

SYSTEMATIC REVISION OF “*CANIS*” *ENSENADENSIS* AMEGHINO, 1888 (CARNIVORA, CANIDAE) AND THE DESCRIPTION OF A NEW SPECIMEN FROM THE PLEISTOCENE OF ARGENTINA



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Abstract. The fossil record of foxes in South America is very rich, with almost all extant South American species recorded. Currently, three fossil species are known in the Plio-Pleistocene of South America: “*Dusicyon*” *cultridens*, *Dusicyon avus* and “*Canis*” *ensenadensis*. In the present work we reviewed the systematics of “*Canis*” *ensenadensis* from the Pleistocene of Buenos Aires province using both qualitative and quantitative approaches. We also described a new fossil specimen (MCA 2082) from Buenos Aires Province (Argentina) that shares some similarities with “*Canis*” *ensenadensis*. We compared the fossil specimens with a large sample of specimens that includes the living species *Lycalopex gymnocercus*, *L. culpaeus*, *Cerdocyon thous*, *L. fulvipes*, *L. vetulus*, *L. sechurae* and *Atelocynus microtis*. We performed a Principal Component Analysis using mandibular and dental measurements, and then a geometric morphometric analysis using photographs of the lateral view of the mandible. Our results indicate that “*Canis*” *ensenadensis* is a valid species and it should be included in the genus *Lycalopex*. We also conclude that MCA 2082 is a member of the genus *Lycalopex*, probably belonging to the species *L. ensenadensis*. These results suggest that the biocron of *L. ensenadensis* reaches the Lujanian Age. Even if our assignation of MCA 2082 is incorrect, this specimen represents a different taxon from those already described for the Lujanian, thus the diversity of foxes during the Lujanian is greater than previously known.

Key words. Foxes. Fossil. Pleistocene. Systematics.

Resumen. REVISION SISTEMÁTICA DE “*CANIS*” *ENSENADENSIS* AMEGHINO 1888 (CARNIVORA, CANIDAE) Y LA DESCRIPCION DE UN NUEVO ESPECIMEN DEL PLEISTOCENO DE ARGENTINA. El registro fósil de zorros en América del Sur es muy rico con prácticamente todas las especies sur americanas actuales representadas en él. En la actualidad se conocen tres especies extintas para el Plio-Pleistoceno de América del Sur. “*Dusicyon*” *cultridens*, *Dusicyon avus* y “*Canis*” *ensenadensis*. En el presente trabajo hemos reestudiado la sistemática de “*Canis*” *ensenadensis* del Pleistoceno de la provincia de Buenos Aires abordando enfoques cualitativos y cuantitativos. Además describimos un nuevo espécimen proveniente de la Provincia de Buenos Aires (Argentina) que comparte ciertas características con “*Canis*” *ensenadensis*. Los especímenes fósiles fueron comparados con una gran muestra de especímenes actuales correspondientes a las especies *L. gymnocercus*, *L. culpaeus*, *Cerdocyon thous*, *L. fulvipes*, *L. vetulus*, *L. sechurae* y *Atelocynus microtis*. Se realizó un Análisis de Componentes Principales, utilizando medidas mandibulares y dentarias, y un análisis de morfometría geométrica, utilizando fotografías de vistas laterales de la mandíbula. Nuestros resultados sugieren que “*Canis*” *ensenadensis* es una especie válida y que debe ser incluida en el género *Lycalopex*. Además concluimos que MCA 2082 es un miembro del género *Lycalopex*, perteneciendo tentativamente a la especie *Lycalopex ensenadensis*. Esto sugiere que el biocron de *Lycalopex ensenadensis* alcanzaría la Edad Lujanense. Incluso si nuestra asignación fuese incorrecta, el espécimen representaría una especie distinta a las descritas para el Lujanense, por lo que la diversidad de zorros del Lujanense es mayor a la previamente conocida.

Palabras clave. Zorros. Fósiles. Pleistoceno. Sistemática.

FOXES are presently represented in South America by seven genera and nine species (Wilson and Mittermeier, 2009; Zunino *et al.*, 1995; Prevosti *et al.*, 2011a). They first appeared in the fossil record of South America in the Late Pliocene of the Pampean Region, when the extinct species “*Dusicyon*” *cultridens* was recorded (Berman, 1994; Cione *et al.*, 2007; Soibelzon and Prevosti, 2007; Prevosti and Soibelzon, 2012). Other two extinct species are recorded in the fossil record of Argentina: *Dusicyon avus* from the Ensenadan?-Platan (early

Pleistocene-late Holocene) of the Pampean region (Berman, 1994; Soibelzon and Prevosti, 2007; Prevosti *et al.*, 2011b) and “*Canis*” *ensenadensis* from the Ensenadan of the Buenos Aires Province (Berman, 1994; Soibelzon and Prevosti, 2007; Prevosti *et al.*, 2011b; Prevosti and Soibelzon, 2012). There are fossil records for almost all the living South American foxes from different fossil sites assigned to the Pleistocene and Holocene of South America (Berman, 1994; Hadler Rodríguez *et al.*, 2004; Soibelzon and Prevosti, 2007; Amorosi

and Prevosti, 2008). Although South American foxes have a relatively good fossil record, an updated and comprehensive systematic revision of the group is missing being the most inclusive works some early mentions from the end of the nineteenth century and the beginning of the twentieth century (*e.g.*, Ameghino, 1889; Kraglievich, 1930), and an unpublished PhD Thesis of the late twentieth century (Berman, 1994) that reviewed the fossil carnivores of Buenos Aires Province (Argentina).

“*Canis*” *ensenadensis* Ameghino, 1888 was described based on an incomplete mandible (MLP 10-56) from Ensenada, Buenos Aires Province, Argentina. Ameghino (1888) mentioned a close tooththrow, small canines, and a robust mandible body as diagnostic characters for the species. Later, other authors discussed the systematics of “*Canis*” *ensenadensis*. Kraglievich (1930) and Cabrera (1931) assigned it to the genus *Cerdocyon* but without mentioning any morphological character to support their decision. Berman (1994) in his unpublished PhD Thesis proposed that the species should be included in the genus *Dusicyon* (*sensu lato*), after comparing it with *Lycalopex gymnocercus* and *L. culpaeus* (both species considered as members of *Dusicyon* by Berman), being this arrangement followed by Nabel *et al.* (2000) and Prevosti *et al.* (2005). Recent phylogenetic analyses changed the nomenclature of South American foxes, restricting the genus *Dusicyon* to two species: *D. australis* (the type species) and *D. avus*, and including the remaining species in the genus *Lycalopex* (Zunino *et al.*, 1995; Slater *et al.*, 2009; Prevosti, 2010). These phylogenetic and nomenclatural changes leave in a dubious status the position and validity of “*Canis*” *ensenadensis*. The systematic review of “*Canis*” *ensenadensis* is relevant to understand of the evolution of South American foxes, and will be useful for broader paleoecological and evolutive studies.

In this contribution we used a descriptive and a qualitative approach, plus traditional and geometric morphometrics, and a large sample of taxa and specimens, to evaluate the taxonomic validity of “*Canis*” *ensenadensis*, its generic position and to amend the diagnosis of the species. We also described a new fossil specimen (MCA 2082) from Mercedes, Buenos Aires Province, Argentina.

MATERIALS AND METHODS

Institutional abbreviations. MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Ar-

gentina; **MCA**, Museo “Carlos Ameghino”, Mercedes, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **AMNH**, American Museum of Natural History, New York, USA; **FMNH**, Field Museum of Natural History, Chicago, USA; **IPUP**, Universidad de Piura, Piura, Peru; **MNHNS**, Museo Nacional de Historia Natural de Santiago, Santiago de Chile, Chile; **MUSM**, Museo de la Universidad de San Marcos, Lima, Peru.

Anatomical abbreviations. **i**, incisor; **c**, canine; **p**, premolar; **m**, molar.

