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The large American opossum *Didelphis* (Didelphimorphia, Didelphidae) in the Late Pleistocene of Uruguay, and paleoecological remarks

Aldo Manzuetti[a,*], Martín Ubilla[a], Daniel Perea[a], Raúl I. Vezzosi[b], Andrés Rinderknecht[c], Martín Ghizzoni[d], Washington Jones[c]

[a] *Facultad de Ciencias (UdelaR). Iguá 4225, CP, 11400, Montevideo, Uruguay*

[b] *Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CONICET, Gob. E.R., UADER), Materi y España, E3105BWA Diamante, Argentina, and Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Ruta Nacional 11 km 10,5, E3100XAD, Oro Verde, Entre Ríos, Argentina*

[c] *Museo Nacional de Historia Natural. 25 de Mayo 582, CP, 11000, Montevideo, Uruguay*

[d] *Escuela Tecnológica Superior de Administración y Servicios, Juan Carlos Gómez 351, CP, 50000, Salto, Uruguay*

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ABSTRACT

The fossil record of the genus *Didelphis*, despite its current diversity (6 species, 5 occurring in South America) and wide distribution (from southern Canada to Patagonia, Argentina), is very scarce. The oldest record of the genus in South America comes from Late Miocene sediments and the youngest records from the Late Holocene and historical times. In Uruguay, the only record is stratigraphically questionable because the material has been lost. The present contribution describes the first materials with a precise stratigraphic context assigned to *Didelphis* cf. *D. albiventris*, based on comparative morphological and numerical analysis. The materials were unearthed from several outcrops of the Sopas Formation (Late Pleistocene, northern Uruguay) and consist of an associated skull and mandible, right hemimandible, and postcranial material. These findings allow us to discuss several aspects related to the biology and ecology of *Didelphis*. These animals, which exhibit a mixed diet, were able to feed at intermediate levels of the food chain in highly diverse environments during the Late Pleistocene.

1. Introduction

The Didelphidae (Metatheria, Didelphimorphia) are the oldest marsupial mammals of the Neotropics (Pasquali and Tonni, 2004; Goin et al., 2007; Rocha and Rumiz, 2010). Extant didelphids include 19 genera and more than 90 species (Astúa, 2010; Rocha and Rumiz, 2010; Goin et al., 2016; Vezzosi et al., 2017) and vary in shape and size, ranging from 10-15 g and up to 2–6 kg (Goin et al., 2009 and references therein; Astúa, 2010; Rocha and Rumiz, 2010). They were grouped into four subfamilies: Caluromyinae, Glironiinae, Hyladelphinae and Didelphinae (Voss and Jansa, 2009; see also Goin et al., 2016).

The genus *Didelphis* has a South American origin (Dias and Perini, 2018) and a wide geographic distribution from southern Canada to Patagonia (Rocha and Rumiz, 2010; Goin et al., 2016; Dias and Perini, 2018). This clade has a controversial systematic history in which most mid-to large-sized American opossums (Didelphinae) have been classified under the genus *Didelphis* (e.g., Thomas, 1888, 1901; Allen, 1901, 1902; Rebin, 1901). Allen (1901, 1902) restricted the name *Didelphis* to a species complex, recognizing two groups from South America with wide distributional ranges (Cerqueira, 1980; Ventura et al., 2002; Flores, 2003; Flores et al., 2007; Cerqueira and Tribe, 2007): the *Didelphis marsupialis* group, with 2 allopatric species (*D. marsupialis* Linnaeus, 1758 and *D. aurita* Wied-Neuwied, 1826); and the *D. albiventris* group, with three species (*D. albiventris* Lund, 1840; *D. pernigra* Allen, 1900, and *D. imperfecta* Mondolfi and Pérez-Hernández, 1984).

Despite the current controversy, five extant species are recognized in South America (*D. albiventris*, *D. aurita*, *D. imperfecta*, *D. marsupialis*, and *D. pernigra*) in a wide diversity of environments (Cerqueira and Tribe, 2007; Gardner, 2007 and references therein).

Unlike North America (see Ferrusquía-Villafranca et al., 2010), South America has a scarce fossil record of large-sized opossums of the genus *Didelphis*. Didelphid remains come from the Late Miocene of Brazil (*Didelphis solimoensis*, Cozzuol et al., 2006) and the Pliocene-Pleistocene of Argentina and Brazil (Ameghino, 1904; Goin, 1991; Villa Nova et al., 2015; Vezzosi et al., 2017). Additionally, there are records of this genus from the Late Holocene and historical times in southern

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[*] Corresponding author.

