ARTICLE

LAGOSTOMUS TELENKECHANUM, SP. NOV., A NEW LAGOSTOMINE RODENT (CAVIOMORPHA, CHINCHILLIDAE) FROM THE ARROYO CHASICÓ FORMATION (LATE MIOCENE; BUENOS AIRES PROVINCE, ARGENTINA)

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ABSTRACT—We describe a new lagostomine rodent (Caviomorpha, Chinchillidae), *Lagostomus telenkechanum*, sp. nov., from the Arroyo Chasicó Formation (late Miocene; Buenos Aires Province, Argentina). Three characters permit its assignment to *Lagostomus*: suborbital canal for the infraorbital nerve limited by a bony lamina, well-developed posterior process of the palatine, and posterior maxillary foramen located at the midpoint of the M3. In addition, we identify the new species based on a unique character combination (e.g., small size, palatines reaching anterior to the level of the midpoint of P4, anterior margin of mesopterygoid fossa at the level of the anterior border of M3, upper cheek teeth more compressed anteroposteriorly and more obliquely implanted in the maxilla than in *L. pretrichodactyla, L. compressidens*, and *L. maximus* but less than in *L. incisus*, and thick cement layer in the hypoflexus). Because the early Miocene–midle Miocene genera, *Prolagostomus* is recognized at that time, we consider this period as an important turnover time in the taxonomic composition of the Chinchillidae. This study increases understanding of the taxonomic diversity of the late Cenozoic lagostomines, contributing to the knowledge of the evolutionary and paleobiogeographic history of chinchillids.

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INTRODUCTION

The subfamily Lagostominae—a group of caviomorph rodents included in the family Chinchillidae—is represented by a single living species, *Lagostomus maximus* (Desmarest, 1817), commonly known as the plains viscacha. *Lagostomus maximus* occurs in a wide variety of lowland habitats in Argentina, Bolivia, and Paraguay (Jackson et al., 1996), including the Pampas and adjoining semiarid Monte and Chaquenean regions (e.g., Spotorno and Patton, 2015). Some peculiar aspects of its biology include a marked sexual dimorphism, gregarious and nocturnal habits, and semifossoriality (Weir, 1974).

The Chinchillidae are known since the early Oligocene (e.g., Flynn et al., 2003; Bertrand et al., 2012), with an abundant fossil record in South America during the greater part of the Cenozoic (e.g., Ameghino, 1887, 1889; Scott, 1905; Vucetich, 1989; Rasia, 2016). Traditionally, fossils of Lagostominae from the late Miocene to late Pliocene have been assigned to *Lagostomopsis* (Kraglievich, 1926), identified either as a genus or as a subgenus of *Lagostomus* Brookes, 1828. Viscachas were diverse during the late Miocene–late Pliocene, with several nominal species recognized in Argentina (see Ameghino, 1883, 1886, 1888, 1891, 1908; Rovereto, 1914). The evolutionary history of Lagostominae during this time period is poorly understood, and many of these species, with some exceptions (see Marshall and Patterson, 1981; Rasia and Candela, 2013, unpubl. data; Rasia, 2016), have not been revised since their original descriptions.

The Arroyo Chasicó Formation (Chasicoan Stage/Age, late Miocene; Tonni et al., 1998; Cione and Tonni, 2005) crops out in southwestern Buenos Aires Province, and its sediments contain abundant and diverse fossil mammals (e.g., Pascual, 1961; Pascual and Bondesio, 1968), which have been poorly studied in comparison with those of other units of the late Miocene of Argentina (e.g., Andalhuala, Cerro Azul, and Ituzaingó formations; Marshall and Patterson, 1981; Cione et al., 2000; Goin et al., 2000; Candela, 2005; Verzi et al., 2008; Brandoni, 2013; Bonini, 2014; Esteban et al., 2014).

The Lagostominae of the Arroyo Chasicó Formation are represented by numerous specimens, which constitute the oldest records for the Pampean region (Pascual, 1966; Bondesio et al., 1980; Vucetich, 1986), but they have not been evaluated in detail, being referred to Lagostominae indet. (Bondesio et al., 1980) and *Lagostomopsis* sp. (e.g., Pascual, 1966; Marshall et al., 1983; Vucetich, 1986; Cione and Tonni, 2001).

In this contribution, we describe numerous remains of Lagostominae from the late Miocene Arroyo Chasicó Formation, which represent a key record in the evolutionary history of the group, and evaluate biostratigraphically and paleobiogeographically related aspects, particularly in the context of the late Cenozoic of central Argentina.

