**Article**

# A new large didelphid of the genus *Thylophorops* (Mammalia: Didelphimorphia: Didelphidae), from the late Tertiary of the Pampean Region (Argentina)

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## Abstract

We describe *Thylophorops lorenzinii* **sp. nov.** (Marsupialia, Didelphidae), the largest known didelphid opossum, living or extinct. Its type specimen comes from Late Pliocene levels at Punta San Andrés, southeastern Buenos Aires Province, Argentina. With an estimated body mass between 4.8 and 7.4 kg, it obviously surpasses that of the (up to now) largest didelphid, the living *Didelphis virginiana* Kerr. In addition to its larger size, the new species differs from *T. chapalmalensis* Ameghino and *T. perplanus* Ameghino in that its lower molars have more labially salient hypoconids and proportionally large hypoconulids which are not antero-posteriorly compressed.

**Key words**: *Thylophorops lorenzinii* **sp. nov.**, Didelphidae, Marplatan Stage/Age, Argentina

## Resumen

Se describe a *Thylophorops lorenzinii* **sp. nov.** (Marsupialia: Didelphidae), la zarigüeya más grande, fósil o viviente, hasta ahora conocida. Su ejemplar tipo procede de niveles del Plioceno Tardío de Punta San Andrés, en el sudeste de la Provincia de Buenos Aires, Argentina. Con una masa corporal estimada entre 4,7 y 7,5 kg, sobrepasa claramente aquella del (hasta ahora) más grande didélfido conocido, *Didelphis virginiana* Kerr. Más allá de su mayor tamaño, la nueva especie difiere de *T. chapalmalensis* Ameghino y *T. perplanus* Ameghino en que sus molares inferiores tienen hipoconúlidos proporcionalmente grandes, los cuales no están comprimidos anteroposteriormente, y en que los hipocónidos son más salientes labialmente.

**Palabras clave**: *Thylophorops lorenzinii* **sp. nov.**, Didelphidae, Piso/Edad Marplatense, Argentina.

## Introduction

Large sized, 2n=22 opossums (Marsupialia: Didelphidae: Didelphinae; Reig et al. 1977, Kirsch & Palma 1995) are widely distributed throughout the Americas, especially in tropical South America. However, their late Cenozoic history and taxonomy is mostly known from fossil sites in higher latitudes such as those of the Pliocene-Pleistocene deposits in the Pampean Region (Goin 1995). A remarkable aspect of these late Cenozoic associations is that didelphines show a decided trend toward more carnivorous-faunivorous feeding habits, as revealed by their dental specializations. One example of this trend is the extinct *Thylophorops* Ameghino, a genus showing affinities with *Didelphis* Linnaeus and *Philander* Brisson (Goin 1991, *contra*

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Simpson 1972). *Thylophorops* is mostly known for its type species, the Late Pliocene (Chapadmalalan Stage/Age) *T. chapalmalensis* Ameghino. A second, smaller species from the Early Pliocene of the Pampean Region, *T. perplanus* Ameghino, was more recently recognized by Goin & Pardiñas (1996; mentioned there as "*T. aff. perplana*"). Here we describe a new, Late Pliocene (Marplatan Stage/Age) species of *Thylophorops*, which represents the largest didelphid opossum known to date, as well as the last (youngest) species of this genus. We comment on its main features, inferred body mass and probable feeding habits.

## Material, methods, provenience, and abbreviations

The type specimen of the new species (Figs. 1–4) belongs to the MLP collections (División Paleontología Vertebrados, Museo de La Plata, Argentina). Specimen of *T. chapalmalensis* MPH 064 in Fig. 4 (left, detail of m3) and Fig. 5 (D–E) belongs to the Museo de Punta Hermengo (Miramar) collections, while specimen of this same species illustrated in Fig. 5 (A–C) is MLP 64-XI-12-1. The figured specimen of *T. perplanus* (Figs. 4 right and 6) is MLP 97-XI-15-1. Body mass (Table 1) was calculated following procedures detailed in Gordon (2003). Feeding habits were inferred from analyses of molar crests and, in worn specimens of other species of the genus, wear facets as detailed in Dewar (2003). The type specimen comes from Punta San Andrés (38º 10' 52.92'' S–57º 39' 11.66'' W; see Verzi & Quintana 2005: fig. 3), General Pueyrredón County, Buenos Aires Province, Argentina. Mammal-bearing deposits at this site belong to Level 2, San Andrés Formation, Sanandresan Stage/Age (latest Pliocene; see Verzi & Quintana 2005: figs. 2, 3). The specimen was extracted from a medium-sized paleocave (110 cm in diameter), most probably generated by a fossorial, extinct xenarthran. Details on the geology, stratigraphy, sedimentology, chronology, and faunal context of this locality were given by Verzi & Quintana (2005 and literature cited therein). Abbreviations: Ma, Mega–annum; c, p, m, lower canine, premolar and molar, respectively; dp3, deciduous premolar. Molar nomenclature follows Goin et al. (2003). L, length; W, width. Measurements are in mm.