E-mail addresses: aldomanzuetti@adinet.com.uy (A. Manzuetti), ubilla@fcien.edu.uy (M. Ubilla), perea@fcien.edu.uy (D. Perea), vezzosiraul@gmail.com (R.I. Vezzosi), apaleorinder@yahoo.com (A. Rinderknecht), martinghizzoni@gmail.com (M. Ghizzoni), wawijo@yahoo.com.ar (W. Jones).

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South America (Hadler et al., 2009; Vezzosi et al., 2017 and references therein). In Argentina, the Didelphinae group is represented by three species: *D. crucialis* (Ameghino, 1904) from the Late Pliocene and *D. reigi* Simpson, 1972 from the Late Pliocene-Early Pleistocene of Buenos Aires (Goin, 1991, 1999) and *Didelphis* cf. *D. marsupialis* from the early Late Pleistocene of Santa Fe (Vezzosi et al., 2017). In Brazil, this group is represented by *Didelphis* cf. *D. albiventris* and the first possible record of *Didelphis* cf. *D. aurita*; both of these species were recently recovered from Late Pleistocene deposits in northern Brazil (Villa Nova et al., 2015).

The fossil record of opossums in Uruguay is restricted to a single reference from Berro (1929), who reported the identification of *Didelphis* in “pampean sediments” (“Formación Pampeana”) but without precise stratigraphic data. Unfortunately, this material is currently lost, precluding taxonomic revision, which adds to its stratigraphic uncertainty (Mones and Rinderknecht, 2004).

In the present contribution, the first fossil remains with stratigraphic context of opossums of the genus *Didelphis* in Uruguay are described, which allows us to discuss different aspects related to its paleobiology and paleoecology. These records came from several fossiliferous outcrops of the Sopas Formation (Late Pleistocene) of northern Uruguay (Fig. 1).

2. Geological context

The Sopas Formation, located in northern Uruguay (in particular Artigas, Salto, Tacuarembó and Paysandú departments), is characterized by conglomerates with clay and calcareous matrices, conglomeratic sandstone, siltstone and sandy siltstone. This unit is predominantly brownish with a thickness of 5–8 m and the sedimentary facies were developed mostly under fluvial and associated depositional context (Martínez and Ubilla, 2004; Ubilla et al., 2016). Based on the mammalian fossil assemblage, this unit is correlated with deposits from the Late Pleistocene sequence of the Pampean region (Lujanian Stage/Age) (Cione and Tonni, 2005; Ubilla et al., 2011). Radiocarbon and optically stimulated luminescence (OSL) ages in some outcrops correlated mainly with MIS-3 (60-25 ka; Cohen et al., 2013; ICC, 2018), and it also includes outcrops at approximately 14 ka (Ubilla et al., 2016). Based on the paleontological content of the Sopas Formation, a wide range of environments can be suggested (lacustrine-fluvial, open areas, semiforested and dense vegetation) (Ubilla and Martínez, 2016).

3. Materials and methods

3.1. Institututional abbreviations

FC-DPV, Facultad de Ciencias- Colección Paleontológica (Vertebrados Fósiles), Montevideo, Uruguay; **MNHN-P**, Museo Nacional de Historia Natural, Sección Paleontología, Montevideo, Uruguay; **CPG**, Colección Paleontológica Ghizzoni, Salto, Uruguay; **MFA-ZV**, Museo Provincial de Ciencias Naturales “Florentino Ameghino”, Área Zoología de Vertebrados, Mamíferos, Santa Fe, Argentina; **MFA-PV**, Museo Provincial de Ciencias Naturales “Florentino Ameghino”, Área Paleontología de Vertebrados, Mamíferos, Santa Fe, Argentina; **CML**, Colección Mamíferos Lillo, Universidad Nacional de Tucumán-Fundación Miguel Lillo, Tucumán, Argentina; **MNHN**, Museo Nacional de Historia Natural, Sección Mamíferos, Montevideo, Uruguay; **ZVC-M**, Colección de Vertebrados de Facultad de Ciencias-Sección Mamíferos, Montevideo, Uruguay.

3.2. Comparative sample

To determine the systematic status of the studied specimens, different extant didelphids with diverse habitats and locomotor habits were analyzed: *Didelphis albiventris*, *D. aurita*, *D. marsupialis*, *Monodelphis dimidiata* (Wagner, 1847) and *Lutreolina crassicaudata* (Desmarest, 1804). Materials that were not available in hand for comparison were consulted through the literature (Voss et al., 2004; Flores, 2009; Flores and Díaz, 2009; Rincón et al., 2009; Villa Nova et al., 2015; Vezzosi et al., 2017). The dental nomenclature follows Goin and Pardiñas (1996) and Villa Nova et al. (2015).

