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

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**ABSTRACT**

*Phoberomys* is a giant caviomorph rodent included in the extinct Neoepiblemidae. 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specimens of *Phoberomys* from the ‘Mesopotamiense’, late Miocene of Entre Ríos Province (Argentina), including several unpublished specimens and the holotypes of the five nominal species (*Ph.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 Neoepiblemidae is monophyletic and includes *Phoberomys*, *Neoepiblema*, and *Perimys*. *Phoberomys* species are recovered as a clade, which is more closely related to *Neoepiblema* than to the Patagonian *Perimys*. In addition, our study shows that *Eusigmonys* is not a Neoepiblemidae, but a Dinomyidae.

**Introduction**

Neoepiblemidae 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), *Neoepiblema* 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 Neoepiblemidae: *Eusigmonys* and *Perumys*. *Eusigmonys oppositus* (see Ameghino 1904, 1905), from the middle Miocene of Argentina, was included in the Dinomyidae by Vucetich (1984), but is considered as a neoepiblemid by several authors (e.g. Bondesio & Bocquentin-Villanueva 1988; Negri & Ferigolo 1999; Sanchez-Villagra et al. 2003). *Perumys gyuulavarii* was described for the upper Pliocene of Peru, and referred as closely related to the neoepiblemid *Phoberomys* and the heptaxodontid *Amblyrhiza* (see Kretzoi & Vörös 1989), but recently Kerber et al. (2016) suggested that it could be assigned to *Phoberomys*.

The Neoepiblemidae are characterised by euhysodont 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 (*Neoepiblema*) 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 Neoepiblemidae 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 bordasi* (Patterson 1942) was considered as possibly belonging to *Neoepiblema* (see Kerber et al. 2016). Other remains referred to *Phoberomys* 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), neoepiblemids reached a great taxonomic diversity.
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. pracoercurus, Ph. insolita, Ph. lozanoi, and Ph. minima; Ameghino 1886; Kraglievich 1932, 1940) and two species of Neoeptiblema (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-Villara 2010; Vucetich et al. 2010).

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

**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 Chinchiloidea, 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 Neoeptiblema (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 paracanalicular 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. Multilamined 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 (hypsoodonty), 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 1966; 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.

**Neoeptiblemids of the ‘Mesopotamiense’**

The Ituzaingó Formation is a unit of fluvial origin mainly composed by sandstone, which crops out on the eastern margin of
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 chrono-logic 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 Neoepiblemidae 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 neoepiblemids (Neoeplebema, Phoberomys, and Perimys) were identified in the ‘Mesopotamiense’ (e.g. Ameghino 1886, 1889; Kraglievich 1926). Two species of Neoeplebema are currently recognised for this unit: Neoeplebema horridula and Neoeplebema ambrosettiatus (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 (Candel 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 Neoepiblemidae: Neoeplebema and Phoberomys.

Systematic paleontology

RODENTIA Bowdich, 1821
HYSTRICOGNATHI Tullberg, 1899
CAVIOMORPHA Wood and Patterson (in Wood, 1955)
CHINCHILLOIDEA Kraglievich, 1940
NEOEPIBLEMIDAE 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. Bondeiso 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 15-251, 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, Perigolo, 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 15-256, 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 4729, fragment of right m1 or m2; 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 know 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 do 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 Josephaortigasia monesi (Rinderknecht & Blanco 2008). The labial face of the incisor is smooth and slightly curved, and the enamel reaches further in the medial face.
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).

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**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.

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

| Material number | Tooth        | APD  | TD  |
|-----------------|--------------|------|-----|
| MACN-Pv 6612    | 1            | 37.68| 35.62|
| MACN-Pv 13480a  | P4/M1/M2     | 17   | 21.4|
| MACN-Pv 4068a   | P4/M1/M2     | 21.5 | 22.2|
| MACN-Pv 3290a   | 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 3461a   | P4/M1/M2     | 13.7 | 15.7|
| MACN-A 5831a    | P4/M1/M2     | 21   | 31.4|
| MLP 15-251      | M3           | 33.96| 19.33|
| MLP 366         | M3           | 34   | 14.5|
| MLP 15-256      | M3           | 34   | 14.5|
| MACN-Pv 9026a   | p4           | 28.7 | 22.2|
| MACN-Pv 2446    | p4           | 36.98| 16.45|
| MLP 15-257a     | p4           | 32.8 | 24.5|
| MACN-Pv 4729a   | 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 15-254a     | m3           | 33.3 | 24.2 |

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

acarrillo and sánchez-Villagra (2015).