Measurement abbreviations. **HCP**, height of the coronoid process; **HMm1**, height of the mandible at the m1 insertion; **HMP2**, height of the mandible at the p2 insertion; **Lc1**, length of the c1; **LCP**, length of the coronoid process; **LM**, length of the mandible; **Lm1**, length of the m1; **Lm2**, length of the m2; **Lp3**, length of the p3; **Lp4**, length of the p4; **Ltrm1**, length of the trigonid of the m1; **Wc1**, width of the c1; **Wm2**, width of the m2; **WMm1**, width of the mandible at the m1 insertion; **Wp3**, width of the p3; **Wp4**, width of the p4; **Wtlm1**, width of the talonid of the m1.

We performed a qualitative comparison between the holotype of the species “*Canis*” *ensenadensis* (MLP 10-56) and several specimens of South American living species of foxes. We considered the intraspecific variation present in the qualitative characters mentioned by Ameghino as diagnostic of “*Canis*” *ensenadensis*. We also compared a new specimen from Mercedes (MCA 2082) with the holotype of “*Canis*” *ensenadensis* and specimens of South American extant foxes. We followed the anatomic nomenclature of Evans (1993) for the osteological anatomy, Wang *et al.* (1999) for the names of the cusps, and the nomenclature proposed by Smith and Dodson (2003) for the orientation of the teeth, with the modifications introduced by Prevosti (2006), Prevosti and Rincon (2007) and Prevosti *et al.* (2011b).

We measured 481 specimens of three living species of foxes: *Lycalopex gymnocercus* (401 specimens), *L. culpaeus* (39 specimens) and *Cerdocyon thous* (41 specimens) housed in the División Mastozoología of the Museo Argentino de Ciencias Naturales (MACN). We used 17 mandibular and dental measurements taken with a digital calliper (0, 01 mm) (Fig. 1.1–2). To summarize the intraspecific variation, we performed a principal component analysis (PCA) from the variance-covariance matrix, using the set of logarithm transformed measurements (following Legendre and Legendre, 1998). To avoid the size

effect we also performed a PCA using the correction by geometric means, as used by Meachen-Samuels and Van Valkenburgh (2009). Both analyses were performed using the software R v.2.10.1 (R Development Core Team, 2010). For specimen MCA 2082 we used the complete measurement set in both analyses. The measurements used were: Lc1, Wc1, Lp3, Wp3, Lp4, Wp4, Lm1, Ltrm1, Wtlm1, Lm2, Wm2, LM, HCP, LCP, HMm1, WMm1 and Hmp2. When MLP 10-56 was included, given its fragmentary nature, a reduced set of measurements was used in both analyses. The measurements used in this case were: Lc1, Wc1, Lp3, Wp3, Lp4, Wp4, Lm1, Ltrm1, Wtlm1, Lm2, Wm2, HMm1, WMm1 and Hmp2 (see abbreviations below).

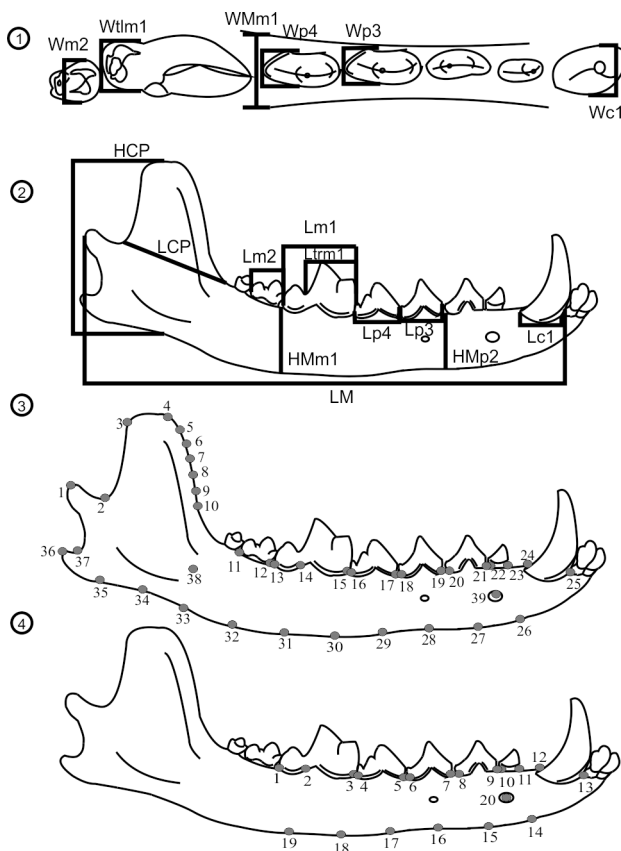


Figure 1. Mandible measurements used in the PCA and landmarks used in the geometric morphometry analyses. **1**, measurements in occlusal view; **2**, measurements in lateral view; **3**, full set of landmarks; **4**, landmarks used in the analysis with the reduced set of landmarks. **Abbreviations:** HCP, height of the coronoid process; HMm1, height of the mandible between the m1 and the m2; Hmp2, height of the mandible between the p2 and the p3; Lc1, length of the c1; LCP, length of the coronoid process; LM, length of the mandible; Lm1, length of the m1; Lm2, length of the m2; Lp3, length of the p3; Lp4, length of the p4; Ltrm1, length of the trigonid of the m1; Wc1, width of the c1; Wm2, width of the m2; WMm1, width of the mandible between the m1 and the m2; Wp3, width of the p3; Wp4, width of the p4; Wtlm1, width of the talonid of the m1.

We also analyzed the shape of the mandible using geometric morphometry (Zelditch *et al.*, 2004). We used photographs of the lateral view of the mandible aligning its sagittal plane with the horizontal plane (*i.e.*, the table). We photographed 233 specimens of the living species: *L. gymnocercus* (147), *L. culpaeus* (39) and *CC.e. thous* (47). *Atelocynus microtis*, *L. fulvipes*, *L. sechurae* and *L. vetulus* were not included because they can be distinguished from the fossils by their size and other qualitative characters. To capture the shape of the mandible we used 39 landmarks, illustrated in Figure 1.3. When only MCA 2082 was included the complete set of landmarks was used and when MLP 1050 was included a reduced set was used (Fig. 1.4). The landmark configurations were superimposed by a generalized Procrustes analysis (Goodall, 1991; Rohlf, 1999). Then we performed a PCA using the software Morpho J v.1.02b (Klingenberg, 2011). The semilandmarks were relaxed during the Procrustes analysis in a preliminary analysis using TpsRelw (Rohlf, 2003), but the results were similar to those obtained with MorphoJ (without relaxing the semilandmarks), so we only included the results obtained with MorphoJ. Size differences were studied using qualitative comparisons between the measurements used in the analyses, and using centroid size boxplots from the values obtained in the geometric morphometry analyses.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

Family CANIDAE Fischer von Waldheim, 1817

Subfamily CANINAE Fischer von Waldheim, 1817

Genus *Lycalopex* Burmeister, 1854

Type species: *Canis vetulus* Lund, 1842, by subsequent designation; Recent; Minas Gerais, Brazil.

Lycalopex ensenadensis (Ameghino, 1888) nov. comb.

Figure 2.1–3

Canis ensenadensis Ameghino, 1888.

Canis (Cerdocyon) ensenadensis (Ameghino, 1888) Kraglievich, 1930.

Cerdocyon (Cerdocyon) ensenadensis (Ameghino, 1888) Rusconi, 1933.

Cerdocyon ensenadensis Prevosti and Reguero, 2000.

Cerdocyon ensenadensis (Ameghino, 1888) Prevosti and Reguero, 2000.

Emended diagnosis. Mandible with tooth row lacking diastemas between the premolars and between the p4 and the m1; slender body (proportionally long and low in relationship to dentition and the rest of the mandible); p3, p4 and m1 long

relative to their width and other dental measurements; m2 narrow in relation to its length and the rest of dental measurements. This species is different from *L. culpaeus* by its convex and sharp posterior cingulum of the p4. *L. ensenadensis* is different from *L. gymnocercus* by having larger teeth when compared to the size of the mandible. It is conspicuously larger than other species of the genus *Lycalopex* (i.e., *L. sechurae*, *L. fulvipes*, *L. vetulus*).