3.3. Analyses

The body mass estimations followed the equations reported by Gordon (2003) based on upper and lower molar measurements of extant didelphids. The humeral robustness index was obtained following the methodology used by Vezzosi et al. (2017) (Supplementary material 1).

Multivariate analyses (principal component analysis, or PCA, and

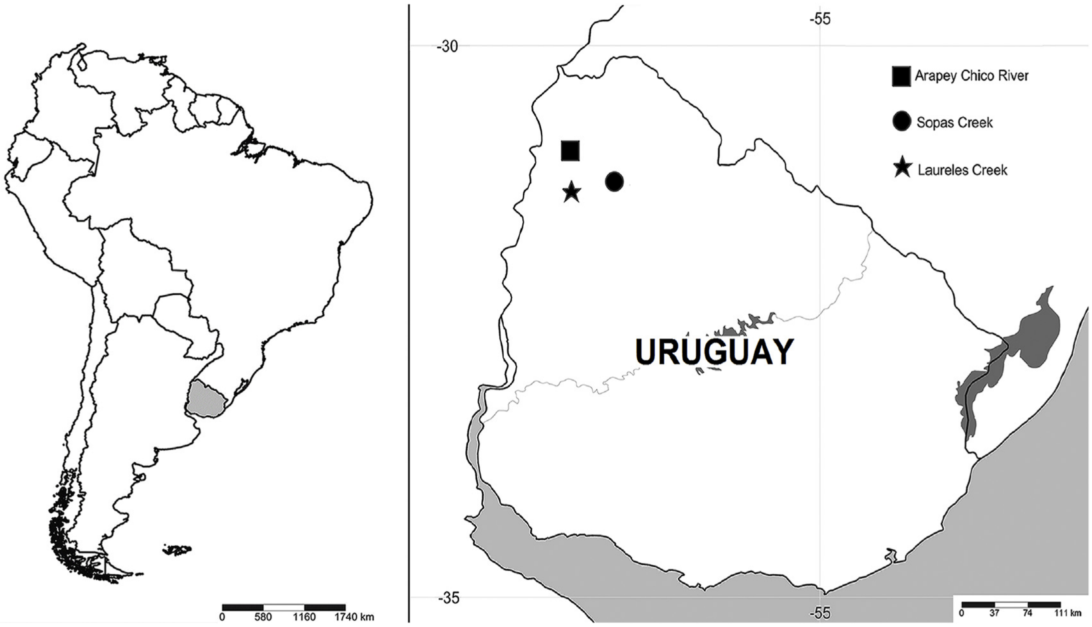

Fig. 1. Map of Uruguay showing the location of the findings: Arapey Chico River, Sopas Creek, Laureles Creek (department of Salto) (Sopas Formation).

hierarchical clustering) were performed on the variance-covariance matrix measurements using the statistical program PAST Version 3.19 (Hammer et al., 2001).

The material used in the numerical and comparative analyses is housed in the following collections: CML, MFA, MNHN, ZVC-M (Supplementary material 2), and from literature (Vezzosi et al., 2017).

3.4. Measurements

All measurements were performed with digital calipers that were accurate to 0.01 mm and expressed in millimeters, following von den Driesch (1976) and Vezzosi et al. (2017) (Supplementary material 3).

Skull measurements: total length (TL); tooth row length PM1-M3 (TRL PM1-M3); tooth row length PM3- M3 (TRL PM3-M3); tooth row length M1-M3 (TRL M1-M3); antero-posterior diameter of the PM3 (PM3 AP); transverse diameter of the PM3 (PM3 ML); antero-posterior diameter of the M1 (M1 AP); transverse diameter of the M1 (M1 ML); antero-posterior diameter of the M2 (M2 AP); transverse diameter of the M2 (M2 ML); antero-posterior diameter of the M3 (M3 AP).

Mandible measurements: total length (TL); tooth row length i-m4 (TRL i-m4); tooth row length pm1-m4 (TRL pm1-m4); tooth row length pm1-pm3 (TRL pm1-pm3); diastema pm1-pm2 (Diast pm1-pm2); tooth row length m1-m4 (TRL m1-m4); antero-posterior diameter of the pm1 (pm1 AP); transverse diameter of the pm1 (pm1 ML); antero-posterior diameter of the pm2 (pm2 AP); transverse diameter of the pm2 (pm2 ML); antero-posterior diameter of the pm3 (pm3 AP); transverse diameter of the pm3 (pm3 ML); antero-posterior diameter of the m1 (m1 AP); transverse diameter of the m1 (m1 ML); antero-posterior diameter of the m2 (m2 AP); transverse diameter of the m2 (m2 ML); antero-posterior diameter of the m3 (m3 AP); transverse diameter of the m3 (m3 ML); antero-posterior diameter of the m4 (m4 AP); transverse diameter of the m4 (m4 ML).

