Systematic and Biostratigraphic Significance of a Chinchillid Rodent from the Pliocene of Eastern Argentina

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Systematic and biostratigraphic significance of a chinchillid rodent from the Pliocene of eastern Argentina

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Two species of chinchillid rodents, *Lagostomus* (*Lagostomopsis*) *incisus* and "*Lagostomus* (*Lagostomopsis*) *spicatus*", have been recorded from the Monte Hermoso Formation (Montehermosan–Lower Chapadmalalan, Early Pliocene) of southern Buenos Aires Province, eastern Argentina. *L.* (*L.*) *incisus* is based on skull remains, while "*L.* (*L.*) *spicatus*" is based on mandible remains and fragmentary skulls. Detailed study of specimens recovered from the upper section of the Monte Hermoso Formation, from the Irene "Formation", and the Chapadmalal Formation (late Early–early Late Pliocene, Buenos Aires Province), some of them represented by associated skull and mandible remains, indicates that *L.* (*L.*) *incisus* and "*L.* (*L.*) *spicatus*" are synonymous, with the valid name being *L.* (*L.*) *incisus*. The differences between both nominal species are here attributed to different ontogenetic states and sexual dimorphism. The stratigraphic provenance of the fossil material of *L.* (*L.*) *incisus* indicates a temporal distribution of this species restricted to the Montehermosan?–Chapadmalalan (Early–early Late Pliocene), instead of the Montehermosan (Early Pliocene).

Key words: Mammalia, Rodentia, Caviomorpha, Chinchillidae, systematics, biostratigraphy, Pliocene, Argentina.

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Introduction

Plains vizcachas (Chinchillidae, Lagostominae) are represented by the single living species *Lagostomus maximus* (Desmarest, 1817), which occurs in the lowlands of southern South America (Argentina, Bolivia, and Paraguay), and ranges in habitat from subtropical humid grasslands to dry thorn scrubs (Nowak 1991; Redford and Eisenberg 1992; Jackson et al. 1996). Fossil plains vizcachas are one of the most typical caviomorph rodents present in Late Miocene–Holocene mammal assemblages of the Pampean region of Argentina, and are abundantly present at several fossil localities. The genus *Lagostomus* Brookes, 1828, and in particular the subgenus *Lagostomus* (*Lagostomopsis*) Kraglievich, 1926 (see Kraglievich 1934; Francis and Mones 1965b, 1966; Vucetich and Verzi 1995), was formerly more diverse than it is today, with six nominal species originally recognized in the Huayquerian (Ameghino 1883, 1886, 1891; Rovereto 1914; Late Miocene), two in the Montehermosan (Ameghino 1888; Early Pliocene sensu Cione and Tonni 1995a, b, 1996, but see Cione and Tonni 2011, 2005), and seven in the Chapadmalalan (Ameghino 1908; late Early-early Late Pliocene sensu Cione and Tonni 1995b, 1996, 2001, 2005). However, few of these species have been revised since their original descriptions (but see Marshall and Patterson 1981), and their taxonomic validity and stratigraphic distributions are still uncertain.

Ameghino (1888) described two species of lagostomines from the Monte Hermoso Formation (Montehermosan–Lower Chapadmalalan, Early Pliocene; Cione and Tonni 1995b) of southern Buenos Aires Province, eastern Argentina (Fig. 1). *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888), a species slightly smaller than *L. maximus*, is based on several incomplete skulls and has not been reported from any other unit since its original description. By contrast, "*L.* (*L.*) *spicatus*" (Ameghino, 1888), about half the size of *L.* (*L.*) *incisus*, is based on several mandibles and very fragmentary skull remains, and was also recognized by Francis and Mones (1965b) in the "Kiyú lithofacies" (Huayquerian, Late Miocene; see Sprechmann et al. 2000) of Uruguay. In addition, Ameghino (1908: 424) also mentioned a lagostomine similar to "*L.* (*L.*) *spicatus*" from the Chapadmalal Formation (Upper Chapadmalalan, early Late Pliocene; Cione and Tonni 1995b, 1996) of Argentina.

Here, we describe fossil material recovered from several

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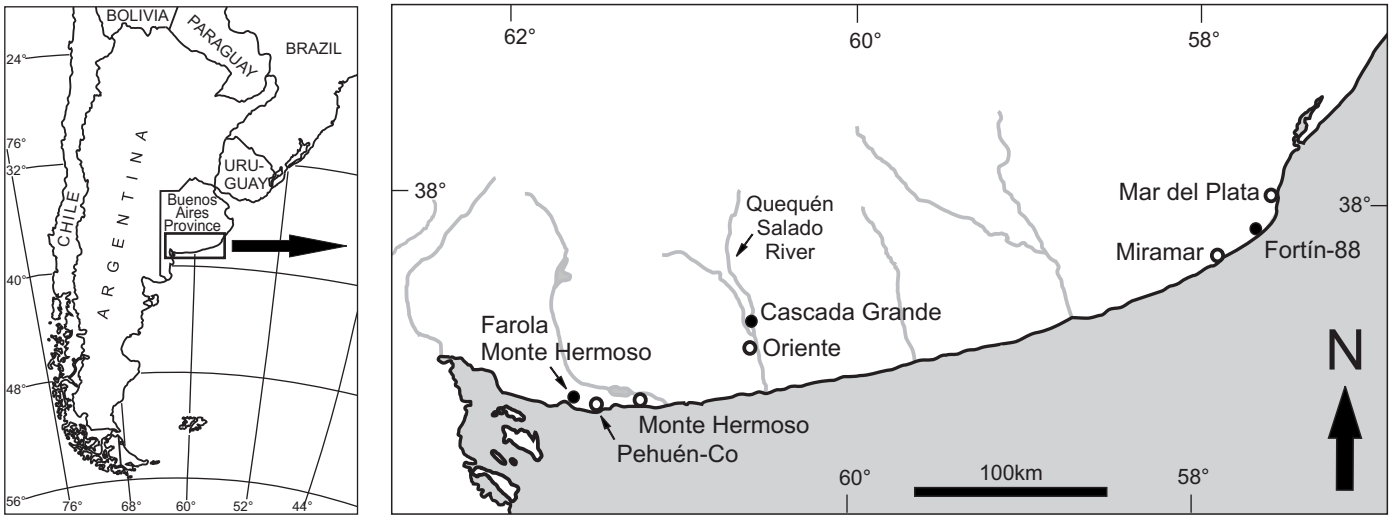

Fig. 1. Map of Buenos Aires Province, Argentina (**A**), showing the localities mentioned in the text (**B**). Black circles indicate fossil localities, while open circles indicate towns and cities.

Pliocene units, including the upper section of the Monte Hermoso Formation, as well as the Irene and Chapadmalal formations, cropping out in southern Buenos Aires Province (eastern Argentina; Fig. 1), and refer it to *Lagostomus* (*Lagostomopsis*) *incisus*. Furthermore, we propose *L.* (*L.*) *incisus* and "*L.* (*L.*) *spicatus*" to be synonymous, and provide an emended diagnosis for *L.* (*L.*) *incisus*. Finally, we establish a precise estimate of the stratigraphic range of this species, and evaluate its biostratigraphic significance based on systematic information and the known stratigraphic provenance of each studied specimen.

Institutional abbreviations.—MACN-A, "Florentino Ameghino" National Collection, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MACN-Mz, Mastozoology, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MACN-Pv, Vertebrate Paleontology, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MASP, Museo de Ciencias Naturales y Antropológicas "Profesor Antonio Serrano" de Paraná, Paraná, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

Other abbreviations.—I/i, upper/lower incisor; M/m, upper/lower molar; P/p, upper/lower premolar; f, female; m, male.

Material and methods

The material assigned here to *Lagostomus* (*Lagostomopsis*) *incisus* was compared with the available holotypes and referred specimens of most of the nominal fossil species of *Lagostomus* registered in Argentina, as well as with the extant *L. maximus*. We were unable to locate the holotypes of *L.* (*L.*) *chapalmalensis* (Ameghino, 1908), *L. egenus* (Ameghino, 1891) and *L. cavifrons* (Ameghino, 1889), and thus had to rely on published illustrations of these specimens instead. A complete list of the material used for comparisons, together with its geographic and stratigraphic provenance, is provided in Appendix 1. Because we question the taxonomic validity of "*Lagostomus* (*Lagostomopsis*) *spicatus*" in this work, it is enclosed in quotation marks. All measurements were taken with a 0.01 mm precision digital caliper.

The measurements of *L. maximus* displayed in Fig. 7 are provided in the Supplementary Online Material (available at http://app.pan.pl/SOM/app58-Rasia_Candela_SOM.pdf)

Geological setting

The present material was recovered from the upper section of the Monte Hermoso Formation (Lower Chapadmalalan, late Early Pliocene), the Irene "Formation" (Chapadmalalan, late Early–early Late Pliocene), and from the Chapadmalal Formation (Upper Chapadmalalan, early Late Pliocene), cropping out in southern Buenos Aires Province (Fig. 2). The respective age of these units and the stratigraphic provenance of the studied specimens are discussed in detail below.