**TABLE 1**: Body mass estimations in selected large didelphids, extant and extinct. BM, body mass; L, length; A, area; g, grams; $r^2$, Determination Index; $LM_x$, Molar length; $AM_x$, Molar Area; N, sample size.

| Taxa | Equation | $r^2$ | $LM_x$ (mm) | $AM_x$ (mm$^2$) | Body Mass (g) |
|---|---|---|---|---|---|
| *Didelphis marsupialis* | Data from Gordon (2003) | | | | 1,265.2 (males) 1,400 (females) |
| *Didelphis virginiana* | Data from Gardner (1982) | | | | 2,970 (males) 2,070 (females) |
| *Didelphis albiventris* | Ln (BM)= 1.59+3.228 x ln(m3 L) | 0.970 | $m_3$= 5.39 | $m_3$=15.35 | 1,442.72 |
| | Ln (BM)= 2.363+1.635 x ln (m3 A) | 0.964 | | | 1,057.30 |
| *Lutreolina crassicaudata* | Ln (BM)= 1.59+3.228 x ln(m3 L) | 0.970 | $m_3$= 3.68 | $m_3$=8.21 | 397.87 |
| | Ln (BM)= 2.363+1.635 x ln (m3 A) | 0.964 | N= 10 | N=10 | 371.96 |
| *Hyperdidelphys inexpectata* | Ln (BM)= 1.59+3.228 x ln(m3 L) | 0.970 | $m_3$= 5.18 | $m_3$=14.89 | 994.18 |
| | Ln (BM)= 2.363+1.635 x ln (m3 A) | 0.964 | N= 1 | N=1 | 879.21 |
| *Hyperdidelphys parvula* | Ln (BM)= 1.59+3.228 x ln(m3 L) | 0.970 | $m_3$=5.17 | $m_3$=15.72 | 984.93 |
| | Ln (BM)= 2.363+1.635 x ln (m3 A) | 0.964 | N= 1 | N=1 | 960.26 |
| *Thylophorops perplanus* | Ln (BM)= 1.59+3.374 x ln (m2 L) | 0.968 | $m_2$=5.47 | $m_2$=15.75 | 1,515.30 |
| | Ln (BM)= 2.403+1.67 x ln (m2 A) | 0.968 | N=1 | N=1 | 1,104.67 |
| *Thylophorops chapalmalensis* | Ln (BM)= 1.59+3.228 x ln(m3 L) | 0.970 | $m_3$=7.59 | $m_3$=32.11 | 3,406.09 |
| | Ln (BM)= 2.363+1.635 x ln (m3 A) | 0.964 | N= 6 | N=6 | 3,087.85 |
| *Thylophorops lorenzinii* **sp. nov.** | Ln (BM)= 1.59+3.228 x ln(m3 L) | 0.970 | $m_3$=9.69 | $m_3$=42.44 | 7,488. 26 |
| | Ln (BM)= 2.363+1.635 x ln (m3 A) | 0.964 | N=1 | N=1 | 4,871. 77 |

**FIGURE 1**: *Thylophorops lorenzinii* **sp. nov.** MLP 08-III-10-1 (Holotype); (A), labial view of the anterior part of the skull and dentary; (B) occlusal view of the dentary; (C) lingual view of the dentary. Scale: 10 mm.

**Systematic paleontology**

*Thylophorops lorenzinii*, **new species**
Figs. 1–4

**Holotype.** MLP 08-III-10-1, a fragment of skull preserving the left maxilla, and a left dentary preserving the second premolar (p2), the deciduous premolar (dp3) and an erupting third molar (m3), all belonging to the same, juvenile specimen. Collected by Leopoldo Soibelzon in January, 2008.

    **Etymology.** Honouring Mr. Silvio Lorenzini, outstanding amateur collector of fossil specimens in Southeastern Buenos Aires Province.

    **Measurements.** Extra-alveolar length of upper canine (C): 10.15; CL: 4.33; CW: 3.41; height of dentary at m3: 11.87; width of dentary at same point: 8.08; length of the p2-m3 series: 40.02 mm; p2L: 7.64; p2W: 3.22; dp3L: 5.76; dp3W: 2.83; m3L (total): 9.69; trigonid m3L: 4.22; talonid m3L: 5.47; talonid m3W: 4.31; trigonid m3W: 4.38 (see also Fig. 3).

    **Diagnosis.** Largest known didelphid; differs from the other species of *Thylophorops* in having its lower molars with proportionally large hypoconulids which are not antero-posteriorly compressed; labially salient hypoconids; p2 is proportionally larger, higher, and posteriorly wider than in *T. chapalmalensis* and *T. perplanus*.