Humerus measurements: proximo-distal distance of the condyle (Dc); total length between the head and the distal condyle (Dhc); total length between head and distal trochlea (Dht); maximum length of the entepicondylar foramen (Def); latero-medial distance between the trochlea and the condyle (Dtc); antero-posterior maximum proximal width (Dh0); antero-posterior width of the humeral head (Dh1); latero-medial width of the head (Dh2); proximal distance between both tuberculum majus and tuberculum minus (Dh3); deltopectoral crest length (Ldc); maximum length of the olecraneon fossa (Lof); antero-posterior width of the shaft below of the crest (Wap); distal width (Wd); latero-medial width of the shaft below of the crest (Wlm).

4. Results

4.1. Systematic paleontology

Order Didelphimorphia Gill, 1872.
Superfamily Didelphoidea Gray, 1821.
Family Didelphidae Gray, 1821.
Subfamily Didelphinae Gray, 1821.
Tribe Didelphini Gray, 1821.
Genus *Didelphis* Linnaeus, 1758
Didelphis cf. *D. albiventris* Lund, 1840.

4.2. Referred material

FC-DPV 875, skull and mandible (Fig. 2).

4.2.1. Geographic and stratigraphic location

Sopas Creek (Department of Salto, Uruguay). Sopas Formation, Late Pleistocene (OSL age: 43.5 to 30.6 ka).

4.2.2. Comparative description

Fig. 2. FC-DPV 875; A) dorsal view of the skull, B) lateral view of the skull, C) lateral view of the mandible and D) occlusal view of the mandible.

Skull: The rostral region is relatively short and robust, as in *D. albiventris* (Astúa, 2015), and part of the left orbit is preserved. The nasals are narrow (Fig. 2A), and the infra-orbital foramen is located near the anterior edge of PM3. However, this character may vary in position in both *D. albiventris* and *D. marsupialis* (Flores and Abdala, 2001). The postorbital constriction is well marked (Fig. 2B). The sagittal crest is moderately well developed and anteriorly projected in a "V" shape (Schimming et al., 2016). The braincase, although broken, seems to be quite small and narrow. *Mandible*: The left hemi-mandible is more complete and better preserved than the right hemi-mandible (Fig. 2C and D). The ramus is high and robust, with the ventral edge slightly curved, similar in size to that of *D. albiventris* (Supplementary material 2) and differing from that of *D. marsupialis,* which shows a slightly more gracile mandible; the mental foramen is not preserved. The masseteric fossa is deep and its anterior edge does not reach the posterior edge of m4 as in extant didelphids. The angular process is inflected medially, as is characteristic of metatherians (Szalay, 1994; Sánchez-Villagra and Smith, 1997, Fig. 2D). The condyle, although broken, is latero-medially expanded; the coronoid process is a thin bone plate that is antero-posteriorly wide and slightly broken (Fig. 2C). *Dental series*: The dental series are partially preserved (Fig. 2C and D), and their general morphology is also typical of Didelphidae Didelphinae marsupials (Szalay, 1994; Tarquini et al., 2018, Fig. 2B, C, D). The material is much larger than *D. crucialis* and *D. solimoensis* (Cozzuol et al., 2006). Compared with *D. crucialis* and *D. reigi*, those species has more trenchant tooth morphology (Goin and Pardiñas, 1996; Cozzuol et al., 2006). The PM3 is well developed, larger than that in *D. albiventris* of similar size, with a high and sharp crown and a marked labial cingulum, much more so than in extant *Didelphis*. The m4 of the left ramus is the best preserved of the lower molars (Fig. 2C and D), with a trigonid longer than wide and more developed than a shorter talonid (Fig. 2C and D). The metaconid is well separated from the other cusps of the trigonid, while the protoconid is the highest cusp. In the talonid, the entoconid seems to be slightly higher than the hypoconid. The hypoconulid is located distally from the entoconid, as in *Didelphis albiventris* and *D. aurita*. In *D. marsupialis,* the entoconid is merged to the hypoconulid instead (Villa Nova et al., 2015).

4.2.3. Measurements (in mm)

Skull: TL, 103; TRL PM1-M3, 31; TRL PM3-M3, 21; TRL M1-M3, 17; PM3AP, 4.25; PM3ML, 3.19; M1AP, 5.04; M1ML, 4.55; M2AP, 4.46; M2ML, 5.11; M3AP, 5.91. Left hemi-mandible: TL, 84.48; TRL i-m4, 47.71; m2AP, 4.85; m2ML, 3.20; m3AP, 5.75; m3ML, 3.47; m4AP, 6.22; m4ML, 3.23. Right hemi-mandible: m1AP, 5.03; m1ML, 3.49; m2AP, 4.70; m2ML, 3.25; m4AP, 5.82; m4ML, 3.14.

