

## SYSTEMATIC REVISION OF THE VIZCACHAS (RODENTIA, CAVIOMORPHA, CHINCHILLIDAE) FROM THE CHAPADMALAL FORMATION, LATE PLIOCENE OF BUENOS AIRES PROVINCE, ARGENTINA

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# SYSTEMATIC REVISION OF THE VIZCACHAS (RODENTIA, CAVIOMORPHA, CHINCHILLIDAE) FROM THE CHAPADMALAL FORMATION, LATE PLIOCENE OF BUENOS AIRES PROVINCE, ARGENTINA

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**Abstract.** Lagostomine rodents (Caviomorpha, Chinchillidae) are very abundant in late Cenozoic vertebrate associations of the Pampean area but the study of their systematics has been mostly limited to a handful of works from the late 19<sup>th</sup> Century and early 20<sup>th</sup> Century. Although seven species of *Lagostomus* were described for the Chapadmalal Formation (late Pliocene; Buenos Aires Province, Argentina), the holotypes of these species do not present precise stratigraphic provenance and have not been studied since their original description. This study of lagostomines from the Chapadmalal Formation with precise stratigraphic provenance gives way to the recognition of at least three species: *Lagostomus incisus*, *L. compressidens* and *L. euplasius*. The comparative study of the holotypes of the previously recognized species in this unit indicates that '*Viscaccia indefinita*' is a junior synonym of *L. compressidens* while '*V. loberiaense*', '*V. definita*' and '*V. chapalmalense*' are junior synonyms of *L. euplasius*. The validity of '*Viscaccia arcuata*' and its inclusion in the Chapadmalal fauna has to be re-evaluated. This work clarifies part of the systematics of the genus *Lagostomus*, thus contributing to the comprehension of the taxonomic diversity of chinchillids during their most recent evolutionary history.

**Key words.** Late Pliocene. Rodentia. Caviomorpha. Chinchillidae. Systematics. Buenos Aires. Argentina.

**Resumen.** REVISIÓN SISTEMÁTICA DE LAS VIZCACHAS (RODENTIA, CAVIOMORPHA, CHINCHILLIDAE) DE LA FORMACIÓN CHAPADMALAL, PLIOCENO TARDÍO DE LA PROVINCIA DE BUENOS AIRES, ARGENTINA. Los roedores lagostominos (Caviomorpha, Chinchillidae) son muy abundantes en las asociaciones de vertebrados en el Cenozoico tardío del área pampeana, pero su estudio sistemático se limita mayormente a algunos trabajos de fines del Siglo XIX y principios del Siglo XX. Se describieron siete especies de *Lagostomus* para la Formación Chapadmalal (Plioceno tardío; provincia de Buenos Aires, Argentina), pero los holotipos de estas especies no tienen procedencia estratigráfica precisa y no han sido estudiados desde su descripción original. Este estudio de lagostominos de la Formación Chapadmalal con procedencia estratigráfica precisa permitió reconocer al menos tres especies: *Lagostomus incisus*, *L. compressidens* y *L. euplasius*. El análisis comparativo de los holotipos de las especies previamente reconocidas en esta unidad indica que '*Viscaccia indefinita*' es un sinónimo junior de *L. compressidens*; y que '*V. loberiaense*', '*V. definita*' y '*V. chapalmalense*' son sinónimos junior de *L. euplasius*. La validez de '*Viscaccia arcuata*' y su inclusión en la fauna Chapadmalalense debe ser re-evaluada. Este trabajo permite esclarecer parte de la sistemática del género *Lagostomus*, contribuyendo así a la comprensión de la diversidad taxonómica de los chinchillidos durante su historia evolutiva más reciente.

**Palabras clave.** Plioceno tardío. Rodentia. Caviomorpha. Chinchillidae. Sistemática. Buenos Aires. Argentina.

THE plains vizcacha, *Lagostomus maximus*, is the only living representative of the subfamily Lagostominae, a group of caviomorph rodents which, together with the subfamily Chinchillinae, is included in the Chinchillidae (e.g., Pocock, 1922). Vizcachas inhabit a wide variety of lowland habitats, including the pampas and adjoining semiarid Monte and Chaqueñean regions of Argentina, southern Bolivia and Paraguay (Jackson, *et al.*, 1996; Ojeda and Bidau, 2013). They are sexually dimorphic, gregarious and nocturnal, and

build complex burrow systems called '*vizcacheras*' (Weir, 1974).

The subfamily Chinchillinae is poorly represented in the fossil record and its oldest representative is an undetermined chinchilline from the early Miocene of Chile (Flynn *et al.*, 2002). Additionally, there are records of the living genus *Lagidium* from the Pleistocene of Peru (Marshall *et al.*, 1984; Walton, 1997) and late Holocene of Argentina (Ortiz *et al.*, 2012) as well as those of the living species *Chinchilla chin-*

*chilla* in the late Holocene of Argentina (Ortiz *et al.*, 2012).

The oldest known Chinchillidae is *Eoviscaccia* (traditionally considered a lagostomine; Vucetich, 1989), from the early Oligocene (Tinguirirican) of Chile (Flynn *et al.*, 2003; Bertrand *et al.*, 2012), the late Oligocene (Deseadan) of Argentina and Bolivia (Vucetich, 1989, 1991; Bond *et al.*, 1998) and the early Miocene (Colhuehuapian) of Argentina (*e.g.*, Kramarz, 2001; Kramarz *et al.*, 2005). The nature of the relationship between *Eoviscaccia* and the remaining Chinchillidae is unclear (see Kramarz *et al.*, 2013). Moreover, two Chinchilloidea with possible affinities with *Eoviscaccia* were recently described (Kramarz *et al.*, 2013; Vucetich *et al.*, 2015) and could represent taxa closely related to the early radiation of Chinchillidae. A more comprehensive analysis of Chinchilloidea is necessary in order to test the phylogenetic position of these basal taxa.

Two undoubted lagostomines are recognized in the early Miocene–middle Miocene ('Pinturan'–Colloncuran): *Prolagostomus* from Argentina, Bolivia and Chile (*e.g.*, Ameghino, 1887, 1889; Scott, 1905; Vucetich, 1984; Flynn *et al.*, 2008; Croft *et al.*, 2009, 2011), and *Pliolagostomus* from Argentina (Ameghino, 1887; Vucetich, 1984).

Lagostomines recorded from the late Miocene to Recent were traditionally included in the genus *Lagostomus* (see Francis and Mones, 1965, 1966, 1968). Besides, two subgenera were recognized: *Lagostomopsis*, from the late Miocene to late Pliocene, and *Lagostomus*, from the late Pliocene to Holocene (*e.g.*, Kraglievich, 1926; Vucetich and Verzi, 1995; Cione and Tonni, 2001; Cione *et al.*, 2000; Candela, 2005). Nevertheless, some authors consider *Lagostomus* and *Lagostomopsis* separate genera (*e.g.*, Kraglievich, 1934; Pascual, 1966).

Lagostomines are very frequent in vertebrate continental associations from the late Miocene–Holocene in the Pampean area (*e.g.*, Bondesio *et al.*, 1980; Vucetich, 1986; Vucetich and Verzi, 1995; Cione and Tonni, 1999). Nevertheless, little attention has been placed upon the systematics of the Lagostominae at the species level since the contributions of Ameghino (1883, 1886, 1888, 1889, 1891, 1908) and Rovereto (1914). Perhaps it is for this reason that their inclusion in biostratigraphic studies has only been at a supraspecific level (*e.g.*, Kraglievich, 1934; Cione and Tonni, 1999).

Ameghino (1908) described seven lagostomine species

from '*Piso Chapalmalense*' (*sensu* Ameghino, 1908; see below) which he included in the genus '*Viscaccia*' (a junior synonym of *Lagostomus*; see Jackson *et al.*, 1996): *Viscaccia euplasia*, *V. compressidens*, *V. definita*, *V. indefinita*, *V. loberiaense*, *V. arcuata* and *V. chapalmalense*. The species described for '*Piso Chapalmalense*' (Ameghino, 1908) do not boast precise stratigraphic or geographic provenance, *Lagostomus incisus* being the only confirmed species for the Chapadmalal Formation (*sensu* Kraglievich, 1952; see Rasia and Candela, 2013).

In the present work, numerous unpublished specimens of chinchillids from the Chapadmalal Formation (Upper Chapadmalalan Stage/Age, late Pliocene; *e.g.*, Cione and Tonni, 2001) with accurate geographic and stratigraphic provenance were studied and compared with the holotypes of the species previously described for '*Piso Chapalmalense*', other fossil species of *Lagostomus* and with the living *L. maximus*. A new taxonomic proposal for the Chapadmalalan vizcachas is hereby provided on such basis. This systematic study will favor a better comprehension of fossil lagostomines from an evolutionary and biostratigraphic perspective.

## MATERIAL AND METHODS

Lagostomine remains recovered from the Chapadmalal Formation (see Systematic Paleontology for precise stratigraphic provenance of each specimen), from the Atlantic coastal area between Punta Mogotes (near Mar del Plata) and Punta Hermengo (near Miramar) in Buenos Aires Province, Argentina (Fig. 1), were studied. Such material was compared with the available holotypes of the species previously recognized for '*Piso Chapalmalense*' (see Ameghino, 1908); that is, '*Viscaccia compressidens*', '*V. indefinita*', '*V. definita*', '*V. euplasia*', '*V. chapalmalense*' and '*V. loberiaense*'. The holotype of '*V. arcuata*' could not be found. Comparisons with holotypes and referred material of *Lagostomus* species from other stratigraphic units, *i.e.*, *L. pretrichodactyla* (including '*V. angulata*' and '*V. insolita*'; see Marshall and Patterson, 1981), *L. antiquus*, *L. laminosus*, *L. debilis*, *L. minimus*, *L. heterogenidens*, *L. cavifrons*, *L. egenus* and *Lagostomus maximus*, were also established (see Appendix 1).

'*Lagostomus pallidens*', from the late Miocene of Entre Ríos Province, is considered *nomen vanum* (see Nasif *et al.*, 2013; Rasia, 2016).