Kraglievich (1940).
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 *Neoepiblema* 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 *Neoepiblema*.

**Phylogenetic analysis**

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

*Neoepiblemidae* 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*, *Neoepiblema*, and *Phoberomys*. *Neoepiblema* and *Phoberomys* conform also a monophyletic group (supported by one synapomorphy: character 43[0]). *Phoberomys* is supported by one unambiguous synapomorphy (character 44[multilamined M3-present]).

The family *Neoepiblemidae* 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* + *Neoepiblemidae*, could respond to the high number of missing data due to the fragmentary nature of the material referred to this taxa. Nevertheless, *Chinchillidae*, *Neoepiblemidae* 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 halfway 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...
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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 'Dabbenea 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 protohypodont and euhypodont cheek teeth of different groups of caviomorphs (e.g. Hydrochiridae, Dinomysidae) 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). Neoepiblemidae shows a similar ontogenetic tooth growth than that detected in other hypsdont caviomorphs. Moreover, it was traditionally considered (e.g. Mones 1980; Bondesio et al. 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. praeccursor, 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, Dinomysidae, Neoepiblemidae, 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 Neoepiblemidae and Chinchillidae are more closely related to each other than to Dinomysidae. Moreover, our analysis showed that Neoepiblemidae is a clade including Perimys, Neoepiblema, and Phoberomys, supporting previous studies (e.g. Bondesio et al. 1975), and that Phoberomys is more closely related to Neoepiblema that to Perimys.

A future, more exhaustive analysis, including more taxa of Neoepiblemidae (i.e. species of Perimys and the genus Doryperimys), other chinchilloids (e.g. Cephalomyidae, Loncolius, Incamys) and more characters, could give a better understanding of the phylogenetic relationship within the Chinchilloidea.

Revised diversity of the Neoepiblemidae

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 Neoepiblemidae.

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

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

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

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

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

Therefore, there are currently four undisputed genera included in the Neoepiblemidae: Perimys, Doryperimys, Neoepiblema and Phoberomys, which share a series of characters: euhypodont 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 Perimys. Eusigmomys oppositus was described by Ameghino (1904, 1905) for the middle Miocene (‘Friesian’) of Santa Cruz Province, Argentina (see Vucetich 1984) as a Chinchillidae (=‘Viscaccidae’; Ameghino 1904). Later, Vucetich (1984) considered this taxon as a Dinomysidae. Several authors (e.g. Bondesio & Bocquentin-Villanueva 1988; Negri & Ferigolo 1999; Carrillo & Sánchez-Villagra 2015) have considered Eusigmomys as a neoepiblemid.

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 Neoepiblemidae 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 Simplusim and Scleromys, supporting the statement of Vucetich (1984).

On the other hand, Perimys gyulavarii was described for the upper Pliocene of Peru as a caviomorph closely related to Phoberomys and Amblyrhiza (Kretzoi & Vrös 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 Perimys 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 Neoepiblema, so Perimys 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 Neoepiblemidae 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 las two without records of neoepiblemids, during the late Miocene (Candela 2005).

The fossil record of the Neoepiblemidae 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 Neoepiblema 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, Neoepiblemidae is represented by Neoepiblema 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 neoepiblemids is lower than previously recognised, and it includes one species of Phoberomys and two species of Neoepiblema. There are no records of Perimys from this unit.

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

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

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

**Acknowledgements**

We want to thank to A. Kramarz (MACN), M. Reguero (MLP) and A. Scarano (MLP) for allowing the access to the collections under their care. We also thank two anonymous reviewers whose comments and corrections improved the final version of the manuscript.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

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**References**

Aeschbach A, Carrillo JD, Sánchez-Villagra MR. 2016. On the growth of the largest living rodent: Postnatal skull and dental shape changes in capybara species (Hydrochoerus spp.). Mamm Biol. 81:558–570.