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MATERIALS AND METHODS

Abbreviations

Institutional Abbreviations—MACN-A, Colección Nacional 'Florentino 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 de Ciencias Naturales de Paraná 'Antonio Serrano,' Paraná; MLP-Mz, Mastozoología, Museo de La Plata, La Plata; MLP-Pv, Paleontología Vertebrados, Museo de La Plata, La Plata. All institutions are located in Argentina.

Anatomical Abbreviations—almpf, anterior limit of mesopterygoid fossa; alPal, anterior limit of palatines; cp (br), coronoid process (broken); D, dentary; hc, horizontal crest; i1, lower incisor; ias, incisor alveolar sheet; M1, first upper molar; m1, first lower molar; M2, second upper molar; m2, second lower molar; M3, third upper molar; m3, third lower molar; mf, mandibular foramen; mn, masseteric notch (for the tendon of the M. masseter medialis pars anterior); mpf, mesopterygoid fossa; Mx, maxilla; P4, fourth upper premolar; p4, fourth lower premolar; Pal, palatine; pmf, posterior maxillary foramen, ppp, posterior process of palatine; rmf, retromolar fossa; soc, suborbital canal; zr (br), ventral zygomatic root (broken).

Other Abbreviations—ACF, Arroyo Chasicó Formation; **APD**, anteroposterior diameter; **SALMA**, South American Land Mammal Age; **TD**, transverse diameter.

Quantitative Analysis

Two linear measurements were taken from the upper (P4–M3) and lower (p4–m3) cheek teeth: the anteroposterior diameter (APD) and the transverse diameter (TD). The linear measurements were log-transformed and analyzed through principal component analysis (PCA) based on the correlation matrix (Bookstein et al., 1985; Legendre and Legendre, 1998). The free access program PAST 3.07 (Hammer et al., 2001) was used for the PCA. Missing data were replaced by iterative imputation (see Ilin and Raiko, 2010), also using PAST 3.07. Independent analyses were conducted for the upper and lower cheek teeth because maxillae and mandibles are not usually associated.

For PCA of the upper cheek teeth, specimens of the following species were included: Lagostomus telenkechanum, sp. nov.; L. pretrichodactyla (Rovereto, 1914); L. incisus Ameghino, 1888; L. euplasius (Ameghino, 1904); L. compressidens (Ameghino, 1904); L. cavifrons Ameghino, 1889; and L. maximus. For PCA of the lower cheek teeth, specimens of the following species were included: Lagostomus telenkechanum, sp. nov.; L. pretrichodactyla; L. antiquus Ameghino, 1883; L. incisus; L. euplasius; L. compressidens; L. debilis Ameghino, 1889; L. minimus Ameghino, 1889; L. heterogenidens Ameghino, 1889; L. egenus Ameghino, 1891; L. cavifrons; and L. maximus. The only extinct species of Lagostomus not included in the PCA were L. laminosus Ameghino, 1891, known by isolated lower cheek teeth, and 'L. pallidens' Ameghino, 1886, considered a nomen vanum (Rasia, 2016; All measurements used in PCA can be found in online Supplemental Data).

LAGOSTOMINES FROM THE LATE MIOCENE AND THE VALIDITY OF *LAGOSTOMOPSIS*

Lagostomopsis was erected as a subgenus of Lagostomus based on skull and postcranial characters (see Kraglievich, 1938). Within this subgenus, Kraglievich (1926) included all the species of Lagostomus described by Ameghino (1908) from the late Pliocene Chapadmalal 'Formation' and stated that this subgenus should probably include also the older species (i.e., those from the Monte Hermoso Formation, the 'Mesopotamiense' and the 'Araucanense'; late Miocene–early Pliocene; Ameghino, 1883, 1886, 1888, 1891; Rovereto, 1914). Later, Kraglievich (1938) considered *Lagostomopsis* as a genus distinct from *Lagostomus*. Conversely, Francis and Mones (1965, 1966, 1968) stated that the differences between *Lagostomus* and *Lagostomopsis* were not sufficient to distinguish two genera, so they considered them to be subgenera. Thus, following these taxonomic proposals, all the Chasicoan (late Miocene) to Chapadmalalan (late Pliocene) records of Lagostominae have been assigned to *Lagostomopsis* (used either as a genus or subgenus of *Lagostomus*), whereas the post-Chapadmalalan records have been referred to *Lagostomus* (e.g., Pascual, 1966; Marshall et al., 1983; Vucetich and Verzi, 1995; Prado and Cerdeño, 1998; Cione and Toni, 2001; Tauber, 2005; Rasia and Candela, 2013).

