A new record of a giant neoepiblemid rodent from Peruvian Amazonia and an overview of lower tooth dental homologies among chinchilloids

MYRIAM BOIVIN, PIERRE-OLIVIER ANTOINE, ALDO BENITES-PALOMINO, LAURENT MARIVAUX, and RODOLFO SALAS-GISMONDI

We report here a new record of the giant caviomorph *Phoberomys* corresponding to a fragmentary mandible from the Monte Salvado area, Peruvian Amazonia (Madre de Dios Department). We describe this specimen and compare it with the material previously attributed to *Phoberomys*. The mandibular fragment is referred to as *Phoberomys* sp. Found as float on a bank of the Río Las Piedras, it has been hypothetically assigned a late Miocene age, due to the local/regional stratigraphic and lithologic context. This specimen constitutes the second record of *Phoberomys* in Peru. For the first time, the pattern of p4s and lower molars in *Phoberomys* was analyzed and compared to a large taxonomic sample (including Paleogene–Recent chinchilloids and other caviomorphs) in order to progress the understanding of the homology of dental structures in this genus. For p4s and lower molars, the position of the protoconid in *Phoberomys* and other chinchilloids (*Drytomomys* sp., *Potamarchus*, *Eumegamys*, *Gyriabrus*, *Isostylomys*, and *Tetrastylus*) is ambiguous, and as a result we propose two alternative homology hypotheses for these taxa: protoconid within the first and second laminae or within the third lamina on juvenile specimens. The knowledge of a comprehensive ontogenetic sequence in extinct and extant chinchilloids, associated with more complete palaeontological records, would likely allow for a clarification of these homology ambiguities.

Key words: Mammalia, Rodentia, *Phoberomys*, mandible, Palaeogene, South America, Peru, Monte Salvado.

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Introduction

The caviomorph rodents (e.g., spiny rats, guinea pigs, chinchillas, and American porcupines) constitute one of the most successful groups of placental mammals from South America. Their Recent specific richness amounts to ca. 11% of the worldwide rodent diversity (ca. 250 species; e.g., Upham and Patterson 2015). They are characterized by a large array of ecomorphologic adaptations, especially of locomotion and diet, illustrating several lifestyles (terrestrial, fossorial, arboreal, and semi-aquatic; e.g., Patton et al. 2015). They present a huge morphological diversity depicting a wide disparity of body mass (ca. 50 g, plains viscacha rat; ca. 65 kg, capybara). During their evolutionary history, several groups from all four extant superfamilies (Hydrocheriinae Gray, 1825 among Cavioidea; Erethizontidae Bonaparte, 1845 among Erethizontoidea; Dinomyidae Peters, 1873 and Neoepiblemidae Kraglievich, 1926 among Chinchilloidea; "Heptaxodontinae" Anthony, 1917 among Octodontoidea and Chinchilloidea; see MacPhee 2011) showed trends toward the achievement of large to giant sizes (Biknevicius et al. 1993;

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Table 1. Records of the extinct neoepiblemid rodent *Phoberomys* from the literature and history of their synonymies or suggested synonymies.

Taxon	Remains	Locality and age	Official or suggested synonymy	Author(s) of synonymy	Additional references	Noted here as
Phoberomys burmeisteri (Ameghino, 1886)	dental and cranial	eastern margin of the Paraná River, Argentina, Ituzaingó Formation, "Mesopotamiense", late Miocene	*Megamys burmeisteri* Ameghino, 1886 "*Euphilus burmeisteri*" (Ameghino, 1886) *Phoberomys burmeisteri* (Ameghino, 1886)	Ameghino 1891 Kraglievich 1926	Ameghino 1898 Candela 2005	*Phoberomys burmeisteri*
			Dabbenea lozanoi Kraglievich, 1940 *Phoberomys lozanoi* (Kraglievich, 1940) *Phoberomys burmeisteri* (Ameghino, 1886)	Bondesio and Bocquentin-Villanueva 1988 Rasia and Candela 2018		
			Dabbenea insolita Kraglievich, 1940 *Phoberomys insolita* (Kraglievich, 1940) *Phoberomys burmeisteri* (Ameghino, 1886)	Bondesio and Bocquentin Villanueva 1988 Rasia and Candela 2018		
			Dabbenea (*Prodabbenea*?) *minima* Kraglievich, 1940 *Phoberomys minima* (Kraglievich, 1940) *Phoberomys burmeisteri* (Ameghino, 1886)	Bondesio and Bocquentin Villanueva 1988 Rasia and Candela 2018		
			Phoberomys praecursor Kraglievich, 1932 *Phoberomys burmeisteri* (Ameghino, 1886)	Rasia and Candela 2018		
			Phoberomys sp.	Rasia and Candela 2018	Cione et al. 2000	
			Phoberomys	Rasia and Candela 2018	Cione et al. 2000	
Phoberomys pattersoni (Mones, 1980)	dental, cranial and postcranial	several localities in Venezuela, Urumaco Formation, late Miocene	*Dabbenea pattersoni* Mones, 1980 *Phoberomys pattersoni* (Mones, 1980)	Bondesio and Bocquentin Villanueva 1988	Sánchez-Villagra et al. 2003 Horovitz et al. 2006 Carrillo and Sánchez-Villagra 2015	*Phoberomys pattersoni*
Phoberomys cf. *pattersoni*	upper teeth and cranial	Tío Gregorio, Venezuela, Urumaco Formation, late Miocene			Horovitz et al. 2006	*Phoberomys* cf. *pattersoni*
Phoberomys sp.	dental, cranial and postcranial	El Mamón, Venezuela Urumaco Formation, late Miocene	*Phoberomys pattersoni* (Mones, 1980) cf. *Phoberomys* *Phoberomys* sp.	Horovitz et al. 2006 Carrillo and Sánchez-Villagra 2015	Bondesio and Bocquentin Villanueva 1988	*Phoberomys* sp. 1
Phoberomys sp.	dental	near El Mamón, Venezuela, Urumaco Formation, late Miocene	*Phoberomys pattersoni* (Mones, 1980) *Phoberomys* sp.	Horovitz et al. 2006	Bondesio and Bocquentin Villanueva 1988	*Phoberomys* sp. 2
Phoberomys sp.	upper teeth and cranial	Norte El Hatillo, Venezuela, Urumaco Formation, late Miocene			Carrillo and Sánchez-Villagra 2015	*Phoberomys* sp. 3

Taxon	Remains	Locality and age	Official or suggested synonymy	Author(s) of synonymy	Additional references	Noted here as
Phoberomys sp.	dental and postcranial	Juruá River and Patos locality, Acre Region, Brazil, Solimões Formation, late Miocene	*Phoberomys burmeisteri* (Ameghino, 1886) *Phoberomys* sp. *Phoberomys minima* (Kraglievich, 1940) *Phoberomys* sp.	Kerber et al. 2017 Kerber et al. 2017	Paula-Couto 1978 Sant'Anna-Filho 1994	*Phoberomys* sp. 4
Phoberomys sp. A	lower teeth and cranial	included NW San Rafael locality, Venezuela, Urumaco Formation, late Miocene			Carrillo and Sánchez-Villagra 2015	*Phoberomys* sp. A
Phoberomys sp. B	upper teeth and cranial	NW San Rafael and El Picache localities, Venezuela, Urumaco Formation, late Miocene			Carrillo and Sánchez-Villagra 2015	*Phoberomys* sp. B
Phoberomys	P4	Upper Pisqui River, Nuevo Edén area, Peru, late? Pliocene	*Perumys gyulavarii* Kretzoi and Vörös, 1989	Kerber et al. 2017		*Phoberomys*
cf. *Phoberomys*	postcranial	El Hatillo, Venezuela, Urumaco Formation, late Miocene		Horovitz et al. 2006		cf. *Phoberomys* 1
cf. *Phoberomys*	postcranial	El Hatillo, Venezuela, Urumaco Formation, late Miocene		Horovitz et al. 2006		cf. *Phoberomys* 2
Neoepiblema	lower teeth	upper Purus River, Acre Region, Brazil, late Miocene	*Phoberomys bordasi* Patterson, 1942	Kerber et al. 2017, 2019; followed by Rasia and Candela 2018 and this work		*Neoepiblema*

Vucetich and Deschamps 2015; Vucetich et al. 2015). Within chinchilloids (i.e., chinchillas and their allies), the mean body mass of the dinomyid *Josephoartigasia* Mones, 2007 would have ranged 350–2584 kg (Rinderknecht and Blanco 2008; Millien 2008; Vucetich et al. 2015), and that of the neoepiblemid *Phoberomys* Kraglievich, 1926 would be 200–655 kg (Sánchez-Villagra et al. 2003; Hopkins 2008; Millien and Bovy 2010; Vucetich et al. 2015). This would make them the largest known rodents of all times.