Ameghino F. 1886. Contribuciones al conocimiento de los mamíferos fósiles de los terrenos terciarios antiguos del Paraná [Contributions to the knowledge of fossil mammals from ancient Tertiary lands of Paraná. Journal name: Bulletin of the National Academy of Science of Córdoba]. Bol Acad Nac Cienc Córdoba. 9:5–228.

Ameghino F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. Bol Mus La Plata. 1:1–26.

Ameghino F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas Acad Nac Cienc Córdoba. 6:1–1027.

Ameghino F. 1891. Mamíferos y aves fósiles argentinas. Especies nuevas, adiciones y correcciones. Rev Argent Hist Nat. 1:240–259.

Ameghino F. 1904. Nuevos especies de mamíferos Cretáceos y Terciarios de la República Argentina. An Soc Cient Arg Córdoba. 57:327–341.

Ameghino F. 1905. Reemplazamiento de un nombre genérico. An Soc Cient Arg Córdoba. 59:75.

Antoine P-O, Abello MA, Adnet S, Altamirano Sierra AJ, Baby P, Billet G, Boivin M, Calderón Y, Candela A, Chabain J, et al. 2015. A 60-million year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. Gondwana Res. 31:30–349. doi:10.1016/j.gr.2015.11.001.

Bondesio D. 2013. Los mamíferos continentales del “Mesopotamiense” (Miocene Tardio) de Entre Ríos, Argentina. Diversidad, edad y
paleobiogeography. In: Brandoni D, Noriega JJ, editors. El Neógeno de la Mesopotamia argentina. Buenos Aires: Asociación Paleontológica Argentina, Publicación Especial. 14: p. 179–191.
Brunetto E, Noriega JJ, Brandoni D. 2013. Sedimentología, estratigrafía y edad de la Formación Ituzaingó en la provincia de Entre Ríos, Argentina. In: Brandoni D, Noriega JJ, editors. El Neógeno de la Mesopotamia argentina, Buenos Aires: Asociación Paleontológica Argentina, Publicación Especial. 14: p. 13–27.
Candela AM. 2000. Los Eretizontidae (Rodentia, Hystrixognathi) fósiles de Argentina Sistemática e historia evolutiva y biogeográfica [PhD thesis]. La Plata: Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.
Candela AM, 2005. Los roedores del “Mesopotamiense” (Mioceno tardío, Formación Ituzaingó) de la provincia de Entre Ríos (Argentina). In: Aceñolaza FG, editor. Temas de la Biodiversidad del Litoral Fluvial Argentino II. Tucumán: Miscelánea. 14; p. 37–88.
Candela AM, Cassini GH, Nasif NL. 2013. Fractal dimension and cheek teeth crown complexity in the giant rodent Eumegamys paranensis. Lethaia. 46:369–377.
Candela AM, Morrone JJ. 2003. Biogeografía de pueceropesínes neotropicales (Rodentia, Hystrixognathi): Integrando datos fósiles y actuales a través de un enfoque panbiogeográfico. Ameghiniana. 40:361–368.
Candela AM, Nasif NL. 2006. Systematics and biogeographic significance of Drytomomys typicus (Scalabrini in Ameghino, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystrixognathi) from Northeast of Argentina. Neues Jahrb Geo P-A. 1:165–181.
Candela AM, Picasso MBJ. 2008. Functional anatomy of the limbs of erethizontidae (Rodentia, Caviomorpha): Indicators of locomotor behavior in Miocene porcupines. J Morphol. 269:552–593.
Carrillo JD, Sánchez-Villagra MR. 2015. Giant rodents from the Neotropics: diversity and dental variation of late Miocene neoepiblemid remains from Urumaco, Venezuela. Paläontol Z. 89:1057–1071. doi: 10.1007/s12542-015-0267-3.