The skull characters used to identify *Lagostomopsis* (e.g., small size, short nasals, long frontals, inflated temporal region, short paroccipital, and mastoid processes; see Kraglievich, 1926; Francis and Mones, 1965, 1966, 1968) are typical characters of juvenile and subadult individuals of the living species *Lagostomus maximus* (see Rasia et al., 2011; Rasia, 2016). Furthermore, a postcranial character mentioned by Kraglievich (1926) as a distinctive feature of *Lagostomopsis*—presence of a humeral supracondyloid canal—is only present in *Lagostomus euplasius*, being open or incomplete in *L. incisus* (Rasia and Candela, 2013, unpubl. data; Rasia, 2016). Moreover, this feature cannot be verified in other species traditionally grouped in *Lagostomopsis* due to the lack of preserved postcranial elements. Thus, neither the skull nor the postcranial characters allow for a clear differentiation between *Lagostomus* and *Lagostomopsis*.

In agreement with these morphological observations, a recent phylogenetic analysis (Rasia, 2016) does not support the validity of *Lagostomopsis* and includes all the late Miocene–Holocene species in the genus *Lagostomus*. Therefore, in this contribution, *Lagostomus* is considered the only valid genus, including all the species previously assigned to *Lagostomopsis* (used either as a genus or as subgenus).

GEOLOGICAL SETTING

The Arroyo Chasicó Formation (ACF) was formally described by Pascual (1961), based on the 'Chasicoense' of Kraglievich (1930). The type section of this unit (Pascual, 1961, 1965; Pascual et al., 1965) crops out on the lower Arroyo Chasicó, in southwestern Buenos Aires Province, Argentina (Fig. 1A). The ACF is composed of fine cross-bedded sandstones, which changes transitionally in the upper levels to sandy limestones with predominant sandy mudstones and limestones. There is a presence of intercalated paleosols in the entire succession (Fidalgo and Porro in Bondesio et al., 1980). Traditionally, two members are recognized within the ACF: the lower Vivero Member and the upper Las Barrancas Member, both distinguishable by their paleontological content and macroscopic features, such as mineralogy, texture, and structures (Fidalgo and Porro in Bondesio et al., 1980; Fidalgo et al., 1987). The 'Viveran' fauna was the basis of the 'Chasicotherium' rothi biozone,' whereas the 'Barrancan' fauna was the basis of the 'Chasicotatus ameghinoi biozone,' delimiting the lower and upper Chasicoan Stage/Age, respectively (Tonni et al., 1998; Cione and Tonni, 2001, 2005; Fig. 1B). Nevertheless, a recent study (Zárate et al., 2007) indicates that there is no lithofacial evidence supporting a member differentiation within the ACF; therefore, the stratigraphic provenance of old fossil collections should be revised. Some studies on fossil vertebrates, especially rodents (e.g., Deschamps et al., 2007, 2009; Verzi et al., 2008), continue to accept the validity of the stratigraphic provenance of the fossils and correlate the Vivero Member with Lithofacies Associations 1 and 2, and the

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FIGURE 1. A, map showing Arroyo Chasicó locality; **B**, chronostratigraphic scheme showing stratigraphic distribution of Lagostominae. South American stages/ages following Cione and Tonni (2001, 2005), Reguero and Candela (2011), and Tomassini et al. (2013).

Las Barrancas Member with the Lithofacies Association 3, described by Zárate et al. (2007).

The age of the ACF was estimated to be between 11 and 3 Ma by Pascual et al. (1996). Later, Tonni et al. (1998) proposed a Tortonian age (late Miocene) for the ACF. Presently, the Chasicoan Stage/Age is placed between 10 and ca. 8.7 Ma (Cione et al., 2000; Cione and Tonni, 2005). Datings on the basal levels of the ACF yielded an age of 9.23 \pm 0.09 Ma (Schultz et al., 2004). A recent interpretation of radiometric and paleomagnetic data of the ACF supports an age between at least 9.43 and 8.7 Ma (Zárate et al., 2007).

The material here studied comes from both the lower Vivero Member and the upper Las Barrancas Member (according to collector data), and some of the material does not have precise stratigraphic provenance within the ACF (those materials that were collected before a member differentiation within the ACF was established).

SYSTEMATIC PALEONTOLOGY

RODENTIA Bowdich, 1821 HYSTRICOGNATHI Tullberg, 1899 CAVIOMORPHA Wood and Patterson (in Wood, 1955) CHINCHILLIDAE Bennett, 1833 LAGOSTOMINAE Wiegmann, 1835 Genus LAGOSTOMUS Brookes, 1828

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

LAGOSTOMUS TELENKECHANUM, sp. nov. (Figs. 2, 3A, 4) Lagostomopsis sp. Pascual, 1966:122, lam. 49e, f.