    **Description of the holotype.** Specimen MLP 08-III-10-1 belongs to a juvenile individual, as evidenced by the persistence of a dp3 and an erupting m3 which is placed immediately anterior to the masseteric crest (i.e. m4 is not observable). Only the anterior part of the snout is preserved (Fig. 1A), which is broken. The dentary (Fig. 1B–C) is partially broken and lacks the incisor region and the angular process; it is quite robust, especially under m3. The posterior end of the symphysis reaches the distal margin of p2. The mental foramen is in line with the mesial root of m1. The distal root of p1, and complete p2, dp3 and m3 are preserved.

    The p2 is large and high. The crown is relatively narrow over the mesial root but is much wider and more robust over the distal root. The posterior cingulum ends near the labial side of the talonid.

    The dp3 is the smallest tooth of this specimen; the trigonid and talonid are similar in length, but the talonid is wider. The metaconid is slightly smaller than the protoconid and is located on the posterolabial margin of the trigonid. The small paraconid is positioned anteromedially. The entoconid is the highest cusp of the talonid; the hypoconid is labially salient.

    The erupting m3 (Fig. 2) is very large, with its trigonid slightly longer than the talonid. All cusps are well preserved. The paraconid is triangular in occlusal view; its postero-lingual side is flat. In contrast, in *T. chapalmalensis* (Fig. 4, left), this side is rounded and the cusp is conical in occlusal view. The protoconid is the highest and largest cusp of the trigonid; it lies on the lingual side and occupies almost the entire trigonid surface. The metaconid is proportionally larger than that of *T. chapalmalensis*. The