Cione AL, Azpeicueta MM, Bond M, Carlini AA, Castiscia JR, Cozzulo MA, de la Fuente M, Gasparini Z, Goin FJ, Noriega J, et al. 2000. Miocene vertebrates from Entre Ríos province, eastern Argentina. In: Aceñolaza FG, Herbst R, editors. El Neógeno de Argentina. Serie Correlación Geológica. Tucumán: INSUGEO, 14; p. 191–237.
D’Orbigny AD. 1842. Voyage dans l’ America Méridionale. Paris, Pitois, Ve. Levrault. 3:1–188.
Farris JS. 1983. The logical basis of phylogenetic analysis. In: Platnick NI, Funk VA, editors. Advances in cladistics. New York: Columbia University Press; p. 7–36.
Ferrugelli J. 1920. Contribución al conocimiento de la geología de Entre Ríos. Bol Acad Nac Cienc Córdoba. 24:55–256.
Geiger M, Wilson LAB, Costeur L, Sánchez R, Sánchez-Villagra MR. 2013. Diversity and body size in giant caviomorphs (Rodentia) from the northern Neotropics – a study of femoral variation. J Vert Paleontol. 33:1449–1456.
Goloboff P, Catalano S. 2016. TNT version 1.5, including a virtual platform of phylogenetic morphometrics. Cladistics. 32:221–238. doi: 10.1111/c12160.
Hennig W. 1968. Elementos de una sistemática filogenética. Buenos Aires: Editorial Universidad de Buenos Aires; 533pp.
Herbst R. 2000. La Formación Ituzaingó (Plioceno). Estratigrafía y distribución. In: Aceñolaza FG, Herbst R, editors. El Neógeno de Argentina. Serie Correlación Geológica. Tucumán: INSUGEO, 14; p. 181–190.
Hershkovitz P. 1958. A geographic classification of Neotropical mammals. Fieldiana Zool. 36:581–620.
Horovitz I, Sánchez-Villagra MR, Martin T, Aguilera OA. 2006. The fossil record of Phoberomys pattersoni Mones 1980 (Mammalia, Rodentia) from Urumaco (Late Miocene, Venezuela), with an analysis of its phylogenetic relationships. J Syst Palaeontol. 4:293–306.
Kerber L, Negri FR, Ribeiro AM, Nasif N, Pereira Souza-Filho J, Ferigolo J. 2016. Tropical fossil caviomorph rodents from the southwestern Brazilian Amazonia in the context of the south American faunas: systematics, biochronology, and paleobiogeography. J Mammal Evol. 24:57–70. doi: 10.1007/s10914-016-9340-2.
Kraglievich L. 1926. Los grandes roedores terciarios de la Argentina y sus relaciones con ciertos géneros pleistocenos de las Antillas. An Mus Nac Buenos Aires. 34:121–135.
Kraglievich L. 1932. Diagnosis of nuevos géneros y especies de roedores cávidos y eumegámidos de la Argentina. Rectificación genérica de algunas especies conocidas y adiciones al conocimiento de otras. An Soc Cient Argentina. 64:155–181, 211–237.
Kraglievich L. 1940. Los roedores de la familia extinguida Neoeoepiblemidae. In: Torcelli AJ, Marelli CA, editors. Obras en Geología y Paleontología. La Plata: Talleres de Impresiones Oficiales; p. 741–764.
Kramarz AG. 2001. Revision of the family Cephalomysidae (Rodentia, Caviomorpha) and new cephalomysids from the Early Miocene of Patagonia. Palaeovertebrata, 30:51–88.
Kramarz AG. 2002. Roedores chinchilloideos (Hystrixognathi) de la Formación Pinturas, Miocene temprano-medio de la provincia de Santa Cruz, Argentina. Rev Mus Arg Cienc Nat, nueva serie. 4:167–180.
Kramarz AG. 2005. A primitive cephalomyid hystrixognath rodent from the early Miocene of northern Patagonia, Argentina. Acta Palaeontol Pol. 50:249–258.
Kramarz AG, Bond M, Arnal M. 2015. Systematic description of three new mammals (Notoungulata and Rodentia) from the early Miocene Cerro Bandera Formation, Northern Patagonia, Argentina. Ameghiniana. 52:585–597.