Monte Hermoso Formation.—When Ameghino (1888) described the lagostomines from the Monte Hermoso Formation (the type section of which is located at Farola Monte Hermoso; Fig. 1), he assumed a Montehermosan Age for the entire unit. While some later authors also considered the Monte Hermoso Formation to represent a single unit (Frenguelli 1928; Zavala 1993; Zavala and Navarro 1993), others divided it into at least two levels of different ages (e.g., Vignati 1925; Leanza 1948; Fidalgo et al. 1975; Fidalgo and Tonni 1982).

Cione and Tonni (1995b) recognized a lower section of Montehermosan age and an upper section of Lower Chapadmalalan age, and and proposed the "Zone of *Neocavia depressidens*" as a new biozone for the Lower Chapadmalalan (Fig. 2A).Whereas their lower section is equivalent to the

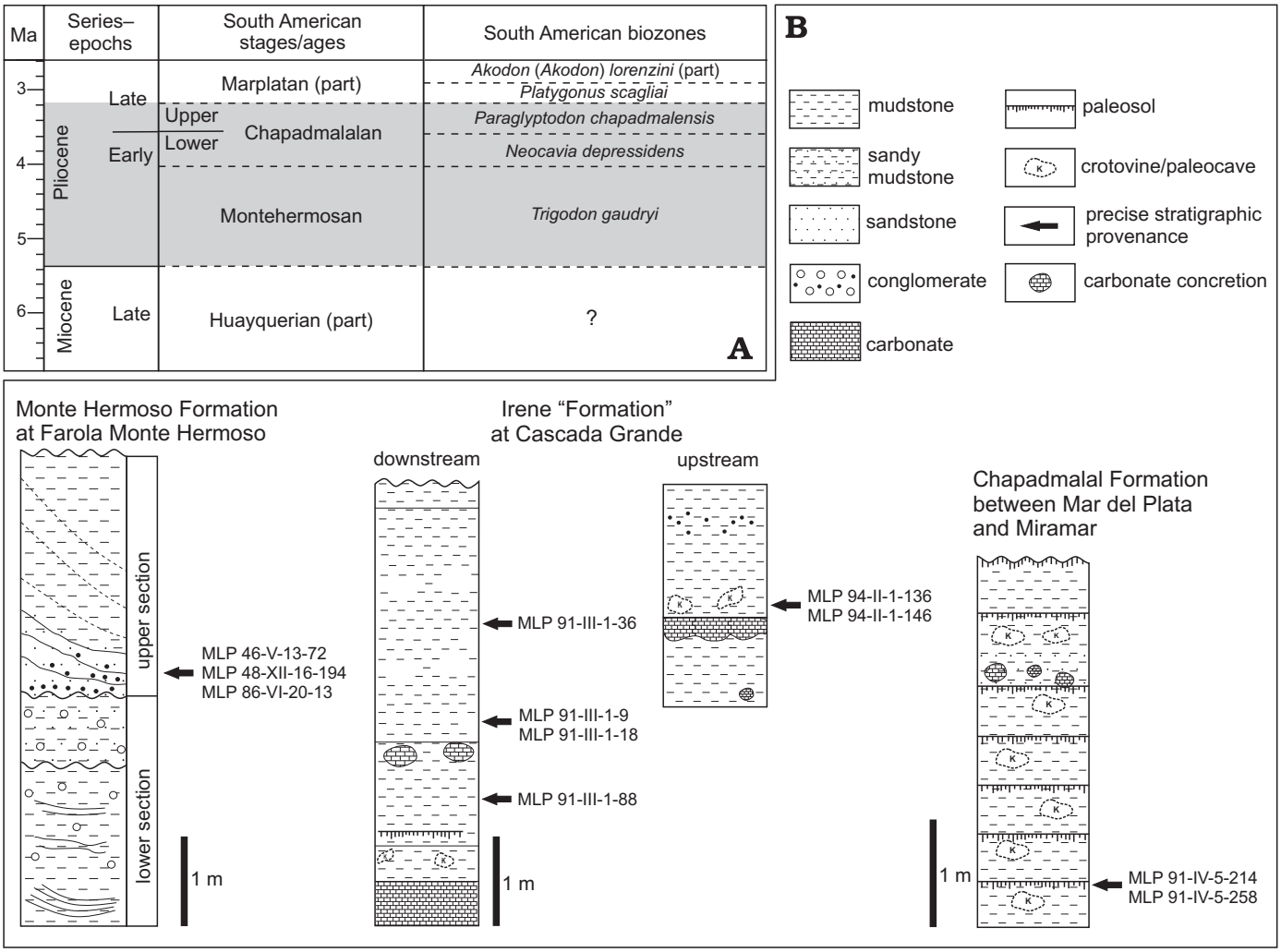

Fig. 2. Profiles of studied formations showing the stratigraphic provenance of *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888). **A**. Chronostratigraphic chart of the Late Miocene–Late Pliocene of South America (modified from Cione and Tonni 1995a). Shaded area indicates the stratigraphic range of *L.* (*L.*) *incisus*. **B**. Schematic profiles of the Monte Hermoso Formation (modified from Cione and Tonni 1995b), Irene "Formation" (from Pardiñas field notes in MLP) and Chapadmalal Formation (modified from Kraglievich 1952; Zárate 1989).

previously proposed "Hermosense típico" (Vignati 1925; Bonaparte 1960), the "formación I" of Leanza (1948) and the "Unidad Litoestratigráfica I" of Fidalgo and Tonni (1982), their upper section corresponds to the "*Chapadmalense*" of Vignati (1925), the "formaciones II and III" of Leanza (1948), the "limolitas estratificadas + limolitas claras" of Bonaparte (1960) and the "Unidad Litoestratigráfica II" of Fidalgo and Tonni (1982). Three of the present specimens were found in the upper section (Fig. 2B), whereas all of the other specimens from this formation (MACN-A 1112, 1654, MACN-Pv 7388; all collected by Ameghino) lack precise stratigraphic information, and could thus have been recovered from either the upper or the lower section.

Irene "Formation".—The age of this unit has been widely discussed. The "Fáunula Irenense", reported from exposures along the Quequén Salado River (Fig. 1), was recognized by Kraglievich (1934) as intermediate in age between the Montehermosan and the Chapadmalalan. Mignone (1949) differentiated two litostratigraphic units for the "Irenean": a lower unit, the "Irenense típico", of the same age as proposed by Kraglievich (1934); and an upper one correlating with the Chapadmalalan. Later, Reig (1955) for the first time referred to the "Irenean" as Irene "Formation" and assigned it to the Montehermosan.

Pascual et al. (1965a) correlated the "Irenean" with the Monte Hermoso Formation on the basis of its faunal content. By contrast, Pascual (1965) and Pascual et al. (1965b) considered the possibility of a partial (or even total) correlation of the Irene "Formation" with the Chapadmalal Formation. Fidalgo et al. (1975) described the type section of the Irene "Formation" at Cascada Grande (Buenos Aires Province; Fig. 1), and assigned it to the Montehermosan. It should be noted that many of the aforementioned works (Pascual 1965; Pascual et al. 1965a, b; Fidalgo et al. 1975) considered the Chapadmalalan to form part of the Montehermosan.

Later, based on the study of marsupials from the Irene "Formation", Goin et al. (1994) and Goin and Pardiñas (1996)

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supported a Chapadmalalan Age for this unit. More recently, part of the Irene "Formation" (at least those levels that have yielded remains of the octodontid rodent *Xenodontomys ellipticus*) was assigned to the Huayquerian (Late Miocene), implying that probably more than one stage/age may be represented by this formation (Verzi et al. 2003, 2008; Verzi and Montalvo 2008; Folguera and Zárate 2009). Prevosti and Pardiñas (2009) further argued that, at some localities, the Irene "Formation" is represented by post-Huayquerian sediments.

The lagostomines previously recovered from the Irene "Formation" were only mentioned as part of faunal lists by Frenguelli (1928), who recognized the presence of *Lagostomus* (*Lagostomopsis*) *euplasius*, and Kraglievich (1934), who recorded the presence of *Lagostomus* (*Lagostomopsis*) sp. Most of the studied specimens from the Irene "Formation", assigned in this work to *L.* (*L.*) *incisus*, come from middle levels of the exposures at Cascada Grande (see Fig. 2B). However, one specimen (MLP 63-VI-10-59) has no precise geographic or stratigraphic provenance.

Chapadmalal Formation.—Ameghino (1908) mentioned a lagostomine similar to "*L.* (*L.*) *spicatus*" from the "Chapadmalal Formation" (between Mar del Plata and Miramar, Buenos Aires Province; Fig. 1), together with another seven new species. Kraglievich (1952) partitioned what Ameghino (1908) considered the "Chapadmalal Formation" (and base of the "Chapalmalan Stage") into several supposed formations (Chapadmalal, Barranca de los Lobos, and Vorohué). Of these, the Chapadmalal Formation, the type series of the Upper Chapadmalalan (early Late Pliocene) is the oldest, and recognized based on the "Zone of *Paraglyptodon chapadmalensis*" (Cione and Tonni 1995b; see Fig. 2A). Two of the specimens studied here come from the lower levels (paleosol 1 of Zárate 1989 = levels I and II of Kraglievich 1952; Fig. 2B) of the Chapadmalal Formation (i.e., Upper Chapadmalalan). By contrast, specimen MLP 88-VI-1-2 has no precise stratigraphic provenance within the Chapadmalal Formation.