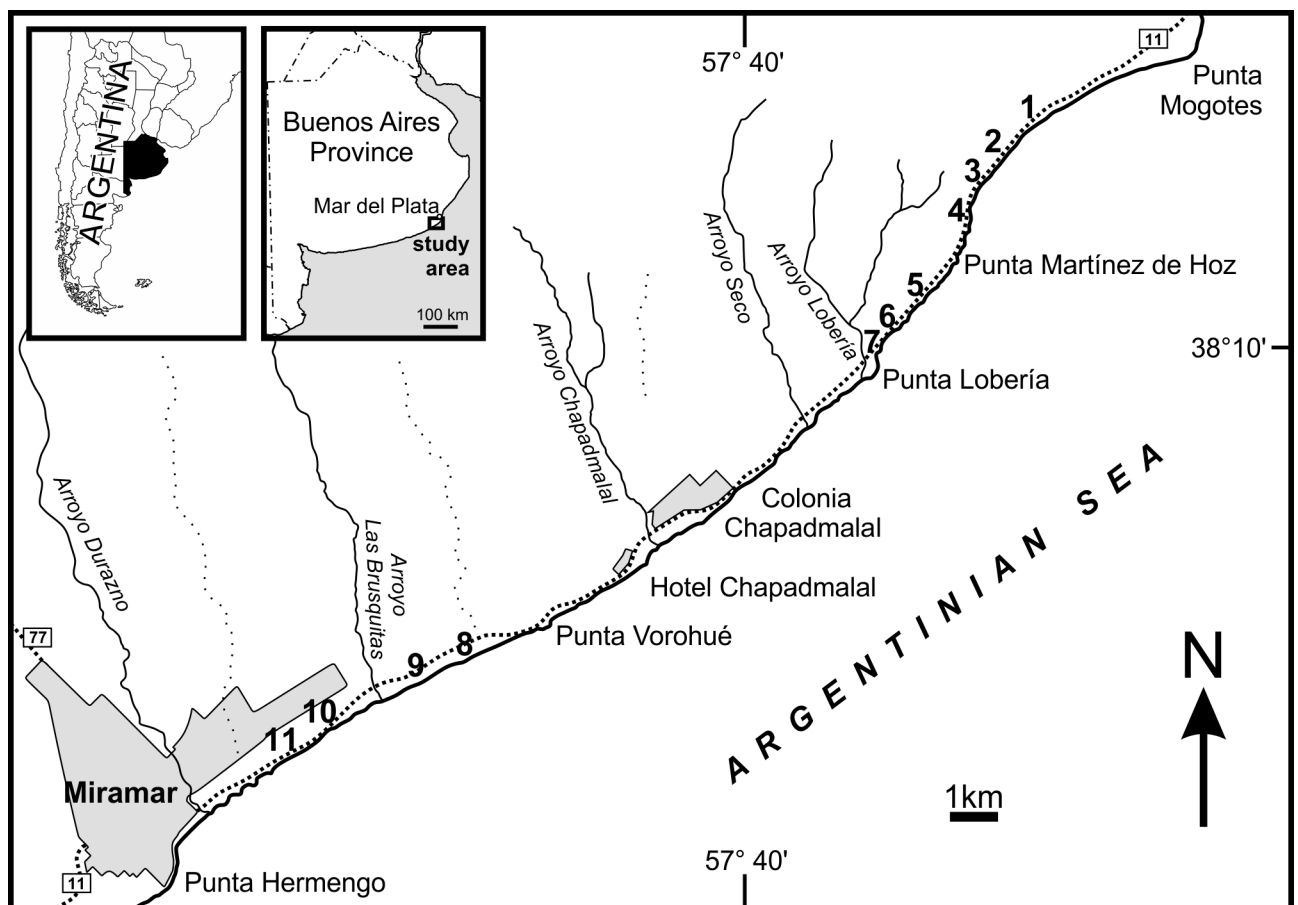
Nominal species originally referred to as '*Viscaccia*' –a

junior synonym of *Lagostomus*, see Jackson *et al.* (1996)– are mentioned between quotation marks. Invalid species (*i.e.*, synonyms, *nomina dubia* and *nomina vana*) are also referred to between quotation marks.

**Institutional abbreviations.** **MACN-A**, Colección Nacional Ameghino, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; **MACN-Ma**, Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; **MACN-Pv**, Colección Nacional Paleovertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; **MASP**, Museo Provincial “Antonio Serrano” de Paraná, Paraná; **MLP-Mz**, Mastozoología, Museo de La Plata, La Plata; **MLP-Pv**, Paleontología Vertebrados, Museo de La Plata, La Plata.

**Quantitative analysis.** We used two linear measurements for the upper (**P4–M3**) and lower (**p4–m3**) cheek teeth: the

anteroposterior diameter (**APD**) and the transverse diameter (**TD**) (see Supplementary Material). Linear measurements were log-transformed and analyzed by means of a principal components analysis (**PCA**) based on a correlation matrix. Analyses were performed using the free access program Past 3.07 (Hammer *et al.*, 2001). Missing data were replaced by iterative imputation (see Ilin and Raiko, 2010) using Past 3.07. Because of the fact that most of the specimens of maxillary fragments and mandibles are not associated, for upper and lower dentition, separate analyses were performed. To evaluate whether PC1 and PC2 of upper and lower cheek teeth proved significantly different among the species from the Chapadmalal Formation, Kruskal-Wallis tests (non-parametric **ANOVA**) were performed via PAST 3.07.



**Figure 1.** Map showing fossil localities in Buenos Aires Province, Argentina. 1, Las Vertientes; 2, Playa Serena; 3, Los Acantilados; 4, Barranca Los Lobos; 5, Las Palomas; 6, Playa de los Lobos; 7, La Estafeta; 8, Arroyo Seco; 9, San Eduardo; 10, Barranca Parodi; 11, Baliza Chica.

**GEOLOGICAL AND STRATIGRAPHICAL CONTEXT**

Coastal cliffs between Mar del Plata and Miramar (Buenos Aires Province, Fig. 1) span an exposition of more than 30 kilometers of 12 to 25 meters of thickness. In this area, Ameghino (1908) defined an intermediate age, between the 'Hermosense' and the 'Ensenadense', for 'Piso Chapalmalense'. Later studies significantly modified the concept of 'Piso Chapalmalense' (e.g., Risso Dominguez, 1949a,b; Kraglievich, 1952, 1959a,b; see Taglioretti *et al.*, 2014; Isla *et al.*, 2015, for a comprehensive account of studies on this subject).

Eight lithostratigraphic units are recognized along the cliffs: formations Chapadmalal, Barranca de los Lobos, Vorohué, San Andrés, Miramar, Arroyo Seco, Santa Isabel and Lobería (e.g., Kraglievich, 1952; Cione and Tonni, 1996, 2001).

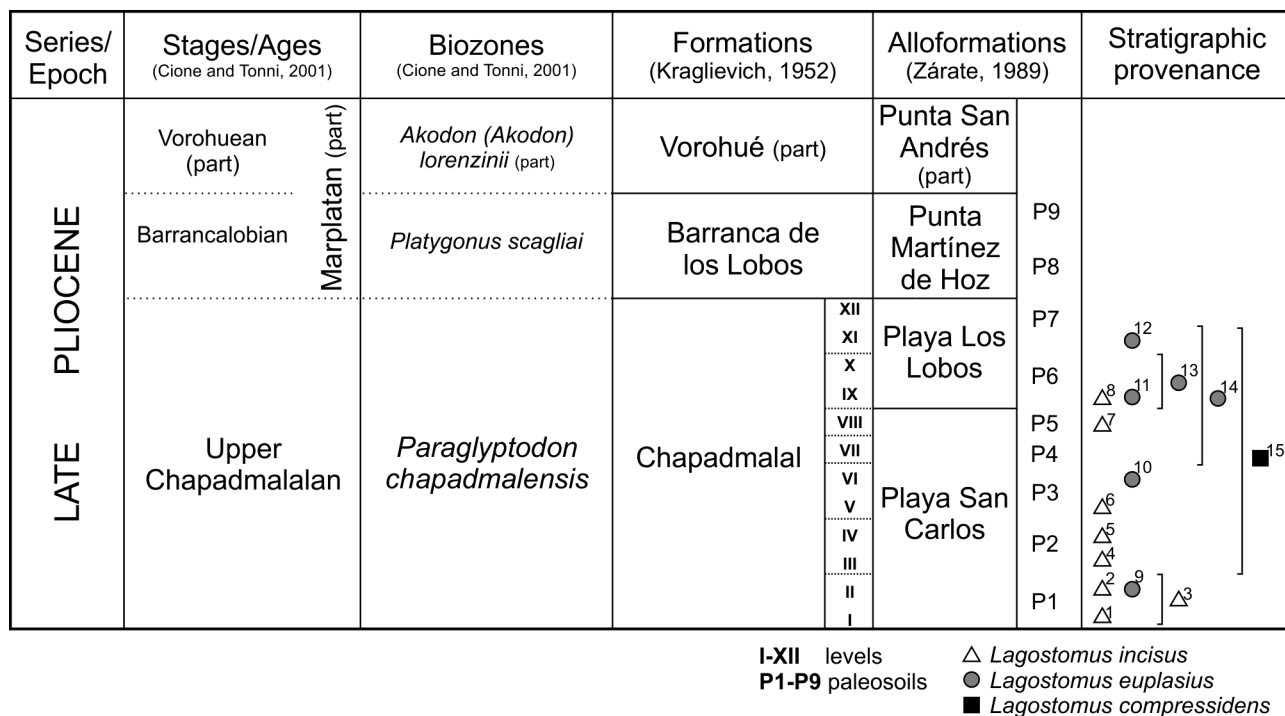
The Chapadmalal Formation is the oldest unit cropping out in this area and it is composed of fine to very fine red limestones deposited in a subaerial environment. Kraglievich (1952) divided the Chapadmalal Formation in alternating

levels (level I to level XV) of fine sandstones (uneven levels, 1–1.5 m thick) and very fine sandstones with a high proportion of limestones (even levels, 0.5–1.5 m thick). Zárata (1989) subdivided the Chapadmalal Formation into two alloformations and recognized seven paleosoils (P1 to P7). The Playa San Carlos Alloformation includes paleosoils P1 to P5 while the Playa Los Lobos Alloformation includes paleosoils P6 and P7 (Fig. 2).

The biostratigraphic basis of the Upper Chapadmalal Stage/Age (late Pliocene) is the 'Paraglyptodon chapadmalensis zone' and it extends from the base of the Chapadmalal Formation (paleosol P1) to paleosol P5 (see Cione and Tonni, 1995a,b,c, 2001).

Datings of paleosol P6 indicated an estimated age of 3.27 (±0.08) Ma (Schultz *et al.*, 1998). Zárata (2005) estimated an age of 4.5 to 3.2 Ma for the Chapadmalal Formation.

The material hereby studied was recovered from several levels of the Chapadmalal Formation (Fig. 2; see detailed stratigraphic provenance in Systematic Paleontology section).



**Figure 2.** Chronostratigraphic scheme of the Chapadmalal Stage/Age and precise stratigraphic provenance of studied specimens. **1**, MLP-Pv 01-I-10-53; **2**, MLP-Pv 01-I-10-38, 01-I-10-41, 01-I-10-54; **3**, MLP-Pv 91-IV-5-214, 91-IV-5-258; **4**, MLP-Pv 01-I-10-37, 01-I-10-52; **5**, MLP-Pv 01-I-10-34, 01-I-10-47; **6**, MLP-Pv 01-I-10-30, 01-I-10-31, 01-I-10-32, 01-I-10-33; **7**, MLP-Pv 01-I-10-35; **8**, MLP-Pv 01-I-10-44; **9**, MLP-Pv 01-I-10-36, 01-I-10-49, 01-I-10-55; **10**, MLP-Pv 01-I-10-56; **11**, MLP-Pv 01-I-10-40, 01-I-10-50; **12**, MLP-Pv 01-I-10-39; **13**, MLP-Pv 91-IV-5-334, 91-IV-5-350, 52-IX-28-62, 52-X-4-21; **14**, MLP-Pv 52-X-1-13, 52-IX-29-74, 52-XI-5-8; **15**, MLP-Pv 90-VI-1-1.