Lagostominae indet. Bondesio, Laza, Scillato Yané, Tonni, and Vucetich, 1980:111.

Etymology—From the tehuelche 'telenke' (small), and 'chanum' (viscacha, actually referring to the mountain viscacha, *Lagidium*), for being one of the smallest species of *Lagostomus*.

Holotype—MLP-Pv 60-VI-18-100, palate with right and left P4–M3.

Hypodigm—The holotype and MLP-Pv 55-IV-28-42, left mandible fragment with broken i1, p4–m2, and broken m3; MLP-Pv 55-IV-28-43, portion of right maxilla with P4–M3; MLP-Pv 55-IV-28-44, fragment of mandibular symphysis with left p4–m1; MLP-Pv 60-VI-18-101, right mandible fragment with p4–m3; MLP-Pv 60-VI-18-107, right mandible fragment with p4 and left mandible fragment with m1–m3; MLP-Pv 76-VI-12-47, left mandible fragment with p4–m3; MLP-Pv 92-XI-19-1, left mandible fragment with broken i1, p4, and broken m1–m2; MLP-Pv 92-XI-19-2, left mandible fragment with p4–m3.

Locality and Horizon—Arroyo Chasicó area, southwest of Buenos Aires Province, Argentina (Fig. 1A). MLP-Pv 55-IV-28-43 and MLP-Pv 55-IV-28-44 come from in front of Radovitzki farm; MLP-Pv 55-IV-28-42 comes from in front of Torres and Stefanazzi farms; MLP-Pv 60-VI-18-101 comes from the left margin of Stefanazzi farm; MLP-Pv 76-VI-12-47 comes from the left bank of Arroyo Chasicó, 400 m upstream from Bajada de los Toros; MLP-Pv 60-VI-18-100, MLP-Pv 60-VI-18-107, MLP-Pv 92-XI-19-1, and MLP-Pv 92-XI-19-2 come from the Arroyo Chasicó area, without more precise geographic provenance.



FIGURE 2. Lagostomus telenkechanum, sp. nov. Photographs and interpretative drawings. MLP-Pv 60-VI-18-100, holotype, palate in ventral (A) and lateral (B) views; MLP-Pv 60-VI-18-101, right mandible in dorsal (C) and lateral (D) views. Abbreviations: cp (br), coronoid process (broken); D, dentary; hc, horizontal crest; ias, incisor alveolar sheet; mf, mandibular foramen; mn, masseteric notch; mpf, mesopterygoid fossa; Mx, maxilla; Pal, palatine; pmf, posterior maxillary foramen, ppp, posterior process of palatine; rmf, retromolar fossa; soc, suborbital canal; zr (br), ventral zygomatic root (broken).

All specimens come from the ACF (Chasicoan Stage/Age, late Miocene; Fig. 1B). Specimens MLP-Pv 55-IV-28-42, MLP-Pv 55-IV-28-43, MLP-Pv 55-IV-28-44, MLP-Pv 60-VI-18-100, MLP-Pv 60-VI-18-101, and MLP-Pv 60-VI-18-107 do not have precise provenance within the ACF because they were collected before the unit was subdivided into two members. Specimens MLP-Pv 92-XI-19-1 and MLP-Pv 92-XI-19-2 come from the Vivero Member of the ACF; and MLP-Pv 76-VI-12-47 comes from the Las Barrancas Member of the ACF.

Diagnosis—Lagostomine differing from all other species of *Lagostomus* by the following character combination: size smaller than all the other species, except for *L. laminosus*; portion of maxilla between cheek tooth alveoli and palatine suture flat; palatines extended anteriorly to the level of the midpoint of P4, forming most of the palate; anterior margin of the mesopterygoid fossa at the level of the anterior border of M3; upper cheek teeth more compressed anteroposteriorly and more obliquely implanted in the maxilla than in *L. pretrichodactyla, L. compressidens*, and *L. maximus*, but less than in *L. incisus*; and cement in

the hypoflexus thicker than in *L. incisus, L. compressidens, L. cavifrons*, and *L. maximus*.

Description and Comparisons

Lagostomus telenkechanum, sp. nov., is one of the smallest species of the genus, with *L. laminosus* (from the 'Conglomerado Osífero' of the Ituzaingó Formation, late Miocene; Cione et al., 2000; Brandoni, 2013; see Fig. 1B) being the smallest species.