Other records.—Francis and Mones (1965b) mentioned the presence of "*Lagostomus (Lagostomopsis) spicatus*" in the Kiyú Formation, in the Department of San José, Uruguay. The Kiyú Formation (now "Kiyú lithofacies") was originally considered Late Pliocene in age (Francis and Mones 1965a–d), but is now recognized as part of the Camacho Formation (Huayquerian, Late Miocene; see Sprechmann et al. 2000). However, we suggest that the material from the "Kiyu lithofacies" does not belong to *L.* (*L.*) *incisus* (="*L.* [*L.*] *spicatus*") (see Discussion).

Systematic paleontology

Order Rodentia Bowdich, 1821

Suborder Hystricognathi Tullberg, 1899

Infraorder Caviomorpha Wood and Patterson (in Wood, 1955)

Superfamily Chinchilloidea Bennet, 1833 (Kraglievich, 1940)

Family Chinchillidae Bennet, 1833

Subfamily Lagostominae Pocock, 1922

Genus *Lagostomus* Brookes, 1828

Type species: *Lagostomus trichodactylus* Brookes, 1828 (= *Dipus maximus* Desmarest, 1817); Recent, South America.

Subgenus *Lagostomus* (*Lagostomopsis*) Kraglievich, 1926

Type species: Not designated.

Lagostomus (*Lagostomopsis*) *incisus* (Ameghino, 1888)

Figs. 3–5, 6.

1888 *Lagostomus incisus* sp. nov.; Ameghino 1888: 9.
1888 *Lagostomus spicatus* sp. nov.; Ameghino 1888: 10 (nov. sin.).
1888 *Lagostomus angustidens* sp. nov.; Moreno 1888: 15.
1888 *Lagostomus intermedius* sp. nov.; Moreno 1888: 15–16 (nov. sin.)
1889 *Lagostomus incisus* Ameghino, 1888; Ameghino 1889: 182, pl. 9: 22.
1889 *Lagostomus angustidens* Moreno, 1888; Ameghino 1889: 182.
1989 *Lagostomus spicatus* Ameghino, 1888; Ameghino 1889: 184, pl. 9: 9, 15 (nov. sin.).
1889 *Lagostomus intermedius* Moreno, 1888; Ameghino 1889: 184 (nov. sin.).

Holotype: The holotypes of *Lagostomus* (*Lagostomopsis*) *incisus* and "*L.* (*L.*) *spicatus*" were originally deposited at the MLP (Ameghino 1889), but both are currently lost. We therefore propose MACN-A 1112 (Fig. 3A) as the neotype, because it was referred by Ameghino (1889: pl. 9: 22) to *L.* (*L.*) *incisus*, and was recovered from the same locality as the holotype.

Type locality: Farola Monte Hermoso, Buenos Aires Province, Argentina.

Type horizon: Monte Hermoso Formation, Montehermosan–Lower Chapadmalalan, Early Pliocene.

Referred material.—MACN-A 1112, anterior portion of skull with both incisors, complete tooth rows, and right fragment of basicranium (referred to *L.* [*L.*] *incisus* in Ameghino 1889: pl. 9: 22; proposed neotype); MACN-A 1654, left mandible with p4–m3, and rostral fragment with right upper incisor (referred to "*L.* [*L.*] *spicatus*" in Ameghino 1889: pl. 9: 9, 15); MACN-Pv 7388, ventral portion of skull, with both incisors and complete tooth rows; MLP 46-V-13-72, right mandible fragment with incisor and p4–m2, isolated right M2, and right tibia; MLP 48-XII-16-194, palatal fragment with right P4–M1, M3, and left M2–3; MLP 86-VI-20-13, anterior portion of rostrum with both incisors; MLP 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, fragments of pelvic girdle, and left femur; MLP 91-IV-5-258, almost complete skull with complete tooth rows, right radius, shaft fragment of right ulna, right femur, portion of left femur, right tibia, left calcaneus, right astragalus, right second, third and fourth metatarsals, and right second, third and fourth proximal phalanges; MLP 63-VI-10-59, incomplete skull with complete

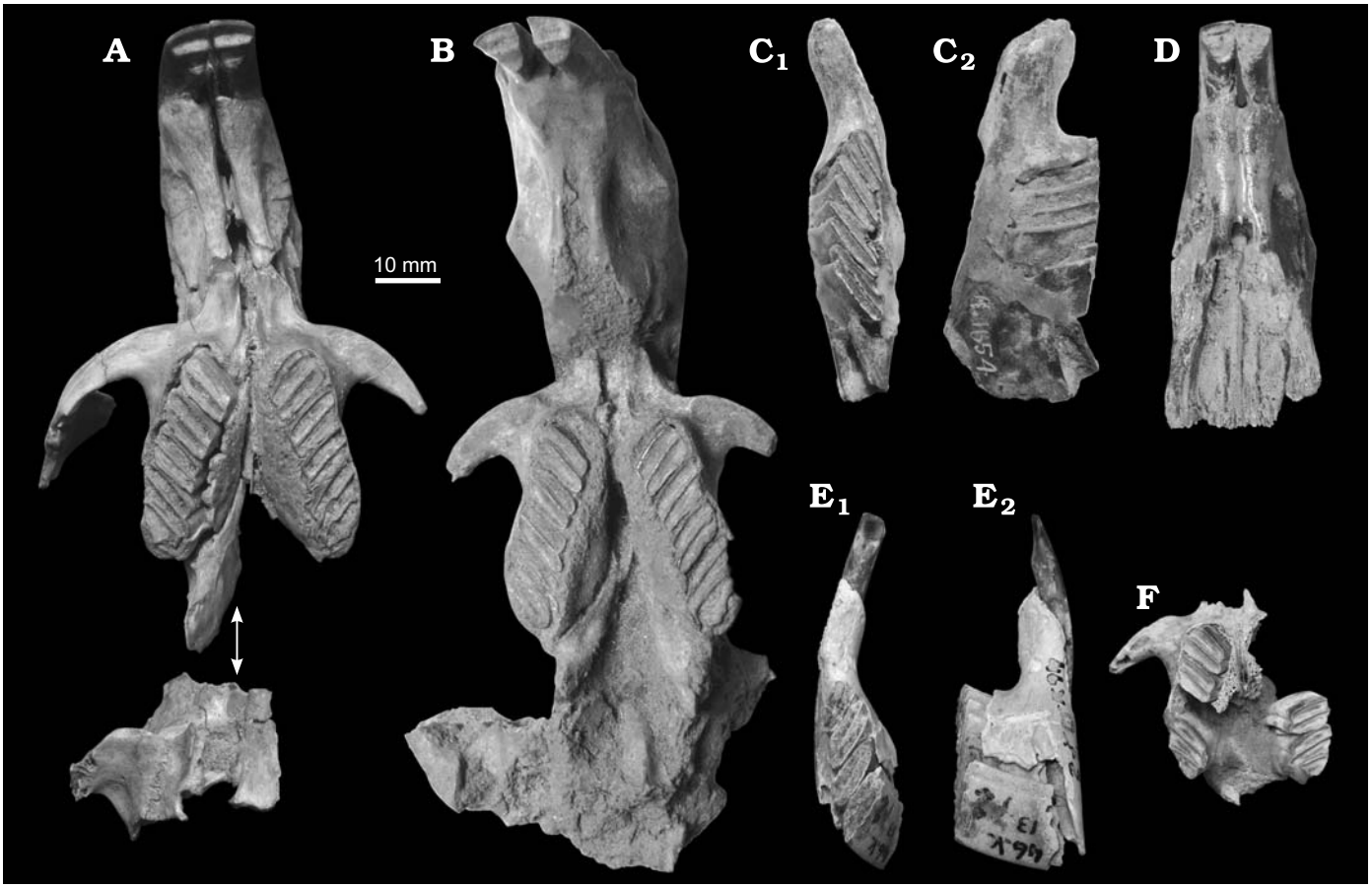

Fig. 3. The chinchillid rodent *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888) from the Monte Hermoso Formation, Buenos Aires Province, Argentina (Early Pliocene). **A**. MACN-A 1112, partial skull with both incisors, complete tooth rows and right portion of basicranium in ventral view. **B**. MACN-Pz 7388, skull with both incisors and complete tooth rows in ventral view. **C**. MACN-A 1654, left mandible in occlusal (C_1) and labial (C_2) views. **D**. MLP 86-VI-20-13, rostrum with both incisors in ventral view. **E**. MLP 46-V-13-72, right mandible with p4–m3 in occlusal (E_1) and labial (E_2) views. **F**. MLP 48-XII-16-194, palate with right P4–M1, M3, and left M2–3 in ventral view.

tooth rows; MLP 91-III-1-18, almost complete skull complete tooth rows; MLP 91-III-1-36, palate with complete tooth rows, portion of rostrum, atlas, axis, cervical vertebra, and right and left portions of pelvic girdle; MLP 94-II-1-136, palatal fragment with complete tooth rows; MLP 91-III-1-9, right mandible with incisor and p4–m3; MLP 94-II-1-146, mandibles with incisors and complete tooth rows, right mandible with p4–m3, right maxilla with P4–M3, two isolated upper incisors, right and left humerus, right portion of pelvic girdle, right and left femur, right and left tibia, distal portion of right fibula, right and left astragalus, left calcaneus, right navicular, right ectocuneiform, right second and third metatarsals, and right second and third proximal phalanges; material represents at least two individuals; MLP 91-III-1-88, mandibles with complete cheek tooth rows, fragment of rostrum with incisors, left humerus, and several phalanges; MLP 91-IV-5-214, left mandible fragment with incisor and p4–m2, and isolated left upper incisor.