talonid is well developed in all dimensions. The entoconid is tall and prominent. The hypoconulid is large and well developed anteroposteriorly. The entoconid and hypoconulid are similar in size, in sharp contrast with *T. capalmalensis*, in which the entoconid is much larger. The hypoconid is located on the labial side of the talonid and is noticeably salient.

**Body mass and inferred feeding habits**

The use of dental measurements to estimate the body mass has been widely analized for many authors mainly due to the predominance of this elements in the mammalian fossil record (see Gingerich et al., 1982; Gingerich and Smith, 1984; Legendre and Roth, 1988; Janis, 1990; Damuth, 1990; Fortelius, 1990). Molar magnitudes are highly correlated with body mass, particularly the antero-posterior length and area, which show high values of determination index ($r^2$) in the regression analysis; the election of one or another measurement is

mainly based on this index. Some authors suggest that length is more reliable because the area is a composite variable that also includes the molar width, and this last one is subject to adaptative variation; on the contrary, length is more constant among the various species (Fortelius, 1990; Damuth, 1990). In the case of marsupials, Gordon (2003) analyzed the the relation of molar measurements to body mass in dental conservative species. She extended the analysis to all molar loci and concluded that there is a high correlation between weight and/or lengh and molar area in all loci, with the highest values of $r^2$ for the first upper and lower molars. Anyway, the posterior molars are also good predictors, as their determination index is always above 0.9.
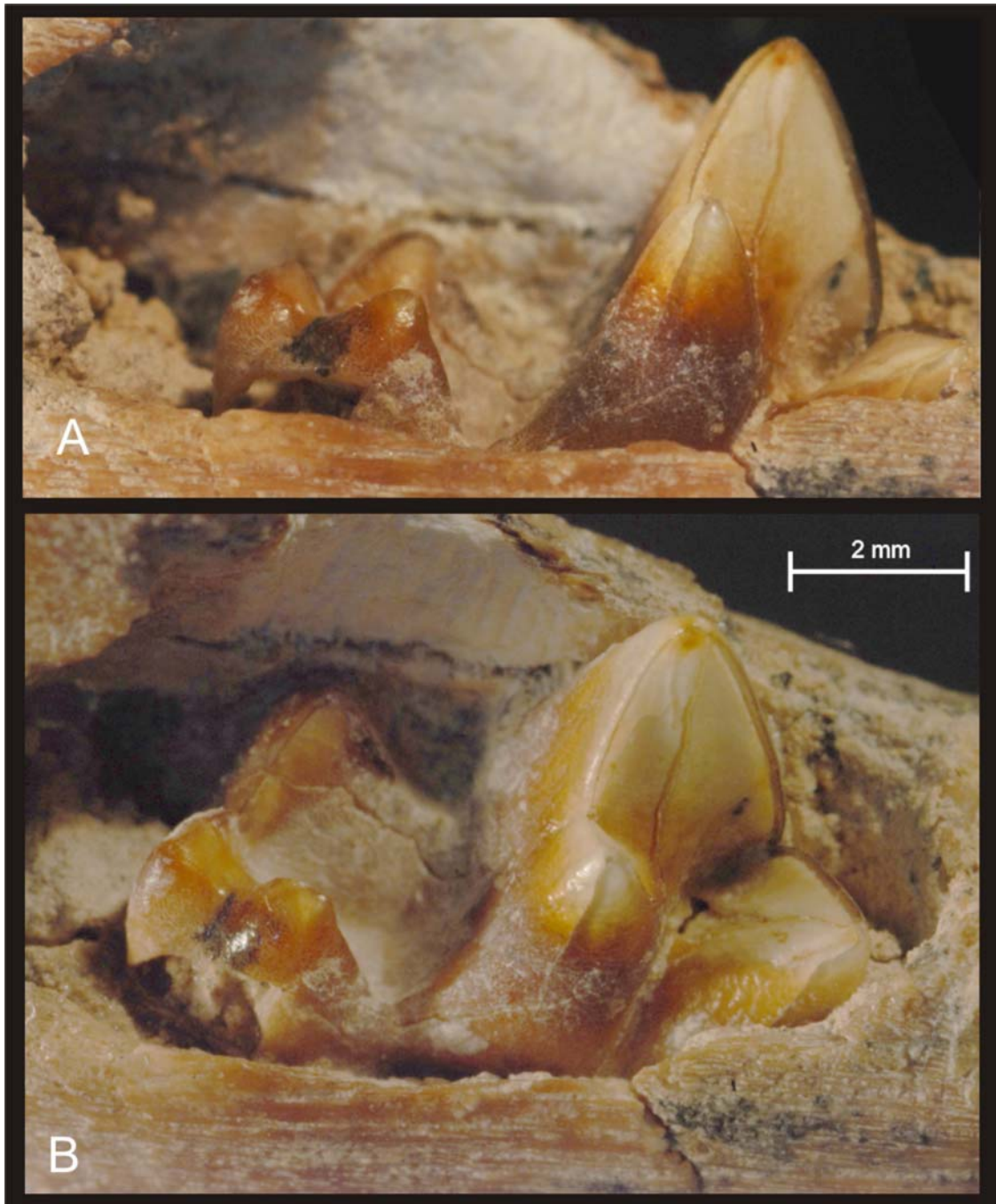