4.2.4. Remarks

The morphologies and dimensions of the skull, mandible and dentition of specimen FC-DPV 875 agree with those of species of *Didelphis* (Cerqueira and Lemos, 2000; Lemos and Cerqueira, 2002; Ventura et al., 2002; Rincón et al., 2009; Astúa, 2010, 2015). The development of some morphological characters (such as the presence of a postorbital constriction, development of the sagittal crest, and shape of the nasals and mandibular condyle), the degree of development of the dentition (Abdala et al., 2001) and its occlusal wear (particularly for the M1-3 series and the left m4) allow us to infer that the FC-DPV 875 material belongs to an adult.

According to equations formulated for didelphids based on the upper and lower molars, the body mass estimation gives an average result of 1.254 kg (range 0.725–2.125 kg; Supplementary material 4), which is coherent with the range of *Didelphis* (Supplementary material 5).

The PCA performed on the left mandible indicated 8 components, among which PC1 explained almost 97% of the variance of the sample (Supplementary material 6). When the values of the first two components were plotted, the studied material fell within the morphospace distribution of *Didelphis albiventris* (Fig. 3A). The loading coefficients of the first component showed that the most influential variables were the TL and TRL i-m4. The cluster analysis concurred with these results and grouped the FC-DPV 875 material with *Didelphis*, particularly associated with *D. albiventris* (Supplementary material 6).

4.3. Referred material

MNHN-P 3000, fragment of right mandible (Fig. 4).

4.3.1. Geographic and stratigraphic location

Laureles Creek (Department of Salto, Uruguay). Sopas Formation, Late Pleistocene.

4.3.2. Comparative description

The mental foramen, filled with sediment, is located below pm1 (Fig. 4A). Distally, the masseteric fossa is deep and does not project to the posterior edge of m4 as in living didelphids. The angular process, the mandibular condyle and the coronoid process are broken (Fig. 4), although the last structure is similar to a thin, bony, broad, anteroposteriorly oriented blade. The ventral edge of the horizontal ramus is slightly convex. The dentition is partially preserved, lacking the incisors and the canine (for which only part of the alveolus is preserved) (Fig. 4B). The molar formula and morphology is also typical of marsupials. This material is much larger than *D. crucialis* and *D. solimoensis* (Cozzuol et al., 2006). Compared with *D. crucialis* and *D. reigi*, the material here described has not so trenchant tooth morphology (Goin and Pardiñas, 1996; Cozzuol et al., 2006).

The premolars are transversely compacted. The pm1 is quite reduced compared with the other premolars and separated by a small diastema. The pm2 is larger than pm3, as in extant didelphids (Goin, 2003; Cozzuol et al., 2006). The molar series increases in size distally. In m2-m4, an anterior labial cingulum is well developed (Fig. 4B). The m4 is well preserved and shows minor occlusal wear, with a trigonid that is slightly longer than wide, as occurs in most Didelphinae opossums except for *Chironectes*, in which the trigonid is as long as wide (Rincón et al., 2009); the talonid is short compared to the trigonid. The metaconid is well separated from the other cusps of the trigonid, similar in height to the paraconid, as occurs in *Didelphis*, differing from that of *Lutreolina*, in which the metaconid is very reduced (Rincón et al., 2009). The protoconid is the highest cusp, although the difference in size compared with the paraconid is much less marked than in *Lutreolina* and extinct didelphids (Rincón et al., 2009). In the talonid, the entoconid is slightly higher than the hypoconid. The hypoconulid, although not well preserved, is separated from the entoconid, as in *Didelphis albiventris* and *D. aurita*. In *D. marsupialis,* these cusps tend to coalesce with one another (Villa Nova et al., 2015).

4.3.3. Measurements (in mm)

TRL pm1-m4, 38.22; TRL pm1-pm3, 16.22; DIAST pm1-pm2, 1.77; TRL m1-m4, 21.98; pm1AP, 4.52; pm1ML, 1.21; pm2AP, 5.42; pm2ML, 1.92; pm3AP, 4.77; pm3ML, 2.33; m1AP, 4.69; m1ML, 2.95; m2AP, 4.81; m2ML, 3.30; m3AP, 5.23; m3ML, 3.32; m4AP, 5.68; m4ML, 2.92.

4.3.4. Remarks

The measurements of the teeth as well as the mandible morphology analyzed here are congruent with those observed in *Didelphis* (Cerqueira and Lemos, 2000; Lemos and Cerqueira, 2002; Ventura et al., 2002; Rincón et al., 2009), differing from the rest of the South American Didelphinae (Marshall, 1978; Macrini, 2004; Rincón et al., 2009). According to dentition development (Abdala et al., 2001) and occlusal wear, particularly those of the premolar and m1-m3 series, the specimen corresponds to an adult.

