitudes in the Urumaco Formation of Venezuela. The specific assignation of the Brazilian and Peruvian records of *Phoberomys* needs to be revised.

The diversity of Mesopotamian neopiblemids is lower than previously recognised, and it includes one species of *Phoberomys* and two species of *Neopiblema*. There are no records of *Perimys* from this unit.

Neopiblemidae is a monophyletic group including *Perimys*, *Neopiblema* and *Phoberomys*, and it is more closely related to Chinchillidae than to Dinomyidae. *Phoberomys* is more closely related to *Neopiblema* than to the Patagonian *Perimys*.

Eusigmomys oppositus is not a Neopiblemide, and possibly belong to the Dinomyidae.

Perimys and *Doryperimys* would become extinct by the middle Miocene, giving place to the middle Miocene-Pliocene genera *Neopiblema* and *Phoberomys*.

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No potential conflict of interest was reported by the authors.

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