Studied material. Holotype of “*Canis*” *ensenadensis* (MLP 10-56). Incomplete mandible lacking both anterior and posterior ends and preserving the left c1 and p2–m1 and the right p1–m2 (Fig. 2.1–3).

Locality and horizon. Ensenada Harbor, Ensenada, Buenos Aires Province, Argentina. The locality has been stated by Ameghino (1889) as the type locality for his Ensenadan Age. Tonni *et al.* (1999) stated that the locality has not been available for study since Ameghino’s times, so they proposed a new type locality for the Ensenadan Age, near Ensenada, in a quarry located in José Hernández, Buenos Aires Province. The age is based on the *Mesotherium cristatum* biozone proposed by Cione and Tonni (2005). The upper limit of this age is near the base of the Brunhes Chron (tentatively at 0.5 My) and its lower limit is placed near 1.8–2 My (Cione and Tonni, 2005; Woodbourne *et al.*, 2006; Prevosti and Soibelzon, 2012).

Description. The fragmentary right mandible of MLP 10-56 bears the p1–m2, an elliptical mental foramen below the p3 mesial root, but the anterior mental foramen is not observable. The left mandible is more complete and preserves the most anterior part of the coronoid process, but the body lacks its anterior end. The dental elements preserved are the c1, which lacks its apical end, and the p2–m1. The tooth row is closed, lacking gaps between the dental elements, except for a small space between p1 and the rest of the premolars. The presence of the m3 is evidenced by the alveolus of this element in the left mandible. The lower canine lacks its apical end and is mesiodistally shorter when compared with other dental elements. The p1 is a small element and it has one root and one distally oriented cusp. The p2 has two roots and one cusp and the distal cingulum is reduced. The p3 and p4 are similar in shape, both show well developed distal cingula and distal accessory cusps. The accessory cusp of the p4 is more developed than the one of the p3, being longer and taller. The distal cingulum is more developed than in the p3. The distal cingulum

of the p4 is well developed and in occlusal view is distally convex. The preserved molars are at an advanced stage of wear. The m1 is large in comparison with the m2. Its trigonid is long when compared with the talonid; the linguodistally oriented metaconid is well developed. The main cusps of the talonid (entoconid and hypoconid) are similar in size and are connected by a transverse cristid. The protostylid is absent. The m2 is short and narrow and its protoconid is subtriangular in transversal section and more developed than the metaconid. Both cusps are connected by a transverse cristid. The entoconid and the hypoconid are well developed and are connected by a transverse cristid. The entoconid is smaller than the hypoconid, which is similar in size to the metaconid.

Comparisons. MLP 10-56 is characterized by its large dental elements related to the size of the mandible. This feature was mentioned by Berman (1994) as characteristic of *L. ensenadensis*. This species shares with *C. thous* a small canine when compared to the rest of the dental elements. The closed tooth row is a character that shows considerable variation in the species of canids used for comparison. It is more frequent in *Cerdocyon* (16 of 57 studied specimens) than in *Lycalopex gymnocercus* (2 of 202 studied specimens) and *Lycalopex culpaeus* (0 of 39 studied specimens).

The flat and wide morphology of the distal cingulum of the p4 of *L. culpaeus* is a character that allows the distinction of this species from other related species. In *L. ensenadensis* the distal cingulum of the p4 is convex and sharp as in *L. gymnocercus*, contrasting with *L. culpaeus* that has a flat distal border.

The closed toothrow of *L. ensenadensis* is a character shared with *A. microtis*. The latter differs from *L. ensenadensis* in that it has short and low premolars in lateral view, which are proportionally shorter and more robust in occlusal view than are those of *L. ensenadensis*. *Lycalopex vetulus*, *Lycalopex sechurae* and *Lycalopex fulvipes* can be distinguished from the holotype of *L. ensenadensis* by its considerable smaller size (Berta, 1987; see below).

L. ensenadensis can be distinguished from “*Dusicyon*” *cultridens* because the latter is smaller and has a conspicuously open tooth row (Berman, 1994).

Lycalopex* cf. *L. ensenadensis

Figure 2.4–5

Studied material. MCA 2082: right mandible with c1–m2. (Fig. 2.4–5).

Locality and horizon. One hundred meters from the 29th Street bridge (Eduardo Carrasco Av.), on the right margin of the Arroyo Frías (34°36'30.0"S–59°25'32.9"W), Mercedes, Buenos Aires Province, Argentina. The specimen was collected from red sand to silt included in the Lujan Rojo sequence of Toledo (2011). The age of this sequence has been established

by Toledo (2011) using OSL and ¹⁴C between 32360± 2150 years and 13860± 50 years BP (non calibrated). An OSL date of 32360± 2150 years was obtained for the Ameghino excavation named Paradero 1, at water level on the Arroyo Frías (Toledo, 2011). This locality is placed downstream from the locality of MCA 2082, 0.5 km away.

