

Is *Galea tixiensis* Quintana, 2001 a synonym of *G. leucoblephara* Burmeister, 1861?

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The genus *Galea* (Rodentia, Caviidae) includes five living and two extinct species of terrestrial and herbivorous caviids that inhabit grasslands and rocky scrub areas at both high and low elevations in South America. Fossil samples from the late Pleistocene-Holocene from central-eastern Argentina have been referred to as *Galea* sp., *G. musteloides* or *G. cf. musteloides* and finally described as a new species under the name of *G. tixiensis*. However, recent studies based on large series of individuals fail to find qualitative morphological differences between *G. leucoblephara* and *G. tixiensis*. Based on these findings, in this contribution we reviewed the taxonomic status of the fossil species *G. tixiensis*. A total of 110 individuals of the three currently recognized subspecies of *G. leucoblephara* (i. e., *G. l. demissa*, *G. l. leucoblephara* and *G. l. littoralis*) from Argentina, Bolivia and Paraguay were examined. Nine craniodental measurements were recorded. Quantitative data were subjected to a principal component analysis (PCA) in order to identify the contribution of each measurement to the total variance. Qualitative characters were evaluated through the comparisons of the diagnostic traits of *G. tixiensis* with the variability derived from the recent samples. PCA showed a high overlap of the multivariate spaces of the three subspecies studied, suggesting that they do not differ significantly in terms of cranial shape. The holotype of *G. tixiensis* was allocated within the morphospace of the recent *G. l. littoralis* samples. Qualitative traits diagnostic of *G. tixiensis* were also recorded in recent samples of *G. leucoblephara*, in particular of *G. l. littoralis*. Based on both qualitative and quantitative cranial traits, we suggest that *G. tixiensis* is a synonym of *G. leucoblephara*. The morphological traits supposedly unique to *G. tixiensis* were also recorded in specimens of living populations of *G. l. littoralis*. The large values of some quantitative cranial traits in fossil samples – compared to living ones – are reinterpreted here as an ecophenotypical response to the more severe climatic conditions of the Holocene.

El género *Galea* (Rodentia, Caviidae) incluye cinco especies vivientes y dos extintas de cávidos terrestres y herbívoros, que ocupan pastizales y matorrales rocosos, tanto en áreas altas como bajas de América del Sur. Algunas muestras fósiles del Pleistoceno-Holoceno del centro-este de Argentina han sido referidas como *Galea* sp., *G. musteloides* o *G. cf. musteloides* y finalmente se describieron como una nueva especie bajo el nombre de *G. tixiensis*. Sin embargo, estudios recientes basados en series grandes de individuos fallaron en encontrar diferencias morfológicas cualitativas entre *G. leucoblephara* y *G. tixiensis*. Sobre la base de estos hallazgos, en esta contribución revisamos el estatus taxonómico de la especie extinta *G. tixiensis*. Se examinaron 110 individuos de las tres subspecies actualmente reconocidas de *G. leucoblephara* (i.e., *G. l. demissa*, *G. l. leucoblephara* y *G. l. littoralis*) de Argentina, Bolivia y Paraguay. Se registraron nueve medidas craneo-dentarias. Los datos cuantitativos se sometieron a un análisis de componentes principales (PCA) con el fin de identificar la contribución de cada medida a la varianza total. Los caracteres cualitativos se evaluaron a través de las comparaciones de los rasgos supuestamente diagnósticos de *G. tixiensis* con la variabilidad representada por las muestras recientes. Los espacios multivariados de las tres subspecies estudiadas se superpusieron ampliamente en el PCA, lo que sugiere que estos taxones no difieren significativamente en la figura del cráneo. El holotipo de *G. tixiensis* se ubicó dentro del morfoespacio correspondiente a muestras recientes de *G. l. littoralis*. Los caracteres cualitativos supuestamente diagnósticos de *G. tixiensis* también se verificaron en muestras recientes de *G. leucoblephara*, en particular de *G. l. littoralis*. Sobre la base de sus rasgos craneanos cualitativos y cuantitativos se sugiere que *G. tixiensis* es un sinónimo de *G. leucoblephara*. Los mayores valores para algunos rasgos craneanos cuantitativos en las muestras fósiles -comparadas con las actuales- son reinterpretados en este trabajo como una respuesta ecofenotípica a las condiciones climáticas más severas durante el Holoceno.

Key words: Caviidae; Cavoidea; Caviomorpha; *Galea leucoblephara littoralis*; Hystricognathi.