Body mass estimation based on the molar series produced an average result of 1.146 kg (range 0.934–1.452 kg; Supplementary material 4), matching the known mass of *Didelphis* (Supplementary material 5).

The PCA showed 6 components, the first of which explained more than 81% of the total variance of the sample (Supplementary material 6). The plot of the first two components grouped the MNHN-P 3000 material into the morphospace shared by *D. albiventris* and *D. marsupialis* (Fig. 3B). The loading coefficients of CP1 showed that the most influential variables were m4AP, m3AP and m2AP (with a significant contribution of their transverse diameter in each case). The cluster analysis also grouped the MNHN-P 3000 material within the *Didelphis* group, particularly associated with *D. albiventris* (Supplementary material 6).

4.4. Referred material

CPG 80-1, left complete humerus (Fig. 5), fragmentary right humerus, and other fragmentary postcranial bones.

4.4.1. Geographic and stratigraphic location

Arapey Chico River (Department of Salto, Uruguay). Sopas Formation, Late Pleistocene (OSL age: 36.9 ka).

4.4.2. Comparative description

The left humerus (CPG 80-1-2) is robust, large and better preserved than the other remains. The humeral head is relatively flat in lateral view and curved backwards (Fig. 5A). The greater and lesser tuberosities are well marked; the first has practically the same height as the humeral head (Fig. 5B). The shaft is straight and bears diverse muscle insertions, with those of the *deltoideus pars spinalis* (Fig. 5B and C), which is more developed than in extant didelphids, being highlighted. By contrast, the insertion of the *teres major* muscle shows a similar morphology as in *Didelphis albiventris* (Fig. 5B and C; Vezzosi et al., 2017). These muscle insertions are quite marked on the right humerus (CPG 80-1-3). Dorsally, the delto-pectoral crest is well developed, reaching the distal part of the shaft (Fig. 5B). The bicipital groove is present but relatively shallow. In the distal dorsal portion, the supracondilar foramen is wide and well developed and has the shape of an