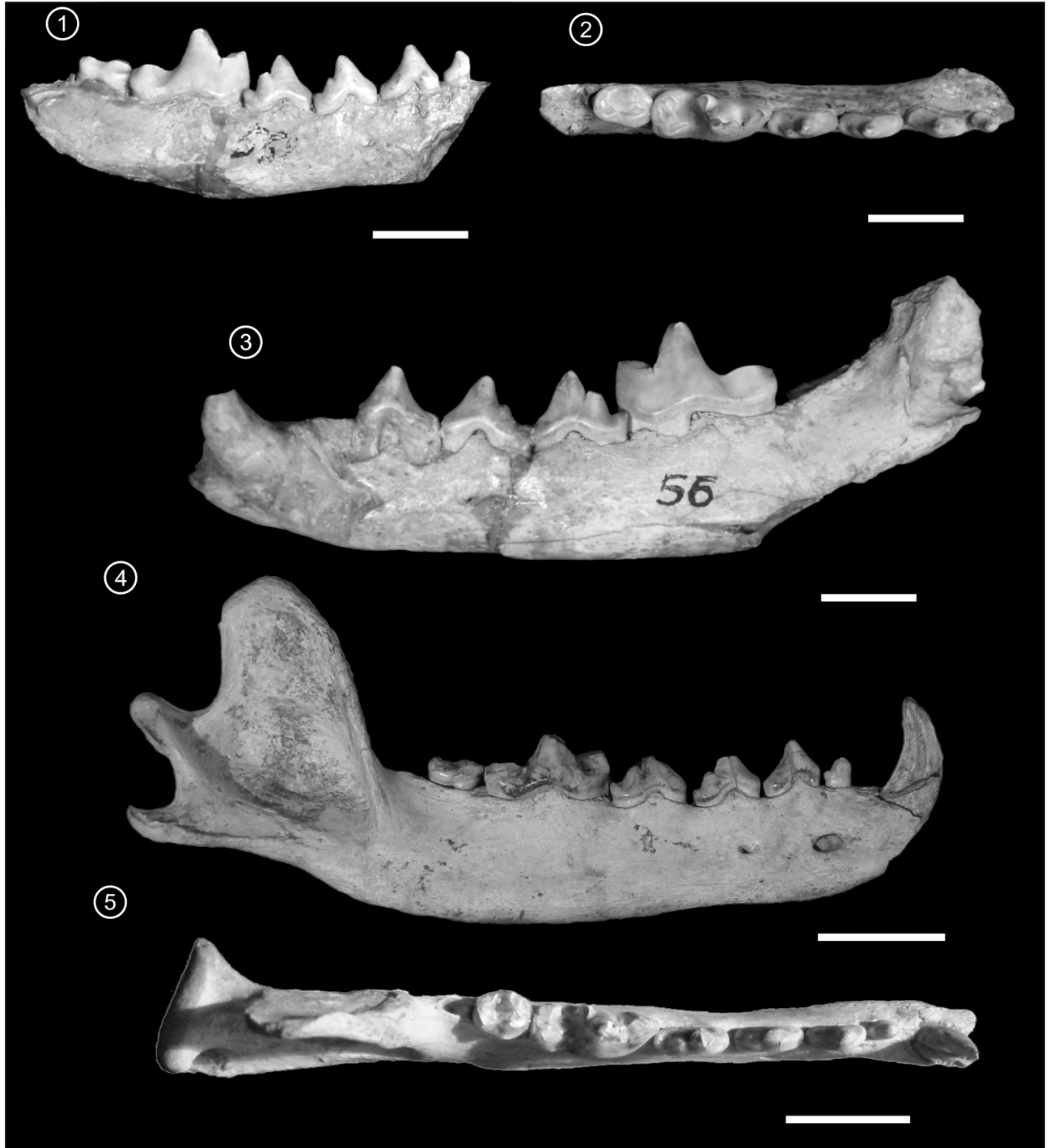


Figure 2. 1–3, *L. ensenadensis* (Ameghino, 1888), MLP 10-56; 1, right mandible in lateral view; 2, right mandible in occlusal view; 3, left mandible in lateral view. 4–5, *L. cf. L. ensenadensis*, MCA 2082; 4, lateral view; 5, occlusal view. Scale bar= 10 mm.

Description. The right mandible is well preserved, lacking only its anterior end and the incisors. The body is dorsoventrally tall and mesiodistally short, which makes it a robust element. It preserves both mental foramina. The anterior mental foramen is bigger, elliptical, and is placed under the root of the p1. The posterior mental foramen is rounded, and is placed under the mesial root of the p3. The low coronoid process is subrectangular in lateral view. The pterygoid fossa is not expanded dorsoventrally, which gives the angular process a compressed morphology. In this specimen the tooth row is open, but the diastemas between the premolars and between the p4 and the m1 are very short. The m3 is not preserved but its alveolus is present. The crown of the canine is broken at its labial half and the element is mesiodistally short when compared to the other dentary elements. The p1 is small and has one root and one cusp that show some degree of wear. The p2 has two roots and one cusp. Both p3 and p4 have distal cusps and a distal cingulum. The distal cingulum of the p4 is convex and acute in occlusal view. In both elements a high degree of wear can be observed. The molars show an advanced degree of wear. The m1 is a large element when compared to the other teeth. Its trigonid is long when compared to the talonid. The well developed metaconid is placed in the protoconid linguo-distal margin. On the labio-distal surface of the protoconid a small protostilid can be observed. Because of wearing the existence of a mesoconid cannot be confirmed. The mesoconulid is absent. The hypoconid is bigger than the entoconid and both cusps are connected by a transversal cristid. The m2 is as long as the talonid of the m1 and it shows a high degree of wear. The protoconid is bigger than the metaconid and both cusps are connected by a transversal cristid. The hypoconid is well developed, having a similar diameter to the protoconid. The entoconid is reduced, having a crest-like shape. The mesiolabial cingulum extends to the distal end of the metaconid.

Comparisons. The morphology observed in the posterior region of the mandible resembles the morphology of the genus *Lycalopex*. This region is different in *C. thous* and *A. microtis*, which exhibit an angular process with a dorsoventrally expanded pterygoid fossa and a well developed subangular lobe, characters absent in MCA 2082. An interesting feature of this specimen is the robust body of the mandible, with both posterior and anterior ends having similar heights. This morphology is similar to the observed in several specimens of *L. culpaeus* and different from the morphology observed in *L.*

gymnocercus, the latter showing the anterior end of the mandible body lower than the posterior end. The reduction of the diastemata in the tooth row is a character that allows us to distinguish this specimen from *L. culpaeus* and most of the specimens of *L. gymnocercus* because both of them have well developed gaps between the dental elements of the tooth row. However, there are two specimens of the last species that have a similar condition.

When comparing MCA 2082 with MLP 10-56 some similarities can be observed. Both materials present a reduction in the gaps of the tooth row; this character is more extreme in MLP 10-56 where the gaps are absent. Another shared feature is the presence of accessory distal cusps on the p3, although this character is very variable in canids (Szuma, 2000, 2002; Prevosti, 2006). MCA 2082 presents a more robust body of the mandible than MLP 10-56, in the latter the mandible tends to be lower (see geometric morphometry analysis below). Another difference is the development of the entoconid of the m2; this cusp is reduced in MCA 2082 but in MLP 10-56 is well developed. The mandible MCA 2082 is conspicuously larger than *L. vetulus*, *L. fulvipes* and *L. sechurae* (see below).

"*Dusicyon*" *cultridens* was diagnosed by its small size and its slender mandible (Gervais and Ameghino, 1880), these characters are different from those observed in MCA 2082, which is a medium-sized form with a particularly robust mandible.

Traditional morphometrics

The first axis of the PCA showed, with the reduced set of variables and without the size correction, a strong influence of size in the distribution of the specimens, with the bigger specimens placed in the positive values (Fig. 3.1). In the second axis, the specimens placed in the positive values presented wider premolars (p3 and p4), wider m2 and talonid of m1, shorter canine (low influence of c1), and lower mandibles (low influence of HMm1 and HMp2). Regarding the distribution of the species in the analysis, a general pattern could be observed, in which the species of *Lycalopex* could be distinguished in the first axis, and the genera *Lycalopex* and *Cerdocyon* were placed separated in the second axis. This analysis, that did not include size correction, showed a strong influence of the size, separating in the first axis the species *L. culpaeus* from *L. gymnocercus* and *C. thous*. This could be observed in the eigenvectors plot, where all the vectors pointed to the same direction in the first axis (Fig. 3.2). In the analysis where measurements

were corrected using geometric means (Figs. 3.3–4), the first axis showed specimens with taller mandibles, longer and wider canines in the positive values. Specimens with negative values in the first axis showed a longer and wider m2 and wider

talonid of the m1. The second axis showed, in the positive values, wider premolars (p3 and p4) and taller mandibles, while the negative values showed a longer m1 with a longer trigonid. Regarding the distribution of the living species, it is interest-