Emended diagnosis.—Lagostomine 20% smaller than *Lagostomus maximus*. Maxillae much more expanded transversely, palatines much more reduced in ventral view, and upper cheek teeth more obliquely implanted in the maxillae than in *L.* (*L.*) *pretrichodactylus*, *L.* (*L.*) *insolitus*, *L.* (*L.*) *angulatus*, *L.* (*L.*) *loberiaensis*, *L.* (*L.*) *euplasius*, *L.* (*L.*) *compressidens*, *L.* (*L.*) *indefinitus*, *L. cavifrons*, and *L. maximus*. Posterior palatine apophyses of the premaxillae very reduced and not at the same dorsoventral level as the diastema, clearly differing from *L.* (*L.*) *pretrichodactylus*, *L.* (*L.*) *insolitus*, *L.* (*L.*) *loberiaensis*, *L.* (*L.*) *euplasius*, *L.* (*L.*) *compressidens*, *L. cavifrons*, and *L. maximus*. Lower cheek teeth much more compressed anteroposteriorly and more obliquely implanted in the mandible than in *L.* (*L.*) *pallidens*, *L.* (*L.*) *antiquus*, *L.* (*L.*) *insolitus*, *L.* (*L.*) *euplasius*, *L.* (*L.*) *definitus*, *L.* (*L.*) *compressidens*, *L. debilis*, *L. heterogenidens*, *L. minimus*, and *L. maximus*. Humerus with canalis supracondyloideus (entepicondyloideus) not entirely closed.

Comparative description

Skull: The skulls of adult specimens (MACN-A 1112, MACN-Pv 7388, MLP 91-III-1-18; Figs. 3A, B, 4A) of *Lagostomus* (*Lagostomopsis*) *incisus* are about 20% smaller than those of *L. maximus*, ranging in length from 73.85 mm (MLP 91-IV-5-258) to 97.92 mm (MLP 91-III-1-18), with an average length of 85.88 mm. The nasals are shorter than the premaxillae (Fig. $4A_2$), as in *L.* (*L.*) *pretrichodactylus*, *L.* (*L.*)

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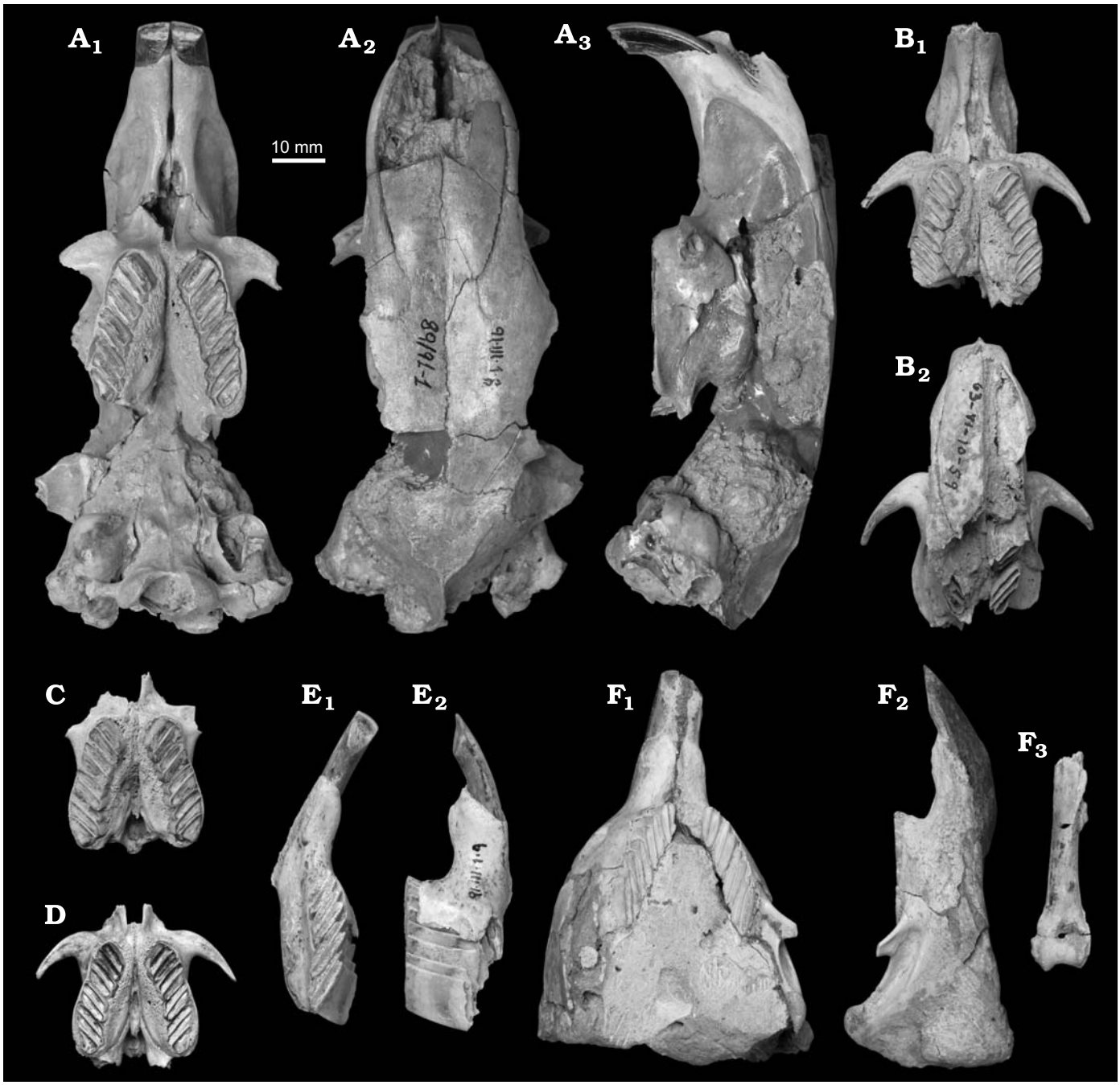

Fig. 4. The chinchillid rodent *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888) from the Irene "Formation", Buenos Aires Province, Argentina (late Early–early Late Pliocene). **A**. MLP 91-III-1-18, skull with complete tooth rows in ventral (A_1), dorsal (A_2), and lateral (A_3) views. **B**. MLP 63-VI-10-59, partial skull with complete tooth rows in ventral (B_1) and dorsal (B_2) views. **C**. MLP 91-III-1-36, palate with complete tooth rows. **D**. MLP 94-II-1-136, palate with complete tooth rows. **E**. MLP 91-III-1-9, right mandible with p4–m3 in occlusal (E_1) and labial (E_2) views. **F**. MLP 91-III-1-88, mandibles with complete tooth rows in occlusal (F_1) and labial (F_2) views, and left humerus (F_3) in anterior view.

insolitus, *L.* (*L.*) *loberiaensis*, and *L.* (*L.*) *euplasius*. In most of the studied specimens of *L. maximus* the nasals are longer than the premaxillae, as in *L.* (*L.*) *compressidens* and *L. cavifrons*. The posterior processes of the premaxillae extend beyond the anterior edge of the dorsal zygomatic root, as is also the case in *L.* (*L.*) *pretrichodactylus*, *L.* (*L.*) *insolitus*, *L.* (*L.*) *loberiaensis*, and *L.* (*L.*) *euplasius*, but not in *L.* (*L.*) *compressidens*, *L. cavifrons*, and *L. maximus*. The frontals are depressed along the midline (Figs. $4A_2$, $5A_2$), being as long as the nasals in young individuals and slightly shorter than the nasals in adult ones. In *L.* (*L.*) *pretrichodactylus*, *L.* (*L.*) *insolitus*, *L.* (*L.*) *loberiaensis*, and *L.* (*L.*) *euplasius* the frontals are slightly longer than the nasals, whereas in *L.* (*L.*) *compressidens*, *L. cavifrons*, and *L. maximus* they are shorter. The parietals are more vaulted than in *L. maximus*. As in *L. maximus*, the sagittal and temporal crests are weakly

developed in young individuals (Fig. $5A_2$), but well developed in adults ones (Fig. $4A_2$).

The posterior palatine apophyses of the premaxillae (located between the interpremaxillary and incisive foramina) are small and not at the same dorsoventral level as the diastema (Figs. 3A, $4A_1$, B_1, $5A_1$), clearly differing from *L.* (*L.*) *pretrichodactylus*, *L.* (*L.*) *insolitus*, *L.* (*L.*) *loberiaensis*, *L.* (*L.*) *euplasius*, *L.* (*L.*) *compressidens*, *L. cavifrons*, and *L. maximus,* in which the posterior palatine apophyses are strong and frequently project to the level of the diastema. The interpremaxillary foramen is always present, unlike in *L. maximus*, in which it can be closed in adults. The incisive foramen is wide and long relative to the length of the diastema. The maxillae are more expanded in palatal view and the palatines are much more reduced (Figs. 3A, B, $4A_1$, B_1, C, D, $5A_1$, B_1) than in the living species. In young individuals, the palatines are fused along the midline and form a posterior process (Figs. $4B_1$, C, D, $5A_1$), as in *L. maximus*. In adults, the maxillae cover the palatines ventrally, thus forming the "cleft palate" described by Ameghino (1888) (see Discussion). The posterior maxillary foramina are small. The tympanic bullae are rounded and inflated in all individuals, as opposed to the more elongate shape observed in adult *L. maximus*.