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Introduction

The genus *Galea* Meyen 1833, with five living and two extinct species, is one of the most diverse genera within the Family Caviidae (Ubilla and Rinderknecht 2014; Dunnum 2015). Its fossil record dates back at least to the Ensenadense (Vucetich et al. 2015) and is composed mainly of fragmentary cranio-mandibular remains (Ubilla and Rinderknecht 2014). The only two known extinct species (i. e., *G. orthodonta* Ubilla and Rinderknecht 2001 and *G. tixiensis* Quintana 2001) are based on well preserved craniodental and postcranial remains. The former of these species,

G. orthodonta, has been found in Pleistocene sediments of Uruguay and southern Bolivia (Ubilla and Rinderknecht 2001; Ubilla and Rinderknecht 2014). The second extinct species, *Galea tixiensis*, was established from remains accumulated throughout the Holocene in rocky outcrops in the southeast of Province of Buenos Aires, in east-central Argentina (Quintana 2001). The materials that led to the description of *G. tixiensis* were instead referred to as either *Galea* sp., *G. musteloides* or *G. cf. musteloides* (e. g., Tonni et al. 1988; Quintana and Mazzanti, 1998; Quintana 2001), highlighting its morphological similarity with individuals of the recent

populations inhabiting this same region, firstly referred to *G. musteloides* and now allocated within *G. leucoblephara* (Dunnun 2015). Quintana (2001) indicated several diagnostic traits for *Galea tixiensis* (see below), in addition to larger size relative to other species in the same genus. Unfortunately, Quintana (2001) did not document what living specimens were compared against the fossil samples, nor some other relevant aspects that are key for the description of a new species, such as holotype measurements (which were not illustrated either). More recently, a species related to *G. tixiensis*, referred to as *G. aff. tixiensis*, was mentioned for the Pleistocene of Province of Corrientes, in northeast Argentina (Francia et al. 2012).

The examination of a vast number of specimens as part of a qualitative and quantitative morphologic review of the genus *Galea* allows us to assume that many of the diagnostic traits of *G. tixiensis* are not unique to this species, and neither is the combination of these traits (see also Ubilla and Rinderknecht 2014). The taxonomic status of *G. tixiensis* is relevant for several reasons (e. g., biogeographic, evolutionary), but mainly because, should this be a distinct species, it would be one of the eight species of mammals that became extinct over the past 500 years in mainland South America (cf. Teta et al. 2014; Prevosti et al. 2015).

The aim of this work is to review the taxonomic status of *Galea tixiensis*. Based on qualitative and quantitative morphological evidence, it is hypothesized that *G. tixiensis* is synonym for *Galea leucoblephara* Burmeister 1861.

Materials and Methods

We studied 110 specimens of *Galea leucoblephara*, including skulls and mandibles, from Argentina, Bolivia and Paraguay. These are deposited in the following collections (for details, see Appendix 1): CFA, Collection of Mammals of Fundación de Historia Natural Félix de Azara (Buenos Aires, Argentina); CMI, Collection of Mammals of Instituto Argentino de Investigación de Zonas Áridas (Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina); CML, Collection of Mammals of Facultad de Ciencias Naturales e Instituto Miguel Lillo (Facultad de Ciencias Naturales e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina); CNP, Collection of Mammals of Centro Nacional Patagónico (Centro Nacional Patagónico, Puerto Madryn, Argentina) MACN-Ma, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina) MNHNP, Collection of Mammals of Museo Nacional de Historia Natural de Paraguay (Asunción, Paraguay); UACH, Collection of Mammals of Universidad Austral de Chile (Valdivia, Chile). Samples were grouped into 3 major geographical groups, allocated to subspecies *G. leucoblephara demissa*, *G. l. leucoblephara* and *G. l. littoralis*, following the taxonomic scheme proposed by Bezerra (2008) and Dunnun (2015). The first of these taxa is distributed across the lowlands of southeastern Bolivia and western Paraguay to the Provinces of Santiago del Estero and Catamarca in Argentina; the second, from southern Catamarca to Córdoba and northern Mendoza and San Luis, in

Argentina; and the third, from southern Mendoza, La Pampa and southeastern Buenos Aires to northeastern Santa Cruz, in Argentina.

The following cranial measurements were recorded for each adult specimen (classes 3-5; cf. (sensu Bezerra 2008) (using a digital caliper accurate to 0.01 mm): AN = nasal width; CIO = interorbital constriction; FL = frontal length; LD = diastema length; AFI = incisive foramen width; LFI = incisive foramen length; LP = palatilar length; SMS = length of the upper toothrow length (alveolar); APM3 = palate width at the third upper molar. The measurements of the holotype of *G. tixiensis* were estimated using the software tpsdig2 from photographs in Bezerra (2008) and Francia et al. (2012), using as reference the scale in the latter.

To summarize the causes of morphometric variation and rank them according to importance, a principal components analysis (PCA) was performed from a variance-covariance matrix of the log-transformed measures. Previously, each individual measurement was corrected by the geometric mean of each individual to avoid the distortion derived from the effect of size (for this methodology, see Meachen-Samuels and Van Valkenburgh 2009). For the purposes of this work, *form* is defined as the appearance, configuration or composition of the traits, including size, whereas *figure* refers to the form excluding size (Vizcaino et al. 2016). This is consistent with the approach of Richtsmeier et al. (2002), in his attempt to circumvent the use of these terms in the colloquial sense.