**PREVIOUS STUDIES OF THE CHAPADMALALAN VIZCACHAS**

Ameghino (1908) described seven species from ‘*Piso Chapalmalense*’, included them in the genus ‘*Viscaccia*’ (see above) and mentioned that some undetermined specimens were very similar to ‘*Lagostomus spicatus*’ (Ameghino, 1908, p. 424), a junior synonym of *Lagostomus incisus* (see Rasia and Candela, 2013; see also Fig. 3).

Kraglievich (1926) studied specimens of lagostomines from the Chapadmalal Formation previously studied by Ameghino (1908) and created, based on cranial and post-cranial characteristics, the subgenus *Lagostomopsis*. Within this subgenus, Kraglievich (1926) included all the Chapadmalal species of *Lagostomus* and, in the same contribution, introduced the possibility of also including all pre-Chapadmalal species (*i.e.*, those from the Monte Hermoso Formation and from ‘*Araucanense*’ and ‘*Mesopotamiense*’; see Ameghino, 1883, 1886, 1888, 1891; Rovereto, 1914). In a later work, Kraglievich (1934) proposed *Lagostomopsis* as a separate genus. Nevertheless, Francis and Mones (1965, 1966, 1968) considered that the differences between *Lagostomus* and *Lagostomopsis* were not sufficient to differentiate two genera and thus maintained *Lagostomopsis* as a subgenus of *Lagostomus*.

Recently, Rasia and Candela (2013) reported the presence of *Lagostomus incisus*, originally described for the Monte Hermoso Formation (Buenos Aires Province; Ameghino, 1888), in the Chapadmalal Formation.

Following the proposal of Francis and Mones (1965, 1966, 1968), all recognized Chapadmalal species (see Figs. 3–5) are herein considered as belonging to the genus *Lagostomus*.

**SYSTEMATIC PALEONTOLOGY**

- Order RODENTIA Bowdich, 1821
- Suborder HYSTRICOGNATHI Tullberg, 1899
- Infraorder CAVIOMORPHA Wood and Patterson in Wood, 1955
- Family CHINCHILLIDAE Bennett, 1833
- Subfamily LAGOSTOMINAE (Wiegmann, 1835)
- Genus *Lagostomus* Brookes, 1828

*Type species.* *Lagostomus trichodactylus* Brookes, 1828 (= *Dipus maximus* Desmarest, 1817).

***Lagostomus incisus* Ameghino, 1888**

Figures 3.1–8, 6.1–2

- 1888. *Lagostomus incisus* Ameghino, p. 9.
- 1889. *Lagostomus angustidens* Moreno, Ameghino, p. 182. *non* Burmeister.
- 1914. *Viscaccia incisa* (Ameghino), Rovereto, p. 137.
- 2013. *Lagostomus spicatus* Ameghino, Rasia and Candela, p. 244.
- 2013. *Lagostomus (Lagostomopsis) incisus* (Ameghino), Rasia and Candela, p. 244.
- 2013. *Lagostomus intermedius* Moreno, Rasia and Candela, p. 244.

**Holotype.** MACN-A 1112, incomplete skull with complete dentition. Monte Hermoso Formation (early Pliocene). Recently, Rasia and Candela (2013), following Mones’s (1986) statement assuring that the holotype was lost, designated MACN-A 1112 as the neotype of *Lagostomus incisus*. However, according to Ameghino (1888, 1889; also Kramarz pers. comm.), the specimen MACN-A 1112 is the original holotype. Thus, it is hereafter pertinent to rectify the taxonomic assignation of MACN-A 1112 as the holotype of *L. incisus* instead of the neotype of this species (Rasia and Candela, 2013). Note that, in both cases, the material considered as type (herein) or neotype (previously) is the same specimen.

**Referred material.** MLP-Pv 88-VI-1-2\*, skull fragment with right P4–M3 and left P4–M2, left mandible fragment with p4–m3, two isolated upper incisors, one caudal vertebra, right humerus, pelvis fragments and left femur; MLP-Pv 91-IV-5-223, right mandible; MLP-Pv 91-IV-5-214\*, left mandible fragment with incisor and p4–m2 as well as left upper incisor; MLP-Pv 91-IV-5-258\*, almost complete skull with right and left incisors and P4–M3, right radius, right ulna fragment, right femur, left femur fragment, left tibia, left calcaneus, right astragalus, right metatarsals II, III and IV, right proximal phalanxes II, III and IV; MLP-Pv 01-I-10-30, left mandible with p4–m3; MLP-Pv 01-I-10-31, left mandible fragment with p4–m3; MLP-Pv 01-I-10-32, incomplete skull with right and left incisors and P4–M3; MLP-Pv 01-I-10-33, complete skull with right and left incisors as well as P4–M3 and right tibia; MLP-Pv 01-I-10-34, right maxillary fragment with M1–M2; MLP-Pv 01-I-10-35, right mandible with incisor and p4–m3, vertebra, scapula, pelvis fragment, humerus, tibia distal fragment, femur proximal



fragment, metatarsal, three hindlimb phalanges; MLP-Pv 01-I-10-37, anterior skull fragment with right and left upper incisors; MLP-Pv 01-I-10-38, left maxillary fragment with P4–M1; MLP-Pv 01-I-10-41, right mandible with incisor fragment and p4–m3; MLP-Pv 01-I-10-44, left mandible with incisor fragment and p4–m3; MLP-Pv 01-I-10-47, skull fragment with right and left P4–M3 and right mandible with p4–m3; MLP-Pv 01-I-10-52, right mandible with incisor fragment, m2 and fragment of m3; MLP-Pv 01-I-10-53, skull fragment; MLP-Pv 01-I-10-54, right mandible fragment with p4–m3, axis fragment, radius fragment and tibia fragment.

Specimens identified with an asterisk (\*) were already referred to *Lagostomus incisus* by Rasia and Candela (2013).

**Geographic occurrence.** Coastal cliffs between Mar del Plata and Miramar, Buenos Aires Province (Fig. 1). MLP-Pv 88-VI-1-2 and 01-I-10-52 from Las Vertientes; MLP-Pv 91-IV-5-214, 91-IV-5-2 and 91-IV-5-258 from Fortin-88; MLP-Pv 01-I-10-30, 01-I-10-31, 01-I-10-37, 01-I-10-38, 01-I-10-41, 01-I-10-47, 01-I-10-53 and 01-I-10-54 from Barranca de Los Lobos (formerly Bajada Martínez de Hoz); MLP-Pv 01-I-10-32, 01-I-10-34 and 01-I-10-35 from Las Palomas; MLP-Pv 01-I-10-33 from San Eduardo; and MLP-Pv 01-I-10-44 from Estafeta.

*Lagostomus incisus* has also been recorded in Farola Monte Hermoso (see Ameghino, 1888; Rasia and Candela, 2013) and Cascada Grande (see Rasia and Candela, 2013) in Buenos Aires Province.

**Stratigraphic occurrence.** Chapadmalal Formation (upper Chapadmalalan, late Pliocene; Fig. 2). MLP-Pv 91-IV-5-214 and 91-IV-5-258 from paleosoil P1; MLP-Pv 01-I-10-53 from level I; MLP-Pv 01-I-10-38, 01-I-10-41 and 01-I-10-54 from level II; MLP-Pv 01-I-10-37 and 01-I-10-52 from level III; MLP-Pv 01-I-10-34 and 01-I-10-47 from level IV; MLP-Pv 01-I-10-30, 01-I-10-31, 01-I-10-32 and 01-I-10-33 from level V; MLP-Pv 01-I-10-35 from level VIII; MLP-Pv 01-I-10-44 from level IX. MLP-Pv 88-VI-1-2 from an undetermined level of the Chapadmalal Formation (see Comments below).

*Lagostomus incisus* have also been recorded in the Monte Hermoso Formation (early Pliocene; see Ameghino, 1888; Rasia and Candela, 2013) and in the Irene 'formation' (Pliocene?; see Rasia and Candela, 2013 but also Verzi and Montalvo, 2008; Verzi et al., 2008; Prevosti and Pardiñas,

2009, for further discussion regarding the age of the Irene 'formation'), both in Buenos Aires Province.

**Diagnosis.** See Rasia and Candela (2013, p. 245) and Rasia (2016, p. 90–91). The diagnoses proposed by Rasia and Candela (2013) could be, after a complete revision of the species of *Lagostomus* is concluded, reassessed in further contributions.

### Description and comparisons

Rasia and Candela (2013) recently presented an emended diagnosis and redescription of this species (see also Rasia, 2016). Therefore, herein, we comment only on some aspects of the anatomy which were not discussed in the abovementioned works.

**Skull.** In contrast with *Lagostomus maximus* or *L. euplasius* (Fig. 4.3), the ventral surface of the zygomatic arch is straight (Fig. 3.3). Yet, both present a ventral projection near the maxillo-jugal suture.

**Postcranial skeleton.** The calcaneus of *Lagostomus incisus* presents a secondary sustentacular facet akin to the one described by Candela and Picasso (2008) for the living chinchillids *L. maximus* and *Chinchilla*.

### Comments

Several species have been synonymized with *Lagostomus incisus* (see Ameghino, 1889; Rasia and Candela, 2013). Ameghino (1889) stated that '*Lagostomus angustidens*' (created by Moreno, 1888) was not only a synonym of *L. incisus* but also a name previously used by Burmeister (1866) and also considered '*Lagostomus intermedius*', which was described by Moreno (1888), a synonym of '*L. spicatus*'. Later, Rasia and Candela (2013) synonymized '*L. spicatus*' with *L. incisus* and thus '*L. intermedius*' was then considered a synonym of *L. incisus*. The holotypes of '*L. angustidens*' (Moreno, 1888) and '*L. intermedius*' are at present lost.