Skull—In the two known specimens with skull portions preserved (MLP-Pv 60-VI-18-100 and MLP-Pv 55-IV-28-43), there is a separate canal for the suborbital nerve in the medioventral surface of the infraorbital foramen, delimited by a well-developed bony lamina (Fig. 2B), as in the other species of the genus (Rasia, 2016) and some Echimyidae (e.g., Patton, 1987) and Caviidae (e.g., Quintana, 1996). There is no separate suborbital canal in *Prolagostomus* Ameghino, 1887 or *Pliolagostomus* Ameghino, 1887. Like in *Lagostomus pretrichodactyla* and *L. euplasius*, in *L. telenkechanum*, sp. nov., the maxilla is flat between the cheek



FIGURE 3. Comparison between *Lagostomus telenkechanum*, sp. nov. (A), and *Lagostomus maximus* (B). Maxilla-palatine suture indicated as a continuous white line. A, MLP-Pv 60-VI-18-100, holotype; B, MACN-Ma 49.13. Abbreviations: almpf, anterior limit of mesopterygoid fossa; alPal, anterior limit of palatines; M1–M3, upper molars; Mx, maxilla; P4, fourth upper premolar; pmf, posterior maxillary foramen; ppp, posterior process of palatines.

tooth alveoli and the palatine suture. In this feature, the new species differs from L. maximus, L. cavifrons, and L. compressidens, which have a shallow depression between the cheek tooth alveoli and the maxilla-palatine suture (Fig. 3). Palatines form a more important portion of the palate (Figs. 2A, 3A) than in L. maximus (Fig. 3) and extinct species of Lagostomus, but not than in Prolagostomus and Pliolagostomus, in which the palate is almost completely formed by the palatines. The palatines reach anteriorly to the midpoint of P4 (Figs. 2A, 3A), whereas in the other species of Lagostomus (i.e., L. pretrichodactyla, L. euplasius, L. compressidens, L. cavifrons, and L. maximus), the palatines reach the posterior end of the P4 (Fig. 3B). Despite that the palatines are broken in the medial portion, it is possible to observe that the posterior process of the palatines is present and well developed (Fig. 2A), as in other species of Lagostomus (Fig. 3B). The degree of development of the posterior process of the palatines varies in the living L. maximus, being either long (Fig. 3B) or short. In contrast, the posterior process of the palatines is poorly developed in Prolagostomus, Pliolagostomus, and the living chinchillines Chinchilla Bennett, 1829, and Lagidium Meyen, 1933. The posterior maxillary foramen is located at the midpoint of the M3 (Figs. 2A, 3A), like in all the other species of Lagostomus (Fig. 3B). In the extinct lagostomines Prolagostomus and Pliolagostomus, and in the living chinchillines Chinchilla and Lagidium, the posterior maxillary foramen is located posterior to the M3. The anterior margin of the mesopterygoid fossa is located at the level of the anterior border of the M3 (Figs. 2A, 3A), like in Prolagostomus and Pliolagostomus. In L. pretrichodactyla, L. euplasius, L. incisus, L. compressidens, L. cavifrons, and L. maximus, the mesopterygoid fossa reaches the midpoint of the M2 (Fig. 3B).

Mandibles—The lower diastema is shorter than the lower cheek tooth series, as in other lagostomines. The masseteric notch for the tendon of the M. masseter medialis pars anterior (sensu Woods, 1972; = pars infraorbitalis, sensu Woods and Howland, 1979) is located between the midpoint of m1 and the posterior end of m2 (Fig. 2D). The mandible body is higher and more robust than that of a juvenile specimen of *Lagostomus maximus* of equal size. The mandibular foramen is located on the lingual portion of the retromolar fossa (Fig. 2C), like in the other Lagostominae. The coronoid process is broken at its base in all specimens (Fig. 2C, D). The horizontal crest, delimiting the lateral masseteric fossa for the insertion of the M. masseter medialis pars posterior (sensu Woods, 1972; = pars zygomaticomandibularis posterior, sensu Woods and Howland, 1979), does not differ from that of other species of *Lagostomus*.