Other skull features, such as foramina of the orbital region and the morphology of the basisphenoid and occipital regions, are indistinguishable from those of *L. maximus*.

Upper dentition: The upper incisors range in transverse diameter from 2.53 mm to 5.46 mm (Table 1). The upper cheek teeth are more obliquely implanted in the maxillae (Figs. 3A, B, $4A_1$, B_1, C, D, $5A_1$, B_1) than in *L.* (*L.*) *pretrichodactylus, L.* (*L.*) *insolitus*, *L.* (*L.*) *angulatus*, *L.* (*L.*) *loberiaensis*, *L.* (*L.*) *euplasius*, *L.* (*L.*) *indefinitus*, *L.* (*L.*) *compressidens*, *L. cavifrons*, and *L. maximus*, with the angle of the tooth laminae with respect to the sagittal plane ranging from 39°–45° in *L.* (*L.*) *incisus*, as opposed to 46°–62° in all of the other species. In P4, the anterior lamina is slightly narrower transversely than the posterior one, which widens labially, and the enamel is thinner on the labial side of the tooth. As in *L. maximus*, there is no enamel on the labial side of the upper molars. The third lamina of M3 is large and resembles that of *L. maximus* in shape.

Lower dentition: The transverse diameter of the lower incisors ranges from 3.42 mm to 5.26 mm (see Table 1). The lower cheek teeth are more compressed anteroposteriorly (see Table 1) and more obliquely implanted in the mandible (Figs. $3C_1$, E_1, $4E_1$, F_1, $5B_1$, C_1, $6A_1$, B_1) than in *L.* (*L.*) *pallidens*, *L.* (*L.*) *antiquus*, *L.* (*L.*) *insolitus*, *L.* (*L.*) *euplasius*, *L.* (*L.*) *compressidens*, *L.* (*L.*) *definitus*, *L. debilis*, *L. heterogenidens*, *L. minimus*, and *L. maximus*. The only other species possessing highly anteroposteriorly compressed lower cheek teeth is *L.* (*L.*) *laminosus* (Ameghino 1891; Vucetich 1984), but the relatively scarcity of the material assigned to this taxon currently prevents more detailed comparisons. The transverse axis of p4 is almost parallel to the sagittal plane, and the anterior lamina of this tooth is anteroposteriorly longer than the posterior one. While the anteroposterior length of the lower molars decreases from front to back, their transverse diameter increases, with m1 being much narrower than m2 and m3.

Mandibles: The mandibles are less divergent than in *L. maximus*. In other preserved features, such as the fossa for the insertion of the masseter medialis pars posterior, the masseteric notch, the morphology of the coronoid process, or the relative length of the diastema, *L.* (*L.*) *incisus* does not differ from *L. maximus*.

Table 1. Dental measurements (in mm) of *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888). Abbreviations: APD, anteroposterior diameter; TD, transverse diameter; I/i, upper/lower incisor; M/m, upper/lower molar; P/p, upper/lower premolar.

Specimen	I1		P4		M1		M2		M3		i1		p4		m1		m2		m3	
	APD	TD	APD	TD	APD	TD	APD	TD	APD	TD	APD	TD	APD	TD	APD	TD	APD	TD	APD	TD
MACN-Pv 7388	4.54	4.82	4.1	8.08	4.32	8.02	3.82	8.32	6.36	9.48	–	–	–	–	–	–	–	–	–	–
MACN-A 1112	5.12	5.26	4.66	8.04	4.36	8.32	3.74	7.72	6.66	10.06	–	–	–	–	–	–	–	–	–	–
MACN-A 1654	3.36	3.72	–	–	–	–	–	–	–	–	3.02	3.42	3.22	7.36	3.42	9.82	3.44	11.12	3.36	10.72
MLP 86-VI-20-13	4.86	5.12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MLP 48-XII-16-194	–	–	4.41	7.31	4.21	7.21	4.29	7.54	6.08	8.72	–	–	–	–	–	–	–	–	–	–
MLP 91-III-1-18	5.13	5.46	4.83	8.15	4.57	8.32	4.45	7.59	7.71	8.92	–	–	–	–	–	–	–	–	–	–
MLP 91-III-1-36	–	–	4.09	7.42	4.06	7.57	4.11	7.1	6.62	8.07	–	–	–	–	–	–	–	–	–	–
MLP 94-II-1-136	–	–	4.02	6.65	3.45	6.85	3.49	7.16	6.39	7.39	–	–	–	–	–	–	–	–	–	–
MLP 63-VI-10-59	–	–	4.19	7.55	4.47	7.13	4.28	7.41	6.98	8.69	–	–	–	–	–	–	–	–	–	–
MLP 88-VI-1-2	–	–	3.95	7.45	3.83	6.98	3.61	7.49	6.63	8.05	–	–	–	7.87	3.51	10.34	3.29	11.58	3.57	11.78
MLP 88-VI-1-2b	2.68	2.53	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MLP 91-IV-5-258	3.52	3.57	3.24	4.64	3.21	4.77	2.66	4.64	4.6	4.81	–	–	–	–	–	–	–	–	–	–
MLP 46-V-13-72	–	–	–	–	–	–	4.02	8.36	–	–	3.66	4.14	3.48	7.94	3.62	10.6	3.65	11.98	–	–
MLP 91-III-1-88	3.91	4.12	–	–	–	–	–	–	–	–	3.54	3.85	3.51	7.86	3.53	10.33	3.24	10.97	3.47	11.18
MLP 91-IV-5-214	3.94	4.29	–	–	–	–	–	–	–	–	3.7	4.14	3.63	8.55	3.51	10.11	3.48	12.14	–	–
MLP 94-II-1-146	3.68	4.11	–	–	–	–	–	–	–	–	3.54	3.89	3.41	8.4	3.59	10.81	3.44	11.77	3.42	11.16
MLP 94-II-1-146b	–	–	–	–	–	–	–	–	–	–	–	–	4.26	8.75	3.81	12.27	3.91	13.76	4.08	13.05
MLP 91-III-1-9	–	–	–	–	–	–	–	–	–	–	5.05	5.26	3.69	8.55	3.59	11.38	3.51	12.66	3.7	11.81

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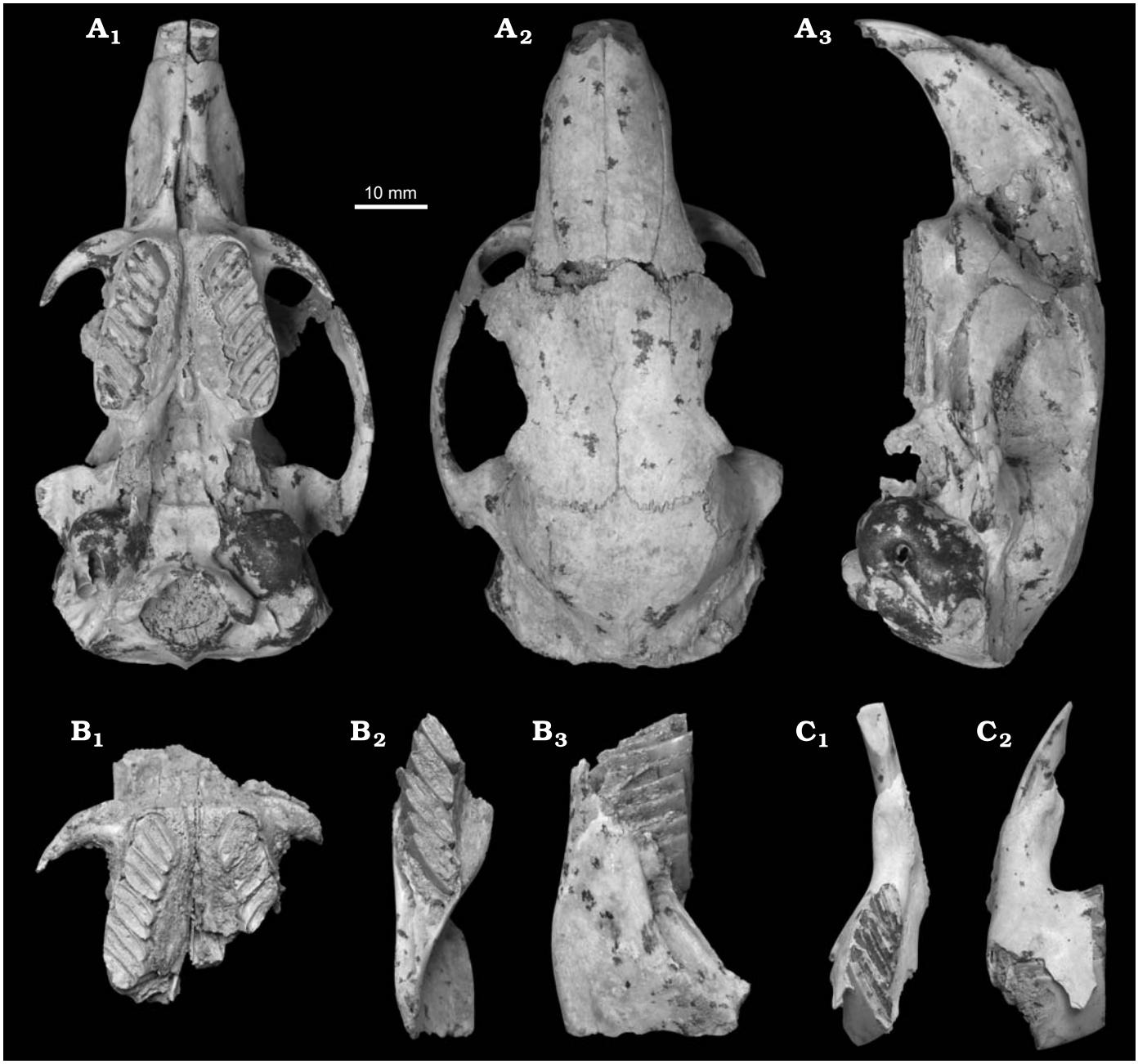