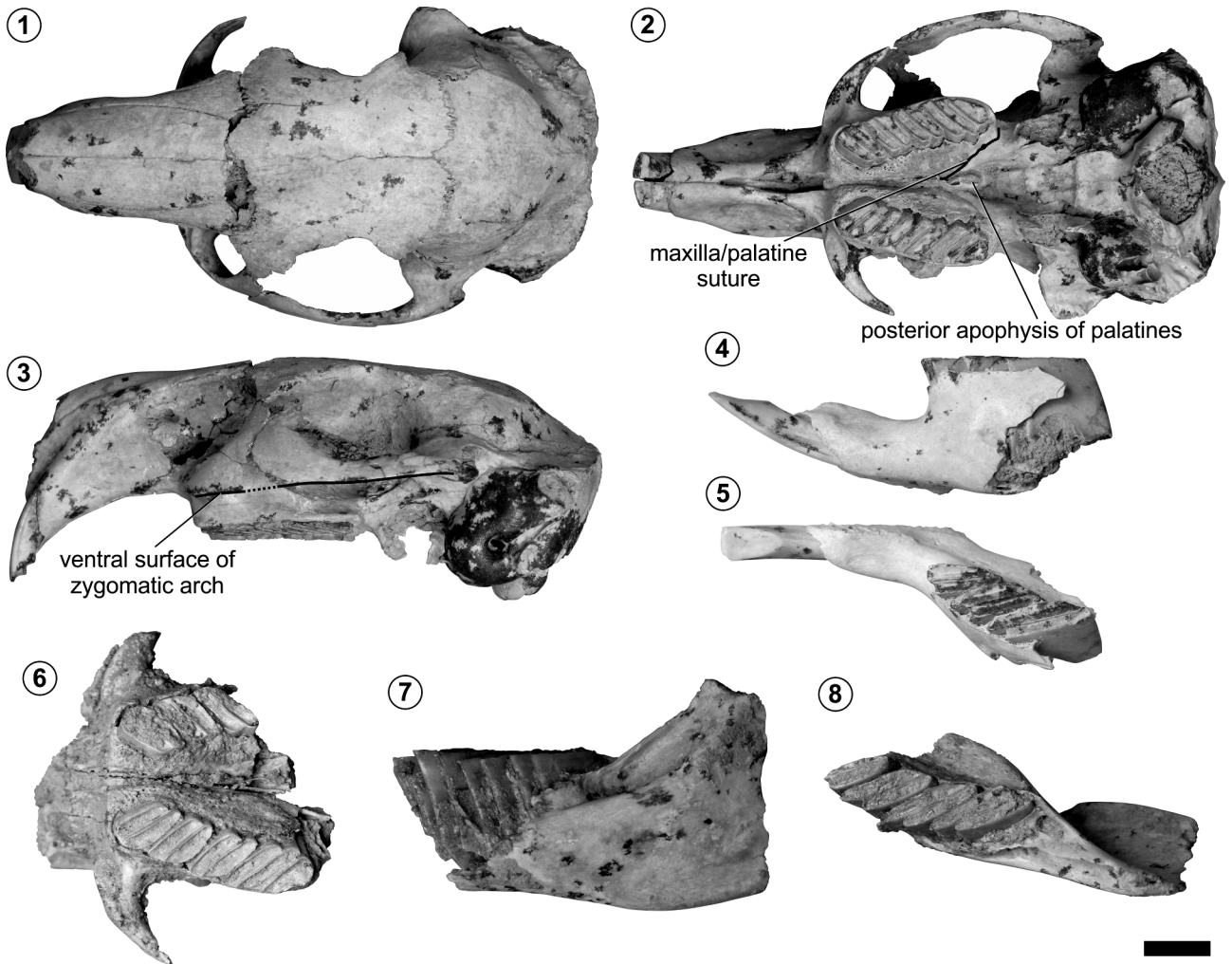
Most of the specimens of *Lagostomus incisus* studied herein were recovered from the Playa San Carlos Alloformation (*sensu* Zárate, 1989) while MLP-Pv 01-I-10-44 was the only specimen recovered from lower levels of the Playa Los Lobos Alloformation (Fig. 2). The specimen MLP-Pv 88-VI-1-2 came from Las Vertientes, where levels III to XI crop out (see Kraglievich, 1952), and would therefore issue from either the Playa San Carlos or the Playa Los Lobos alloformations.

***Lagostomus euplasius* (Ameghino, 1908)**

Figures 4.1–11, 6.3–4

- 1908. *Viscacia* (sic) *euplasia* Ameghino, p. 424–425.
- 1908. *Viscacia* (sic) *loberiaense* Ameghino, p. 425.
- 1908. *Viscacia* (sic) *definita* Ameghino, p. 424.
- 1908. *Viscacia* (sic) *chapalmalense* Ameghino, p. 424.
- 1914. *Viscaccia euplasia* Ameghino, Rovereto, p. 192, fig. 74.4, lam. 26 fig. 5, 5a.
- 1914. *Viscaccia loberianese* Ameghino, Rovereto, p. 193, fig. 74.3.
- 1914. *Viscaccia definita* Ameghino, Rovereto, p. 192.
- 1914. *Viscaccia chapalmalense* Ameghino, Rovereto, p. 192.
- 1926. *Lagostomus* (*Lagostomopsis*) *euplasius* (Ameghino), Kraglievich, p. 48, lam. 1, figs. 3, 4.

**Emended diagnosis.** Lagostomine of middle to small size; smaller than *Lagostomus maximus*, *L. egenus*, *L. cavifrons*, *L. debilis*, *L. compressidens* and *L. incisus*; larger than *L. laminosus*; and similar in size to *L. pretrichodactyla*, *L. antiquus*, *L. heterogenidens* and *L. minimus*. Premaxillaries posteriorly longer than nasals. Palate formed by maxillaries and palatines in equal proportion. Incisors with yellowish enamel. Hipoflexa and hipoflexids with thicker cement than in *L. antiquus*, *L. incisus*, *L. compressidens*, *L. debilis*, *L. heterogenidens*, *L. minimus*, *L. cavifrons* and *L. maximus*. Upper cheek teeth more compressed anteroposteriorly than in *Lagosto-*



**Figure 3.** *Lagostomus incisus* from the Chapadmalal Formation. 1–3, MLP-Pv 91-IV-5-258; 1, skull in dorsal view; 2, skull in ventral view; 3, skull in lateral view; 4–5, MLP-Pv 91-IV-5-214; 4, left mandible in lateral view; 5, left mandible in dorsal view; 6–8, MLP-Pv 88-VI-1-2; 6, palate in ventral view; 7, left mandible in lateral view; 8, left mandible in dorsal view. Scale bar= 1 cm.



*mus pretrichodactyla*, *L. compressidens* and *L. maximus* yet less than in *L. incisus* and forming a more acute angle with the sagittal plane than in *L. antiquus*, *L. pretrichodactyla*, *L. compressidens*, *L. cavifrons* and *L. maximus* though less than in *L. incisus*. Lower cheek teeth are less compressed antero-posteriorly than in *L. incisus* and *L. laminosus* and more compressed than in *L. pretrichodactyla*, *L. compressidens*, *L. cavifrons* and *L. maximus* and thus similar to *L. antiquus*, *L. debilis*, *L. heterogenidens* and *L. minimus*. Lower cheek teeth laminae forming a more acute angle with the sagittal plane than in *L. maximus*, *L. cavifrons*, *L. compressidens*, *L. pretrichodactyla*, *L. minimus*, *L. heterogenidens* and *L. debilis* but less than in *L. incisus*, thus being similar to *L. antiquus*. Humerus shows a fully formed supracondyloid canal.

**Holotype.** MACN-Pv 6163, complete skull with right and left incisors and P4–M3, mandibles with right and left incisors and p4–m3 (Fig. 4.1–4).

**Referred material.** MACN-Pv 5986 (holotype of '*Viscaccia definita*'), right mandible fragment with incisor and p4–m2 (Fig. 4.6–7); MACN-Pv 5985 (holotype of '*V. chapalmalense*'), left mandible with p4–m2, symphyseal portion of right mandible and two isolated lower incisors (Fig. 4.11); MLP-Pv 54-X-13-1 (holotype of '*V. loberiaense*'), incomplete skull with left incisor, right and left P4–M3, atlas fragment, axis fragment, seven lumbar vertebrae, one sacral vertebra, six caudal vertebrae, left humerus, left metacarpal IV, pelvis, right and left femurs, right and left tibiae, right fibula fragment, right astragalus, right calcaneus, right navicular, right proximal phalanx of digit III, right upper incisor, P4 and M3 (Fig. 4.8–10); MLP-Pv 52-IX-28-62, maxillae with left P4–M3 and right P4–M2 as well as left premaxillary fragment; MLP-Pv 52-IX-29-74, two right lower incisors, two right tympanic bullae, two lumbar vertebrae, right scapula fragment, left humerus, left humerus distal fragment, three incomplete right and left humeri, left tibia, right astragalus, right calcaneus, right tarsals II and III, left tarsal II; MLP-Pv 52-X-1-13, palate with left P4–M3 and right P4–M1 and M3, right premaxillary fragment with incisor, fragments of posterior portion of the skull; MLP-Pv 52-X-4-21, anterior portion of the skull with right and left incisors, right P4–M3, left P4–M2, right mandible with incisor and p4–m3, sacral vertebrae, left tibia, left astragalus, left calcaneus, left tarsals II, III and IV, complete digit III of hindlimb; MLP-Pv 52-XI-5-8, left mandible with incisor and p4–m3, right

femur and right tibia from different individuals; MLP-Pv 91-IV-5-334, anterior fragment of the skull with right and left incisors and P4–M3, atlas, axis and seven cervical vertebrae; MLP-Pv 01-I-10-36, anterior portion of the skull with right and left incisors, right P4–M1, left P4–M3, occipital portion of the skull and right tympanic bulla; MLP-Pv 01-I-10-39, palate fragment with right and left P4–M2; MLP-Pv 01-I-10-40, fragment of right maxillary with P4–M1, fragment of right mandible with incisor and p4, fragment of left mandible with p4–m3, acetabular portion of pelvis; MLP-Pv 01-I-10-49, skull roof fragment, left tibia fragment, right and left humeri, isolated teeth; MLP-Pv 01-I-10-50, anterior portion of the skull with right and left P4–M3; MLP-Pv 01-I-10-55, right mandible fragment with p4–m3, posterior skull portion, ulna, radius, left femur distal portion, left tibia, articulated left foot, isolated tarsal element; MLP-Pv 01-I-10-56, right mandible fragment with p4–m2.

**Geographic occurrence.** Coastal cliffs between Mar del Plata and Miramar, Buenos Aires Province, Argentina (Fig. 1).

Holotype of *Lagostomus euplasius* (MACN-Pv 6163), MACN-Pv 5986 (holotype of '*Viscaccia definita*') and MACN-Pv 5985 (holotype of '*V. chapalmalense*') were recovered from 'Chapalmalal'. MLP-Pv 54-X-13-1 (holotype of '*V. loberiaense*') was recovered from an undetermined site on the Atlantic coast between Mar del Plata and Miramar. MLP-Pv 01-I-10-36 comes from Los Acantilados; MLP-Pv 01-I-10-55, from Playa Serena; and MLP-Pv 01-I-10-39, 01-I-10-49 and 01-I-10-56, from Barranca de los Lobos (formerly Bajada Martínez de Hoz). MLP-Pv 01-I-10-50 was recovered from Estafeta; MLP-Pv 01-I-10-40, from San Eduardo; and MLP-Pv 91-IV-5-334 and MLP-Pv 91-IV-5-350, from Las Brusquitas. MLP-Pv 52-IX-28-62 and MLP-Pv 52-X-4-21 were collected between Las Brusquitas and Vuelta Mala while MLP-Pv 52-IX-29-74 and MLP-Pv 52-X-1-13 were collected between Las Brusquitas and Punta Vorohué. MLP-Pv 52-XI-5-8 comes from Miramar.

*Lagostomus euplasius* have been also recorded in Farola Monte Hermoso (Mones, 1980; Rasia, 2016) and Cascada Grande (Frenguelli, 1928; Rasia, 2016), in Buenos Aires Province, Argentina, as well as in the Maldonado Department in Uruguay (Francis and Mones, 1966).

**Stratigraphic occurrence.** Chapadmalal Formation (upper Chapadmalal State/Age, late Pliocene; Fig. 2).

Holotype of *Lagostomus euplasius* (MACN-Pv 6163),

MACN-Pv 5986 (holotype of '*Viscaccia definita*'), MACN-Pv 5985 (holotype of '*V. chapalmalense*') and MLP-Pv 54-X-13-1 (holotype of '*V. loberiaense*') come from '*Piso Chapalmalense*'.