The anatomical terminology corresponds to the one used by Cherem and Ferrigolo (2012). The qualitative and quantitative morphological traits of *Galea tixiensis* were taken from the literature (i. e., Quintana 2001) and discussed from the comparison with recent specimens.

Results

The first two PCA axes accounted for 63.1% of the variation in craniodontal measurements (Figure 2; Table 2). The overlap of the polygons corresponding to the three subspecies currently recognized was moderate to high, suggesting that there are no major differences in figure. In this context, the holotype of *G. tixiensis* was allocated with *G. l. littoralis* specimens (Figure 2), toward positive values in PC 1. All the variables were negatively correlated with PC 1, except AFI, which was positively correlated.

The states for morphological traits originally referred to as diagnostic for *G. tixiensis* were also observed in living specimens of *G. leucoblephara*. The morphological variability recorded in different qualitative features of the fossil taxon is well within the variability documented for the living populations of *G. leucoblephara*, but especially of *G. l. littoralis* (for a summary see Table 3).

Discussion

The most striking feature of *G. tixiensis* relative to other species in the same genus is its larger overall size (Quintana

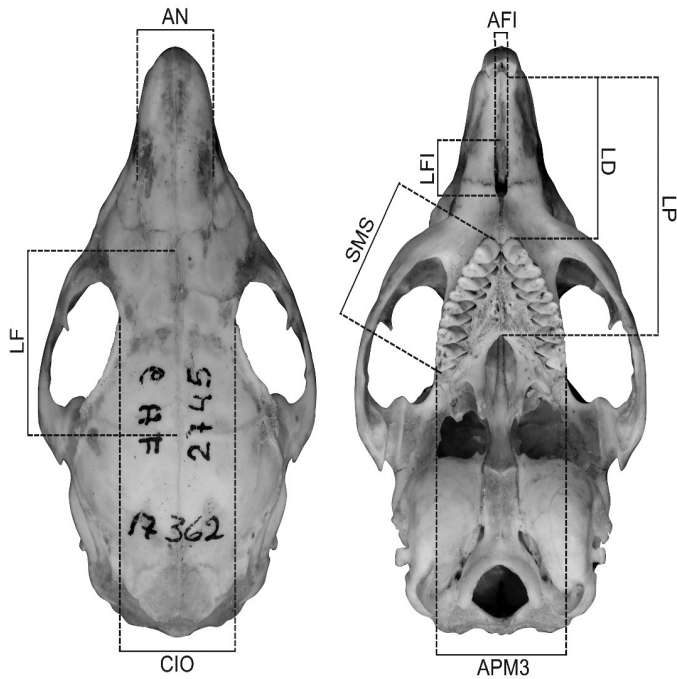


Figure 1. Cranial measurements used in this study, shown on a skull of *Galea leucoblephara* (MACN 17362). For a reference of the abbreviations, see Materials and Methods.

2001:404). However, a size-adjusted PCA indicates that, in terms of figure, the *G. tixiensis* holotype does not differ from other individuals referred to as *G. leucoblephara*. This is not a minor issue, as certain quantitative traits are among the phenotypic variables most frequently associated with physiological or environmental changes (e. g., [Maestri et al. 2016](#)). Also, some differences might be magnified by the different sample sizes considered by previous authors. For example, for a set of 35 individuals of *G. leucoblephara*, [Quintana \(2001\)](#) reported a higher mean upper alveolar tooththrow length of 11.77 mm, with a range between 10.4 to 11.7 mm ($n = 35$; note the contradiction between the mean and maximum values recorded), while for the same species, with a sample three times larger ($n = 110$), we recorded an average of 11.82 mm and a range of 10.1 to 15.54 mm ($n = 110$). This evidences that although the mean value remains clearly lower for *G. leucoblephara*, the range of measurements for this species covers completely the range reported for *G. tixiensis* (mean = 13.18 mm; 12.2–15.1 mm range; $n = 107$).

Our review of extensive series of specimens indicates that none of the qualitative traits supposedly diagnostics of *G. tixiensis*, nor the combination of them, is unique to this taxon. For example, the morphology of the zygomatic arch and the diastema and its associated foramina does not differ significantly from the one observed in living specimens of *G. l. littoralis* (cf. Figures 3 and 4; Table 3). In this subspecies, the shape of the incisive foramen varies between tapered and diamond-shaped, together with the presence of a conspicuous interpremaxillar foramen, accompanied by accessory foramina with a lateral and posterior arrangement, in a disposition similar to that reported for *G. tixiensis* (Figure 3). This contradicts what has been pointed out by [Quintana](#)