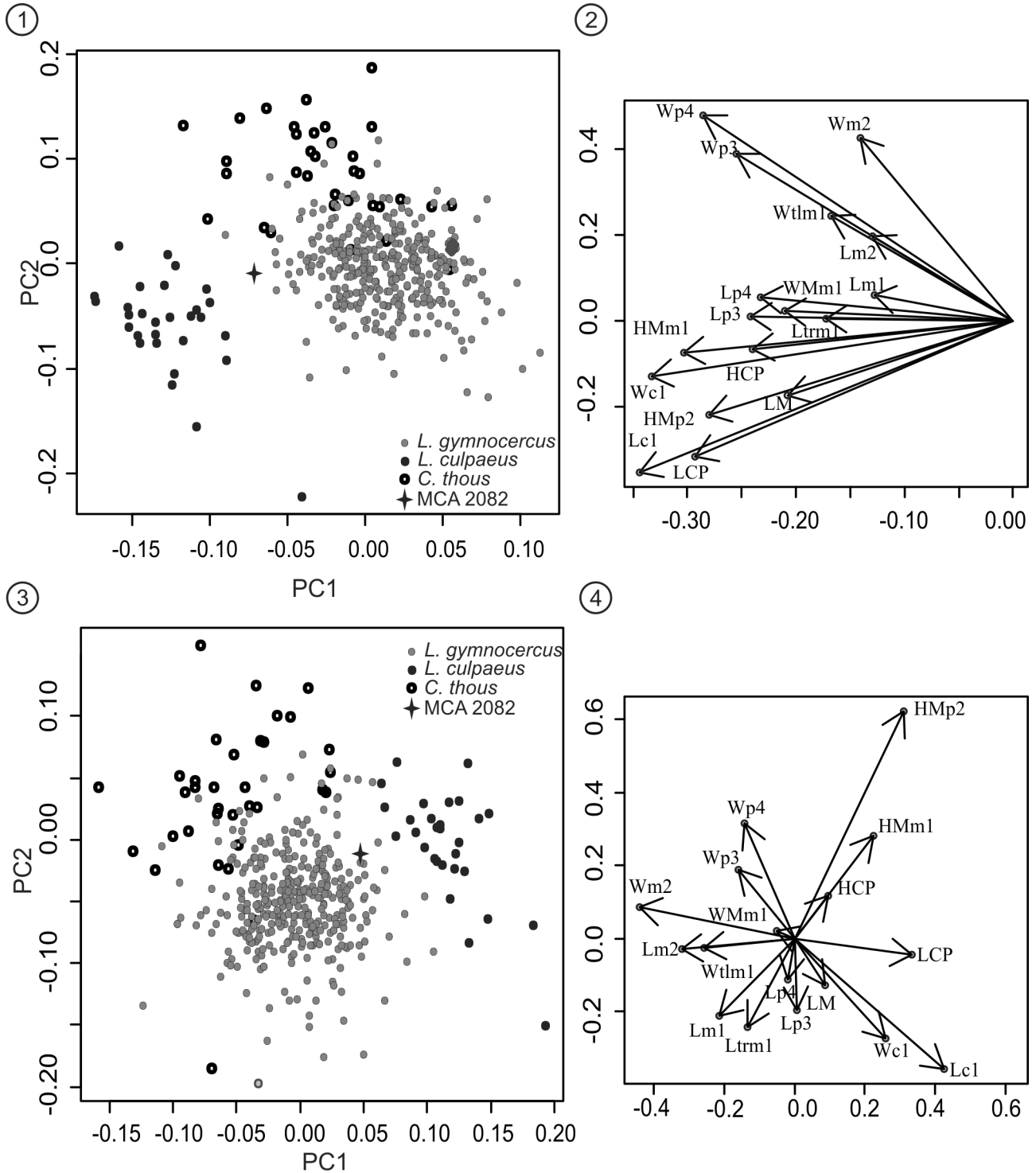


Figure 3. Results of the measurements PCA including both fossil specimens. **1**, plot of the first two axis of the analysis without the correction by geometric means; **2**, plot of the eigenvectors of the analysis without the correction by geometric means; **3**, plot of the first two axis of the analysis with the correction by geometric means; **4**, plot of the eigenvectors of the analysis with the correction by geometric means.

ing how even when the size effect was controlled, their distribution showed the same general pattern observed in the analysis without correcting the size effect. Both fossil specimens were placed in the overlapping area between *L. gymnocercus* and *L. culpaeus*, but MCA 2082 was placed closer to *L. culpaeus* than to *L. gymnocercus*, while MLP 10-56 was closer to *L. gymnocercus*.

In the analysis performed with the complete set of measurements (Fig. 4.1–2), the first axis was strongly influenced by size, with all the vectors oriented towards the negative values where the bigger specimens were placed. The second axis showed specimens with wider premolars (p3 and p4), a wider talonid of the m1 and a wider m2 in the positive values. Specimens placed in the negative values showed a longer and wider c1, a longer coronoid process and taller mandibles. The living species showed the same pattern of distribution than the one observed in the analyses with the reduced set of measurements. MCA 2082 was placed closer to *L. gymnocercus*, in the overlapping area between this species and *L. culpaeus*.

In the PCA where the size correction was included (Fig. 4.3–4), specimens placed on the positive values of the first axis had longer and wider canines, taller mandibles, a narrower talonid of m1, a larger m2, and a larger coronoid process. Specimens with wider and shorter p3–4, shorter m1, and taller mandibles were placed on the positive values of the second component. The distribution of the living species was very similar to the one observed in the other analyses. Again, MCA 2082 was placed in the overlapping area between *L. culpaeus* and *L. gymnocercus*, but closer to *L. gymnocercus*.

Geometric morphometrics

Both analyses (the one including the complete mandible and only MCA 2082 and the one that includes the anterior region of the mandible and both fossils) showed a similar pattern regarding the shape-changes of the mandible. The first axis showed specimens with shorter mandibles and a robust anterior region in the positive values. In this region of the morphospace the canines were shorter (Fig. 5.1). Specimens placed in positive values of the first axis of the analysis that includes the complete mandible, showed its posterior region expanded dorsoventrally and the condyle was oriented dorsally. The third axis in the complete mandible analysis and the second axis in the analysis of the anterior region of the mandible showed, in the negative values, specimens with mandibles that tend to be

shorter and taller, and had shorter canines and premolars and the m1 with a shorter talonid. The positive values showed an opposite pattern, with specimens with longer and lower mandibles, longer canines and premolars, and a longer talonid in m1 (Fig. 5.2).

The species distribution was similar to the one observed in the linear morphometry analyses. Geometric morphometry analyses separated the genus *Lycalopex* from the genus *Cerdocyon* and also separated the species *L. culpaeus* and *L. gymnocercus*. The first axis separated the genus *Cerdocyon*, which was placed in the positive values, from the genus *Lycalopex* that was placed in the negative values. The second axis of the analysis of anterior region of the mandible and the third axis of the analysis of the complete mandible separated the species *Lycalopex gymnocercus* (positive values) and *Lycalopex culpaeus* (negative values). MCA 2082 was placed in the analysis of the complete mandible in the overlapping area between the genera *Cerdocyon* and *Lycalopex*, in the first axis, and in the third axis was placed near the specimens of *L. culpaeus*. In the analysis of the anterior part of the mandible and including both fossil specimens, MCA 2082 was placed, in the first axis, in the zone occupied by specimens of *Cerdocyon thous*, and in the second axis in the region occupied by *Lycalopex culpaeus*. MLP 10-56 was placed with the genus *Lycalopex* in the first axis and in the zone of *L. culpaeus* in the second axis.

Quantitative analysis of size

When plotting the centroid size of the analysis including the fossil specimens and only the anterior half of the body of the mandible (Fig. 6.1), MLP 10-56 presented a centroid size value similar to the upper quartile of *L. gymnocercus*, coinciding with the maximum values of *C. thous*. MCA 2082 was outside the upper quartile of *C. thous* and *L. gymnocercus*, and the lower quartile of *L. culpaeus*.

The analysis including the complete mandible and MCA 2082 (Fig. 6.2) showed that the centroid size of this specimen was similar to the upper quartiles of *L. gymnocercus* and *C. thous*, and below the minimum values observed in *L. culpaeus*.

When comparing the size of the fossil specimens with the median, quartile, maximum and minimum values of the measurements obtained from the specimens of the living species (Supplementary Information Online), both MLP 10-56 and MCA 2082 could be separated from *L. vetulus*, *L. fulvipes* and *L. sechurae* given its larger size. When comparing MLP

10-56 with *Atelocynus microtis*, some measurements (e.g., Lp3, Lp4, Lm1) escaped the range of variation observed in the living species. There were also similarities with some values that were coincident with the minimum values of *A. microtis* (e.g.,

HMm1, Wp3, Wp4, Lm2). MCA 2082 showed a similar situation, where some measurements (e.g., Lp3, Lp4 and Lm1) were higher than the observed in *A. microtis* and some of them were similar to the minimum values of the living species (e.g.,