MLP-Pv 91-IV-5-334, MLP-Pv 91-IV-5-350, MLP-Pv 52-IX-28-62 and MLP-Pv 52-X-4-21 were recovered from levels IX to X of the Chapadmalal Formation (see Fig. 2).

MLP-Pv 52-X-1-13, MLP-Pv 52-IX-29-74 and MLP-Pv 52-XI-5-8 were collected between levels VII and XI of the Chapadmalal Formation (see Fig. 2).

MLP-Pv 01-I-10-36, 01-I-10-49 and 01-I-10-55 come from level II; MLP-Pv 01-I-10-56, from level VI; MLP-Pv 01-I-10-40 and 01-I-10-50, from level IX; and MLP-Pv 01-I-10-39, from level XI.

*Lagostomus euplasius* have been also recorded in the Monte Hermoso Formation (early Pliocene; see Mones, 1980; Rasia, 2016), the Irene 'formation' (Pliocene?; see Rasia, 2016) and the Maldonado Formation (late Pliocene; Francis and Mones, 1966).

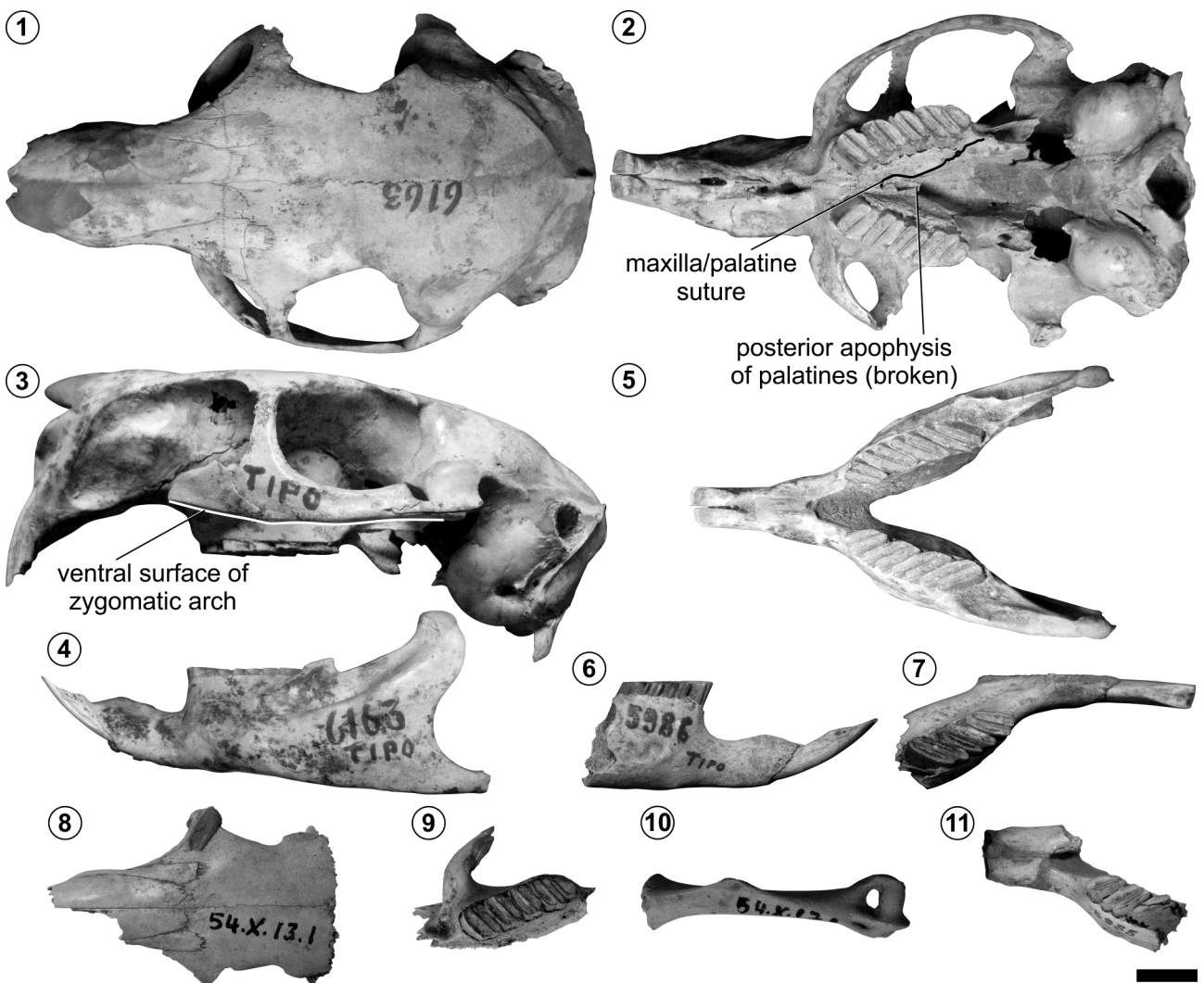


Figure 4. *Lagostomus euplasius* from the Chapadmalal Formation. 1–5, MACN-Pv 6163 (holotype); 1, skull in dorsal view; 2, skull in ventral view; 3, skull in lateral view; 4, mandibles in lateral view; 5, mandibles in dorsal view; 6–7, MACN-Pv 5986, holotype of '*Viscaccia definita*'; 6, mandible in lateral view; 7, mandible in dorsal view; 8–10, MLP-Pv 54-X-13-1, holotype of '*Viscaccia loberiaense*'; 8, skull fragment in dorsal view; 9, left palate portion in ventral view; 10, left humerus in posterior view; 11, MACN-Pv 5985, holotype of '*Viscaccia chapalmalense*', left mandible and right mandibular fragment in dorsal view. Scale bar= 1 cm.

### **Description and comparisons**

**Skull.** This is a small to medium sized lagostomine smaller than *Lagostomus maximus*, *L. cavifrons*, *L. egenus*, *L. debilis*, *L. compressidens* and *L. incisus*.

In comparison with the total length of the skull, the rostrum is short, thus resembling that of subadult individuals of *Lagostomus maximus* (Rasia, 2016). The nasals are wide and bulky in their anterior portion and become narrower from the middle point toward the posterior portion (Fig. 4.1, 4.8). Nasals are, as in *Lagostomus pretrichodactyla* and *L. incisus*, equal in length or as much as 12.5% shorter than the frontals. In *Lagostomus maximus*, nasals are as long as the frontals in juvenile specimens but 50% longer than the frontals in adult specimens. In *L. compressidens* and *L. cavifrons*, nasals are longer than the frontals. The premaxillaries extend beyond the posterior end of the nasals (Fig. 4.1, 4.8), as in *Lagostomus pretrichodactyla* and *L. incisus*. In *L. compressidens*, *L. cavifrons* and most specimens of *L. maximus*, premaxillaries and nasals reach the same level posteriorly.

Zygomatic arches are rather parallel to the sagittal plane, as in juvenile specimens of *Lagostomus maximus*. In adult specimens of the living species, the zygomatic arches are posteriorly divergent. As in *Lagostomus maximus* and differing from *L. incisus* (see above), the ventral surface of the zygomatic arch is slightly projected ventrally at the level of the maxillary-jugal suture (Fig. 4.3).

Temporal crests are long and well defined and the sagittal crest is short and well marked (Fig. 4.1). Both of the aforementioned features are common to subadult specimens and adult females of *Lagostomus maximus*.

The posterior palatine apophysis of the premaxillaries occur at the same dorso-ventral level as the diastema or slightly protrude ventrally, as in *Lagostomus maximus*, *L. compressidens*, *L. pretrichodactyla*, and *L. cavifrons*. In *L. incisus*, the premaxillary posterior palatine apophysis is situated dorsally with respect to the diastema (see Rasia and Candela, 2013). The interpremaxillary foramen is narrow but well developed. The incisive foramen is narrow and occupies less than half the length of the diastema. Palatines reach anteriorly toward the posterior level of the P4, as in *Lagostomus pretrichodactyla*, *L. compressidens*, *L. cavifrons* and *L. maximus*, and present a posterior apophysis (Fig. 4.2). The palate is rather vaulted, with maxillaries and palatines forming a flat surface, as in *Lagostomus pretrichodactyla*.

In *L. maximus* and *L. compressidens* there is a shallow depression in the maxillary between the cheek teeth alveoli and the maxillary-palatine suture.

The tympanic bullae are rounded (Fig. 4.2), as in *Lagostomus incisus* and young specimens of *L. maximus*. In adult specimens of *L. maximus*, bullae are posterolateral-anteromedially elongated. The paraoccipital apophyses are strong and posteroventrally oriented (Fig. 4.3), as in *Lagostomus maximus*.

**Mandibles.** In comparison with the length of the lower cheek teeth series, the diastema is shorter than in *Lagostomus incisus* and *L. compressidens*. The masseteric crest is less developed than in *L. maximus*. The angular apophysis is slender. The coronoid apophysis is low in the mandible ramus and boasts a wide base, as in *L. maximus*. The postcondyloid apophysis is rounded and well developed, as in *L. compressidens*.

**Upper teeth.** The enamel of the upper incisors is yellowish. Although the color may be caused by diagenetic factors, it is noteworthy that the only specimens marked by yellowish enamel in the incisors are those which were assigned to *Lagostomus euplasius* (based on cheek teeth and skull characters). Such fact suggests that the color was original to such surface and is thus a diagnostic feature of this species.

The cheek teeth are more anteroposteriorly compressed than in *Lagostomus pretrichodactyla*, *L. compressidens*, *L. cavifrons* and *L. maximus* but less than in *L. incisus* (see Figs. 4.2, 4.9, 6.3, 7). Cheek teeth laminae form a more acute angle with the sagittal plane than that which can be observed in *Lagostomus maximus*, *L. cavifrons*, *L. compressidens*, *L. pretrichodactyla* and *L. antiquus* though less acute than in *L. incisus*.

The enamel band is thick but to a lesser extent than in *Lagostomus pretrichodactyla*. The cement of the hypoflexus is thicker than that of *Lagostomus antiquus*, *L. incisus* and *L. compressidens*. As in *L. pretrichodactyla*, hypoflexa are straight, with a short posterior curvature in the labial portion which is less marked than that of *Lagostomus maximus*. The anterior loph of the upper molars is more labially projected than the posterior loph, as in *Lagostomus pretrichodactyla* and *L. maximus*.

**Lower teeth.** As in the upper incisors, the enamel of the lower incisors is yellowish.

The cheek teeth are less compressed anteroposteriorly

than those of *Lagostomus laminosus* and *L. incisus* (see Figs. 4.5, 4.7, 4.11, 6.4, 7). Additionally, they are more compressed than in *L. maximus*, *L. pretrichodactyla*, *L. compressidens* and *L. cavifrons*, and similar to those of *L. antiquus*, *L. heterogenidens*, *L. minimus* and *L. debilis*.

Cheek teeth laminae form a more acute angle with the sagittal plane than that which is formed in *Lagostomus maximus*, *L. pretrichodactyla*, *L. compressidens*, *L. heterogenidens*, *L. minimus* and *L. debilis*. Yet, such angle is less acute than that of *L. incisus*, thus being similar to *L. antiquus*.