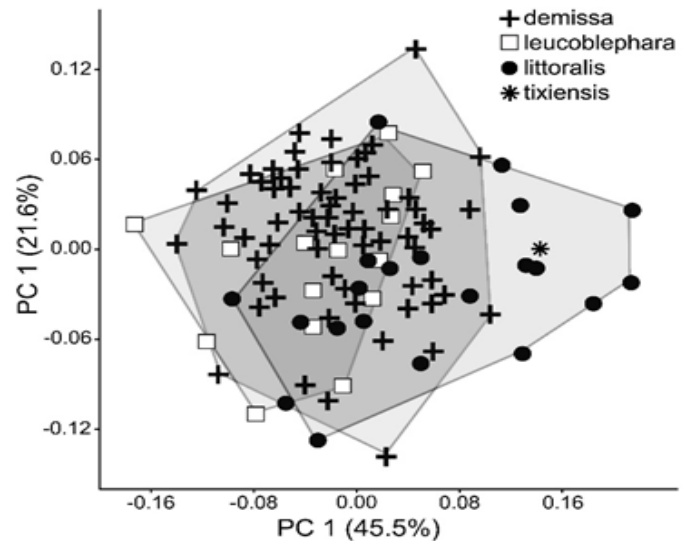


Figure 2. Polygons and individual scores for adult specimens ($n = 111$) in three subspecies of *Galea leucoblephara* and the holotype of *G. tixiensis* for principal components 1 and 2 (obtained from a variance-covariance matrix on nine craniodental measurements corrected by the geometric mean).

(2001:402 to 404), who indicated that the diamond shape of the incisive foramen was exclusive to the fossil species and that the accessory foramina were not present in other species, nor did this displayed the overall disposition as *G. tixiensis*. Also, the robustness of the zygomatic arch, as well as the development of the paraorbital apophysis on the ascending branch of the zygomatic portion of the maxilla and the size of the jugal were relatively variable in samples of the living specimens, with some individuals (e. g., MACN-Ma 13335; cf. Figure 4B) displaying a disposition similar to the one observed in *G. tixiensis* (cf. [Quintana 2001](#); Fig. 3A). Other traits (e. g., shape of the mesopterygoid fossa, shape of the nasolacrimal foramen, appearance of the tympanic bulla, morphology of the mandibular ramus and molars) did not show major differences between *G. tixiensis* and *G. leucoblephara* (cf. [Quintana 2001](#); this work). For all the above mentioned, we consider that there is no qualitative morphological evidence to suggest that *G. tixiensis* is a different species from *G. leucoblephara*.

For [Quintana \(2001\)](#), *G. tixiensis* became extinct toward

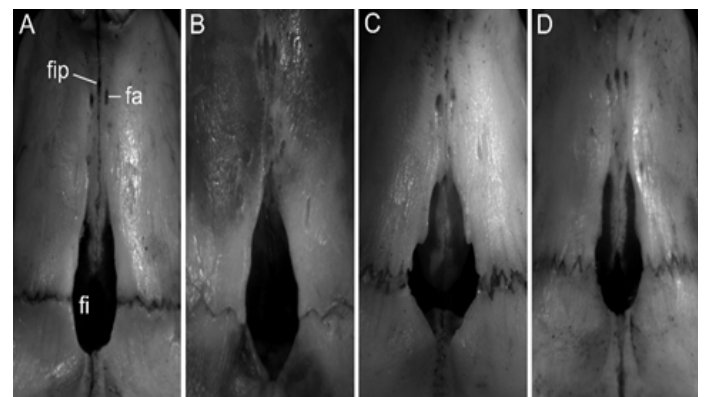


Figure 3. Individual variation in the morphology of incisive foramina and associated structures in specimens of *Galea leucoblephara littoralis* (from left to right: MACN-Ma 13226, 22607, 16405, 13664). Abbreviations: fa = lateral accessory foramina; fip = interpremaxillar foramen.

Table 1. Statistical summary for nine craniodental measurements (in mm; for a reference of the abbreviations, see Materials and Methods) in adult specimens of the genus *Galea*. Other abbreviations: N = number of specimens measured; SD = standard deviation; Min = minimum recorded value; Max. = maximum recorded value.

	<i>G. leucoblephara demissa</i>					<i>G. leucoblephara leucoblephara</i>					<i>G. leucoblephara littoralis</i>					<i>G. tixiensis</i>
	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	
AN	71	7.39	0.56	6.27	8.91	18	7.18	0.42	6.52	8.08	21	6.98	0.44	6.42	8.20	7.83
CIO	71	10.89	0.79	8.89	13.06	18	10.32	0.87	8.55	12.36	21	10.64	0.50	9.47	11.49	11.74
LF	71	16.34	0.90	13.58	18.36	18	16.36	2.13	10.03	19.91	21	17.08	0.90	15.69	19.23	16.86
LD	71	12.93	1.11	10.84	15.25	18	13.55	1.05	11.81	15.25	21	13.27	0.89	11.35	15.13	15.85
AFI	71	1.44	0.22	1.02	2.04	18	1.40	0.21	1.00	1.75	21	1.72	0.38	1.16	2.51	2.39
LFI	71	4.50	0.56	3.14	6.19	18	4.38	0.58	3.02	5.43	21	4.15	0.48	3.16	5.20	5.05
LP	71	11.79	0.92	10.10	15.52	18	11.95	1.22	10.41	15.54	21	11.81	0.72	10.70	13.52	13.96
SMS	71	20.92	1.58	17.72	24.48	18	20.79	2.57	12.20	23.83	21	21.29	1.19	17.83	23.45	15.00
APM3	71	12.60	0.75	10.97	14.22	18	12.77	0.69	11.48	13.88	21	12.90	0.70	11.88	14.56	25.58