The Neoepiblemidae are documented from the early Miocene up to the Pliocene, in Argentina (e.g., Ameghino 1886; Kramarz 2002; Rasia and Candela 2018), Brazil (e.g., Patterson 1942; Kerber et al. 2017), Chile (Flynn et al. 2002), Peru (Kretzoi and Vörös 1989; Tejada-Lara et al. 2015; Antoine et al. 2016), Colombia (Moreno-Bernal et al. 2012), and Venezuela (e.g., Mones 1980; Vucetich et al. 2010; Carrillo and Sánchez-Villagra 2015). In addition to *Phoberomys*, other fossil genera have often been related to *Neoepiblema* Ameghino, 1889 within the Neoepiblemidae: *Eusigmomys* (Ameghino, 1904) Ameghino, 1905 (e.g., Bondesio and Bocquentin Villanueva 1988; Negri and Ferigolo 1999; Sánchez-Villagra et al. 2003; but see Vucetich 1984); *Perimys* Ameghino, 1887 (e.g., McKenna and Bell 1997; Flynn et al. 2002; Kramarz 2002; Vucetich et al. 2010); *Perumys* Kretzoi and Vörös, 1989; and *Doryperimys* Kramarz et al. 2015. The genus *Eusigmomys* is monospecific. Its type species, *E. oppositus* (Ameghino, 1904), was

described based on only one specimen, an upper molar from the Fénix River in Argentina (Río Frías Formation, middle Miocene; Rovereto 1914; Pascual and Díaz de Gamero 1969). As illustrated in Rovereto (1914: 35, fig. 11), this specimen displays a S-shaped like pattern on occlusal view, as noted by Pascual and Díaz de Gamero (1969). The specimen was considered as lost (Vucetich 1980, 1984), but Rasia and Candela (2018) recently analyzed an upper molar housed in the MACN (i.e., MACN-A 11189), which is very similar to the holotype of *E. oppositus.* This kind of S-shaped pattern does not match with neoepiblemid upper teeth, and is more characteristic to upper teeth of some dinomyids, such as *Simplimus* or *Scleromys* (Rasia and Candela 2018). Besides, the flexi are broader in neoepiblemids than those of MACN-A 11189 (Luciano Rasia, personal communication 2018). *Perumys gyulavarii* from the Upper Pisqui River in the Nuevo Edén area (Peruvian Amazonia; late? Pliocene) was described by Kretzoi and Vörös (1989) based on a single tooth (possibly a P4; Kerber et al. 2017). However, due to its large size, it would preferably be a representative of *Phoberomys* (Kerber et al. 2017; Table 1). This tooth would be the only record of *Phoberomys* in Peru, the other mentions of neoepiblemids being material assigned to *Neoepiblema* (Tejada-Lara et al. 2015; Antoine et al. 2016). *Doryperimys* appears morphologically close to *Perimys* (Kramarz et al. 2015), and two recently published cladistic analyses (Kerber et al. 2018; Rasia and Candela 2018) support close rela-
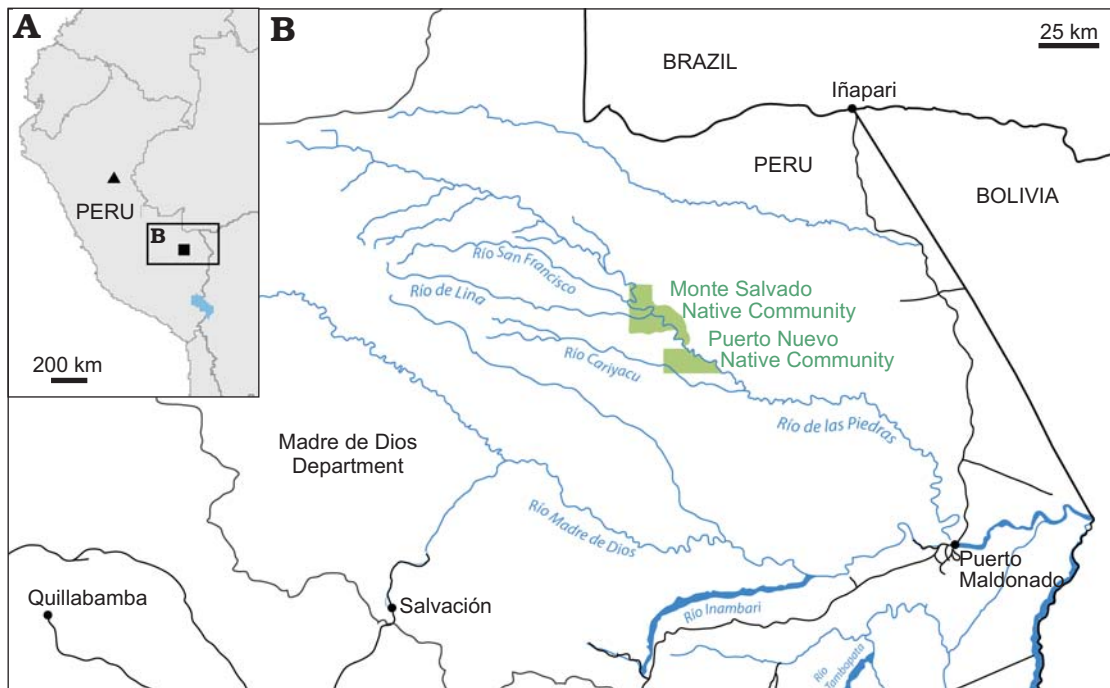
Fig. 1. **A**. General map of Peru showing geographic location of *Phoberomys*-yielding localities: Monte Salvado, Madre de Dios Department (square) and Pisqui River, Nuevo Edén area, Loreto Department (triangle). **B**. Location map of the Monte Salvado Native Community area in Peruvian Amazonia, where the fragmentary left mandible MHNC-MS-001 was found. Based on data from the Instituto Geográfico Nacional del Perú.

tionships of *Perimys* with *Neoepiblema* and *Phoberomys*. Therefore, after their revision of the Neoepiblemidae, Rasia and Candela (2018) recognized four undisputed genera in this family: *Neoepiblema*, *Phoberomys*, *Perimys*, and *Doryperimys*.

At least two species of *Phoberomys* are currently recognized: *P. burmeisteri* (Ameghino, 1886) and *P. pattersoni* (Mones, 1980) (see Rasia and Candela 2018 and citations therein; Table 1). *Phoberomys burmeisteri* is from the Ituzaingó Formation (eastern margin of the Paraná River, Argentina; "Mesopotamiense", late Miocene; Ameghino 1886; Kraglievich 1926; Rasia and Candela 2018). Several other species were previously described from this formation: *P. praecursor* (Kraglievich, 1932), *P. insolita* (Kraglievich, 1940), *P. lozanoi* (Kraglievich, 1940), and *P. minima* (Kraglievich, 1940). Nevertheless, Rasia and Candela (2018) concluded that they are all synonyms of *P. burmeisteri*. *Phoberomys pattersoni* is recorded in several late Miocene localities of the Urumaco Formation in Venezuela (Mones 1980; Bondesio and Bocquentin Villanueva 1988; Carrillo and Sánchez-Villagra 2015). It is documented by several tooth rows and postcranial remains (Mones 1980; Bondesio and Bocquentin Villanueva 1988; Sánchez-Villagra et al. 2003; Horovitz et al. 2006; Carrillo and Sánchez-Villagra 2015). Giant neoepiblemid specimens from Brazil (Solimões Formation, Acre Region) and Venezuela (Urumaco Formation) are assigned to *Phoberomys*, but remain in open nomenclature (Table 1): cf. *Phoberomys* (Horovitz et al. 2006), *Phoberomys* sp. (Horovitz et al. 2006; Carrillo and Sánchez-Villagra 2015; Kerber et al. 2017), *Phoberomys* sp. A (Carrillo and Sánchez-Villagra 2015), *Phoberomys* sp. B

(Carrillo and Sánchez-Villagra 2015), and *Phoberomys* cf. *pattersoni* (Horovitz et al. 2006). Patterson (1942) described *P. bordasi* from the Acre Region (Brazil; late Miocene), but according to Kerber et al. (2017, 2019), later followed by Rasia and Candela (2018), it shows more affinities with *Neoepiblema*.

A new record of the giant rodent *Phoberomys* is reported here. It corresponds to a fragmentary mandible from the Monte Salvado area, Peruvian Amazonia (Madre de Dios Department; Fig. 1). In this paper, we provide a description of this specimen and we compare it with the material previously attributed to *Phoberomys*. We discuss the homologies of lower teeth in *Phoberomys* based on juvenile specimens and a comparison with a large taxonomic sample (including chinchilloids and other caviomorphs), and propose for the first time an associated nomenclature.