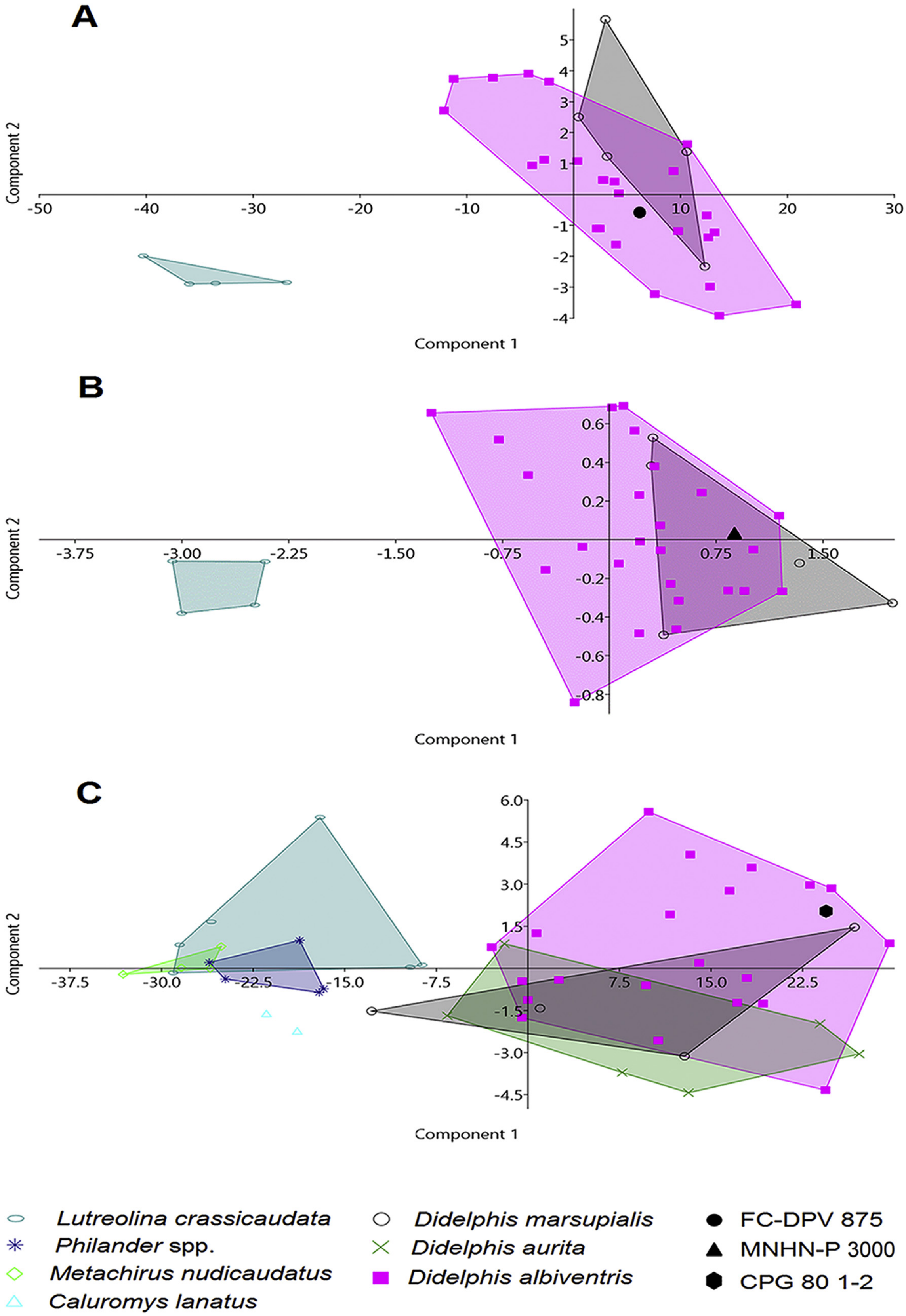

Fig. 3. Biplot of the first two components of the PCA: A) FC-DPV 875, B) MNHN-P 3000 and C) CPG 80 1–2.

oval section, as in extant didelphids (Vezzosi et al., 2017). In the right humerus, this foramen is more expanded dorsoventrally. The supracondilar bridge, which is straight to convex in form, is projected diagonally to the delto-pectoral crest as in extant Didelphinae. The supinator ridge is straight to convex, similar to that of *D. aurita* (Vezzosi et al., 2017). The proximal process of this ridge is high and rounded,

Fig. 4. MNHN-P 3000 in A) lateral and B) occlusal views.

Fig. 5. CPG 80 1–2 in A) inner lateral, B) frontal and C) posterior views.

most similar to that of *D. albiventris* among the living didelphids (Vezzosi et al., 2017). The capitulum is cylindrical, as in *Didelphis*, and connected with the trochlea by a deep groove. The entepicondilar surface is short and not as developed as in extant didelphids (Vezzosi et al., 2017). In the posterior view, the olecranon fossa is relatively deep (Fig. 5C).

4.4.3. *Measurements (in mm)*

Dc, 4.95; Dhc, 68.10; Dht, 69; Def, 4.70; Dtc, 13.95; Dh0, 16.40; Dh1, 12.60; Dh2, 12.75; Dh3, 15.60; Ldc, 35.35; Lof, 9; Wap, 6.20; Wd, 22.30; Wlm, 5.90.

4.4.4. *Remarks*

Sutures are apparent in both epiphyses of the left humerus, which means that the CPG 80-1-2 material belongs to a subadult.

The humeral robustness index (8.551) is close to the average of the indices calculated for *D. albiventris* (8.283) and *D. marsupialis* (8.314). However, the value of this index for the fossil material is in the expected range only for the large-sized Didelphidae species *D. albiventris* (Supplementary material 4).

The PCA shows 14 components, among which PC1 explains more than 96% of the total variance of the sample (Supplementary material 6). Between PC1 and PC2, CPG 80-1-2 is located in the morphospace of the largest species *Didelphis albiventris*, differing from *L. crassicaudata*, *Philander* spp. and *Caluromys lanatus* (Olfers, 1818) (Fig. 3C). The loading coefficients of PC1 show that Dht and Dhc are the most influential variables. The cluster analysis groups CPG 80-1-2 in the *Didelphis* group, with *D. albiventris* in particular (Supplementary material 6).

5. Discussion

5.1. *Anatomical comments*

The morphological characters and measurements of the fossil specimens described here are congruent with those of *Didelphis* (Cerqueira and Lemos, 2000; Lemos and Cerqueira, 2002; Ventura et al., 2002; Rincón et al., 2009; Astúa, 2010, 2015; Vezzosi et al., 2017). Moreover, the numerical analyses support a strong similarity with *Didelphis albiventris* (Fig. 3).

Thus, *Didelphis* species should be considered to differ mainly in external characters such as their coloration, kind of fur or overall body size, among others (McManus, 1974; Flores and Abdala, 2001; Lemos and Cerqueira, 2002; Ventura et al., 2002; Rocha and Rumiz, 2010; Dias et al., 2018). However, the body pattern of didelphids is quite conservative in strictly morphological terms (Medellín, 1991; Cerqueira and Lemos, 2000; Astúa et al., 2000; Flores and Abdala, 2001; Astúa, 2015; Amador and Giannini, 2016). This lack of specialization is evident in, for example, the skull anatomy and dental morphology of the didelphids (Amador and Giannini, 2016 and references therein).