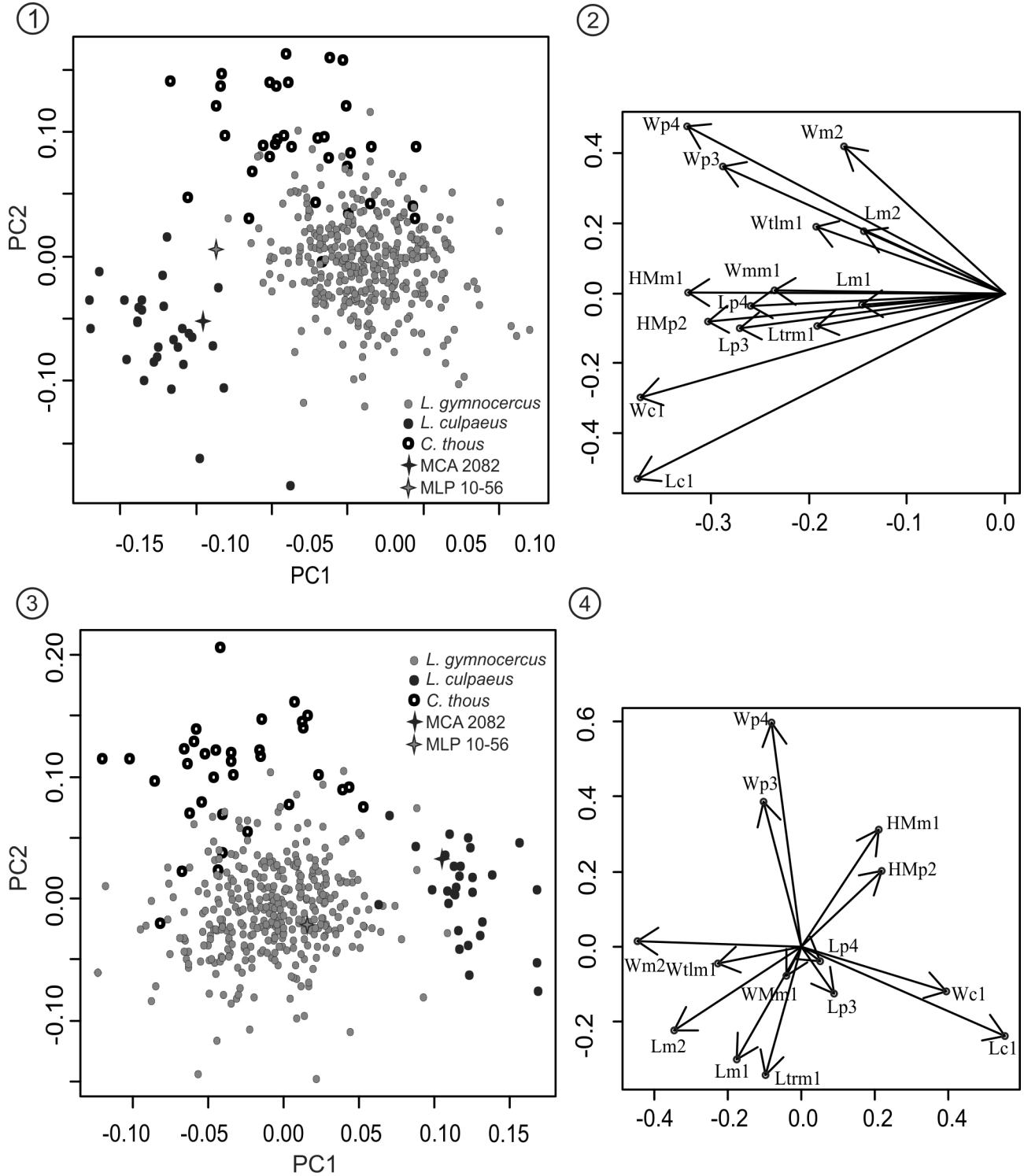


Figure 4. Results of the measurements PCA including only MCA 2082. **1**, plot of the first two axis of the analysis without the correction by geometric means; **2**, plot of the eigenvectors of the analysis without the correction by geometric means; **3**, plot of the first two axis of the analysis with the correction by geometric means; **4**, plot of the eigenvectors of the analysis with the correction by geometric means.

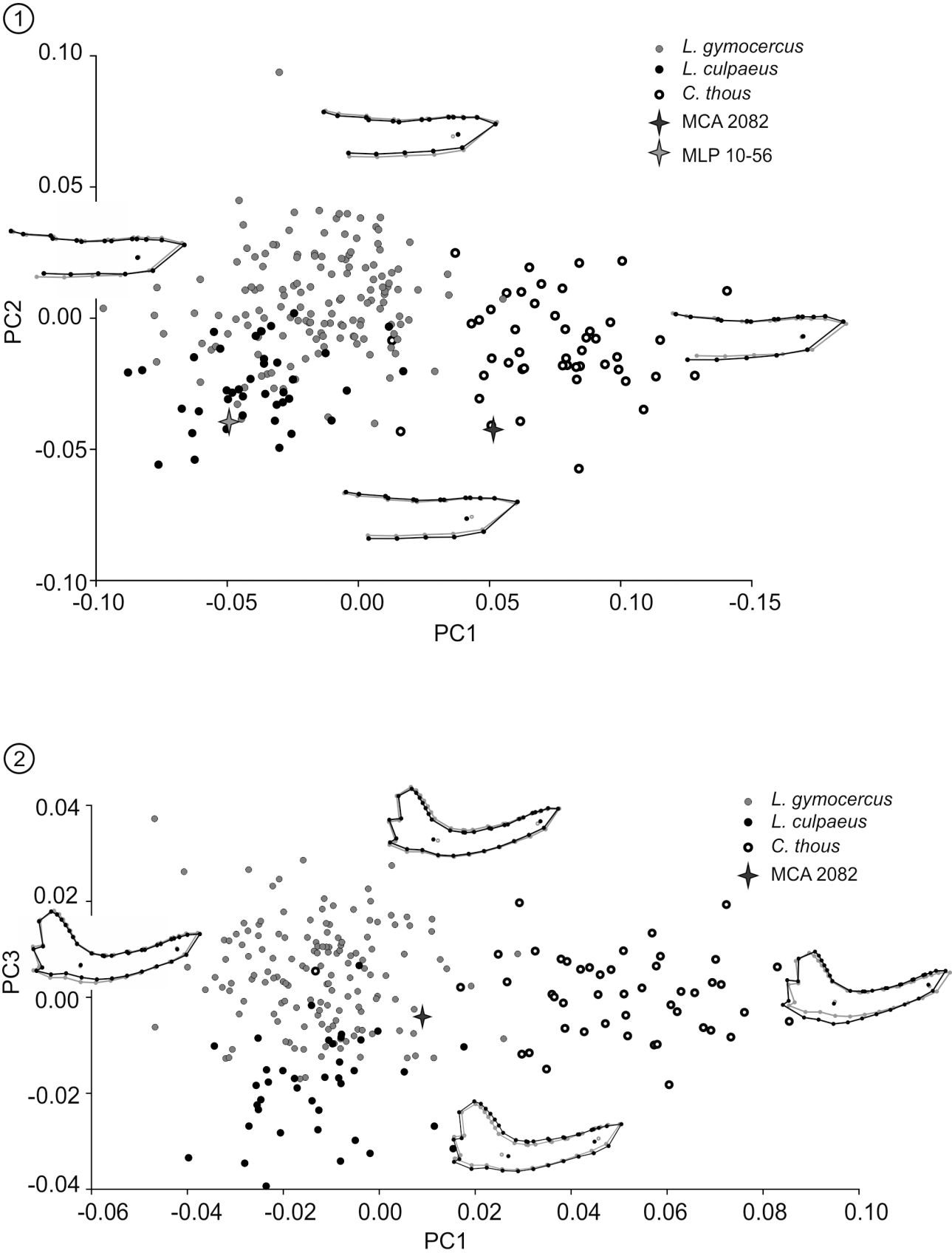


Figure 5. Results of the analysis of geometric morphometrics. **1**, analysis including both fossil specimens; **2**, analysis including only MCA 2082.