Institutional abbreviations.—FMNH, Field Museum of Natural History, Chicago, USA; IGM, Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Museo Geológico, Bogotá, Colombia; LACM, Museum of Natural History Los Angeles County, Los Angeles, USA; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MHNC, Museo de Historia Natural de la Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru; MLP, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MNHN, Museo Nacional de Historia Natural, Montevideo, Uruguay; PU, Princeton University, Princeton, USA (specimens are today deposited at the Yale Museum of Natural History, New Haven, USA); UCMP, University of California Museum of Paleontology,

Berkeley, USA; UFAC, Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Rio Branco-AC, Brazil; UFAC-CS, Laboratório de Pesquisas Paleontológicas, Universidade Federal do Acre, Campus Floresta, Cruzeiro do Sul, Brazil.

Other abbreviations.—HI, hypsodonty index of tooth. We follow standard convention in abbreviating tooth families as I, C, P, and M, with upper and lower case letters referring to upper and lower teeth, respectively.

Geological setting

The concerned mandible (MHNC-MS-001) was found floating on a bank of the Río Las Piedras, in the vicinity of the Monte Salvado Native Community (Fig. 1). It is therefore difficult to ascertain the stratigraphic age of this specimen. Nevertheless, it may have originated from the upper Miocene–Pliocene Madre de Dios Formation, which crops out extensively around the river beds in that area (Romero Pittman et al. 1998; Campbell et al. 2001; Roddaz et al. 2010). This formation is considered as a lateral equivalent of the Solimões Formation in Acre, Western Brazil (e.g., Bissaro-Júnior et al. 2019). The matrix of MHNC-MS-001 was a beige marly limestone, compatible with a lacustrine floodplain depositional environment. That lithological facies matches perfectly the lowermost horizons of the Madre de Dios Formation ("Unit A"; light grey to beige shale and limestone lenses, with pedogenetic calcareous nodules; Romero Pittman et al. 1998: 54, fig. 4) overlying the so-called Acre Conglomerate (Campbell et al. 2001). This conglomerate, further known to yield vertebrate assemblages in a wide array of river banks all around (Romero Pittman et al. 1998: 54, fig. 4; Campbell et al. 2001; Negri et al. 2010; Ribeiro et al. 2013), unconformably overlies middle–upper Miocene levels assigned to the Ipururo Formation. The latter deposits are dominated by red siltstone, sandstone and conglomeratic channels ("Red Beds"; Campbell et al. 2001), which discards any assignment of MHNC-MS-001 to the underlying formation. As for other deposits assigned to the Madre de Dios Formation and attributed to the overlying Units B and C, they have a terrigenous origin and they lack carbonate components (Campbell et al. 2001); they typically consist of unconsolidated and oxidized sand and gravel or sandy clay (Romero Pittman et al. 1998), which is neither compatible with the specimen matrix.

A volcanic ash topping the Acre Conglomerate ca. 150 km to the NW of the Monte Salvado territory was dated at 9.01 ± 0.28 Ma by using $^{40}Ar/^{39}Ar$ radioisotopy on feldspar grains ("Cocama Ash"; Campbell et al. 2001). It was allocated to the Unit A of the Madre de Dios Formation, which may correspond to the level yielding MHNC-MS-001. Another ash was dated at 3.12 ± 0.02 Ma along the Río Las Piedras, 50 km SE to the Monte Salvado area ("Las Piedras Ash", late Pliocene); it is situated well above in the regional section, in the Unit C of the Madre de Dios Formation (Campbell et al. 2001).

In other words, considering the local and regional stratigraphic context and even if a Pliocene age cannot be fully discarded, a late Miocene age, younger than 9 Ma, can be hypothesized for MHNC-MS-001. This age would be consistent with the biostratigraphic age of the Acre Local Fauna, which has repeatedly yielded *Phoberomys* remains in Brazil (Huayquerian South American Land Mammal Age; Negri et al. 2010; Ribeiro et al. 2013; Carrillo and Sánchez-Villagra 2015; Kerber et al. 2017). Interestingly, Bissaro-Júnior et al. (2019) have recently provided maximum ages, through U/Pb datings on detrital zircon grains, for two major Neoepiblemidae-yielding localities from Acre, namely Talismã (10.8 ± 0.5 Ma) and Niterói (8.1 ± 0.5 Ma), further supporting the late Miocene age of the Acre assemblages.

Material and methods

The mandible (MHNC-MS-001) is housed in the Museo de Historia Natural de la Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru (MHNC) since 2015. However, in August 2016, it was sent to the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM), through Marcelo Stucchi, for identification, and a cast was then prepared at this occasion (MUSM 3739). The fossil specimen has been returned to the MHNC.

For each tooth, measurements were taken with a digital caliper. We followed the protocol of Kerber et al. (2017) for the measurements of the maximum anteroposterior length (mesio-distal length sensu Kerber et al. 2017) and maximum linguolabial width (linguo-labial width sensu Kerber et al. 2017). For the lower molars, the anterior width, medium width, and posterior width correspond to the maximum width at the level of the first, second, and third laminae, respectively. For the p4, we divided the tooth into three equal parts along its length, and measured the maximum width of each part. All the dental measurements are given in Table 2.

In caviomorphs, the presence of laminae or lobes, resulting from the fusion of dental structures and their enlargement, is found in high-crowned taxa (e.g., chinchilloids, cavioids). However, the crown height of teeth cannot be

Table 2. Dental measurements (in mm) of MHNC-MS-001. As the anterior part of p4 is greatly missing, the anterior width was not measured. Due to the state of preservation of the specimen, all measurements should be considered and used with caution.

Tooth	Maximum anteroposterior length	Maximum linguolabial width	Anterior width	Medium width	Posterior width
p4	30.8	19.1	–	15.7	18.9
m1	26.1	20.2	13.5	18.2	18.4
m2	27.5	20.5	17.5	20.5	19.6
m3	34.7	21.5	20.5	20.7	21.5

measured directly on the MHNC-MS-001 specimen, and thus the hypsodonty index of tooth (Janis 1986) could not be calculated. Moreover, without X-ray analyses, it was not possible to evaluate the presence or absence of tooth roots on the MHNC-MS-001 specimen. Therefore, we could not define if lower teeth are mesodont (HI = 1), protohypsodont (HI >1, with roots), or euhypsodont (HI >1, without root). So, in the following text (Systematic Palaeontology section), we decided to use the term "high-crowned" to define the crown height of the MHNC-MS-001 teeth. Given that neoepiblemids are characterized by euhypsodont teeth (Mones 1968, 1982; Koenigswald 2011), the lower teeth of the MHNC-MS-001 specimen could be expected to be euhypsodont.

The terminology used here for the rodent mandible follows the nomenclature proposed by Woods and Howland (1979) and Pérez (2010). The caviomorph taxa used for comparisons in the Systematic Palaeontology section are listed in Table 1. The material from the Acre Region assigned to *P. bordasi* by Patterson (1942) shows a smaller size with respect to ascertained *Phoberomys* remains, similar to that of *Neoepiblema*, and a p4 bearing three laminae. Based on these features, Kerber et al. (2017, 2019) suggested that this material was more closely related to *Neoepiblema*. Like Rasia and Candela (2018), we agree with such a generic assignment.

For the recognition of dental homologies, we followed Boivin and Marivaux (2018) using different criteria: topology/connectivity between structures (Rieppel 1988, 1994), the position of structures relative to each other, and their orientation, shape, and size (in surface and height). Several comparisons have allowed the proposition of hypotheses regarding the lamina homologies of lower teeth in *Phoberomys*:

– an analysis of the pre-existing material of *Phoberomys*, and notably the comparison between the juvenile specimen assigned to *P. burmeisteri* (MACN-Pv 2645, Rasia and Candela 2018: 5, fig. 4F, G) and lower rows of adult *Phoberomys*;

– comparisons of lower teeth of *Phoberomys* with those of other chinchilloids and caviomorphs. For these comparisons, we used the same material as sampled by Boivin and Marivaux (2018), to which specimens of other chinchilloids were added (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app64-Boivin_etal_SOM.pdf). Some chinchilloids characterized by lower teeth with a bilophodont pattern (i.e., *Pliolagostomus*, *Prolagostomus*, and *Lagostomus*) were not considered here due to the difficulty in the recognition of the dental structures.