The cement layer of the hypoflexids is thicker than that of *Lagostomus antiquus*, *L. incisus*, *L. compressidens*, *L. heterogenidens*, *L. minimus* and *L. debilis* though similar to that of *Lagostomus pretrichodactyla*.

**Postcranial skeleton.** The humerus presents a fully formed supracondyloid canal above the medial epicondyle (Fig. 4.10). In *Lagostomus incisus*, the supracondyloid canal is open or incomplete (see Rasia and Candela, 2013), and in *L. maximus* the canal is absent (see Kraglievich, 1926).

The calcaneus exhibits a secondary sustentacular facet distal to the sustentacular facet, as in the living chinchillids *Lagostomus maximus* and *Chinchilla* (see Candela and Picasso, 2008). Although this secondary facet is present in other fossil species of the genus, such as *Lagostomus incisus* (see above), it cannot be observed in other genera of Chinchillidae (i.e., *Eoviscaccia*, *Prolagostomus* and *Pliolagostomus*) because of the lack of preserved postcranial elements.

Other postcranial elements do not evidence significant differences with *Lagostomus maximus* or with other fossil species of the genus.

### Comments

Most of the material of *Lagostomus euplasius* herein studied was recovered from the Playa San Carlos Alloformation and from basal levels of the Playa los Lobos Alloformation (Fig. 2). Only the specimens MACN-Pv 6163, MACN-Pv 5985, MACN-Pv 5986 and MLP-Pv 54-X-13-1 (holotypes of *Lagostomus euplasius*, '*Viscaccia chapalmalense*', '*V. definita*' and '*V. loberiaense*') do not boast precise stratigraphic provenance within the Chapadmalal Formation.

The holotype of '*Viscaccia loberiaensis*' (MLP-Pv 54-X-13-1; Fig. 4.8–9) is indistinguishable from the holotype of *Lagostomus euplasius* (MACN-Pv 6163; Fig. 4.1–3) with

respect to skull morphology and cheek teeth characteristics. Probably being a juvenile specimen of these same species, their synonymy is hereby proposed.

The holotypes of '*Viscaccia loberiaense*', '*V. definita*' (Fig. 4.6–7) and '*V. chapalmalense*' (Fig. 4.11) share the presence of incisors with yellowish enamel and the lower cheek teeth features with the holotype of *Lagostomus euplasius* (Fig. 4.4–5). Therefore, their synonymy is hereby proposed.

*Lagostomus euplasius* was reported, based on different specimens (MLP-Pv 52-X-5-54 to 63), from the Monte Hermoso Formation by Mones (1980) and Rasia (2016).

### *Lagostomus compressidens* (Ameghino, 1908)

Figures 5.1–5, 6.5–6

1908. *Viscacia* (sic) *compressidens* Ameghino, p. 424.

1908. *Viscacia* (sic) *indefinita* Ameghino, p. 424.

1914. *Viscaccia compressidens* Ameghino. Rovereto, p. 191, fig. 74.2.

1914. *Viscaccia indefinita* Ameghino. Rovereto, p. 192, fig. 74.1.

**Emended diagnosis.** Lagostomine smaller than *Lagostomus maximus* and *L. cavifrons* though approximately equal in size to *L. incisus*, *L. debilis* and *L. egeus* and larger than *L. antiquus*, *L. laminosus*, *L. pretrichodactyla*, *L. euplasius*, *L. heterogenidens* and *L. minimus*. Nasals extend posteriorly to the same level as the premaxillaries, thus differing from those of *L. pretrichodactyla*, *L. incisus* and *L. euplasius*. Maxillaries with a depression between cheek teeth alveoli and the palatines. Palatines more developed than maxillaries in palatal view. Palate less vaulted than in *Lagostomus maximus* and *L. cavifrons*. The root of the lower incisor reaches the posterior level of m2. Upper cheek teeth less compressed anteroposteriorly than in *L. euplasius* and *L. incisus*. Upper cheek teeth more perpendicular to the sagittal plane than in *L. euplasius* and *L. incisus*. Lower cheek teeth less compressed anteroposteriorly than in *L. antiquus*, *L. laminosus*, *L. incisus* and *L. euplasius*. Lower cheek teeth more perpendicular to the sagittal plane than in *L. incisus*, *L. euplasius* and *L. antiquus*. Cement present in the hypoflexus and hypoflexid, thinner than in *L. pretrichodactyla*.

**Holotype.** MLP-Pv 54-X-13-2, incomplete skull with right incisor and both complete cheek teeth series, left mandible with incisor and complete p4–m3 series (Fig. 5.1–4).

**Referred material.** MLP-Pv 54-X-13-4 (holotype of '*Viscaccia indefinita*'), palate with both cheek teeth series (Fig. 5.5); MLP-Pv 90-VI-1-1, right mandible with incisor and p4–m3.



**Geographic provenance.** The holotype and MLP-Pv 54-X-13-4 were recovered from an indetermined site between Mar del Plata and Miramar. MLP-Pv 90-VI-1-1 came from Las Vertientes (Fig. 1).

**Stratigraphic provenance.** Chapadmalal Formation (upper Chapadmalalan, late Pliocene; Fig. 2). Both the holotype and MLP-Pv 54-X-13-4 were recovered from 'Piso Chapadmalense' sensu Ameghino (1908). MLP-Pv 90-VI-1-1 was collected from undetermined levels of the Chapadmalal Formation (see Comments below).

**Description and comparisons**

**Skull.** The description is mostly based on the holotype (MLP-Pv 54-X-13-2), which is the most complete specimen.

*Lagostomus compressidens* is a medium sized lagostomine approximately equal to adult females or subadult males of the living *L. maximus* and to adult individuals of *L. incisus*.

Nasals are broken in their anterior portion but the length of the preserved part is longer than that of the frontals, as in *L. cavifrons* and *L. maximus*. The nasals are approxi-

mately of equal width in all their length, as in *L. incisus* and *L. maximus*. Premaxillaries do not extend posteriorly beyond the nasals as occurs in *Lagostomus pretrichodactyla*, *L. euplasius* and *L. incisus*. Instead, the premaxillaries extend posteriorly to the same level as the nasals (Fig. 5.1), like in *L. maximus* and *L. cavifrons*. Lacrimals are elongated as in *Lagostomus maximus*.

While temporal crests are long and well developed, the sagittal crest is, as observed in subadult males and adult females of *Lagostomus maximus* (see Rasia *et al.*, 2011), short and well marked (Fig. 5.1). The skull roof is rather vaulted in lateral view, as in adult females and subadult males of *L. maximus*.

Posterior palatine apophysis of the premaxillary occurs at the same dorsoventral level as the diastema, like in *Lagostomus maximus*, *L. cavifrons*, *L. euplasius* and *L. pretrichodactyla*. The interpremaxillar foramen is narrow but well developed. The incisive foramen is wide and short.

The palatines extend anteriorly, reaching the level of the posterior margin of the P4 and forming an important portion of the palate. In palatal view, the maxillary present a

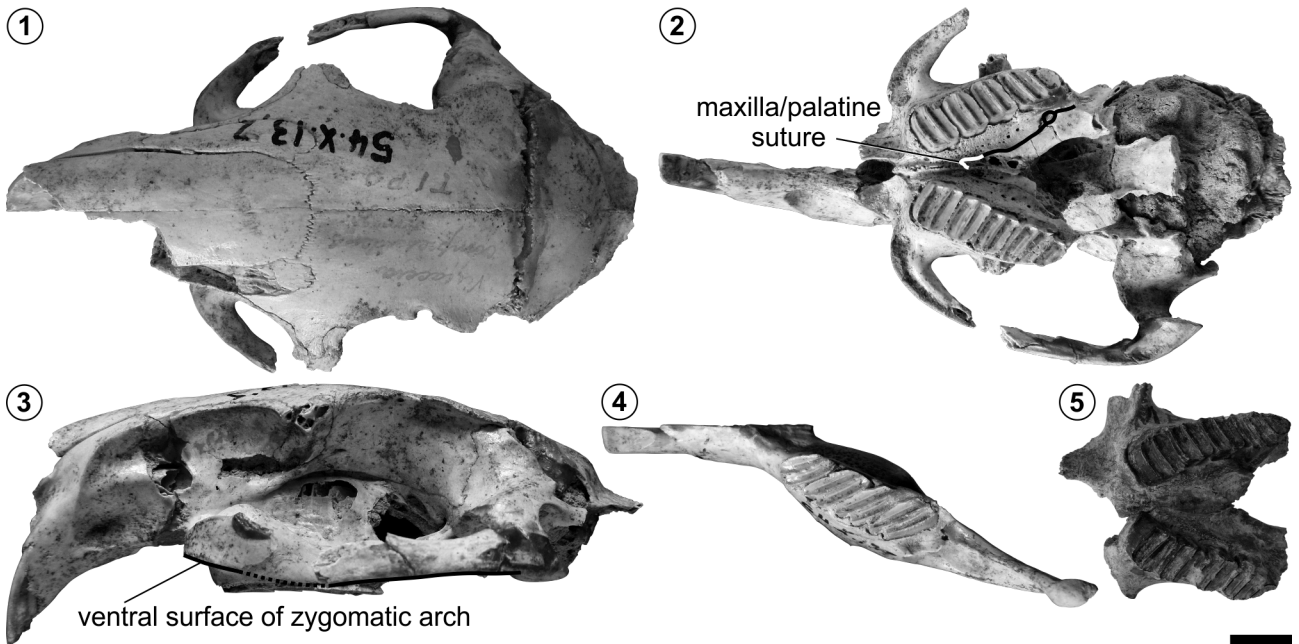


Figure 5. *Lagostomus compressidens*. 1–4, MLP-Pv 54-X-13-2 (holotype); 1, skull in dorsal view; 2, skull in ventral view; 3, skull in right lateral view (shown as left); 4, left mandible in dorsal view; 5, MLP-Pv 54-X-13-4, holotype of '*Viscaccia indefinita*', palate in ventral view. Scale bar= 1 cm.



shallow depression between the cheek teeth alveoli and the maxillary-palatine suture. Such depression is also observed in *Lagostomus maximus* and *L. cavifrons*. Maxillae and palatines form a rather horizontal structure and the palate is not vaulted.

**Mandibles.** In comparison with the total length of the cheek teeth series, the diastema is shorter than that of *Lagostomus maximus* but longer than that of *L. incisus* and *L. euplasius*. Compared with *L. maximus*, the mandibular condyle is higher than the cheek teeth series. The postcondyloid process is more developed than in *L. maximus*.

**Upper teeth.** In comparison with specimens of *Lagostomus maximus* of similar size, the upper incisors present a greater transverse diameter and are shorter (less projected from the alveolar sheet).

The upper cheek teeth series is longer than in *Lagostomus maximus*, compared to the total length of the skull, and approximately equal to that of *L. incisus*.