Despite this scenario, six cranio-dental characters (the shape of the palatine process, development of the supra-orbital and suborbital process, shape of the internal acoustic meatus, shape of the lower petrosal groove and shape of PM2) that allow the differentiation of *D. albiventris* from *D. marsupialis* have been recognized (Flores and Abdala, 2001). The preservation of the skull in the FC-DPV 875 material does not allow the identification of such differences. However, the presence in the talonid of m4 of a hypoconulid separated from the entoconid in the FC-DPV 875 and MNHN-P 3000 material allows both materials to be assigned to *D. albiventris* (or inclusive *D. aurita*), in marked contrast with *D. marsupialis*.

The postcranial skeleton also shows a generalized pattern (Cozzuol et al., 2006 and references therein). Because of this, the species of the genus *Didelphis* show a wide variety of locomotor behaviors, such as arboreal, terrestrial, or aquatic behaviors, or a combination thereof (Szalay, 1994; Argot, 2001; de Muizon and Argot, 2003; Cozzuol et al., 2006; Flores, 2009). It should be noted that some preferences in those patterns have been reported (Supplementary material 5). Overall, the CPG 80 1–2 material shows a morphology (i.e., straight supracondilar bridge, relatively deep olecranon fossa, general morphology of the capitulum) related to the generalized pattern of terrestrial opossums with climbing abilities (Argot, 2001; Flores, 2009; Vezzosi et al., 2017). This similarity is also clearly shown by the humeral robustness index (Supplementary material 4). In summary, a clearly terrestrial locomotor behavior with scansorial skills is inferred for this material, as found in *Didelphis*.

5.2. *Paleoecological aspects*

Didelphis inhabits a wide variety of ecosystems, such as forested or open areas and arid environments in temperate or tropical climates (Gardner, 2007), mainly near water sources (Rocha and Rumiz, 2010; Chemisquy and Martin, 2016), which is in accord with the environmental amplitude inferred for the Sopas Formation (Ubilla and Martínez, 2016; Ubilla et al., 2016). Although living Didelphinae didelphids could occur in sympatry, certain distribution patterns have been identified in *Didelphis* species, showing a preference for a particular type of habitat (Dias and Perini, 2018). For example, *D. marsupialis* and *D. aurita* prefer humid/tropical forests in northern and southeastern South America, while *D. albiventris*, *D. imperfecta* and *D. pernigra* are most commonly found in open areas (such as savannah) of the Chacoan geographic subregion of northern South America (Guiana Shield) and environments of the Andean region, respectively (Gardner, 2007; Dias and Perini, 2018). Thus, it is expected that a segregation pattern with this or similar characteristics has probably occurred in the past.

Finally, *Didelphis* species play an essential role in the structure of the community of small mammals, being considered an important predator in middle levels of the trophic chain (Salvador et al., 2009 and references therein; Cantor et al., 2010 and references therein). The *Didelphis* diet is based mainly on small vertebrates such as rodents, birds, frogs, or lizards (including carrion), invertebrates (insects, crabs, spiders) and also fruits or grains (Cozzuol et al., 2006; Rocha and Rumiz, 2010; Siciliano Martina, 2013). However, even though juvenile and adult specimens of *Didelphis* have similar food habits, adults have a greater ability to feed on vertebrates (Siciliano Martina, 2013). As known before, this kind of generalist diet is considered one of the main factors contributing to the success of the group (McManus, 1974; Cantor et al., 2010). In this context, *Galea* sp., *Microcavia criolloensis* Ubilla et al. (1999), *Reithrodon* sp. and *Lundomys molitor* (Winge, 1887) (4 small rodents) are recorded in the Sopas Formation (Prevosti et al., 2009 and references therein; Ubilla and Martínez, 2016), so the possibility that these species could have been potential prey of *Didelphis* species during the Late Pleistocene in the territory of current Uruguay cannot be ruled out.

6. Conclusions

The materials described here (skull, mandibles and humerus) correspond to the *Didelphis* group (probably to the species *D. albiventris*), which is substantiated by morphological comparisons and numerical analysis. They represent the first stratigraphically reliable fossil record for the genus in Uruguay, all of which belong to the Sopas Formation (Late Pleistocene). Living *Didelphis* opossums, beyond presenting a generalist diet, have the capacity to prey in middle trophic levels in a wide variety of environments. Thus, during the Late Pleistocene in the territory of Uruguay, the potential prey of these opossums could have been small rodents, among other small animals.

Declaration of Interest statement

There are no conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2019.102437.

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