**FIGURE 2**: *Thylophorops lorenzinii* **sp. nov.** MLP 08-III-10-1 (Holotype); detail of the erupting m3 in lingual (A), and occlusal-lingual views (B). Scale: 2 mm.

In the estimation of the body mass of *T. lorenzinii*, we have followed Gordon's sample including didelphids (except *Caluromys*) and dasyurids. The exclusion of *Caluromys* results from its peculiar dentition, wich

shows a sharp decline in molar size in m3–4 as compared to m2. Because of this, *Caluromys* is an outlier and, as such, significantly alters the correlation index (Gordon, 2003). All other didelphids, including *T. lorenzinii*, are more dentally conservative in showing a size progression from m1 to m3. In short, the exclusion of *Caluromys* from the sample increase the predictive potential of the equations. Finally, the equations are derived from a pooled sample (didelphid + dasyurid) because the resulting range in the values of the independent variable is wider than that obtained from the single didelphid sample. As *T. lorenzinii* exceeds in molar size that of all other living or extinct didelphid, the former would be out of range in the didelphid regression.
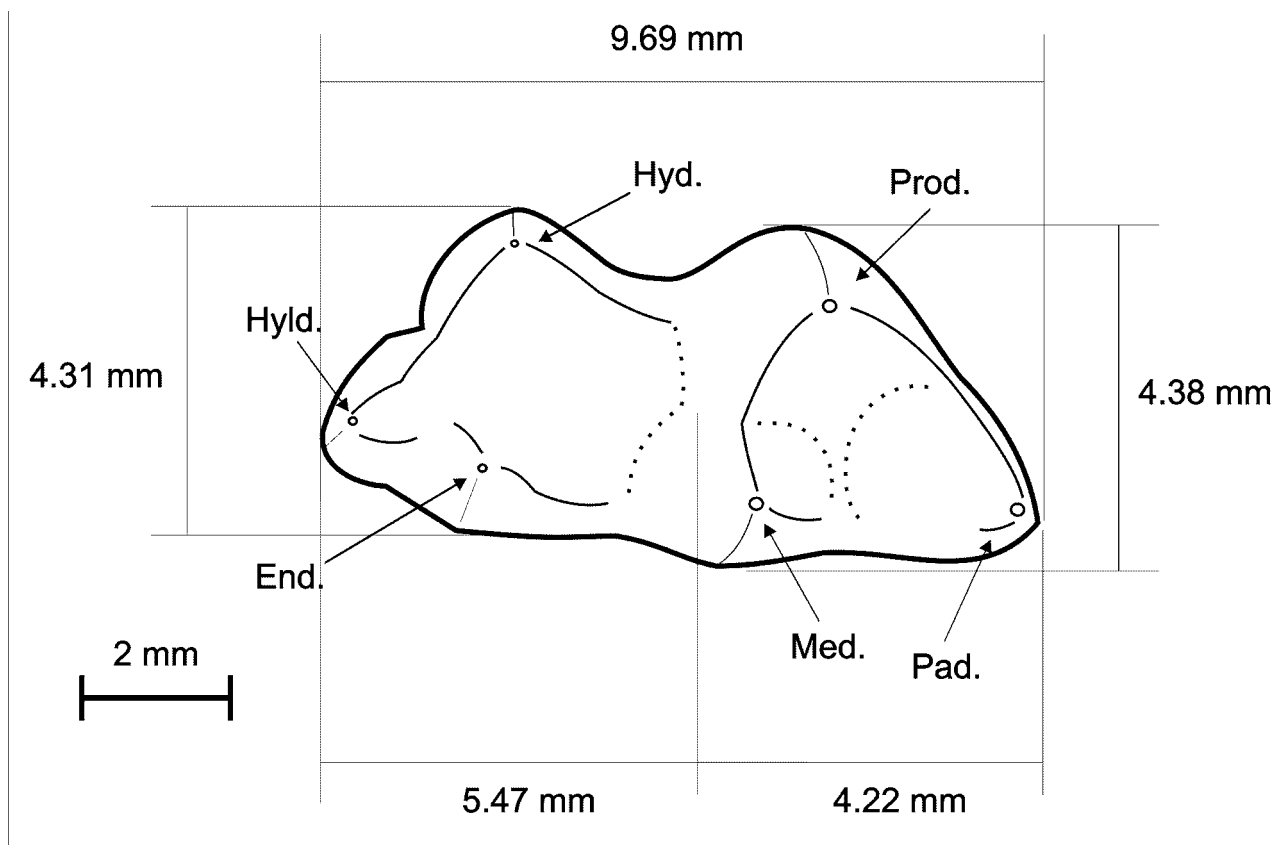