The nomenclature used to name dental structures is based on Boivin and Marivaux (2018). In the Systematic Palaeontology section below, we identified the laminar cristids of lower teeth in neoepiblemids by a number (e.g., first, second) with respect to their position on the tooth from mesial to distal.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Infraorder Hystricognathi Tullberg, 1899

Parvorder Caviomorpha Wood and Patterson in Wood, 1955

Superfamily Chinchilloidea Bennett, 1833

Family Neoepiblemidae Kraglievich, 1926

Genus *Phoberomys* Kraglievich, 1926

1886 *Megamys* Laurillard in d'Orbigny, 1842; Ameghino 1886: 39. part.
1891 *Euphilus* Ameghino, 1889; Ameghino 1891: 246. part.
1926 *Phoberomys* Kraglievich, 1926; Kraglievich 1926: 127.
1988 *Dabbenea* Kraglievich, 1926; Bondesio and Bocquentin-Villanueva 1988: 33.
2017 *Perumys* Kretzoi and Vörös, 1989; Kerber et al. 2017: 7.

Type species: *Megamys burmeisteri* Ameghino, 1886; "Mesopotamiense", late Miocene, eastern margin of the Paraná River, Ituzaingó Formation, Argentina.

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

Stratigraphic and geographic range.—Late Miocene–?Pliocene of Argentina, Brazil, Peru, and Venezuela.

Phoberomys sp.

Fig. 2.

Material.—MHNC-MS-001, left mandibular fragment with incisor (portion) and p4 (portion)–m3, from Monte Salvado Native Community, Madre de Dios Department, Peru. Although found as float, based on its matrix, this specimen most likely originates from the lower unit of the Madre de Dios Formation, late Miocene in age (see Geological setting).

Measurements.—See Table 2.

Description.—*Dentary*: MHNC-MS-001 is a left mandibular fragment preserving m1–m3 and the distal portion of p4 (Figs. 2, 3). It is undistorted but fractured at several points. The body of the mandible is anteriorly broken at the level of the posterior part of the lower diastema. Posteriorly, the angular apophysis and most of the ascending ramus, including the mandibular condyle, are missing. The coronoid process is broken at its base posterodorsally.

The mandibular body is robust. The mandibular symphysis is stout, broken anteriorly, and ends at the level of m1. Labially, the notch for the insertion of the tendon of the zygomatico-mandibularis pars infraorbitalis is wide, below m1–m2, and ventrally situated on the labial edge of the mandible. The anterior tip of the masseteric crest and that of the lateral crest end below the m2, and they link the notch for the insertion of the tendon of the zygomatico-mandibularis pars infraorbitalis, at the level of its posteroventral and posterodorsal regions, respectively. The masseteric crest is posteriorly broken. It is posteroventrally directed and prominent in its anterior part. It is sub-horizontal and more reduced toward its posterior region. The lateral crest, posterodorsally directed, is markedly oblique. Its posterior part
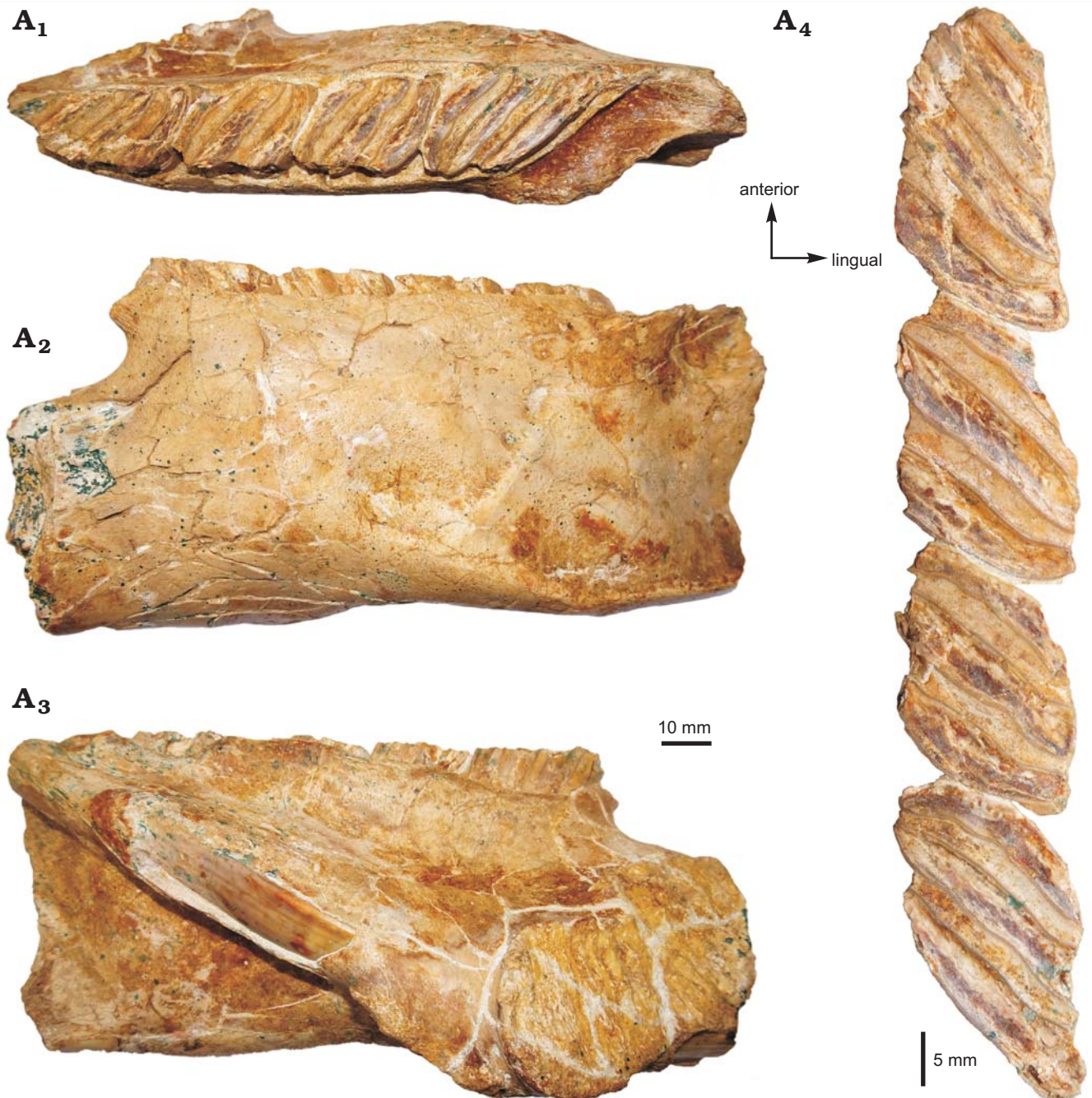
Fig. 2. Photograph of the MHNC-MS-001 attributed to caviomorph rodent *Phoberomys* sp., from Monte Salvado, Peruvian Amazonia, late Miocene or Pliocene; fragmentary left mandible in occlusal (A_1), labial (A_2), and lingual (A_3) views, p4–m3 in occlusal view (A_4).

is not visible. The anterior part of the horizontal crest is absent. By contrast, its posterior part is conspicuous, although broken, and it delimits ventrally the fossa for the insertion of the zygomatico-mandibularis muscle. This fossa is moderately deep. The preserved part of the ascending ramus, which runs toward the coronoid process, begins below the m3. The retromolar fossa, posteriorly located with respect to the m3, is well developed. Lingually, the alveolar sheath of the lower incisor is partially broken, showing the lower incisor at two locations. The bottom of this alveolar sheath is situated at the level of the distal portion of the m3.