the 18th century, in accordance with the earliest records of exotic wildlife in the southeast of the Province of Buenos Aires, during a period of cold and dry climate referred to as the Little Ice Age. If his hypothesis is correct, *G. tixiensis* would have been replaced in those same ecosystems by *G. l. littoralis*, the species currently recorded in the south of the pampas region (Galliari et al. 1991). In other words, the colonization of *G. l. littoralis* would have occurred in the last 200 years after the extinction of *G. tixiensis*, since there are no references of both species coexisting in sympatry in any of the sites studied by Quintana (2001; see also Quintana, 2016a, 2016b). This hypothesis is hardly parsimonious, especially in view of the morphological results discussed above. It is more likely that *G. leucoblephara* had experienced changes in size throughout the Holocene, a phenomenon that is well documented for mammals of the Northern Hemisphere (Martin and Barnosky 1993). In fact, the record of Holocene mammals of larger sizes than their living counterparts has already been mentioned for hilly and interhilly

areas of Buenos Aires. A number of authors have highlighted the findings in various archaeological and fossils sites, of specimens of the rodent *Dolichotis patagonum* (e. g., Lobería; Tonni 1985) and the xenarthran *Zaedyus pichiy* (e. g., La Toma, Fortín Necochea, Laguna del Trompa, San Martín; see Vizcaino et al. 1993) based on skeletal remains of larger size vs living specimens. A similar finding has been described for the cervid *Ozotocerus bezoarticus* and the sigmodontine rodent *Holochilus vulpinus* in several sites in the hilly area of Córdoba, central Argentina, for the same period of time (Teta et al. 2005; Medina and Merino 2012).

The climatic conditions for the largest part of the Holocene in the Pampean region were colder and drier than the current climate (cf. Tonni et al. 1999). In this context, it would not be unlikely that some mammal lineages likely developed phenotypic and physiological responses consistent with this scenario, including the variation in size, but not necessarily implying speciation events.

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Table 2. Results of the principal component analysis performed on adult individuals (n = 111) of three subspecies of *Galea leucoblephara* and the holotype of *G. tixiensis*. For a reference of the abbreviations, see Materials and Methods.

	PC 1	PC 2	PC 3
AN	-0.14	0.01	0.43
CIO	-0.06	-0.06	0.71
LF	-0.11	-0.13	-0.41
LD	-0.14	-0.26	-0.31
AFI	0.94	0.05	-0.04
LFI	-0.17	0.90	-0.15
LP	-0.12	-0.24	-0.11
SMS	-0.09	-0.13	-0.08
APM3	-0.10	-0.14	-0.05
Autovalues	0.01	0.00	0.00
% Variance	45.14	21.60	10.59

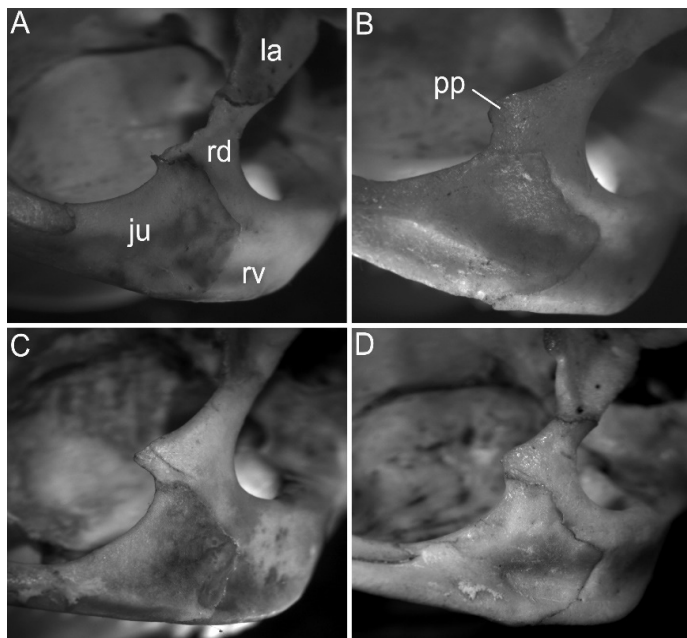


Figure 4. Individual variation in the morphology of the orbit in specimens of *Galea leucoblephara littoralis*: A) MACN-Ma 16405; B) MACN-Ma 13335; C) MACN-Ma 22607; D) MACN-Ma 13226. Abbreviations: ju = jugal; la = lacrimal; pp = paraorbital apophyses; rd/rv = dorsal/ventral root of the zygomatic portion of the maxilla.