Fig. 5. The chinchillid rodent *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888) from the Chapadmalal Formation, Buenos Aires Province, Argentina (early Late Pliocene). **A**. MLP 91-IV-5-258, skull in ventral (A_1), dorsal (A_2) and lateral (A_3) views. **B**. MLP 88-VI-1-2, palate with right P4–M3 and left P4–M2 in ventral view (B_1), and left mandible with p4–m3 in occlusal (B_2) and labial (B_3) views. **C**. MLP 91-IV-5-214, left mandible with p4–m2 in occlusal (C_1) and labial (C_2) views.

Postcranial material: The canalis supracondyloideus or entepicondyloideus (Figs. $4F_3$, 6D) is not entirely closed, as opposed to *L.* (*L.*) *loberiaensis* and *L.* (*L.*) *euplasius*, in which the canal is fully closed, as well as the extant *L. maximus* and the other living chinchillids, *Chinchilla* and *Lagidium*, in which the canal is absent.

Remarks.—*Lagostomus* (*Lagostomopsis*) *incisus* was originally described by Ameghino (1888) as a species slightly smaller than *Lagostomus maximus*, and characterized by the presence of a "cleft palate", as well as more slender and shorter premaxillae, and more compressed and more obliquely implanted upper cheek teeth than in the living species. "*L.* (*L.*) *spicatus*" was distinguished by Ameghino (1888, 1889) by being just half the size of *L.* (*L.*) *incisus*, the presence of strongly striated incisors, more dorsally directed coronoid processes, and more compressed and more obliquely implanted lower cheek teeth than in *L. maximus*. Note that the differences between *L.* (*L.*) *incisus* and "*L.* (*L.*) *spicatus*" observed by Ameghino (1888, 1889) correspond mainly to differences in the size of the skull and the width of the incisors, as well as the

enamel striation pattern of these teeth. According to Ameghino (1888, 1889), *L.* (*L.*) *incisus* has incisors with a transverse width exceeding 5 mm, while in "*L.* (*L.*) *spicatus*" the transverse width of the incisors ranges from 3.5–4 mm. The diagnostic value of these features in light of the ontogenetic variability and sexual dimorphism observed in the living *L. maximus* is discussed below.

Geographic and stratigraphic range.—MACN-A 1112, MACN-A 1654, MACN-PV 7388, MLP 46-V-13-72, MLP 48-XII-16-194, and MLP 86-VI-20-13 come from Farola Monte Hermoso (Fig. 1), with the first three having no precise stratigraphic provenance within the Monte Hermoso Formation (Montehermosan–Lower Chapadmalalan, Early Pliocene), while the last three come from the upper section of the Monte Hermoso Formation (Lower Chapadmalalan, late Early Pliocene, Cione and Tonni 1995b; see Fig. 2); MLP 88-VI-1-2 was recovered from Las Vertientes (near Mar del Plata; Fig. 1), from the Chapadmalal Formation (Upper Chapadmalalan, early Late Pliocene; Fig. 2); MLP 91-IV-5-214 and MLP 91-IV-5-258 come from Fortín-88 (Fig. 1), from the lower levels of the Chapadmalal Formation (Upper Chapadmalalan, early Late Pliocene); MLP 63-VI-10-59 was recovered from Quequén Salado River (Fig. 1), from the Irene "Formation" (Chapadmalalan, late Early–early Late Pliocene); MLP 91-III-1-9, MLP 91-III-1-18, MLP 91-III-1-36, MLP 91-III-1-88, MLP 94-II-1-136, and MLP 94-II-1-146 come from Cascada Grande (Fig. 1), from the middle levels of the Irene "Formation" (Chapadmalalan, late Early–early Late Pliocene; Fig. 2).

Discussion

Synonymy of *Lagostomus* (*Lagostomopsis*) *incisus* with "*L.* (*L.*) *spicatus*".—Comparisons of fossil specimens with the living *Lagostomus maximus* indicate that the differences in skull size and the width of the incisors used by Ameghino (1888, 1889) to distinguish *L.* (*L.*) *incisus* from "*L.* (*L.*) *spicatus*" can be attributed to different ontogenetic states of a single species. Both features vary considerably between young and adult specimens of *L. maximus*, with the differences clearly being the result of ontogenetic variation. Substantial ontogenetic increase in tooth size has also been observed in other fossil caviomorphs, including the neoepiblemid *Perimys* (Kramarz 2002) and the hydrochoerid *Cardiatherium* (Vucetich et al. 2005), indicating the presence of this condition in a variety of hypsodont caviomorph lineages. Furthermore, the striation pattern of the incisors, a feature supposedly distinctive of "*L.* (*L.*) *spicatus*", is variable both among the fossil specimens examined here and specimens of the extant *L. maximus*, implying that this character cannot be used to differentiate fossil species. Finally, the relative length and width of the premaxillae also varies among the fossil specimens included in this study, as well as among juveniles and adults of *L. maximus* (see below), suggesting the degree of development of the rostrum to be the result of ontogenetic changes within a single species.

Note that, apart from the differences mentioned above, Ameghino (1888, 1889) pointed out that *L.* (*L.*) *incisus* and "*L.* (*L.*) *spicatus*" were very similar in general morphology, leading Francis and Mones (1965b) to suggest that more detailed comparative studies could lead to a synonymization of both species. Our study supports this idea, which is further corroborated by the morphology of specimens MLP 88-VI-1-2 (Fig. 5B), and MLP 94-II-1-146 (Fig. 6). While their palatal anatomy and upper tooth morphology are similar to that of *L.* (*L.*) *incisus* (Ameghino 1889: pl. 9: 22; Fig. 3A), their lower teeth resemble those of "*L.* (*L.*) *spicatus*" (Ameghino 1889: pl. 9: 9, 15; Fig. 3C). This indicates that *L.* (*L.*) *incisus* and "*L.* (*L.*) *spicatus*" indeed form a single species, with the valid name being *L.* (*L.*) *incisus* by page priority.

Ontogenetic variation and sexual dimorphism in *Lagostomus* (*Lagostomopsis*) *incisus*.—In addition to the traits proposed above to vary according to ontogenetic stage, we have identified several other features expressing a similar kind of variation. In general, differences observed between juvenile (e.g., MLP 91-IV-5-258) and adult (e.g., MACN-Pv 7388 and MLP 91-III-1-18) individuals of *L.* (*L.*) *incisus* resemble those found in *L. maximus*, with young individuals of both species having a more slender and shorter rostrum with a less-developed fossa for the origin of the medial masseter, smaller teeth, a more inflated parieto-occipital region, and more weakly developed temporal and sagittal crests as compared to adult specimens. While likely linked to ontogeny, it is possible that some of this variation, such as differences in skull size or the development of the rostrum and the temporal and sagittal crests, may also be due to sexual dimorphism. The latter is very pronounced in the extant plains vizcacha, *L. maximus*, with males being much larger and more massively built than females (e.g., Jackson et al. 1996; Fig. 7). We therefore suggest that the differences observed among specimens of *L.* (*L.*) *incisus* may be explained by a mixture of ontogenetic variation and sexual dimorphism.