Lower tooth row: The p4–m3 of MHNC-MS-001 are damaged mesially and distally. The m3 is also slightly broken on its lingual edge. The four teeth are high-crowned and taeniodont (i.e., absence of anterior arm of the hypoconid). The cuspids/stylids are not visible because they are subsumed within enlarged lophids, thereby forming laminar cristids (i.e., laminae). The latter are mesiolabially directed (slightly oblique forward with respect to the long axis of the tooth row). Compared with the size of teeth, each cristid displays a continuous and relatively thin enamel layer (without noticeable heterogeneous thickness on the leading and trail-
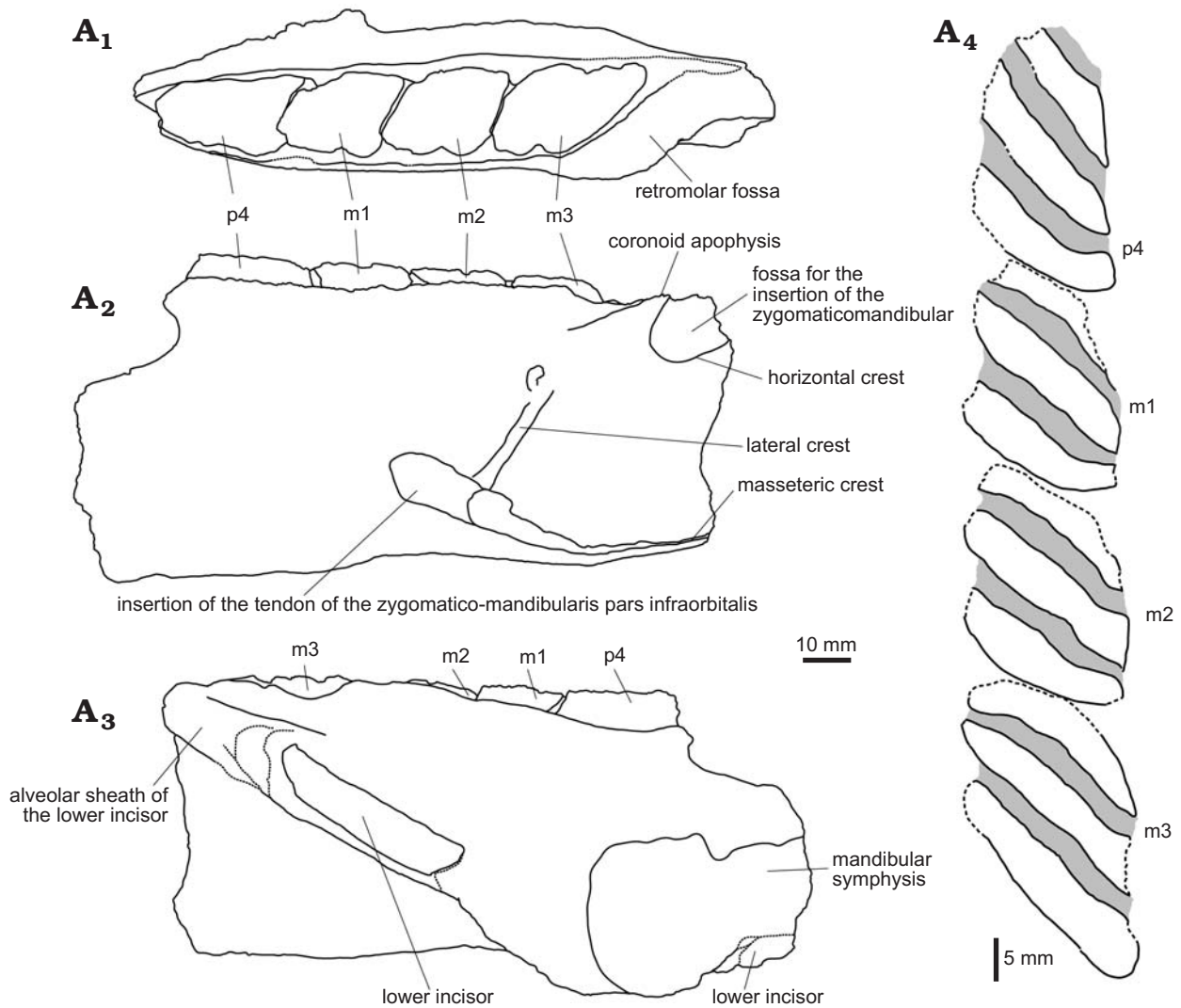
Fig. 3. Explanatory drawings of the MHNC-MS-001 attributed to caviomorph rodent *Phoberomys* sp., from Monte Salvado, Peruvian Amazonia, late Miocene or Pliocene; fragmentary left mandible in occlusal (A_1), labial (A_2), and lingual (A_3) views, p4–m3 in occlusal view (A_4). The dotted lines indicate incomplete parts.

ing edges), coating a thick dentine layer. The inter-cristid regions (i.e., flexids) are laminar and filled by cement.

On p4, despite the damage, three cristids and three inter-cristid cement layers are distinct on this tooth, suggesting that it likely displayed four cristids when it was complete (i.e., the first cristid is missing). Due to the fragmentary state of the p4, the presence or absence of labial connections between cristids cannot be determined. The lower molars display three cristids and two inter-cristid cement layers. Although the cristids have their lingual and labial tips mostly fractured, they seem to be connected neither lingually nor labially with each other. The m2 is slightly longer than m1, and these two teeth have a similar width. The m3 is much longer and slightly wider than m1 and m2.

Remarks.—Taeniodont and high-crowned lower teeth with laminar, oblique, and thick cristids suggest chinchilloid affinities for MHNC-MS-001. The lower teeth have a typical neoepiblemid occlusal pattern characterized by the presence

of laminar and thick inter-cristid cement, as well as a continuous enamel layer (i.e., without heterogeneous thickness between leading and trailing edges). The huge size (Table 2) and the presence of a tetralophodont p4 suggest a generic assignment of the MHNC-MS-001 specimen to *Phoberomys*. The two included species, *P. burmeisteri* and *P. pattersoni*, have a similar dental size (Carrillo and Sánchez-Villagra 2015; Rasia and Candela 2018). They are differentiated by characters on M3 and p4 (see Mones 1980; Carrillo and Sánchez-Villagra 2015; Rasia and Candela 2018). The M3s of *P. pattersoni* have straighter laminae than those of *P. burmeisteri*. There are mesial indentations on the sixth or seventh laminae of M3s in *P. burmeisteri*, whereas the edges of the distal laminae are straight in *P. pattersoni*. In *P. pattersoni*, the two mesial laminae are labially united on p4, and the distal ones are free. Representatives of *Phoberomys burmeisteri* show this connection but they can also have a labial connection between the second and third laminae. Due to the poor preservation of MHNC-MS-001, the

latter feature cannot be assessed. Besides, the specimen does not exhibit the morphological characters that would clearly differentiate it from *P. burmeisteri, P. pattersoni, Phoberomys* sp. 1, *Phoberomys* sp. 2, and *Phoberomys* sp. A from the Urumaco Formation (Venezuela; Bondesio and Bocquentin Villanueva 1988; Horovitz et al. 2006; Carrillo and Sánchez-Villagra 2015), and the UFAC 1817 m1 or m2 assigned to *Phoberomys* sp. 4 from the Solimões Formation (Brazil; Kerber et al. 2017). Teeth of *Phoberomys* sp. A (and *Phoberomys* sp. B) from the Urumaco Formation are smaller in size than those of MHNC-MS-001. In caviomorphs, some groups with hypsodont teeth show a wide range of dental size during ontogeny (i.e., teeth grow in length and width in addition to crown height), often associated with morphological variations (e.g., Kraglievich and Parodi 1940; Vucetich et al. 2005; Fields 1957; Nasif and Abdala 2015). Therefore, based on only one specimen, the size criterion is somewhat useless for differentiating MHNC-MS-001 from other species of *Phoberomys* (Carrillo and Sánchez-Villagra 2015; Rasia and Candela 2018). Lastly, MHNC-MS-001 being a fragmentary mandible, comparison with taxa only known by upper teeth or postcranial remains is de facto limited: the neoepiblemid from the Upper Pisqui River, Peru (originally described as *Perumys gyulavarii* Kretzoi and Vörös, 1989; see Kerber et al. 2017), and cf. *Phoberomys* sp. 1, cf. *Phoberomys* sp. 2, *Phoberomys* sp. 3, and *Phoberomys* sp. B from the Urumaco Formation (Horovitz et al. 2006; Carrillo and Sánchez-Villagra 2015). In light of these various points, MHNC-MS-001 is provisionally identified here as *Phoberomys* sp.

Homologies of lower teeth in *Phoberomys* and other chinchilloids

Lower molars.—As in *Neoepiblema*, the lower molars of *Phoberomys* have three laminae in adult specimens. The study of the material of *Phoberomys* from the Ituzaingó Formation led by Rasia and Candela (2018) allowed for the recognition of a juvenile specimen, the MACN-Pv 2645 m1 or m2. Based on this tooth, Rasia and Candela (2018) highlighted two early ontogenetic stages of *Phoberomys burmeisteri*. The first was reconstructed from the occlusal surface of the tooth and characterized by a pattern with five laminae (Fig. 4A). The second was rebuilt from the outline of the dental base, and it is characterized by four laminae (Fig. 4B). During ontogeny, lower molars of *P. burmeisteri* show transformations from a pentalophodont pattern (Fig. 4A) to a tetralophodont pattern (Fig. 4B), and then to a trilophodont pattern (Fig. 4C; Rasia and Candela 2018). These transformations would be explained by fusions between mesial laminae (Rasia and Candela 2018). In this species, the cuspids/stylids are subsumed within lophids, and

as such they form laminae even in early ontogenetic stages (Fig. 4A, B). Hence, cuspids/stylids and lophids cannot be directly recognized, but the comparison with other chinchilloids and other caviomorphs allows to propose hypotheses regarding an approximate position of these structures on the tooth with pentalophodont pattern (Fig. 4A). We could successively recognize (Fig. 4A$_2$) that:

– the first lamina would include the metaconid + the metalophulid I + a part of the protoconid;
– the composition of the second lamina is ambiguous and would depend on its morphology in earlier ontogenetic stages. If the first and second laminae would be also lingually linked in the earlier ontogenetic stages, then the metaconid would be common to both laminae. In this case, the second laminae would correspond to a part of the metaconid + the metaconid cristid. However, if this lamina is lingually separated from the first, it would be a neolophid, developed from a neoconid;
– the third lamina would include the second transverse cristid + a part of the protoconid. The second transverse cristid could correspond either to a posterior arm of the protoconid, or to a neomesolophid, or to a posterior arm of the protoconid + a neomesolophid (Boivin and Marivaux 2018). In the last two cases, a mesostylid would be present, associated to the neomesolophid;
– the fourth lamina would include the entoconid + the hypolophid + the ectolophid;
– the fifth lamina would include the posterolophid + the hypoconid + the anterior outgrowth of the hypoconid.