Cheek teeth sub-quadrangular and with straight margins similar to those of *Lagostomus maximus* and *L. cavifrons*. Cheek teeth are also less compressed anteroposteriorly than in *Lagostomus euplasius* and *L. incisus*, thus being approximately equal to those of *L. pretrichodactyla*, *L. cavifrons* and *L. maximus* (see Figs. 5.2, 5.5, 6.5, 7). Upper cheek teeth laminae are more perpendicular with respect to the sagittal plane than in *Lagostomus incisus* and *L. euplasius*, hence being approximately equal to those of *L. antiquus*, *L. pretrichodactyla*, *L. cavifrons* and *L. maximus*.

The third lobe of the M3 is well developed and marked by a larger anteroposterior diameter than that of the first two lobes.

There is cement in the hipoflexus of all cheek teeth and it is thinner than in *Lagostomus pretrichodactyla* and *L. euplasius*, being similar to that of *L. incisus*.

**Lower teeth.** In parallel to what occurs with the upper incisors, the lower incisors are wider and shorter (less projected from the alveolar sheet) than in a specimen of *Lagostomus maximus* of equal size. A difference with respect to the other species of *Lagostomus* is given by the fact that the root of the lower incisor does not extend beyond the m2.

With respect to the total length of the mandible, the cheek teeth series is longer than that of *Lagostomus maximus* yet shorter than that of *L. euplasius* and *L. incisus*.

Cheek teeth are less compressed anteroposteriorly than

in *Lagostomus antiquus*, *L. laminosus*, *L. incisus*, *L. euplasius*, *L. debilis*, *L. heterogenidens* and *L. minimus*, thus being similar to those of *L. pretrichodactyla*, *L. cavifrons*, *L. egenus* and *L. maximus* (see Figs. 5.4, 6.6, 7).

Cheek teeth laminae form a less acute angle with respect to the sagittal plane than in *Lagostomus antiquus*, *L. incisus* and *L. euplasius*. The angle is rather similar to that of *L. pretrichodactyla*, *L. cavifrons* and *L. maximus*.

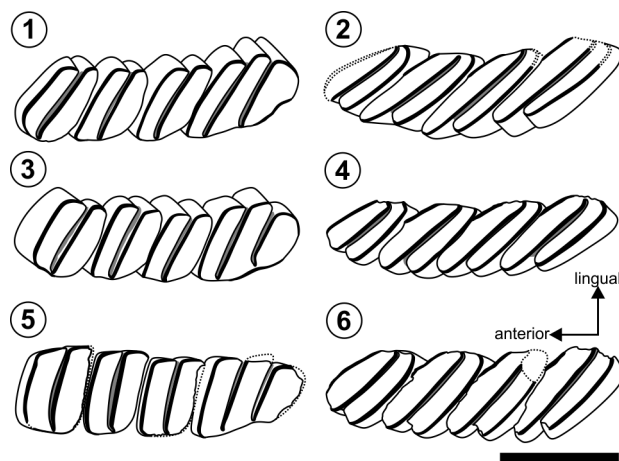
There is cement in the hypoflexid of all cheek teeth and it is thinner than in *Lagostomus pretrichodactyla* and *L. euplasius*.

**Comments**

The holotype of '*Viscaccia indefinita*' (MLP-Pv 54-X-13-4; Fig. 5.5) shows proportions, anatomic features of the upper cheek teeth and palatal morphology identical to those characterizing the holotype of *Lagostomus compressidens* (Fig. 5.2). Therefore, the synonymy of both species is hereby proposed.

The specimen MLP-Pv 90-VI-1-1, referred to as *Lagostomus compressidens* herein, is identical in size and in the morphology of lower cheek teeth and proportions of the lower incisor and mandible to the holotype of this species.

The holotype of *Lagostomus compressidens* (MLP-Pv 54-X-13-2) and the holotype of '*Viscaccia indefinita*' (MLP-Pv



**Figure 6.** Compared schematic occlusal views of *Lagostomus* species from the Chapadmalal Formation. 1–2, *Lagostomus incisus*, MLP-Pv 88-VI-1-2; 1, scheme of right upper cheek teeth; 2, scheme of left lower cheek teeth; 3–4, *Lagostomus euplasius*, MACN-Pv 6163; 3, scheme of right upper cheek teeth; 4, scheme of left lower cheek teeth; 5–6, *Lagostomus compressidens*, MLP-Pv 54-X-13-2; 5, scheme of right upper cheek teeth; 6, scheme of left lower cheek teeth. Scale bar= 1 cm.

54-X-13-4) were recovered from '*Piso Chapalmalense*' sensu Ameghino (1908). The specimen MLP-Pv 90-VI-1-1 was collected from Las Vertientes (see Fig. 1), where levels III to XI of the Chapadmalal Formation (sensu Kraglievich, 1952) crop out (see Fig. 2).

*Lagostomus compressidens* was recorded exclusively from the Chapadmalal Formation (late Pliocene).

**'*Viscaccia arcuata*'** Ameghino, 1908 *nomen dubium*

1908. *Viscacia* (sic) *arcuata* Ameghino, p. 425.

1914. *Viscaccia arcuata* Ameghino. Rovereto, p. 193.

**Holotype.** Currently lost.

**Comments**

Ameghino (1908) originally described this species based on skull remains and stated that it is small sized and presents a short, wide and vaulted skull. However, these features are also present in juvenile specimens of the living *Lagostomus maximus* and of fossil species such as *L. incisus* and *L. euplasius*. Therefore, '*Viscaccia arcuata*' cannot be differentiated from other species based on such description and, given that the holotype has not been found in the

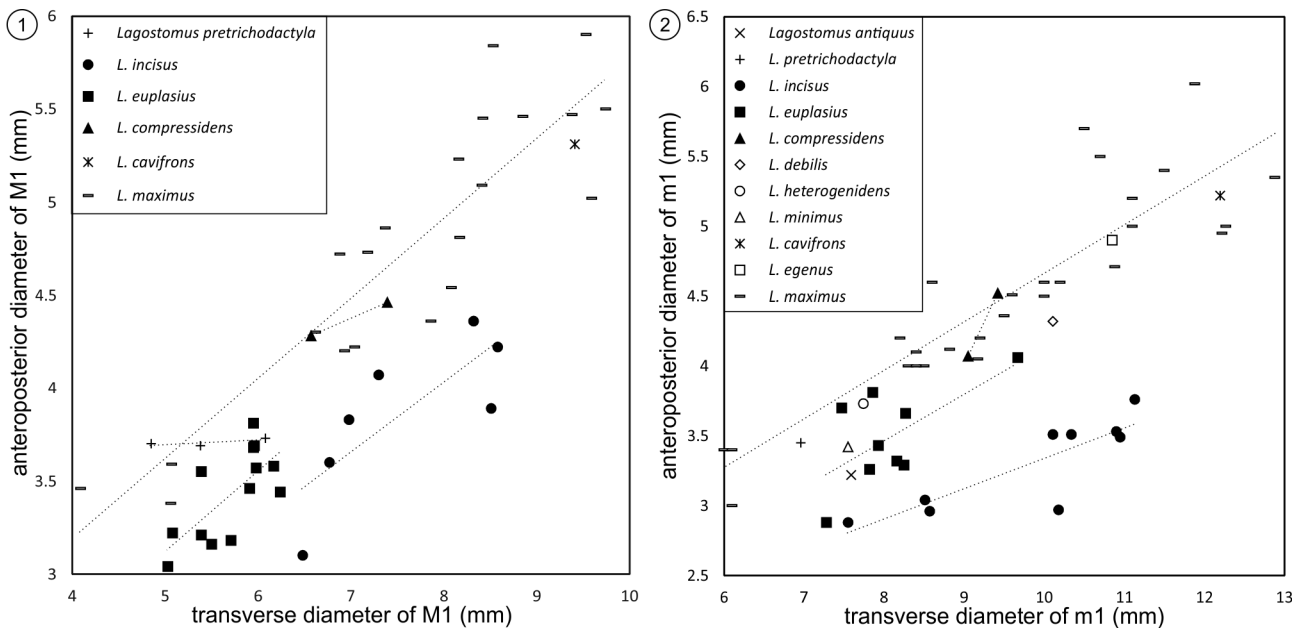
MACN collection, is thus herein considered *nomen dubium*.

According to Mones (1986), the specimen MACN-Pv 5983 is the holotype of this species. Nevertheless, this catalogue number corresponds to a right mandible and does not match the description of Ameghino (1908) based on skull remains.

**QUANTITATIVE ANALYSIS**

**Upper cheek teeth.** For the analysis based upon upper cheek teeth and given that all variables yield high positive loads (see Table 1), the first principal component (PC1) represents essentially size. The smaller specimens present lower values of PC1 while the larger ones present higher scores. The largest species with known upper cheek teeth are *Lagostomus maximus*, *L. cavifrons*, *L. compressidens* and *L. incisus* (see Fig. 8).

The second principal component (PC2) represents variations in the APD of P4–M2 and in the TD of M2–M3 (see Table 1). The species with more anteroposteriorly compressed upper cheek teeth is *Lagostomus incisus*, with negative scores. *Lagostomus euplasius* and *L. cavifrons* exhibit a moderate anteroposterior compression of upper cheek teeth. The rest of the species (*L. pretrichodactyla*, *L. compressidens*



**Figure 7.** Bivariate graphic of dental measurements (in mm) for species of *Lagostomus*. 1, first upper molar (M1) and 2, first lower molar (m1). Dotted lines indicate linear regression trend line for each species using least squares.

TABLE 1 – Factor loadings of PC1 and PC2.

	PCA of upper cheek teeth		PCA of lower cheek teeth		
	PC1	PC2	PC1	PC2	
<i>P4 APD</i>	0.296	<b>0.399</b>	<i>p4 APD</i>	<b>0.387</b>	0.298
<i>P4 TD</i>	<b>0.360</b>	-0.111	<i>p4 TD</i>	<b>0.383</b>	-0.144
<i>M1 APD</i>	<b>0.319</b>	<b>0.383</b>	<i>m1 APD</i>	<b>0.326</b>	<b>0.380</b>
<i>M1 TD</i>	<b>0.382</b>	-0.255	<i>m1 TD</i>	<b>0.335</b>	-0.225
<i>M2 APD</i>	<b>0.338</b>	<b>0.403</b>	<i>m2 APD</i>	<b>0.318</b>	<b>0.390</b>
<i>M2 TD</i>	<b>0.376</b>	<b>-0.336</b>	<i>m2 TD</i>	<b>0.333</b>	<b>-0.396</b>
<i>M3 APD</i>	<b>0.365</b>	0.245	<i>m3 APD</i>	<b>0.324</b>	<b>0.344</b>
<i>M3 TD</i>	<b>0.382</b>	<b>-0.530</b>	<i>m3 TD</i>	<b>0.409</b>	<b>-0.518</b>
Eigenvalue	0.303	0.024	Eigenvalue	0.270	0.050
Variance	90%	7%	Variance	81%	15%

Loadings higher than 0.3 are in boldface.

and *L. maximus*) present less compressed cheek teeth and yield positive scores (see Fig. 8).

**Lower cheek teeth.** In the analysis of the lower cheek teeth and given that all variables yield high positive loads (see Table 1), PC1 represents size. The smaller specimens present lower values while the larger ones yield higher ones (see Fig. 8). The species of larger size with known lower cheek teeth are *Lagostomus maximus*, *L. cavifrons*, *L. egenus*, *L. debilis*, *L. compressidens* and *L. incisus*.