Table 3. Diagnostic traits of *Galea tixiensis* (from Quintana, 2001) and expression of these same traits in a sample of 20 adult specimens of *G. leucoblephara littoralis* (for further details see Appendix 1).

	<i>G. tixiensis</i>	<i>G. l. littoralis</i>
Size	Larger than in living populations of <i>G. l. littoralis</i>	Smaller than in <i>G. tixiensis</i>
Zygomatic arches	Robust	Robust to moderately robust
Jugal	Proportionately short and wide	Proportionately short and wide to short and thinner
Ascending branch of the zygomatic portion of the maxilla	Proportionately short, with a well-defined paraorbital apophysis	Proportionately short, with a moderately to well-defined paraorbital apophysis
Ventral surface of the diastema	Flat in front of the incisive foramina	Flat in front of the incisive foramina
Incisive foramen	Large and diamond-shaped	Large, tapered to diamond-shaped
Interpremaxillar foramen	Large with two accessory foramina located with a lateral and posterior disposition, forming a structure that is connected to the incisive foramen through two open channels that cover the premaxilla on the lower side of the diastema	Large to medium in size, with two accessory foramina located to the sides and back, with the same disposition and connection with the incisive foramen as in <i>G. tixiensis</i> .

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Literature cited

- BEZERRA, A. 2008. Revisão taxonômica do gênero *Galea* Meyen, 1832 (Rodentia, Caviidae, Caviinae) Dissertation, Universidad de Brasilia, Brasília, Brazil.
- CHEREM, J. J., AND F. FERIGOLO. 2012. Descrição do sínclano de *Cavia aperea* (Rodentia, Caviidae) e comparação com as demais espécies do gênero no Brasil. *Papeis Avulsos de Zoologia* 52:21-50.
- DUNNUM, J. L. 2015. Family Caviidae G. Fischer, 1817. Pp. 690–726 in *Mammals of South America, Volume 2 - Rodents* (Patton, J.L., U.F.J. Pardiñas y G. D’Elía, eds.). The University of Chicago Press, Chicago, Illinois.
- FRANCIA, A., A. A. CARLINI, A. E. ZURITA, AND D. H. VERZI. 2012. *Galea* (Rodentia, Caviidae) in the late Pleistocene of Corrientes Province (Argentina): taxonomic and paleobiogeographic implications. *Neues Jahrbuch für Geologie und Paläontologie* 266/2:173-184.
- GALLIARI, C. A., W. D. BERMAN, AND F. J. GOIN. 1991. Situación ambiental de la provincia de Buenos Aires. A. Recursos y rasgos naturales en la evaluación ambiental. Mamíferos. Comisión de Investigaciones Científicas de la provincia de Buenos Aires, año I, 5:1-35.
- MAESTRI, R., R. FERNEL, G. L. GONÇALVES, L. GEISE, T. R. O. DE FREITAS, AND A. C. CARNAVAL. 2016. Predictors of intraspecific morphological variability in a tropical hotspot: comparing the influence of random and non-random factors. *Journal of Biogeography* 43:2160–2172.
- MARTIN, R. A., AND A. D. BARNOSKY. 1993. *Morphological Change in Quaternary Mammals of North America*. Cambridge, UK: Cambridge University Press.
- MEACHEN-SAMUELS, J., AND B. VAN VALKENBURGH. 2009. Craniodental indicators of prey size preference in the Felidae. *Biological Journal of the Linnean Society* 96:784-799.
- MEDINA, M. E., AND M. L. MERINO. 2012. Zooarqueología de Puesto La Esquina 1 (ca. 360 AP, Pampa de Olaen, Córdoba). Su importancia biogeográfica y paleoecológica. *Intersecciones en Antropología* 13:473-484.
- PREVOSTI, F. J., M. A. RAMÍREZ, M. SCHIAFFINI, F. MARTIN, D. E. UDRIZAR SAUTHIER, M. CARRERA, C. SILLERO-ZUBIRI, AND U. F. J. PARDIÑAS. 2015. Extinctions in near time: new radiocarbon dates point to a very recent disappearance of the South American fox *Dusicyon avus* (Carnivora: Canidae). *Biological Journal of the Linnean Society* 116:704-720.
- QUINTANA, C. 2001. *Galea* (Rodentia, Caviidae) del Pleistoceno Superior y Holoceno de las sierras de Tandilia oriental, provincia de Buenos Aires, Argentina. *Ameghiniana* 38:399-407.
- QUINTANA, C. 2016a. Tafonomía de los microvertebrados del sitio arqueológico, Cueva Tixi (Pleistoceno tardío–Holoceno tardío), Tandilia Oriental (provincia de Buenos Aires, Argentina). *Publicación Electrónica de la Asociación Paleontológica Argentina* 16:14–51.
- QUINTANA, C. 2016b. Microvertebrados del sitio arqueológico Cueva El Abra, Tandilia oriental: tafonomía y paleoambiente. *Comechingonia, Revista de Arqueología* 20:203-229.
- QUINTANA, C., AND D. L. MAZZANTI. 1998. Roedores Caviidae del Pleistoceno Superior y Holoceno de sitios arqueológicos de Tandilia oriental, provincia de Buenos Aires. *V Jornadas Geológicas y Geofísicas Bonaerenses* 259-263.
- RICHTSMIEIER, J.T., V.B. DELEON, AND S.R. LELE. 2002 The promise of geometric morphometrics. *Yearbook of Physical Anthropology* 45:63-91.
- TETA, P., M. MEDINA, S. PASTOR, D. RIVERO, AND H. PARADELA. 2005. *Holochilus brasiliensis* (Rodentia, Cricetidae) en conjuntos arqueofaunísticos del Holoceno tardío de la provincia de Córdoba (Argentina). *Mastozoología Neotropical* 12:271-275.