The inclusion of the ectolophid in the fourth lamina is based on the comparison with Palaeogene and Miocene chinchilloids such as *Eoincamys* (Fig. 5A), *Incamys* (Fig. 5B), *Eoviscaccia* (Fig. 5C), *Scleromys* (Fig. 5D), *Drytomomys aequatorialis* (Fig. 5E), and *Microscleromys* (Fig. 5F; see Boivin 2017 and Boivin et al. 2019). These taxa are characterized by tetralophodont/trilophodont lower molars, with oblique loph(-id)s. It is worth noting that on their lower molars, the ectolophid is often aligned with the hypolophid (i.e., mesiolabially-distolingually oriented). The mesiolabial-distolingual alignment of these structures forms a central and oblique (diagonal) cristid connecting the entoconid to the protoconid. The second cristid is limited to a neomesolophid stemming from the mesostylid and often mesiolabially linked to the metalophulid I. On some pristine specimens of *Eoviscaccia* (MACN CH 1879; Fig. 5C), *Scleromys* (UCMP 40550; Fig. 5D), *Drytomomys* (UCMP 41636; Fig. 5E), and *Microscleromys* (IGM 250303; Fig. 5F), the metalophulid I is disconnected to the protoconid. A connection between these two structures is then generated with wear. The possibility exists that the protoconid could be exclusively connected to the entoconid via the ectolophid and hypolophid in Miocene and Pliocene chinchilloids displaying tetralophodont or pentalophodont lower molars (at least at early ontogenetic stages) like in *Phoberomys* (Fig. 4A$_1$), *Drytomomys* sp. (described by Kerber et al. 2017; Fig. 5G), *Potamarchus* (Fig. 5H), *Eumegamys* (Fig. 5I), *Gyriabrus*
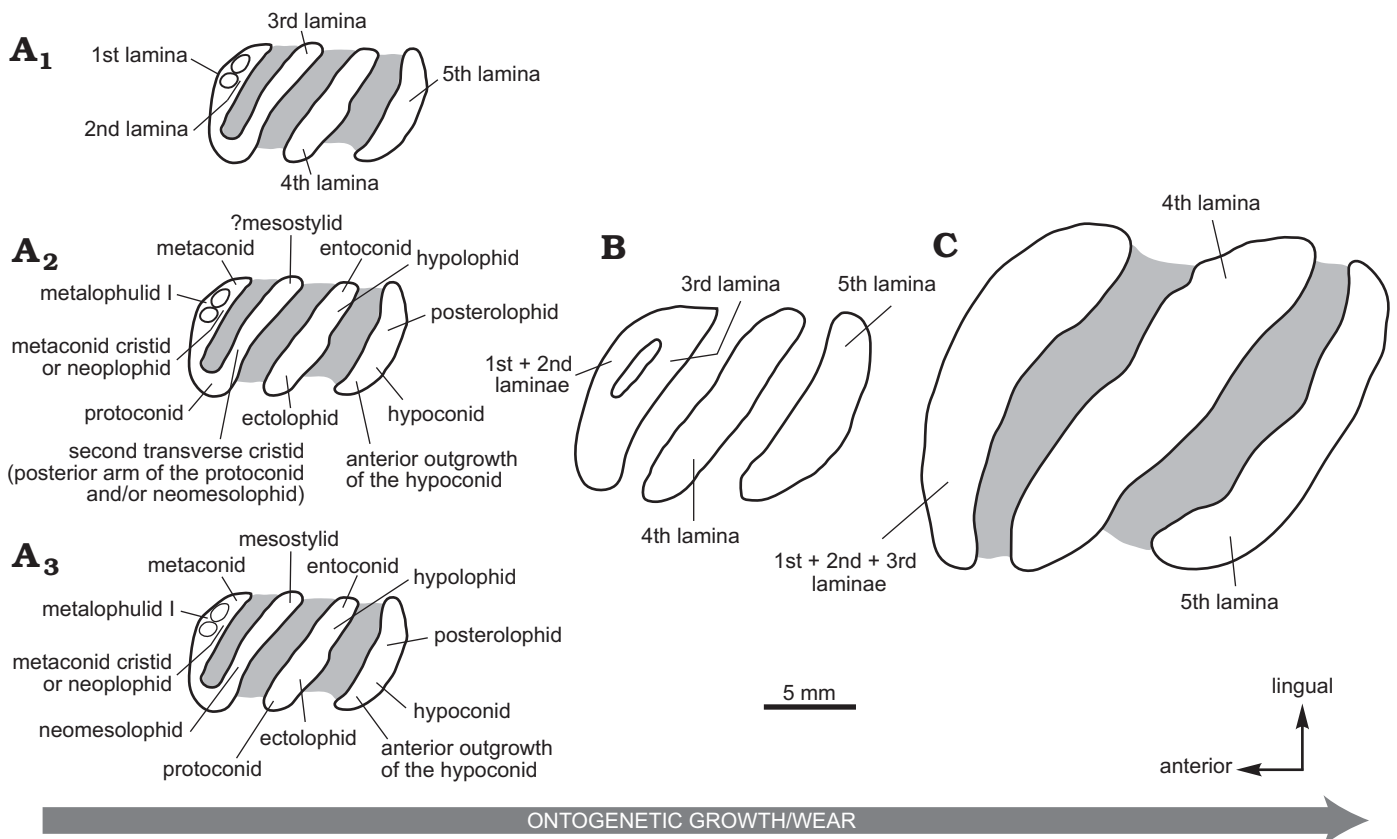
Fig. 4. Explanatory drawings of occlusal morphologies of lower molars at three ontogenetic stages in *Phoberomys*. **A**. Pentalophodont pattern in a juvenile specimen: MACN-Pv 2645, right m1 or 2 (occlusal surface) of *Phoberomys burmeisteri*; the laminae (A_1), homology hypothesis 1 (A_2), and homology hypothesis 2 (A_3). **B**.Tetralophodont pattern in a juvenile specimen: MACN-Pv 2645, right m1 or 2 (outline pattern of the dental base) of *P. burmeisteri*. **C**. Trilophodont pattern in an adult specimen: MACN-Pv 3475, right m1 or 2 of *P. burmeisteri*. The direction of the arrow indicates the direction of development associated with an increase of the ontogenetic growth and dental wear. Note that the position of the fused structures is speculative. Based on Rasia and Candela 2018: fig. 4.

(Fig. 5J), *Isostylomys* (Fig. 5K) or *Tetrastylus* (Fig. 5L). Therefore, according to this second hypothesis (Figs. $4A_3$, $5G_3$, $H_3–L_3$):
– the first lamina would include the metaconid + the metalophulid I;
– as for the first hypothesis, the composition of the second lamina is ambiguous: it would include either a part of the metaconid + the metaconid cristid, or a neolophid + a neoconid;
– the third lamina would include a mesostylid + the neomesolophid. The neomesolophid would be connected at the labial extremity of the metalophulid I;
– the fourth lamina would include the entoconid + the hypolophid + the ectolophid + the protoconid;
– as for the first hypothesis, the fifth lamina would include the posterolophid + the hypoconid + the anterior outgrowth of the hypoconid.