PC2 represents variations in the APD of the m1–m3 and in the TD of the m2–m3 (see Table 1). *Lagostomus incisus* is the species with more compressed lower cheek teeth, with the lowest values. The species in which a moderate compression of the lower cheek teeth is observed are *L. antiquus*, *L. euplasius* and *L. egenus*. The species with less compressed lower cheek teeth are *L. pretrichodactyla*, *L. debilis*, *L. heterogenidens*, *L. minimus*, *L. cavifrons* and *L. maximus* (see Fig. 8).

The Kruskal-Wallis test for the PC1 and PC2 of the PCA of the upper and lower cheek teeth indicates that the medians of the three species from the Chapadmalal Formation are significantly different, except for the PC1 of lower cheek teeth (see Table 2) which represents essentially size.

According to these results, the three species recorded from the Chapadmalal Formation can be distinguished in terms of general size and anteroposterior compression of the cheek teeth. This supports the diagnostic value of the aforementioned characteristics (see Systematic Paleontology section).

## DISCUSSION AND CONCLUSIONS

The comparative study of unpublished material with precise stratigraphic control from the Chapadmalal Formation allowed the identification of at least three of the seven species which were originally described by Ameghino (1908) for '*Piso Chapalmalense*': *Lagostomus incisus*, *L. euplasius* and *L. compressidens*. The first one was originally described for the Monte Hermoso Formation (Ameghino, 1888) and later reported from the Irene 'formation' and the Chapadmalal Formation (Rasia and Candela, 2013). The second species was originally described for '*Piso chapalmalense*' (*sensu* Ameghino, 1908) and later recorded in the Monte Hermoso Formation (Mones, 1980; Rasia, 2016), the Irene 'formation' (Frenguelli, 1928; Rasia, 2016) and the Maldonado Formation (Uruguay; Francis and Mones, 1966). The third species

was described for '*Piso Chapalmalense*' (*sensu* Ameghino, 1908) and is the only species recorded exclusively in the

Chapadmalal Formation.

Ameghino (1908) diagnosed *Lagostomus euplasius* as being of very small size and presenting a deep palate and premaxillae extending posteriorly (on dorsal view); '*Viscaccia definita*' was diagnosed as being marked by very striated lower incisors with a concave anterior surface; '*V. chapalmalense*', by its small size, deep palate and M3 with the three lobes in the same plane; and '*V. loberiaense*', by its very small size, long skull and yellowish enamel of the incisors. These four species share some of the features mentioned above, at least in the ones enough complete enough to be comparable. Therefore, the holotypes of '*Viscaccia loberiaense*' (MLP-Pv 54-X-13-1), '*V. definita*' (MACN-Pv 5986) and '*V. chapalmalense*' (MACN-Pv 5985) are herein referred to *Lagostomus euplasius*.

*Lagostomus compressidens* was originally diagnosed (Ameghino, 1908) in terms of presenting compressed molars and a wide, shallow and flat palate. '*Viscaccia indefinita*' was described as being similar to *L. compressidens* though smaller and with a deeper palate. Such differences are herein interpreted to be related to intraspecific variation and the holotype of '*Viscaccia indefinita*' (MLP-Pv 54-X13-4) is, in this study, referred to *Lagostomus compressidens*.

The nominal species '*Viscaccia arcuata*' was described for '*Piso Chapalmalense*' (Ameghino, 1908) but the fact that the holotype of this species is currently lost and the original description (very small size and a short, wide and vaulted skull) does not admit its differentiation from other species derives in its labeling as a *nomen dubium*. The presence of this species in the Chapadmalal Formation is not confirmed and has yet to be re-evaluated.

The presence of *Lagostomus incisus* and *L. euplasius* in the Monte Hermoso and Chapadmalal formations (see Ameghino, 1888, 1908, Mones, 1980; Rasia, 2016; Rasia and Candela, 2013) indicates a Montehermosan–Chapadmalalan stratigraphic range for these two species. Additionally, the presence of *L. incisus* and *L. euplasius* in the Irene 'formation' (see Frenguelli, 1928; Rasia, 2016; Rasia and Candela, 2013) suggests a Montehermosan–Chapadmalalan age for at least part of this unit. *Lagostomus incisus* and *L. euplasius* represent the only species recorded during the entire Montehermosan–Chapadmalalan interval and constitute the typical chinchillids during this lapse in central Argentina.

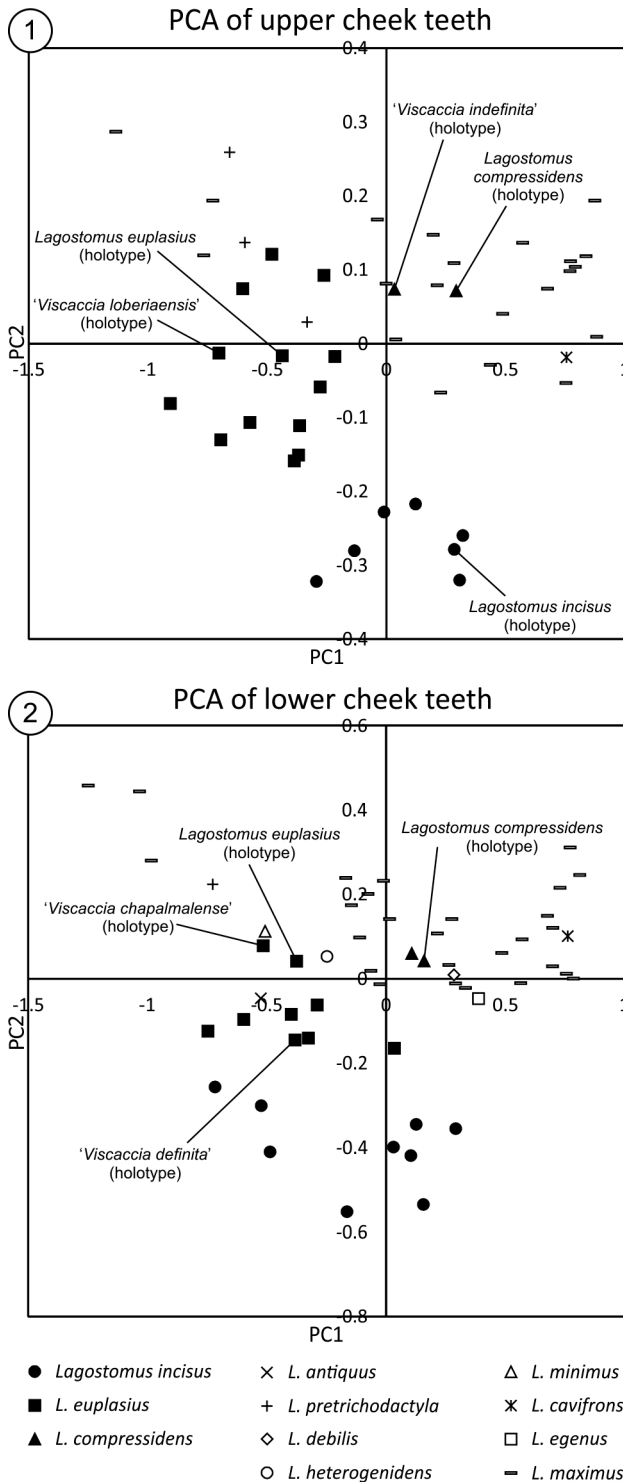


Figure 8. Plot of scores of PC1 and PC2 for dental measurements of species of *Lagostomus*. 1, upper cheek teeth; 2, lower cheek teeth.

TABLE 2 – Kruskal-Wallis test for PCA of species from Chapadmalal Formation.

	H - Hc	p	L. inc vs L. eup	L. inc vs L. com	L. eup vs L. com
PC1 - uct PCA	<b>13.78</b>	0.001019	0.0008741	0.8836	0.03375
PC2 - uct PCA	<b>14.37</b>	0.0007594	0.0003626	0.05704	0.2696
PC1 - lct PCA	5.525	0.06312	0.1333	0.2888	0.04513
PC2 - lct PCA	<b>15</b>	0.0005535	0.0004123	0.04513	0.1255

Boldface indicates values higher than critical value.  $\alpha=0.05$ ; degrees of liberty= 2; critical value=5.991. Abbreviations: H, chi2; Hc, tie corrected; L. eup, *Lagostomus euplasius*; L. com, *Lagostomus compressidens*; L. inc, *Lagostomus incisus*; lct, lower cheek teeth; uct, upper cheek teeth.

The specific diversity of the Montehermosan–Chapadmalal lagostomines (with two species in the Montehermosan and at least three in the Chapadmalal) is less significant than what was previously proposed; that is, with two species originally described for the Montehermosan (Ameghino, 1888) and seven, for the Chapadmalal (Ameghino, 1908). Nonetheless, such numbers are still higher than those referred to the diversity observed in recent times, with only one species (e.g., Weir, 1974; Jackson *et al.*, 1996).

The study of fossil Lagostominae could provide useful biostratigraphic information for the Pampean area given the great abundance of this group of rodents in late Cenozoic continental associations for which a more precise stratigraphic provenance is now known.

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## Appendix 1

### *List of specimens used for comparison and for the PCA.*

*Lagostomus antiquus* (late Miocene): MASP 32 (holotype).

*Lagostomus laminosus* (late Miocene): MACN-A 8883 (holotype); MACN-Pv 5884.

*Lagostomus pretrichodactyla* (late Miocene): MACN-Pv 8339 (holotype); MACN-Pv 8337; MACN-Pv 8345.

*Lagostomus debilis* (Pleistocene) MACN-A 1255 (holotype).

*Lagostomus heterogenidens* (Pleistocene): MACN-A 1187 (holotype).

*Lagostomus minimus* (Pleistocene): MACN-A 1098 (holotype).

*Lagostomus cavifrons* (Pleistocene): MACN-A 1651 (holotype).

*Lagostomus egenus* (Pleistocene): MACN-A 417 (holotype).

*Lagostomus maximus* (recent): MACN-Ma 49.289; MACN-Ma 49.291; MACN-Ma 50.10; MACN-Ma 50.13; MACN-Ma 50.14; MACN-Ma 50.15; MACN-Ma 50.17; MACN-Ma 50.18; MACN-Ma 50.20; MACN-Ma 50.21; MLP-Mz 14; MLP-Mz 19; MLP-Mz 37; MLP-Mz 38; MLP-

Mz 39; MLP-Mz 41; MLP-Mz 42; MLP-Mz 45; MLP-Mz 54; MLP-Mz 59; MLP-Mz 61; MLP-Mz 64; MLP-Mz 230; MLP-Mz 254; MLP-Mz 269; MLP-Mz 338; MLP-Mz 379; MLP-Mz 565; MLP-Mz 720; MLP-Mz 1473; MLP-Mz 1602; MLP-Mz 1603; MLP-Mz 1604; MLP-Mz 1605; MLP-Mz 1634; MLP-Mz 1642; MLP-Mz 1651; MLP-Mz 1657; MLP-Mz 1659; MLP-Mz 1728.

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