- TETA, P., A. FORMOSO, M. TAMMONE, D. C. DE TOMMASO, F. J. FERNÁNDEZ, J. TORRES, AND U. F. J. PARDIÑAS. 2014. Micromamíferos, cambio climático e impacto antrópico: ¿Cuánto han cambiado las comunidades del sur de América del Sur en los últimos 500 años? *Therya* 5:7-38.
- TONNI, E.P. 1985. Mamíferos del Holoceno del Partido de Lobería, provincia de Buenos Aires. Aspectos paleoambientales y bioestratigráfico del Holoceno del sector oriental de Tandilia y área Interserrana. *Ameghiniana* 22:284-288.
- TONNI, E.P., M. BARGO, AND J. PRADO. 1988. Los cambios ambientales en el Pleistoceno tardío y Holoceno del S.E. de la Prov. de Buenos Aires a través de una secuencia de mamíferos. *Ameghiniana* 25:99-110.
- TONNI, E. P., A. L. CIONE, AND A. J. FIGINI. 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the Late Pleistocene and Holocene. *Paleogeography, Palaeoclimatology, Palaeoecology* 147:257-281.
- UBILLA, M., AND A. RINDERKNECHT. 2001. Consideraciones sobre el género *Galea* Meyen, 1831 (Rodentia, Caviidae), su registro en el Pleistoceno de Uruguay y descripción de una nueva especie extinguida. *Boletín de la Real Sociedad Española de Historia Natural* 96:111-122.
- UBILLA, M., AND A. RINDERKNECHT. 2014. Comparative analysis of *Galea* (Rodentia, Caviidae) and expanded diagnosis of *Galea ortodonta* Ubilla and Rinderknecht, 2001 (Late Pleistocene, Uruguay). *Geobios* 47: 255–269.
- VIZCAÍNO, S. F., Y M. S. BARGO. 1993. Los armadillos de la toma (partido de Coronel Pringles) y otros sitios arqueológicos de la provincia de Buenos Aires. Consideraciones paleoambientales. *Ameghiniana* 30:435-443.
- VIZCAÍNO, S. F., M. S. BARGO, G. H. CASSINI, AND N. TOLEDO. 2016. Forma y función en paleobiología de vertebrados. Editorial de la Universidad Nacional de La Plata (EDULP).
- VUCETICH, M. G., M. ARNAL, C. M. DESCHAMPS, M. E. PEREZ, AND E. C. VIEYTES. 2015. Evolution of Caviomorph rodents: A complete phylogeny and timetree for living genera. Pp. 11-62 in *Biology of Caviomorph rodents: Diversity and evolution* (Vasallo, A.I. y D. Antenucci, eds.). Sociedad Argentina para el Estudio de los Mamíferos Series A, Mammalogical Research/ Investigaciones Mastozoológicas, Buenos Aires, Argentina.

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Appendix 1.

List of the *Galea* specimens studied in the present work, and their record localities in Argentina, Bolivia and Paraguay. These materials are deposited in the following collections: CFA, Collection of Mammals of Fundación de Historia Natural Félix de Azara (Buenos Aires, Argentina); CMI, Collection of Mammals of Instituto Argentino de Investigación de Zonas Áridas (Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina); CML, Collection of Mammals of Facultad de Ciencias Naturales e Instituto Miguel Lillo (Facultad de Ciencias Naturales e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina); CNP, Collection of Mammals of Centro Nacional Patagónico (Centro Nacional Patagónico, Puerto Madryn, Argentina) MACN-Ma, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina) MNHNP, Collection of Mammals of Museo Nacional de Historia Natural de Paraguay (Asunción, Paraguay); UACH, Collection of Mammals of Universidad Austral de Chile (Valdivia, Chile):