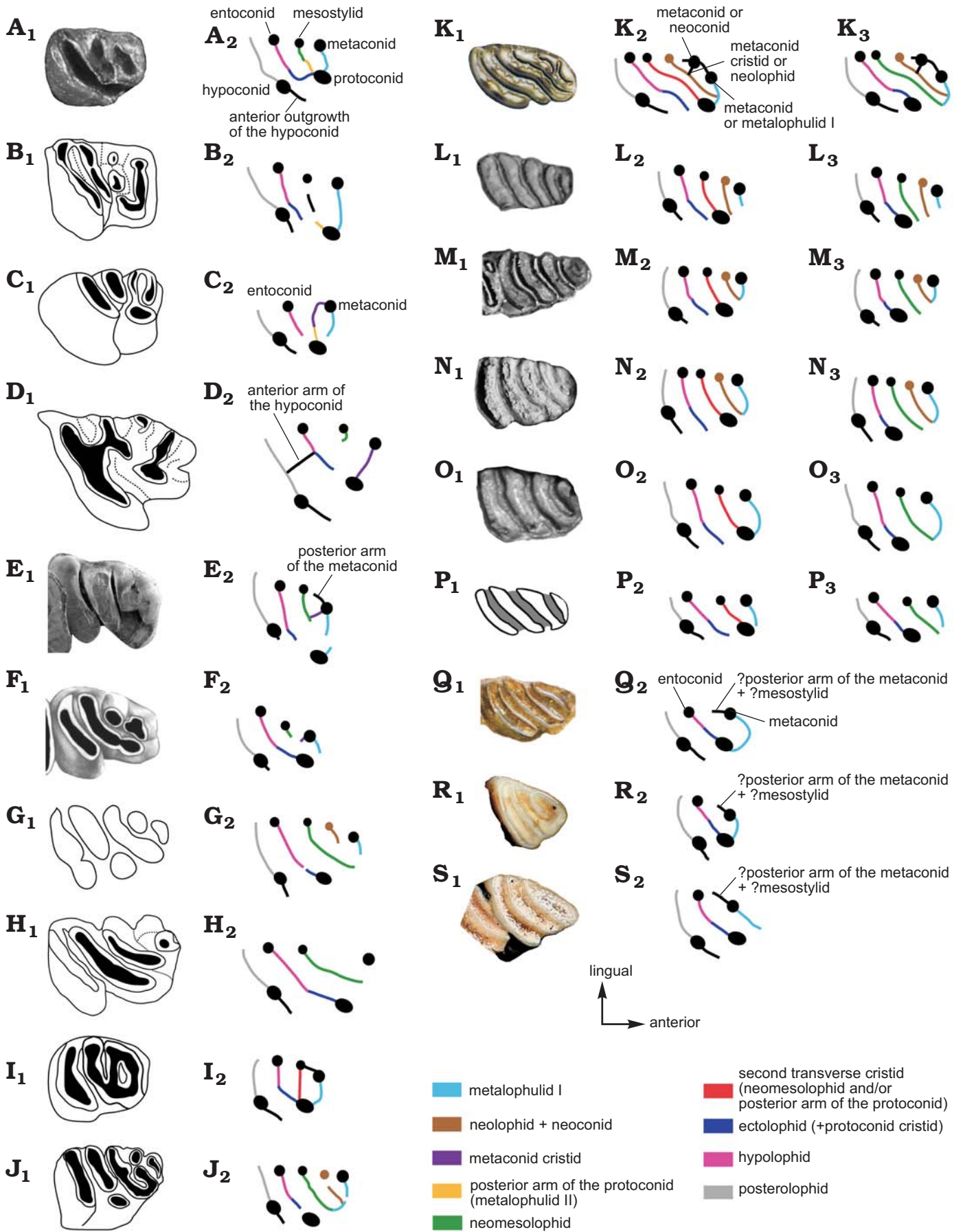However, this second hypothesis appears unlikely because:
– a substantial distal displacement of the protoconid should be expected in these taxa. This hypothesis would be less parsimonious than the first one;
– in the two earliest ontogenetic stages of *Dinomys* figured by Nasif and Abdala (2015: 11, 13, fig. 9 [FMNH 147996], fig. 11a [MACN 12962]), the protoconid is either slightly or strongly linked to the second transverse cristid, and clearly separated from the hypolophid + the ectolophid (Fig. 5M). In the following ontogenetic stages, the protoconid is strongly connected to the second transverse cristid and to the metalophulid I (Fig. 5N; Nasif and Abdala 2015: 13, fig. 11c [MACN 12961]).

In the absence of early ontogenetic stages with visible cuspids in *Phoberomys*, *Drytomomys* sp. (Kerber et al. 2017), *Potamarchus*, *Eumegamys*, *Gyriabrus*, *Isostylomys*, and *Tet-*

Fig. 5. Photographs (A_1, $G_1–L_1$, O_1, P_1), explanatory drawings ($B_1–F_1$, M_1, N_1), and interpretative schematic drawings ($A_2–P_2$, $G_3–L_3$) of occlusal morphologies of lower molars in some chinchilloids; homology hypothesis 1 ($A_2–P_2$); homology hypothesis 2 (G_3, $H_3–L_3$). **A**. *Eoincamys pascuali*, LACM 143299 (based on Frailey and Campbell 2004: 112, appendix 2). **B**. *Incamys bolivianus*, PU 21726 (based on Patterson and Wood 1982: 423, fig. 19b). **C**. *Eoviscaccia australis,* MACN CH 1862 (based on Kramarz 2001: 238, fig. 1A). **D**. "*Scleromys*" *colombianus*, UCMP 40550 (based on Fields 1957: 318, fig. 14b). **E**. *Drytomomys aequatorialis*, UCMP 41636 (based on Fields 1957: 328, fig. 16a). **F**. *Microscleromys cribriphilus*, IGM 250303 (based on Walton 1997: 393, fig. 24.2L). **G**. *Drytomomys* sp., UFAC 2742 (Kerber et al. 2017: 59, fig. 1h). **H**. *Potamarchus murinus*, UFAC 1820 (Kerber et →
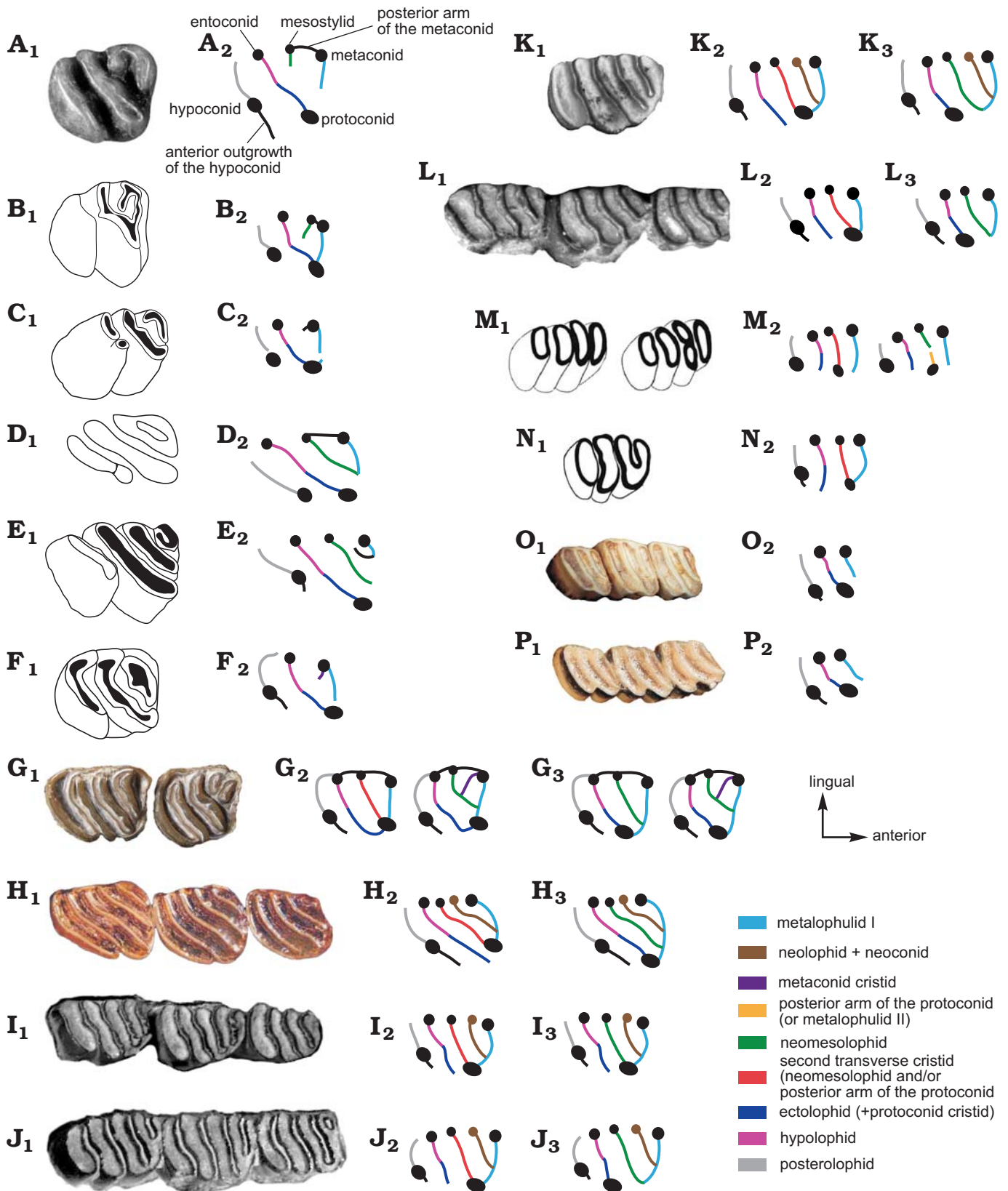
al. 2016: 196, fig. 4B2). **I**. *Eumegamys paranensis,* MLP 15-245 (Nasif et al. 2013: 152, fig. 2.15). **J**. *Gyriabrus holmbergi*, MLP 15-252 (Nasif et al. 2013: 152, fig. 2.9). **K**. *Isostylomys laurillardi*, MNHN 2687 (Rinderknecht et al. 2018: 252, fig. 5). **L**. *Tetrastylus laevigatus*, MLP 52-X-1-59 (Nasif et al. 2013: 152, fig. 2.12). **M**. *Dinomys branickii*, MACN 12962 (Nasif and Abdala 2015: 13, fig. 11a). **N**. *Dinomys branickii*, MACN 12961 (Nasif and Abdala 2015: 13, fig. 11c). **O**. *Chinchilla lanigera*, MLP 11.VILL.99.41. **P**. *Lagidium* sp., MLP 22-IV-47-2. Note that the position of the fused structures is interpreted. Not to scale.