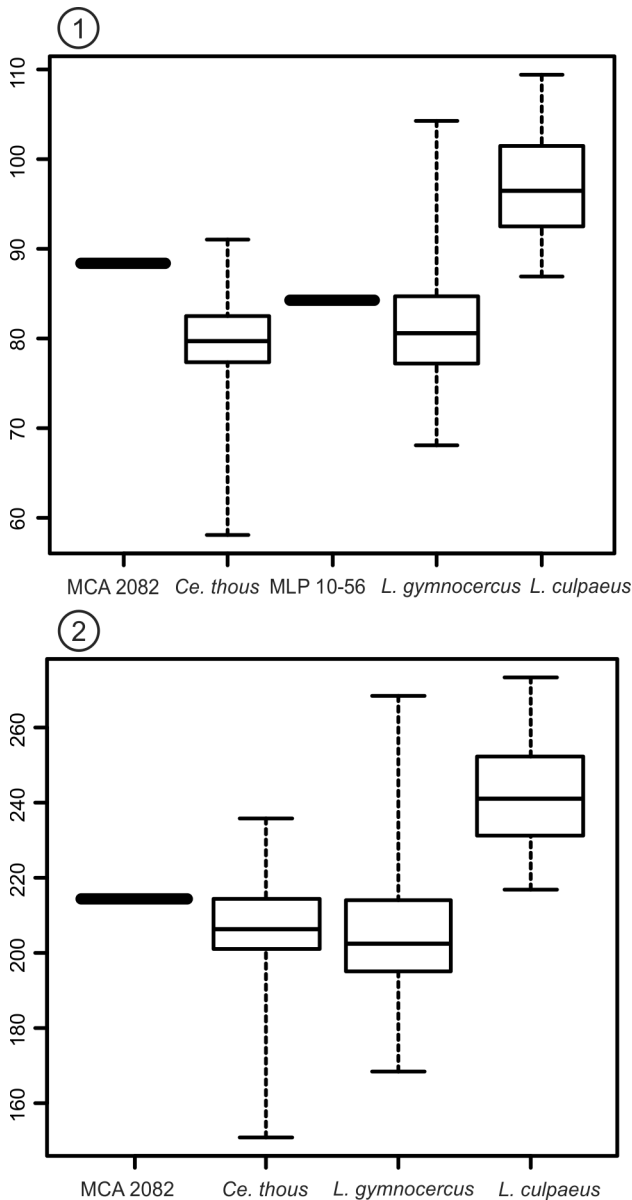


Figure 6. Boxplot of the centroid size. **1**, analysis including both fossil specimens; **2**, analysis including only MCA 2082.

Wp3, Wp4, Ltrm1, Wtlm1, Lm2, LM, TCP, LCP). The mandible measurements (HMm1, HMm2, WMm1) of MLP 10-56 were similar to the minimum values of *L. culpaeus*, while the dental values were closer to the median (e.g., Lp3, Lp4, Wp4, Ltrm1, Lm2) or maximum values (Lm1, Wtlm1 and Wm2). A similar pattern was observed in MCA 2082, where some dental measurements had values closer to the first quartile values of *L. culpaeus* (e.g., Lp3, Lp4) or the maximum values (e.g., Lm1), and some mandibular measurements (e.g., LM, TCP, LCP) being lower than the minimum values of this

living species. A different scenario was observed when comparing the fossil specimens with *L. gymnocercus*. The comparison of the holotype of *L. ensenadensis* with *L. gymnocercus* showed that the mandible measurements (HMm1, WMm1, HMP2) of MLP 10-56 were similar to the third quartile of this living species, but other dental measurements (e.g., Lp3, Lp4 and Lm1) were higher than the maximum values observed in *L. gymnocercus*. The situation of the MCA 2082 was similar, with some dental values being higher than the maximum values of *L. gymnocercus* (Lp3, Lp4, Lm1) and some mandible measurements are similar to the third quartile (e.g., HCP, LCP) or the maximum values of *L. gymnocercus* (e.g., the length of the mandible). The comparison of the fossils with *C. thous* showed similar results. Some dental measurements (e.g., Lc1, Lp3, Lp4, Lm1) obtained from MLP 10-56 were higher than the maximum values of *C. thous*, and the height of the mandible at the insertions of the p2 and m1 were similar to the median values. MCA 2082 also had some dental measurements higher than the maximum of *C. thous* (e.g., Lc1, Lp3, Lm1). The length of the mandible was similar to the third quartile, the length of the coronoid process was similar to the median values and the height of the coronoid process was similar to the minimum values of this living species. Other mandible measurements (HMm1 and HMP2) were higher than the maximum values of *C. thous*.

DISCUSSION

The morphometric analyses showed a similar pattern of distribution of the living species and some degree of separation between them (Figs. 3–5), this also evidences the existence of a considerable amount of intraspecific variation. This separation is useful in the context of discussing the systematic position of the fossil specimens analyzed in this work. As mentioned in the description of the results of the quantitative analyses, both fossil specimens were placed in the morphospace occupied by the genus *Lycalopex*. MLP 10-56 presents some problems with its generic assignment. Several authors discussed this issue (see above) and the assignment proposed by Berman (1994) seems to be the most accurate. Considering the systematic arrangement proposed by Zunino *et al.* (1995), “*Canis*” *ensenadensis* should be considered a member of the genus *Lycalopex*. The long and narrow premolars, the long m1 and the proportionally short m2 (Fig. 3) are characters that allow us to relate this species to *Lycalopex* (Kraglievich, 1930;

Berta 1987). *Cerdocyon* is characterized for having wide pre-molars and short molars (Kraglievich, 1930; Berta, 1987). Unfortunately the mandible of the holotype of *L. ensenadensis* is incomplete and the posterior region is absent (Fig. 2), so it is not possible to check the characters that are diagnostic of *Cerdocyon* (e.g., Kraglievich, 1930; Berta, 1987). However, the available information suggests that specimen MLP 10-56 belongs to the genus *Lycalopex* based on the mentioned qualitative characters and the results of the quantitative analyses, but this should be confirmed in a phylogenetic context and with the discovery of new fossil specimens.

The situation of MCA 2082 is different since the specimen is more complete. Only in one geometric morphometry analysis (when only the anterior part of the mandible was included) MCA 2082 was placed within the genus *Cerdocyon*. The position of MCA 2082 in that analysis is considered here as a result of the robust morphology of the anterior region of the mandible of the specimen and not a result of taxonomic affinities with *Cerdocyon*. MCA 2082 lacks the qualitative characters used to identify the genus *Cerdocyon*, such as an expanded pterygoideal fossa of the angular process and a subangular lobe. Another difference is the position and orientation of the mandible condyle, which resembles the position and orientation observed in species of the genus *Lycalopex* (e.g., *L. culpaeus* and *L. gymnocercus*), and is different from the observed in *C. thous* (Kraglievich, 1930; Berta, 1982). Given the position in the analyses of the fossil specimens studied here, we propose that both (MLP 10-56 and MCA 2082) are members of the genus *Lycalopex*. This proposal is also supported by the qualitative evidence. The morphology of the mandible of MCA 2082 is similar to the morphology observed in *L. gymnocercus* and *L. culpaeus* with a dorsoventrally compressed angular process given the lack of expansion of the pterygoid fossa, the lack of a subangular lobe and the above mentioned position and orientation of the mandibular condyle.

When comparing the holotype of “*Canis*” *ensenadensis* (MLP 10-56) with the living species of the genus *Lycalopex*, there are some characters that allow us to distinguish between them. As mentioned above, *L. culpaeus* is different from MLP 10-56 in the morphology of the distal cingulum of the p4 because it is convex in MLP 10-56 and flat in *L. culpaeus* (Fig. 7). The size of the mandible body in comparison to the size of the teeth is an important character to consider, as was mentioned by Berman (1994) when he observed that the teeth

where similar in size to those of *L. culpaeus*, but the mandible was proportionally smaller, with a size close to that of *L. gymnocercus*. This could explain the position of MLP 10-56 in the overlapping area between both species in the quantitative analyses. The comparison of the sizes using the measurements of the specimens studied supports the intermediate position of *L. ensenadensis* between *L. culpaeus* and *L. gymnocercus*. The mandibular measurements of *L. ensenadensis* are coincident with the minimum values of *L. culpaeus* and with the third quartile of *L. gymnocercus*. Some dental elements have higher values than the maximum observed in *L. gymnocercus* but these values are coincident with the median or quartile values of *L. culpaeus*.