**FIGURE 3**: *Thylophorops lorenzinii* **sp. nov.** MLP 08-III-10-1 (Holotype); schematic drawing of the m3 showing the cusp homologies and measurements. Abbreviations: *End.*, entoconid; *Hyd.*, hypoconid; *Hyld.*, hypoconulid; *Med.*, metaconid; *Pad.*, paraconid; *Prod.*, protoconid. Scale: 2mm.

For comparative purposes we extended our calculations to the remaining species of *Thylophorops*: *T. chapalmalensis* (Fig. 5) and *T. perplanus* (Fig. 6), as well as to two species of *Hyperdidelphys*, another large, extinct didelphid. The molar locus used is the m3 with the exception of *T. perplanus*, in which the analyzed molar values are those of the m2. Table 1 summarizes the equations, associated coefficients, and estimated body masses for selected large didelphids. Estimations were obtained both from molar length and molar area. Because of the lack of published data on measurements of individual molars for *D. virginiana*, the largest living opossum, this species was not added to the pooled sample. Weight measurements for this species in Table 1 were taken from Gardner (1982).

Even though the regression coefficients are similar for all estimations, in *T. lorenzinii* we note significant differences between the calculated weight from m3 length and that of m3 area. This is not the case of other results based on the same equations for other large didelphid species, living or extinct (see Table 1). This can be due to the high sensitivity of the least square regression to extreme values on the independent variable. For didelphids + dasyurids, the logarithmic range in the m3 length equation fluctuates from 0.3 to 2.4, while for the m3 area it does from 0.2 to 4.4 (Gordon, 2003). The logarithmic values for *T. lorenzinii* are 2.2 for the m3

length and 3.7 for the m3 area. Both values fall within the extremes of the regression line (Fig. 7), but the m3 area is closer to the mean value of its respective regression. As the predictive potential for marginal values of the independent variable is lower than that of the central ones, we understand that the most realistic estimation of the body mass of *T. lorenzinii* is that one obtained from the m3 area.
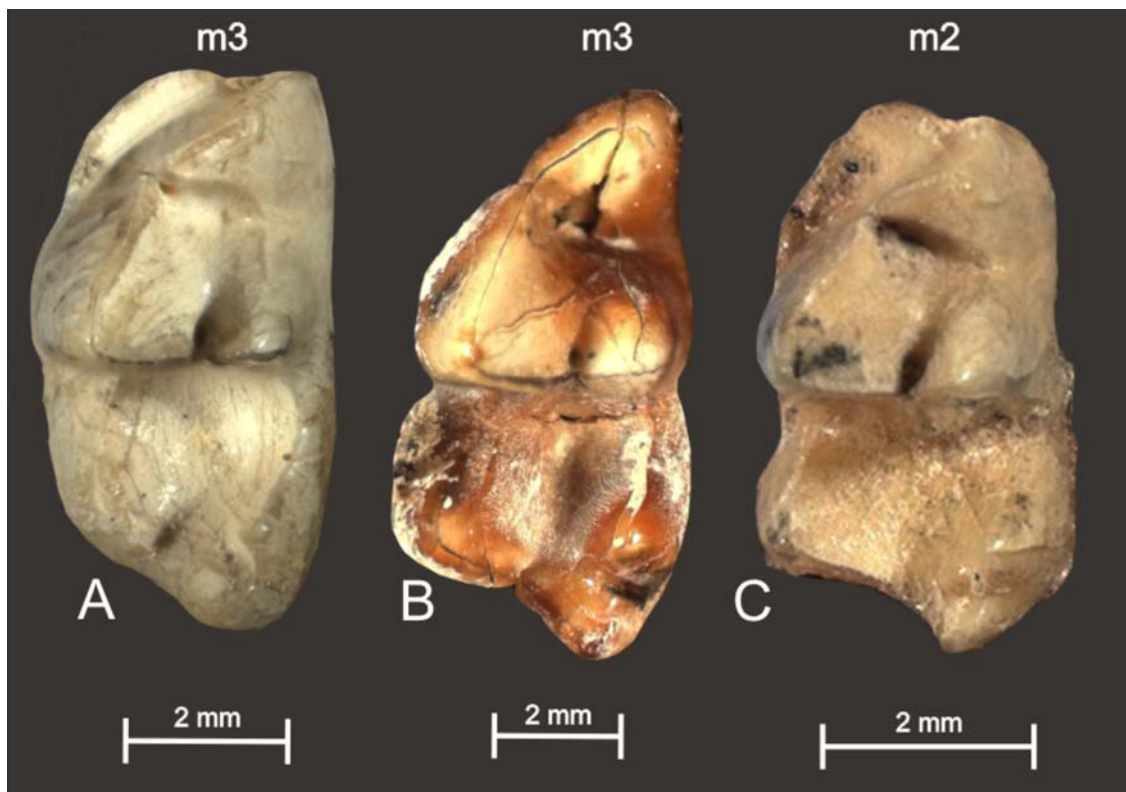