A₂ labels: entoconid, mesostylid, metaconid, hypoconid, protoconid, anterior outgrowth of the hypoconid

C₂ labels: entoconid, metaconid

D₂ label: anterior arm of the hypoconid

E₂ label: posterior arm of the metaconid

K₂ labels: metaconid or neoconid, metaconid cristid or neolophid, metaconid or metalophulid I

Q₂ labels: entoconid, ?posterior arm of the metaconid + ?mesostylid, metaconid

R₂ label: ?posterior arm of the metaconid + ?mesostylid

S₂ label: ?posterior arm of the metaconid + ?mesostylid

Orientation: lingual, anterior

Legend:
- metalophulid I (blue)
- neolophid + neoconid (brown)
- metaconid cristid (purple)
- posterior arm of the protoconid (metalophulid II) (yellow)
- neomesolophid (green)
- second transverse cristid (neomesolophid and/or posterior arm of the protoconid) (red)
- ectolophid (+protoconid cristid) (dark blue)
- hypolophid (magenta)
- posterolophid (grey)

rastylus, the second hypothesis cannot be entirely ruled out. These two homology hypotheses, which differ by the protoconid position, may occur in different chinchilloid taxa.

On the occlusal surface of MACN-Pv 2645 (Fig. $4A_1$), the first and second laminae are partially fused and they are only separated by two small fossettids. Hence, the transformation from a pentalophodont pattern to a tetralophodont pattern would be explained by a complete fusion of the first and second laminae. From the outline of the dental base of MACN-Pv 2645 (Fig. 4B), a partial fusion between the mesialmost lamina ($1^{st} + 2^{nd}$ laminae) and the third one is observed: both laminae are strongly connected labially and linked lingually. The transformation from a tetralophodont pattern to a trilophodont pattern would be explained by a complete fusion of the $1^{st}/2^{nd}$ laminae with the third one (Fig. 4C).

p4s.—The analysis of dental homologies on p4 in chinchilloids reveals the same ambiguities regarding the position of the protoconid in some chinchilloids with tetralophodont or pentalophodont p4s (at least at early ontogenetic stages), such as *Phoberomys* (Fig. 6P), *Potamarchus* (Fig. 6K), *Eumegamys* (Fig. 6L), *Gyriabrus* (Fig. 6M), *Isostylomys* (Fig. 6N), and *Tetrastylus* (Fig. 6O). In these taxa, the protoconid is either disconnected (homology hypothesis 1; Fig. $6K_2$–P_2) or connected to the ectolophid-hypolophid (homology hypothesis 2; Fig. $6K_3$–P_3). In the former case, the second lamina on tetralophodont p4s (Fig. $6O_2$–P_2) and the third lamina on pentalophodont p4s (Fig. $6K_2$–N_2) would correspond to the mesostylid + the second transverse cristid + the protoconid. In the second case, the second lamina on tetralophodont p4s (Fig. $6O_3$–P_3) and the third lamina on pentalophodont p4s (Fig. $6K_3$–N_3) would correspond to the mesostylid + the neomesolophid.

Due to (i) the inclusion of several structures (i.e., cuspids/stylids and lophids) in each lamina, (ii) the ambiguity in the identification of some structures (i.e., position of the protoconid), and (iii) the fact that precise limits between these structures are undiscernible, it is preferable to describe teeth of *Phoberomys* in terms of laminae than of cuspids/stylids and lophids. The knowledge of a comprehensive ontogenetic sequence in extinct and extant chinchilloids, associated with more complete palaeontological records would certainly allow to clarify the ambiguities regarding these dental homologies.

Conclusions

The neoepiblemid mandibular fragment from Monte Salvado, Madre de Dios, Peru is referred to as *Phoberomys* sp. Found as float on a bank of the Río Las Piedras, it has been hypothetically assigned a late Miocene age, due to the local/regional stratigraphic and lithologic context. This specimen constitutes the second record of *Phoberomys* in Peru, the first corresponding to one upper tooth from the Upper Pisqui River in the Nuevo Edén area (Kretzoi and Vörös 1989; Kerber et al. 2017). For the first time, the pattern of p4s and lower molars in *Phoberomys* was analyzed and compared to a large taxonomic sample (including Palaeogene–Recent chinchilloids and other caviomorphs) as a means of furthering the understanding of the homology of dental structures in this genus. For p4s and lower molars, the position of the protoconid in *Phoberomys* and other chinchilloids (*Drytomomys* sp., Kerber et al. 2017, *Potamarchus*, *Eumegamys*, *Gyriabrus*, *Isostylomys*, and *Tetrastylus*) is ambiguous, and we thus propose two alternative homology hypotheses for these taxa. The knowledge of a comprehensive ontogenetic sequence in extinct and extant chinchilloids, associated with more complete palaeontological records would likely allow for a clarification of these homology ambiguities. As the recognition of the dental homologies is a necessary prerequisite in any phylogenetic studies and in the understanding of dental character evolution, we encourage further discussions in that respect.

Acknowledgements

← Fig. 6. Photographs (A_1, E_1, K_1–O_1, Q_1–S_1), explanatory drawings (B_1–D_1, F_1–J_1, P_1), and interpretative schematic drawings (A_2–S_2, K_3–P_3) of occlusal morphologies on p4s in *Phoberomys* and other chinchilloids; homology hypothesis 1 (A_2–S_2); homology hypothesis 2 (K_3–P_3). **A**. *Eoincamys pascuali*, LACM 143301 (based on Frailey and Campbell 2004: 112, appendix 2). **B**. *Incamys bolivianus*, PU 20975 (based on Patterson and Wood 1982: 423, fig. 19b). **C**. *Eoviscaccia australis,* MACN CH 1875 (based on Kramarz 2001: 239, fig. 3A). **D**. *Perimys intermedius*, MACN Pv SC2037 (based on Kramarz 2002: 169, fig. 2C). **E**. *Garridomys curnunuquem*, MOZ-PV-938 (Kramarz et al. 2013: 253, fig. 4C). **F**. *Scleromys quadrangulatus*, MLP 82-VI-3-2 (Kramarz 2006: 18, fig. 3C). **G**. "*Scleromys*" *colombianus*, UCMP 39909 (based on Fields 1957: 318, fig. 14a). **H**. *Drytomomys aequatorialis*, UCMP 41636 (based on Fields 1957: 328, fig. 16a). **I**. *Microscleromys paradoxalis*, IGM 250308 (based on Walton 1997: 293, fig. 24.2H). **J**. "*Simplimus indivisus*", MLP 15-244a (based on Vucetich 1984: 125, lamina Vj). **K**. *Potamarchus* cf. *adaminae*, UFAC-CS 057 (Kerber et al. 2017: 21, fig. S7B). **L**. *Eumegamys paranensis,* MLP 15-245 (Nasif et al. 2013: 152, fig. 2.15). **M**. *Gyriabrus holmbergi*, MLP 15-252 (Nasif et al. 2013: 152, fig. 2.9). **N**. *Isostylomys laurillardi*, MNHN 2187 (Rinderknecht et al. 2018: 252, fig. 5). **O**. *Tetrastylus laevigatus*, MLP 52-X-1-59 (Nasif et al. 2013: 152, fig. 2.12). **P**. *Phoberomys burmeisteri*, MACN-Pv 4729 (Rasia and Candela 2018: 5, fig. 4C). **Q**. *Neoepiblema acreensis* (=*Neoepiblema ambrosettianus*), UFAC 3525 (Kerber et al. 2017: 36, fig. S13E; Kerber et al. 2019). **R**. *Chinchilla lanigera*, MLP 11.VILL.99.41. **S**. *Lagidium* sp., MLP 22-IV-47-2. Note that the position of the fused structures is interpreted. Not to scale.

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