Diagnostic features of *Lagostomus* (*Lagostomopsis*) *incisus*.—One of the most distinctive features characterizing *Lagostomus* (*Lagostomopsis*) *incisus* is the presence of a "cleft palate". This feature was originally described by Ameghino (1988, 1889), who stated that *L.* (*L.*) *incisus* and "*L.* (*L.*) *spicatus*" lacked a bony palate because the maxillae did not contact medially posterior to P4, instead being divided by a deep cleft. Later, Rovereto (1914) mentioned the presence of a similar "cleft" in *L.* (*L.*) *angulatus* and *L.* (*L.*) *insolitus* (both junior synonyms of *L.* [*L.*] *pretrichodactylus* according to Marshall and Patterson [1981]). Kraglievich (1926) argued that this cleft could have been produced by postmortem alteration. A comparison of *L.* (*L.*) *incisus* with *L.* (*L.*) *angulatus* and *L.* (*L.*) *insolitus* indicates that their palatal morphologies are very different, with the palate of the latter two resembling that of *L. maximus,* albeit being somewhat more vaulted. Unlike in those species, the maxillae in *L.* (*L.*)

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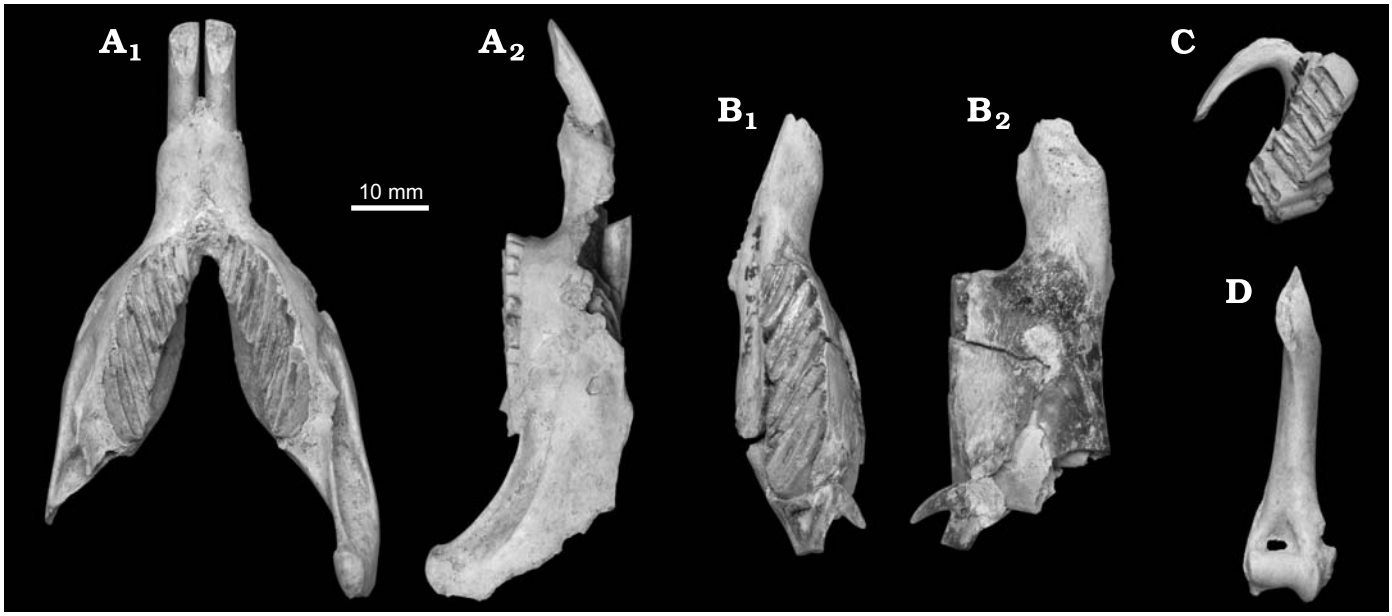

Fig. 6. The chinchillid rodent *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888) from the Irene "Formation", Buenos Aires Province, Argentina (late Early–early Late Pliocene); MLP 94-II-1-146. **A**. Mandibles with incisors and complete tooth rows in occlusal (A_1) and labial (A_2) views. **B**. Right mandible with p4–m3 in occlusal (B_1) and labial (B_2) views. **C**. Right maxilla with P4–M3 in ventral view. **D**. Right humerus in anterior view.

incisus extend towards the sagittal plane and cover part of the palatines in ventral view, thus forming the "cleft palate" described by Ameghino (1888) (see Description and Fig. 8A–C). We therefore consider this feature to be diagnostic of *L.* (*L.*) *incisus*, as originally proposed. Note that juvenile *L.* (*L.*) *incisus* show a palatal morphology similar to that of adult *L. maximus* (palatines fused and forming a posterior process), suggesting that heterochrony may have been involved in the evolution of this feature. More data will be necessary to test this idea.

Our study confirms the oblique implantation of the cheek teeth and anteroposteriorly compressed lower cheek teeth as diagnostic features of *L.* (*L.*) *incisus* (Fig. 8D–F), as originally proposed by Ameghino (1888). In addition, reduced posterior palatine apophyses of the premaxillae not extending to the dorsoventral level of the diastema are here identified as a distinctive feature of *L.* (*L.*) *incisus*. This feature is not variable within the available sample and does not show any variation between juvenile and adult specimens (Fig. 8A–C). Finally, the presence of a partially closed humeral canalis supracondyloideus, which in life contains the arteria brachialis and nervus medianus, allows to distinguish *L.* (*L.*) *incisus* from the living *L. maximus* (in which the canal is absent), and from the extinct *L.* (*L.*) *euplasius* and *L.* (*L.*) *loberiaensis* (in which the canal is fully closed). Kraglievich (1926) noticed the presence of a partially closed canalis supracondyloideus in Chapadmalalan lagostomine material of uncertain affinity, although the degree to which the roof of the canal was developed varied among those specimens. More detailed studies of postcranial material belonging to other species of *Lagostomus* are required before the systematic significance of this feature can be assessed on a broader scale.

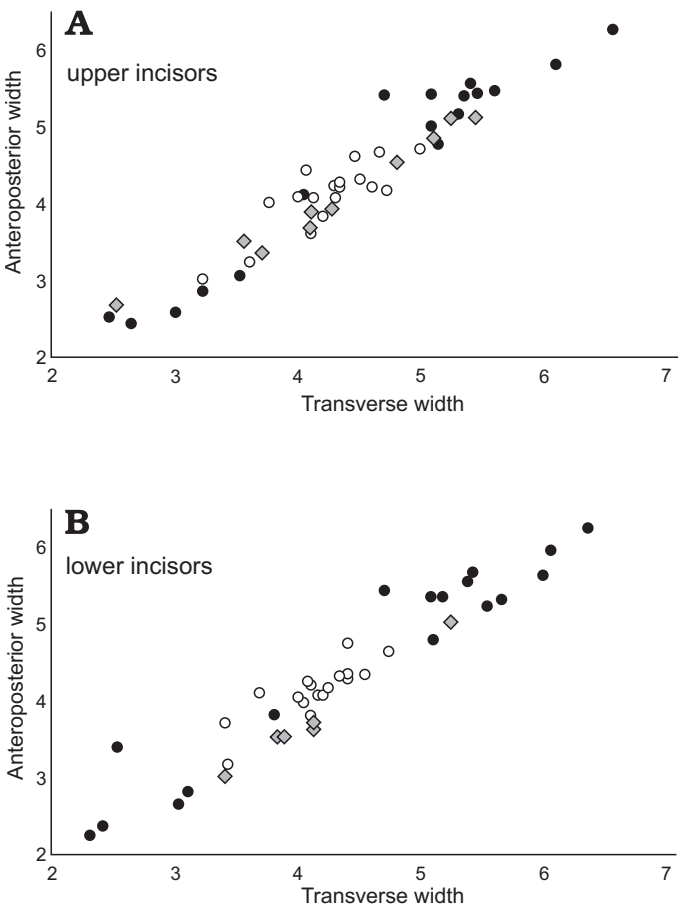

Fig. 7. Scatterplot of transverse and anteroposterior diameters of the upper (**A**) and lower (**B**) incisors of *Lagostomus* (*Lagostomopsis*) *incisus* (gray squares), and *Lagostomus maximus* male (black circles) and female (open circles) specimens.