**FIGURE 4**: Lower left molars of *Thylophorops chapalmalensis* (left, detail of specimen MPH 064), *T. lorenzinii* **sp. nov.** (centre, detail of the type specimen), and *T. perplanus* (right, detail of specimen MLP 97-XI-15-1). Because of the erupting stage of the m3 of *T. lorenzinii* in the type specimen, the anterobasal cingulum is not visible. Scale: 2 mm.

In order to test the ability of Gordon's (2003) equations for the prediction of body mass, we measured the m3 length and area of ten MLP specimens belonging to *Lutreolina crassicaudata* (a species not included in Gordon's sample) and *Didelphis albiventris*. Results are shown in Table I. Known weight of *L. crassicaudata* ranges from 200 and 540 g (Grzimek et al., 2003) and that of *D. albiventris* is between 1265.2 (males) and 1400 (females; Gordon, 2003). It can be seen that both equations predict equally well the body size of these two species, which, in the didelphid + dasyurid sample, are close to the mean values in molar size. This reinforces the idea that the high body mass value obtained for *T. lorenzinii* from m3 length is due to its marginal position within the sample range.

The largest living didelphid is *Didelphis virginiana*, whose body mass published estimations vary between 0.8–6.4 kg for males, and 0.3–3.7 kg for females (Wilson & Ruff 1999). Notwithstanding, it is unclear whether or not some of these weights are based on captive animals. McNab (1978) averaged in 3.7 kg the body mass of this species. Earlier, McManus (1974) mentioned an average body mass of 2.8 kg for males and 1.9 kg for females of this same species. By far, the most complete published measurements of body mass for *D. virginiana* are those of Gardner (1982), in which he gave average weights for 374 males and 296 females from North America, all of them sorted by region. Averaging the numbers given for each lot, mean values for body weight are 2.97 kg for males, and 2.07 for females, with an average body weight of 2.52 kg. With an estimated mean body mass of 4.8 kg, *T. lorenzinii* almost doubles that of the largest living didelphid. In conclusion, *T. lorenzinii* is the largest known didelphid, living or extinct.
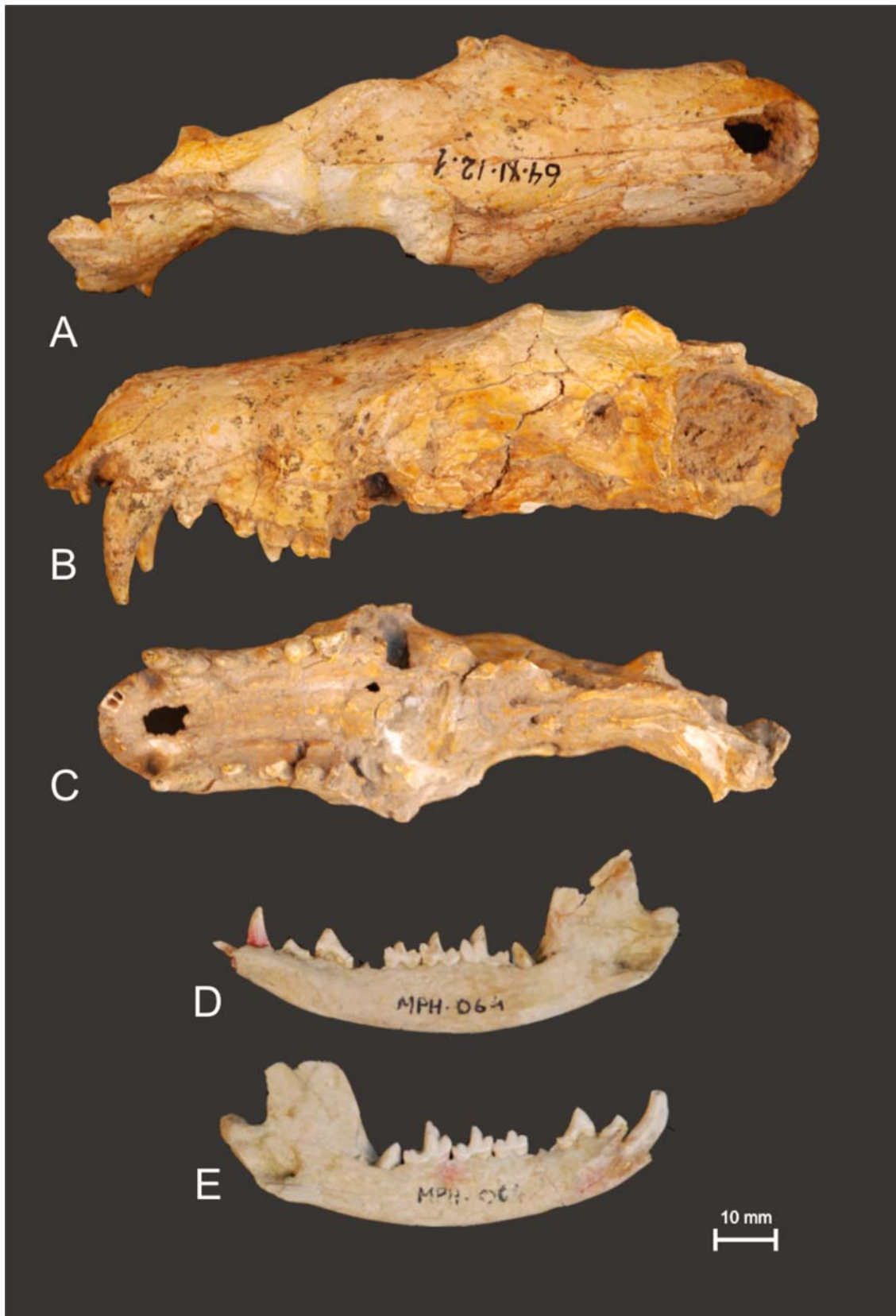
**FIGURE 5**: *Thylophorops chapalmalensis* Ameghino. A–C, detail of the rostrum and medial portion of the skull of an adult individual (MLP 64-XI-12-1) in dorsal (A), lateral (B), and ventral (C) views; D–E, detail of both mandibles of a juvenal specimen (MPH 064; D, right mandible in lingual view; E, left mandible in lingual view). In both mandibles, the erupting molar is m4. Scale: 10 mm.