In summary, the teeth of *L. ensenadensis* are bigger than the teeth of *L. gymnocercus*, but the mandible of the fossil species is similar in size to the values observed in this taxon. This proportion between tooth size and mandible size allowed us to separate the fossil specimen from *L. gymnocercus*. When considering this character and the presence of characters that are very uncommon in the species of *Lycalopex* studied here, like the presence of an additional distal cusp in the p3 and the absence of diastemata between the teeth, we interpret MLP 10-56 as a member of a species different from *L. culpaeus* and *L. gymnocercus*. Two interesting features of this specimen are the large size of its m1 and the long and narrow premolars compared with the other dental elements of the mandible, as observed in the quantitative analyses. In this context we propose the new combination *Lycalopex ensenadensis*.

As pointed above, the teeth of MCA 2082 have a size comparable to the sizes observed in *L. culpaeus* and mandibles similar in size to *L. gymnocercus*. Another common character with MLP 10-56 is the presence of an accessory cusp in the p3, a character mentioned above as rare in *L. culpaeus* and *L. gymnocercus*. It also differs from *L. culpaeus* by the morphology of the distal cingulum of the p4, which is convex in MCA 2082 and flat in *L. culpaeus* (Fig. 7). A difference between the fossil specimens is the presence in MCA 2082 of an open tooth-row, but in this case the diastemas are reduced resembling the condition observed in some specimens of *L. gymnocercus* and *C. thous*. MCA 2082 also differs from MLP 10-56 by its robust and taller mandible body. MLP 10-56 is characterized by its slender mandible body, contrary to the observation made by Ameghino (1888). But taking into account the large intraspecific variation observed in living species, it is possible that these

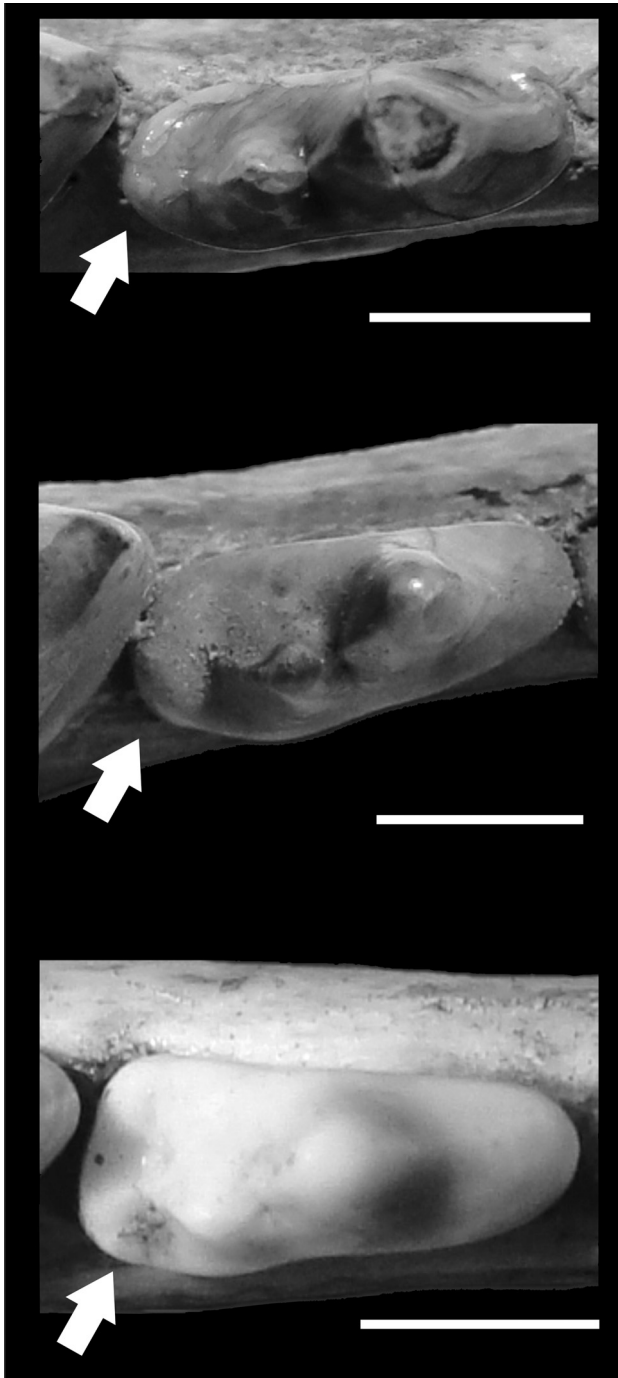


Figure 7. Distal cingulum of the p4 of **1**, MLP 10-56; **2**, MCA 2082; **3**, *L. culpaeus*. Scale bar= 10 mm.

differences are not taxonomically significant. MCA 2082 is interpreted here as a form different from *L. gymnocercus*, *L. culpaeus* and *C. thous* given the characters mentioned above. Due to the fragmentary nature of the type specimen of *L. ensenadensis*, and the lack of information about its intraspecific variation, it is hard to confirm or reject possible phylogenetic affinities between MCA 2082 and *L. ensenadensis*. They share

some common characters but they also have some differences. More information is needed about *L. ensenadensis* to solve this problem. Here we interpret MCA 2082 as a member of the genus *Lycalopex* with some affinities with *L. ensenadensis*. If this interpretation is correct, *L. ensenadensis* has a biochron that goes from Ensenadan Age (early-middle Pleistocene, 1800–500 ka) to the Lujanian (late Pleistocene, 130–8.5 ka). All these hypotheses need to be tested in a phylogenetic context.

The first foxes in South America are recorded in the Vorohuan (late Pliocene 2.9–2.4 Ma) of Buenos Aires Province (Berman, 1994; Soibelzon and Prevosti, 2007). This record corresponds to the extinct species “*Dusicyon*” *cultridens* and this is the only species recorded in this age. The record in the Sanandresian (late Pliocene, 2.4–1.8 Ma) is limited to a “*Dusicyon*” sp., that showed some similarities with *L. gymnocercus* from the Buenos Aires Province, Argentina (Soibelzon *et al.*, 2007), but a systematic review is needed. During the Ensenadan (early–middle Pleistocene, 1800–500 ka) a higher diversity is recorded, with the presence of the species *L. gymnocercus*, “*Dusicyon*” *cultridens*, *L. ensenadensis* and some unconfirmed records of *D. avus* from the Pampean Region (Ameghino, 1888, Berman, 1994; Soibelzon and Prevosti, 2007). More fieldwork is needed to confirm the canid diversity during the Bonaerian (middle Pleistocene, 500–130 Ka), a poorly known Age with very few localities recorded and few dated fossils (see Prevosti and Soibelzon, 2012). The Lujanian Age shows a more diverse scheme, with almost all the living South American species represented in different South American localities (*i.e.*, *L. gymnocercus*, *L. sechurae*, *L. vetulus*, *L. culpaeus* and *C. thous*; Hoffstetter, 1952; Berta, 1987; Trejo and Jackson, 1998; Cartelle, 1999; Soibelzon and Prevosti, 2007), and the extinct species, *D. avus*. The new fossil here described indicates that the diversity of foxes during the Lujanian of South America was even higher, because it is referred to *Lycalopex* cf. *L. ensenadensis*, a species that was previously restricted to the Ensenadan (see above). Even if our tentative assignation of this mandible to *L. ensenadensis* was wrong, its morphology indicates that it belongs in a taxon different from those recorded in the Lujanian, increasing the number of fox species from five to six for this Age.

CONCLUSIONS

Lycalopex ensenadensis is considered here as a valid species included in the genus *Lycalopex*. MCA 2082 is considered as

a member of the genus *Lycalopex*, but its specific assignation is not completely clear and we assign it to *Lycalopex* cf. *L. ensinadensis*. The new specimen described here increases the diversity of Lujanian foxes to six species and, if our systematic hypothesis is correct, extends the biochron of *L. ensinadensis* to the Lujanian Age.

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