Upper Teeth—The upper incisors are not known. The upper cheek teeth have two rectangular lobes, except for the M3, which has three lobes, like all lagostomines. The upper cheek teeth are more compressed anteroposteriorly than in L. pretrichodactyla, L. compressidens, and L. maximus, but less than in L. incisus, and approximately equal to L. cavifrons and L. euplasius (see Table 1). In addition, the upper cheek teeth are more obliquely implanted in the maxillae with respect to the sagittal plane than in L. maximus, L. compressidens, and L. pretrichodactyla, but less than in L. incisus, and approximately equal to those of L. cavifrons and L. euplasius. The cement layer of the hypoflexus is slightly thinner than the enamel layer of the teeth. Cement is thicker than in L. incisus, L. compressidens, L. cavifrons, and L. maximus. The enamel layer is thick on the anterior face of both lobes and in the lingual face of all upper cheek teeth, and it is very thin or absent on the labial face of upper cheek teeth

Specimen	P4		M1		M2		M3	
	APD	TD	APD	TD	APD	TD	APD	TD
MLP-Pv 55-IV-28-43 MLP-Pv 60-VI-18-100	2.73 3.15	4.17 4.46	2.58 3.07	4.6 4.76	2.54 3.04	4.56 4.68	4.37 4.26	4.39 4.93
	p4		m1		m2		m3	
	APD	TD	APD	TD	APD	TD	APD	TD
MLP-Pv 60-VI-18-107 MLP-Pv 60-VI-18-101 MLP-Pv 76-VI-12-47 MLP-Pv 55-IV-28-42 MLP-Pv 55-IV-28-44 MLP-Pv 92-XI-19-1	2.3 2.39 2.76 2.64 2.21 2.66	4.47 5.07 5.32 4.97 4.74 5.73	2.32 2.68 2.99 2.87 2.65	5.09 6.65 6.78 5.89 5.62	2.29 2.72 2.75 2.68	4.98 6.82 6.91 5.66	2.24 2.86 2.75	4.63 6.67 6.2

TABLE 1. Measurements (in mm) of cheek teeth of Lagostomus telenkechanum, sp. nov.

(Fig. 4A). The P4 has almost straight borders. The anterior lobe is rectangular, and the posterior lobe is lingually thinner and subtriangular. In M1 and M2, the anterior lobe is more labially projected than the posterior one, like in most species of *Lagosto*-*mus*, but not as projected as in *Prolagostomus*. A very narrow dentine bridge joins the second and third lobes of the M3 labially (Fig. 4A), as in young individuals of *L. maximus*. In *Prolagosto*-*mus* and *Pliolagostomus*, the second and third lobes of the M3 are labially continuous by a thick bridge of dentine. The third lobe of the M3 is triangular and is not as developed as in *L. maximus*, *L. cavifrons*, *L. compressidens*, and *L. incisus*.

Lower Teeth—The lower incisor is deeply implanted in the mandible, reaching the posterior end of m3, like in the other species of the genus, except for Lagostomus compressidens (Rasia and Candela, unpubl. data). The enamel of the anterior face of the incisor is yellowish, like in L. euplasius (Rasia, 2016; Rasia and Candela, unpubl. data). The lower cheek teeth have two lobes like all lagostomines. Also, they are more compressed anteroposteriorly than in L. maximus, L. cavifrons, L. egenus, L. debilis, L. minimus, L. heterogenidens, L. compressidens, and L. pretrichodactyla, but less compressed than in L. laminosus and L. incisus, and similar to those of L. antiquus and L. euplasius (see Table 1). The lower cheek teeth are more obliquely implanted in the mandible than in L. pretrichodactyla, L. compressidens, L. cavifrons, and L. maximus, but less than in L. incisus, and approximately equal to L. antiquus, L. euplasius, L. debilis, L. heterogenidens, and L. minimus. There is no enamel on the anterior face of the posterior lobe in the lower cheek teeth. The enamel is thick in the posterior face of the first and second lobes, and in the lingual portion of the anterior face of lower cheek teeth. In addition, the enamel is thin in the lingual face of all check teeth (Fig. 4B). There is a layer of cement in the hypoflexid of all lower cheek teeth (Fig. 4B), which is thicker than in L. incisus, L. compressidens, L. debilis, L. minimus, L. heterogenidens, L. cavifrons, and L. maximus, but similar to L. pretrichodactyla, L. antiquus, and L. euplasius.

QUANTITATIVE ANALYSES

Upper Cheek Teeth

For the PCA using upper cheek teeth, the first principal component (PC1) essentially represents size, given that all variables have high positive loadings (see Table 2). The smaller specimens have lower scores on PC1, and the larger ones have higher scores. The smallest species analyzed is *Lagostomus telenkechanum*, sp. nov., with a size equivalent to that of some juvenile specimens of *L. maximus*. The

biggest species are L. maximus, L. cavifrons, L. compressidens, and L. incisus (see Fig. 5A).

The second principal component (PC2) represents variation in APD of P4, APD and TD of M1 and M2, and TD of M3 (see Table 2). The species with the greatest anteroposterior compression of the upper cheek teeth is *Lagostomus incisus*, with negative scores. *Lagostomus telenkechanum*, sp. nov., *L. euplasius*, and *L. cavifrons* have moderately anteroposteriorly compressed upper cheek teeth. The rest of the species (*L. pretrichodactyla*, *L. compressidens*, and *L. maximus*) have less compressed cheek teeth, with positive scores (see Fig. 5A).