**FIGURE 6**: *Thylophorops perplanus* (Ameghino). MLP 87-XI-15-1, a juvenile specimen preserving a partial skull (A, dorsal; B, lateral, and C, ventral views) and fragments of both mandibles (D, left mandible in labial view; E, right mandible in labial view). Scale: 10mm.
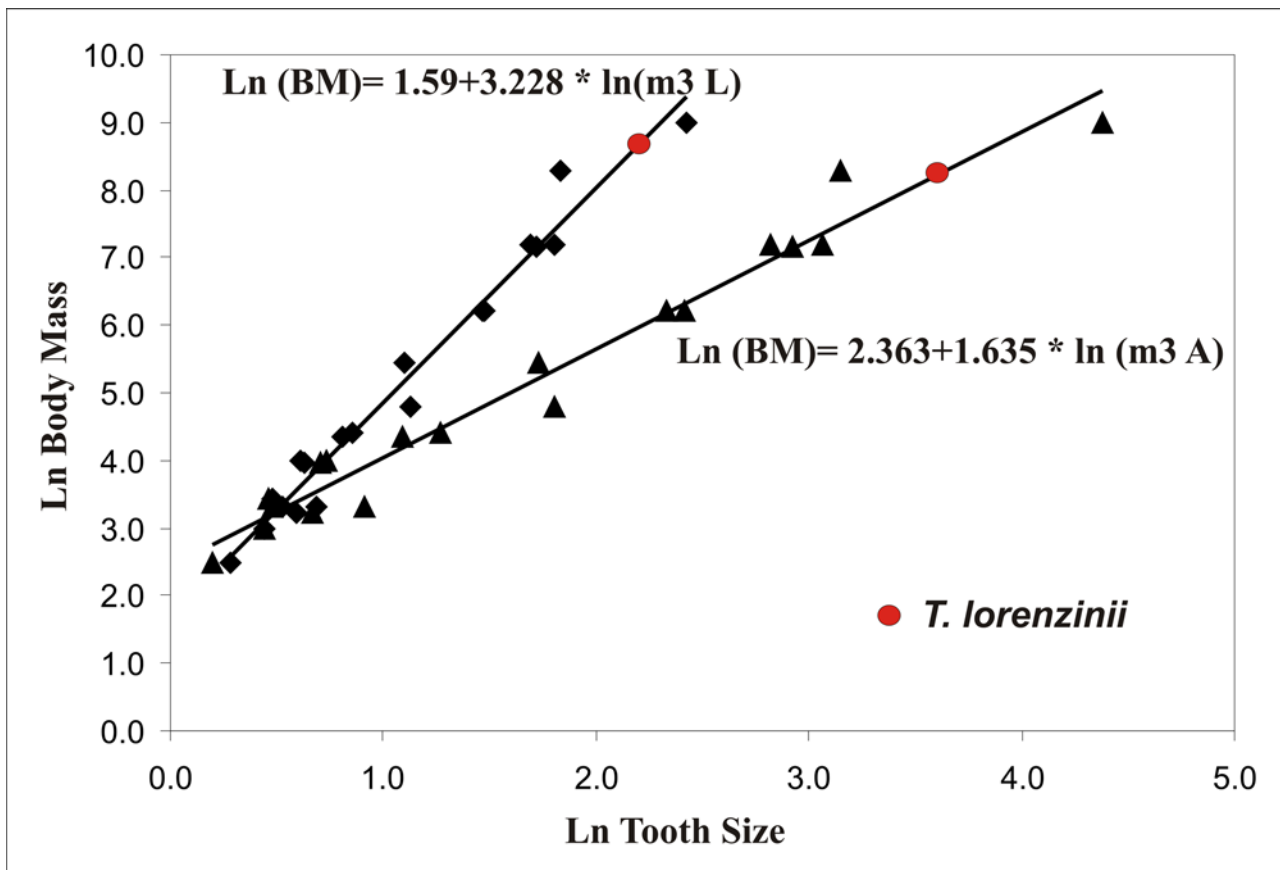
**FIGURE 7**: Regression plots showing the relationships between mean body mass and molar size (length and area). The red circle indicates the position of *T. lorenzinii*. See Table 1 for abbreviations.

Feeding habits of *T. lorenzinii* are inferred mainly by comparison with other species of the genus *Thylophorops*. The wear facet pattern observed in *T. chapalmalensis* (Zimicz, pers. obs.) is consistent with an omnivorous diet trending to carnivory, as the most developed wear facets in this species correspond to those of shearing activity (79.1% of the total wear facets). Although grinding surfaces (talonid, protocone) are developed in all three species of *Thyophorops*, they were less omnivorous than *Didelphis albiventris*, as indicated by an even larger development of grinding facets in the latter.

**Remarks**

The new species *T. lorenzinii* is clearly referable to the genus *Thylophorops* on the basis of the following aspects: (1) its large size; (2) it lacks the somewhat bunoid cusps and less trenchant crests typical of the species of *Didelphis*, and (3) its talonid basin is proportionally larger than that of the species of *Hyperdidelphys*. On the other side, it shares most of the molar features that characterize other known species of *Thylophorops* (see Goin & Pardiñas, 1996).

Specimen MLP 08-III-10-1 is the only specimen so far known that can be unequivocally assigned to *Thylophorops lorenzinii*. A couple of specimens of *T. chapalmalensis* have proportionally large size (see Simpson 1972, Goin 1991); however, none of them show the diagnostic features of the holotype of *T. lorenzinii* in their lower molars or approach its absolute size. *T. lorenzinii* is only known from the Sanandresan Substage of the Marplatan Stage/Age. Further research should explore its possible function as an index species for the Sanandresan or, alternatively, for the whole Marplatan Stage (Late Pliocene).

Previous studies of the faunal association recovered from levels of the San Andrés Formation reveal a peculiar assemblage characterized by the large numbers of first records of taxa. Caviomorph rodents have been recently reviewed by Verzi & Quintana (2005: 303); they concluded that the San Andrés caviomorph assemblage is the "…most clearly indicative of arid environments so far recorded. Its episodic character and composition, and the available palaeomagnetic data, reinforce the hypothesis that it is probably coeval with the profound Late Pliocene cooling and drying pulse detected worldwide around 2.5 Ma." (Verzi & Quintana 2005: 303). Based on that climatic event, Verzi & Quintana (2005) inferred that the caviomorph fauna of San Andrés is composed mostly of immigrant taxa from western Argentina, taxa that reached the more eastern Chapadmalalan area during the expansion of arid environments by ca. 2.5 Ma. The sudden appearance of *T. lorenzinii* in the fossil record seems to agree with these inferences, although we do not know the source area of this species in South America –either the Monte environments of western Argentina or, alternatively, the less arid, more forested Chaco habitats of northern Argentina and Paraguay.

## Acknowledgements

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