Kramarz AG, Vucetich MG, Arnal M. 2013. A new early Miocene chinchilloid hystrixognath rodent; an approach to the understanding of the early chinchillid dental evolution. J Mammal Evol. 20:249–261.
Kretzoi M, Vóris I. 1989. On a new caviomorph rodent from Peru. Fragmenta Mineralogica et Palaeontologica. 14:111–116.
MacPhee RED. 2011. Basicranial morphology and relationships of Antillean Heptaxodontidae (Rodentia, Ctenohystrica, Caviomorpha). Bull Am Mus Nat Hist. 363:1–70.
McKenna MC, Bell SK. 1997. Classification of mammals above the species level. New York: Columbia University Press; p.1–XII; 1–631.
Millien V, Boyv H. 2010. When teeth and bones disagree: body mass estimation of a giant extinct rodent. J Mammal. 91:11–18.
Mones A. 1980. Un Neoeoepiblemidae del Plioceno Medio (Formación Urumaco) de Venezuela (Mammalia: Rodentia: Caviomorpha). Ameghiniana. 16:277–279.
Nasif NL. 2010. Los Dinomyidae (Rodentia, Caviomorpha) del Miocene superior del Noroeste argentino Su anatomía cráneo-dentaria [PhD thesis]. Tucumán: Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán.
Nasif NL, Candela AM, Rasia I, Madozzo Jaén MC, Bonini R. 2013. Actualización del conocimiento de los roedores del Mioceno Tardío de la Mesopotamia argentina: aspectos sistemáticos, evolutivos y paleobiogeográficos. In: Brandoni D, Noriega JJ, editors. El Neógeno de la Mesopotamia argentina. Buenos Aires: Asociación Paleontológica Argentina, Publicación Especial. 14; p. 153–169.
Negri FR, Ferigolo J. 1999. Anatomia craniana de Neoeoepiblema ambrostetians (Ameghino 1889) (Rodentia, Caviomorpha, Neoeoepiblemidae) do Miocene superior-Plioceno, Estado do Acre, Brasil, e revisão das espécies do gênero. Bol Mus Para Emilio Goeldi, Sér Ciênc Terra. 11:3–81.
Patterson B. 1942. Two tertiary mammals from northern South America. Amer Mus Novit. 1173:1–8.
Pérez LM. 2013. Nuevo aporte al conocimiento de la edad de la Formación Paraná, Miocene de la provincia de Entre Ríos, Argentina. In: Brandoni D, Noriega JJ, editors. El Neógeno de la Mesopotamia argentina. Buenos Aires: AsociaciónPaleontológica Argentina, Publicación Especial. 14; p. 7–12.
Rinderknecht A, Blanco RE. 2008. The largest fossil rodent. Proc R Soc B. 275:923–928.
Sánchez-Villagra MR, Aguilera O, Horovitz I. 2003. The anatomy of the world’s largest extinct rodent. Science. 301:1708–1710.
Vucetich MG. 1985. Cephalomyopsis hipselodontus gen. et sp. nov. (Rodentia, Caviomorpha, Cephalomyidae) de la Edad Colhuehuapense (Oligoceno tardio) de Chubut, Argentina. Ameghiniana. 22:243–245.
Vucetich MG, Carlini AA, Aguilera O, Sánchez-Villagra MR. 2010. The tropics as reservoir of otherwise extinct mammals: the case of rodents from a new Pliocene faunal assemblage from Northern Venezuela. J. Mammal. Evol. 17:265–273.
Vucetich MG, Deschamps CM, Olivares AI, Dozo MT. 2005. Capybaras, size, shape, and time: a model kit. Acta Palaeontol Pol. 50:259–272.
Vucetich MG, Verzi DH. 1993. Un nuevo Chinchillidae del Colhuehuapense (Mioceno Inferior?) de Gaiman (Chubut): su aporte a la comprensión de la dicotomía vizcachas – chinchillas. Ameghiniana. 30:115.
Wood AE. 1955. A revised classification of the rodents. J Mammal. 36:165–187.
Woods CA. 1972. Comparative myology of jaw, hyoid, and pectoral appendicular regions of New and Old World hystricomorph rodents. Bull Am Mus Nat Hist. 147:115–198.
Woods CA, Howland EB. 1979. Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. J Mammal. 60:95–116.