Galea leucoblephara demissa ($n = 77$): Argentina: Catamarca: Hualfín, Casa de Piedra (CML 917). Chaco: General Güemes, Misión Nueva Pompeya (MACN-Ma 22589). Formosa: Matacos, Ingeniero Guillermo N. Juárez (MACN-Ma 47.391). Jujuy: San Pedro, Ingenio La Esperanza (CFA 4704). La Rioja: Chilecito, Chilecito (MACN-Ma 34.189, 34.272); Coronel Felipe Varela: Villa Unión (MACN-Ma 34.190, 34.193); Famatina, Las Pirquitas (MACN-Ma 34.194, 34.200); Famatina, Tres Cerros (MACN-Ma 34.196, 34.198). Salta: Anta, Los Colorados, 17 km E Santo Domingo (CML 3052); El Quebrachal (MACN-Ma 36.312, 36.313, 36.314, 36.315, 36.685, 36.752, 36.755, 36.761, 36.764, 36.766, 36.767, 36.771, 36.772, 36.774, 36.775, 36.776, 36.778, 36.779, 36.783, 36.784, 36.785, 36.786, 36.790, 36.791); General José de San Martín, Dragones (MACN-Ma 36.262); Metán, Metán (MACN-Ma 17362); Metán, La Represa, 500 mts. (MACN-Ma 30.363, 30.368); Orán, Orán (MACN-Ma 16227); Río Pescado (CFA 4307); Tabacal (MACN-Ma 16227); Finca San Javier, 8,5 km SE Joaquín V. González (CMI 3021); San Javier-Pozo Largo, 19 km SE Joaquín V. González (CMI 3023); Puesto Yuchán, camino a Salta forestal, 35 km N Joaquín V. González (CMI 3022). Santiago del Estero: Banda, Sotelillo (CML 509); Choya, Villa La Punta (CFA 10809); Pellegrini, Santa Isabel (MACN-Ma 17351, 17352); sin localidad precisa (MACN-Ma 35.137, 35.138). Tucumán: km 81 de la R307, Tafi del Valle, 12 km O de Quebradita (CMI 4160); Trancas: Cerro Vipos, 1000 m s.n.m. (MACN-Ma 30.167, 30.169-30.171); Cumbres Calchaquies, cercanas a Vipos (MACN-Ma 30.167); Leales (CFA 111); Villa M. Paz (CFA 4370). Paraguay: Alto Paraguay: Estancia "Tres Marias" (TK 62443); Palmar de Las Islas (TK 65319, 65391). Boquerón: (TK130781, 130786, 130807, 13785); Parque Cué (TK 63298, 63371); Parque Nacional "Teniente Enciso" (TK 65029); Parque Nacional "Teniente Enciso", 3 Km. al Sur del fortín Teniente Enciso (MNHNP 753); Parque Nacional "Teniente Enciso", cerca del Puesto Siracua (TK66471); Rodeo Trebol, 5 Km. al NE de Loma Plata (TK 130764). Parque Nacional "Defensores del Chaco", 500

mts. al Oeste de Madrejón (MNHNP 755); Presidente Hayes, Estancia "Samaklay" (TK 122211, 122212, 122226).

Galea leucoblephara leucoblephara ($n = 11$): Argentina: Córdoba: Pocho, Tala Cañada (MACN-Ma 14745); San Alberto, Pampa de Achala (MACN-Ma 14706); San Javier, La Paz (MACN-Ma 29.10); Santa María, Alta Gracia, Falda del Carmen (MACN-Ma 14705). Mendoza: Mendoza (IZH 17); Santa Rosa, Reserva de Biosfera de Ñacuñan (UACH 6168); Tunuyán, Manzano Histórico (CMI 4160). San Juan: 9 de Julio, Monte de Oro (CMI 7065), San Juan (MACN-Ma 29.876); San Luis: General Pedernera, Villa Mercedes (MACN-Ma 50.49); Merlo, El Rincón (MACN-Ma 29.51).

Galea leucoblephara littoralis ($n = 22$): Argentina: Buenos Aires: Bahía Blanca (MACN-Ma 25281); Balcarce, Napaleofú (MACN-Ma 16405); Benito Juárez, Benito Juárez (MACN-Ma 54.134, 54.135); General Pueyrredón, Sierra de los Padres (MACN-Ma 13064); Necochea, Quequén (MACN-Ma 28.11); Torquinst, Abra de la Ventana (MACN-Ma 14936); Villarino, Algarrobo (MACN-Ma 22607). Chubut: Biedma, Arroyo Valdes (US s/n); Puerto Madryn, Playa Kaiser (CNP s/n, CNP s/n); Escalante, Valle Hermoso (MACN-Ma 29.927); La Pampa: Caleu Caleu (MACN-Ma 13335, 13336, 15500); Hucal, Laguna Colorada Grande (MACN-Ma 15500); Lihuel Calel, Parque Nacional Lihué-Calel (MACN-Ma 20845); Pichi Mahuida, Estación de Aforos N°44 (CNP 3619). Neuquén: Collón Curá (CFA 5567). Río Negro: Avellaneda: Choele Choel (MACN-Ma 28.141). Santa Cruz: Deseado, 20 km al Norte de Caleta Olivia (MACN-Ma 22838).