FIGURE 4. *Lagostomus telenkechanum*, sp. nov. Schematic drawings of cheek teeth. **A**, MLP-Pv 60-VI-18-100, holotype, upper right cheek teeth; **B**, MLP-Pv 60-VI-18-101, lower right cheek teeth. Black: enamel; gray: cement; and white: dentine.

TABLE 2. Factor loadings for PC1 and PC2 of PCA of upper and lower cheek teeth.

Uppe	r cheek tee	th	Lower cheek teeth			
Dimension	PC1	PC2	Dimension	PC1	PC2	
P4 APD	0.296	0.422	p4 APD	0.371	0.334	
P4 TD	0.382	-0.149	p4 TD	0.376	-0.102	
M1 APD	0.312	0.366	m1 APD	0.308	0.385	
M1 TD	0.371	-0.240	m1 TD	0.350	-0.249	
M2 APD	0.325	0.389	m2 APD	0.311	0.399	
M2 TD	0.368	-0.319	m2 TD	0.363	-0.401	
M3 APD	0.366	0.284	m3 APD	0.313	0.341	
M3 TD	0.395	-0.523	m3 TD	0.420	-0.481	
Eigenvalue	0.319	0.023	Eigenvalue	0.353	0.052	
% variance	90.273	6.625	% variance	84.773	12.471	

Lower Cheek Teeth

In the PCA of the lower cheek teeth, PC1 represents size, given that all variables have high positive loadings (see Table 2). The smaller specimens have lower scores, and the larger species have higher scores. As in the PCA of upper cheek teeth, *Lagostomus telenkechanum*, sp. nov., is the smallest species (see Fig. 5B). The larger species are *L. maximus*, *L. cavifrons*, *L. egenus*, *L. debilis*, *L. compressidens*, and *L. incisus*.

The PC2 represents variation in the APD and TD of the m1-m3 (see Table 2). *Lagostomus incisus* has the most compressed lower cheek teeth, with negative values of PC2. Species with a moderate compression of the lower cheek teeth are *L. telenkechanum*, sp. nov., *L. antiquus*, and *L. euplasius*, with values of PC2 close to 0. Species with less compressed lower

cheek teeth are *L. pretrichodactyla*, *L. debilis*, *L. heterogenidens*, *L. minimus*, *L. cavifrons*, *L. egenus*, and *L. maximus*, with positive scores of PC2 (see Fig. 5B).

According to these results, *Lagostomus telenkechanum*, sp. nov., can be distinguished from other species of *Lagostomus* by the general size and anteroposterior compression of the cheek teeth (more compressed than *L. pretrichodactyla, L. compressidens*, and *L. maximus*, but less than in *L. incisus*), supporting the diagnostic value of these characters (see Systematic Paleontology).

DISCUSSION AND CONCLUSIONS

Generic Identity and Specific Status of Chasicoan Vizcachas

The study of the Lagostominae from the ACF indicates that these are clearly distinguishable from the early and middle Miocene genera *Prolagostomus* and *Pliolagostomus* and that they belong to *Lagostomus* due to the presence of (1) suborbital canal limited by a bony lamina; (2) well-developed posterior process of the palatine; and (3) posterior maxillary foramen located at the midpoint of the M3 (see Rasia, 2016).

The comparative study shows that *Lagostomus telenkechanum*, sp. nov., constitutes a new species due to the following character combination: (1) small size; (2) portion of maxilla between cheek tooth alveoli and palatine suture flat; (3) palatines reaching anteriorly to the mid-point of the P4; (4) palatines forming most of the palate; (5) anterior margin of the mesopterygoid fossa at the level of the anterior border of M3; (6) upper cheek teeth more anteroposteriorly compressed; (7) upper cheek teeth more obliquely implanted than in *L. pretrichodactyla, L. compressidens*, and *L. maximus*, but less than in *L. incisus*; and (8) cement in the hypoflexus thicker than in *L. incisus, L. compressidens, L. cavifrons*, and *L. maximus*.



In addition, the referred material differs from other species of *Lagostomus* by the following character combination: (1) lower incisor with yellowish enamel; (2) lower cheek teeth more compressed anteroposteriorly than in *L. maximus*, *L. cavifrons*, *L. egenus*, *L. debilis*, *L. minimus*, *L. heterogenidens*, *L. compressidens*, and *L. pretrichodactyla*, and less than in *L. laminosus* and *L. incisus*; and (3) lower cheek teeth more obliquely implanted than in *L. pretrichodactyla*, *L. compressidens*, *L. cavifrons*, and *L. maximus*, but less than in *L. incisus*.