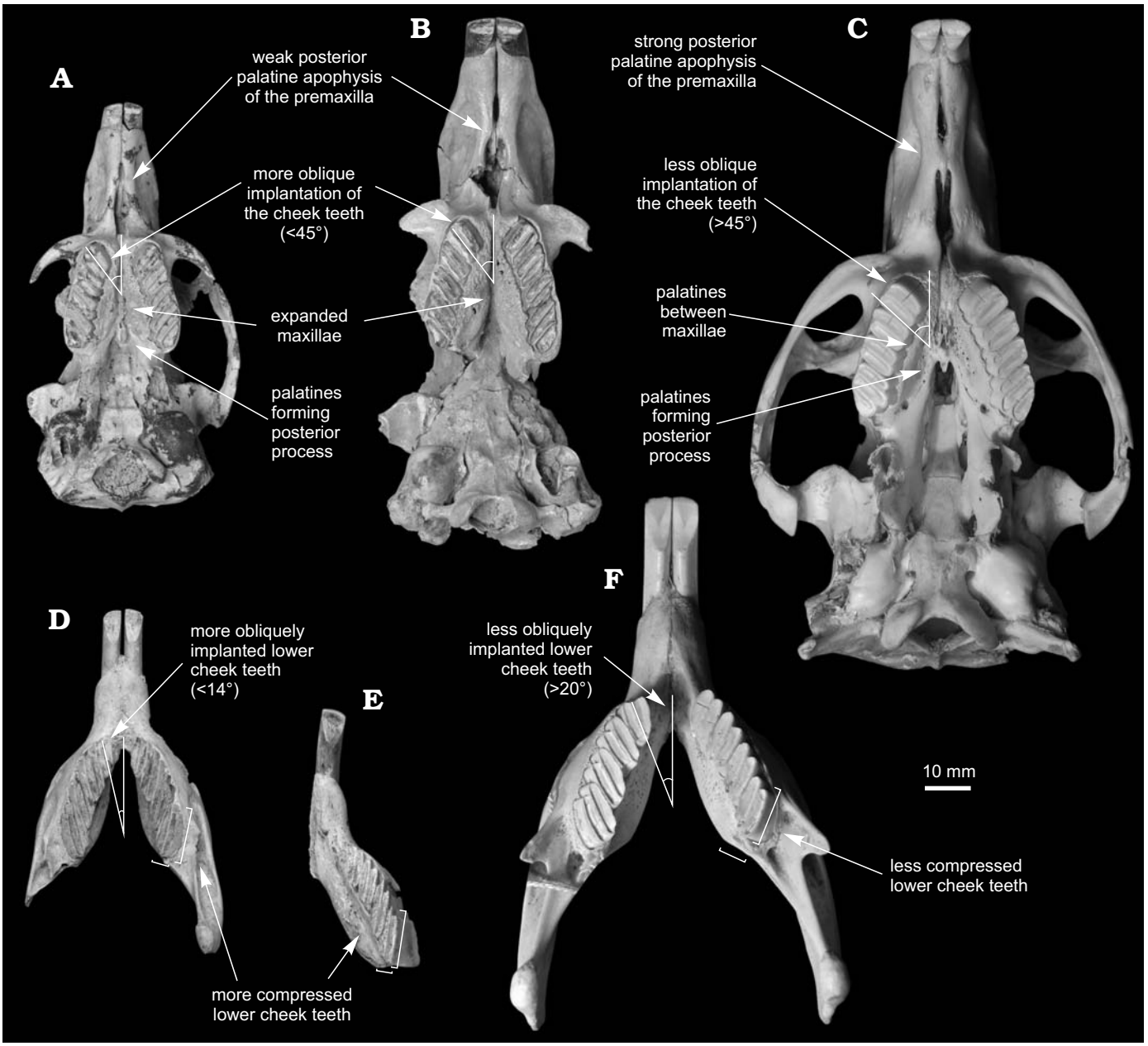

Fig. 8. Differences between *Lagostomus* (*Lagostomopsis*) *incisus* (Ameghino, 1888) from the Pliocene of Buenos Aires Province, Argentina (A, B, D, E) and the living *Lagostomus maximus* (Desmarest, 1817) (C, F). **A**–**C**. Skulls in ventral view. **A**. MLP 91-IV-5-258, juvenile. **B**. MLP 91-III-1-18, adult. **C**. MACN-Mz 49.48, adult. **D**–**F**. Mandibles in occlusal view. **D**. MLP 94-II-1-146, juvenile. **E**. MLP 91-III-1-9 adult. **F**. MACN-Mz 49.48, adult.

"*Lagostomus* (*Lagostomopsis*) *spicatus*" from the "Kiyú lithofacies".—The specific assignment of the lagostomines from the "Kiyú lithofacies" to "*L.* (*L.*) *spicatus*" was mostly based on the size of the specimens and the striation of the incisors. However, as discussed above, these characters are extremely variable in the living *Lagostomus maximus*, and hence of little systematic value. In addition, the skull figured by Francis and Mones (1965b: 158, figs. 1, 2) differs from *L.* (*L.*) *incisus* (= "*L.* [*L.*] *spicatus*") in having less obliquely implanted cheek teeth, and less-developed maxillae in palatal view. Therefore, there are no features justifying the assignment of the material from the "Kiyú lithofacies" to *L.* (*L.*) *incisus*, and its precise specific status will need to be established as part of a broader systematic study of the Lagostominae.

Conclusions and future research

Systematics.—The size differences previously thought to distinguish *Lagostomus* (*Lagostomopsis*) *incisus* from "*L.* (*L.*) *spicatus*" can be attributed to ontogenetic variation within a single species, as also observed in the extant *Lagostomus maximus*. Furthermore, some of these differences may also be

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the result of sexual dimorphism. Together, these observations suggest "*L.* (*L.*) *spicatus*" to be a *junior* synonym of *L.* (*L.*) *incisus*, with the latter species being diagnosed by several characters of the skull and teeth.

According to Vucetich (1984), there has been a tendency towards an increase in body size, as well as a shortening of the cheek tooth laminae in the evolution of lagostomines from the Early–Middle Miocene genus *Pliolagostomus* to the extant *Lagostomus maximus*, assuming the existence of a *Pliolagostomus–Lagostomopsis–Lagostomus* lineage. However, our study suggests that *L.* (*L.*) *incisus* from the Pliocene of eastern Argentina was almost as big as the modern plains vizcacha, while possessing much shorter lower cheek teeth, hinting at a more complex evolutionary sequence. Future phylogenetic analyses including both fossil and living lagostomines will be crucial in reconstructing the evolution of body size and the occlusal molar pattern of this lineage. The relationships of *L.* (*L.*) *incisus* with other lagostomines are still obscure, and can only be tested following a systematic review of the subfamily as a whole.

Biostratigraphic significance.—While there are confirmed records of *Lagostomus* (*Lagostomopsis*) *incisus* from the upper section of the Monte Hermoso Formation (Lower Chapadmalalan, late Early Pliocene), as well as the Chapadmalal Formation (Upper Chapadmalalan, early Late Pliocene), some specimens have no precise provenance within the Monte Hermoso Formation, and might therefore have been recovered from the lower section of the latter (Montehermosan, Early Pliocene). The presence of *L.* (*L.*) *incisus* in the Irene "Formation" further supports a Chapadmalalan age for this taxon.

The restriction of *L.* (*L.*) *incisus* makes this species a useful biostratigraphic marker, and highlights the potential of late Neogene lagostomines as tools in reaching a more precise calibration of the biostratigraphic scheme proposed for the late Cenozoic of the Pampean region.

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Appendix 1

List of material used for comparative study.

Lagostomus (*Lagostomopsis*) *antiquus*: MASP 32 (type), left mandible with m1–3, Entre Ríos Province, "Mesopotamian", Late Miocene.

Lagostomus (*L.*) *pallidens*: MASP 30 (type), right symphyseal mandible fragment with incisor; MASP 31, left mandible fragment with p4–m3, Entre Ríos Province, "Mesopotamian", Late Miocene.

Lagostomus (*L.*) *laminosus*: MACN-A 8883 (type), two isolated lower molars; MACN-A 5883, 5884, two isolated lower molars, Entre Ríos Province, "Mesopotamian", Late Miocene.

Lagostomus (*L.*) *angulatus*: MACN-Pv 8337 (type), palate with complete tooth rows, Catamarca Province, Huayquerian, Late Miocene.

Lagostomus (*L.*) *pretrichodactylus*: MACN-Pv 8339 (type), skull partially preserved with complete tooth rows, Catamarca Province, Huayquerian, Late Miocene.

Lagostomus (*L.*) *insolitus*: MACN-Pv 8345 (type), skull partially preserved with complete tooth rows and left mandible fragment with p4–m2, Catamarca Province, Huayquerian, Late Miocene.

Lagostomus (*L.*) *loberiaensis*: MLP 54-X-13-1 (type), skull roof, maxillae with complete tooth rows and humerus, Buenos Aires Province, Pliocene.

Lagostomus (*L.*) *euplasius*: MACN-Pv 6163 (type), skull and mandibles with complete tooth rows, Buenos Aires Province, Pliocene.

Lagostomus (*L.*) *compressidens*: MLP 54-X-13-2 (type), skull and left mandible with complete tooth rows, Buenos Aires Province, Pliocene.

Lagostomus (*L.*) *indefinitus*: MLP 54-X-13-4 (type), palate with complete tooth rows, Buenos Aires Province, Pliocene.

Lagostomus (*L.*) *definitus*: MACN-Pv 5986 (type), right mandible with p4–m2, Buenos Aires Province, Pliocene.

Lagostomus (*L.*) *arcuatus*: MACN-Pv 5983, maxilla fragment, Buenos Aires Province, Pliocene. *Lagostomus angustidens* (Burmeister 1866, non Moreno 1888): MACN-Pv 2373 (type), left mandible with p4–m3, Buenos Aires Province, Late Pleistocene.

Lagostomus minimus: MACN-A 1098 (type), left mandible with p4–m3, Buenos Aires Province, Middle Pleistocene.

Lagostomus heterogenidens: MACN-A 1187 (type), left mandible with p4–m3; 1188, right mandible with p4–m3, Buenos Aires Province, Late Pleistocene.

Lagostomus debilis: MACN-A 1255 (type), right mandible with p4–m2, Buenos Aires Province, Late Pleistocene.

Lagostomus striatus: MACN-A 813, postcranial remains, Buenos Aires Province, Late Pleistocene.

Lagostomus cavifrons: MLP 52-IX-30-36, partially preserved skull, Santa Fe Province, Late Pleistocene.

Lagostomus maximus: MACN-Mz 48.274 (male), 48.276 (m), 48.277 (female), 48.279 (m), 48.280 (m), 48.281 (m), 49.5 (m), 49.8 (m), 49.12 (f), 49.13 (?), 49.14 (f), 49.16 (f), 49.17 (f), 49.43 (f), 49.44 (f), 49.45 (f), 49.46 (f), 49.48 (m), 49.141 (m), 53.8 (f), 53.9 (f), 53.10 (m), 53.11 (m), 53.13 (m), 53.19, 53.20 (f), 53.21 (f), 53.24 (m), 53.25 (m), 53.27 (f), 53.33 (m), 53.34 (f), 53.35 (f), 53.36 (f), 53.37 (f), Recent.