Thus, the qualitative and quantitative analyses support the validity of *Lagostomus telenkechanum*, sp. nov., as a new species of *Lagostomus* from the ACF. The identification of this species increases understanding of the taxonomic richness of *Lagostomus* since their earliest evolutionary history.

Biostratigraphic and Paleobiogeographic Remarks

Our study indicates that there are no confirmed records of *Prolagostomus* or *Pliolagostomus* in the ACF, in contrast to statements by several authors (Bondesio et al., 1980; Chick et al., 2008; Croft et al., 2011). The youngest records of *Prolagostomus* come from middle Miocene levels of Argentina (Vucetich, 1984; Vucetich et al., 1993), Bolivia (e.g., Marshall and Sempere, 1991; Croft et al., 2011), and Chile (Flynn et al., 2008). The youngest record of *Pliolagostomus* also comes from middle Miocene levels in Argentina (Vucetich, 1984).

In this regard, the Chasicoan Stage/Age (late Miocene) marks an important turnover of the taxonomic composition of the subfamily Lagostominae. *Prolagostomus* and *Pliolagostomus*—the typical genera of the early and middle Miocene—are no longer recorded during this stage/age, instead *Lagostomus telenkechanum*, sp. nov., is recognized as the oldest representative of the living genus *Lagostomus* and the oldest recorded lagostomine of the Pampean region. Currently, there are no definite records of lagostomines from the Laventan (middle Miocene) and Mayoan (early late Miocene) South American land mammal ages (SAL-MAs), but new findings would shed light on the precise onset of this taxonomic turnover.

The taxonomic study of fossil Lagostominae indicates that *Lagostomus telenkechanum*, sp. nov., is not identified in the younger units assigned to the Huayquerian Stage/Age (e.g., Andalhuala, Cerro Azul, and Ituzaingó formations; see Rasia, 2016). Until now, Huayquerian species are represented by *L. pretrichodactyla*, *L. antiquus*, and *L. laminosus* (Ameghino, 1883, 1891; Rovereto, 1914; Rasia, 2016; see Fig. 1B). Therefore, *Lagostomus telenkechanum*, sp. nov., seems to be restricted to the Chasicoan Stage/Age, and the end of the Miocene period could indicate a new and younger taxonomic turnover of Lagostominae, associated with an increasing specific richness of the genus.

The Chasicoan Stage/Age marks the beginning of the traditional 'Edad de las Planicies Australes,' the Age of the Southern Plains (Pascual and Bondesio, 1982), which was coeval with a global climatic deterioration and more marked seasonality than in the middle Miocene (e.g., Janis, 1993; Pascual et al., 1996), that occurred after the withdrawal of the Miocene 'mar Paranaense' (Paranean Sea; Pascual et al., 1996; Aceñolaza, 2000; Candela et al., 2012). Whether some of these environmental and biogeographic events were related to taxonomic changes in the lagostomines has not yet been examined, and could be better understood in the context of other groups of rodents. Caviomorphs recovered from the ACF, with some exceptions (Pascual, 1961, 1967; Pascual and Bondesio, 1968; Bondesio et al., 1980; Deschamps et al., 2007; Verzi et al., 2008; Pérez et al., 2014) have not been intensively studied. Therefore, analysis of the possible faunistic turnover between the Chasicoan and the Huayquerian occurring in other lineages of caviomorphs is pending.

The correct identification of the late Cenozoic species of lagostomines and their accurate stratigraphic provenance indicates that they are restricted to different times of the late Miocene– Pleistocene (see Fig. 2B). This suggests that the fossil species of *Lagostomus* could be good biostratigraphic tools for central Argentina during this period, where these rodents are particularly abundant.

Other records of Lagostominae, of uncertain specific status, have been reported from assemblages assigned to the Chasicoan Stage/Age, such as Assemblage A of the Loma de las Tapias Formation (San Juan Province; see Contreras and Baraldo, 2011) and the El Jarillal Member of the Chiquimil Formation (Catamarca Province; see Herbst et al., 2000; Esteban et al., 2014). Further studies of these materials could clarify their taxonomic status, confirming whether the distribution of *Lagostomus telenkechanum*, sp. nov., was restricted to the Pampean region or extended to the west and northwest of Argentina, or even to other areas of South America with late Miocene lagostomine records (Marshall and Sempere, 1991).

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