



Galea (Rodentia, Caviidae) in the late Pleistocene of Corrientes Province (Argentina): taxonomic and paleobiogeographic implications

Analía Francia, Alfredo A. Carlini, Alfredo E. Zurita and Diego H. Verzi

With 6 figures and 1 table

FRANCIA, A., CARLINI, A.A., ZURITA, A.E. & VERZI, D.H. (2012): *Galea* (Rodentia, Caviidae) in the late Pleistocene of Corrientes Province (Argentina): taxonomic and paleobiogeographic implications. – N. Jb. Geol. Paläont. Abh., **266**: 173–184; Stuttgart.

Abstract: The Caviidae (Rodentia) are taxonomically diverse caviomorphs. Their fossil record is abundant and their oldest representatives date back to the middle/late Miocene. The genus *Galea* MEYEN includes small-sized species, exclusively distributed in South America. In this work we describe new remains of *Galea* (Rodentia, Caviidae) from the Toropí Formation (late Pleistocene, ca. 52 ka) of Corrientes Province, Argentina, and discuss the paleobiogeography of late Pleistocene species. The remains consist of a partial maxillary with complete P4-M3 dental series, anterior portion of the zygomatic arches, one associated left upper incisor, and one isolated left P4. Anatomical differences in relation to the remaining recognized species, differences in temporal and latitudinal distribution, as well as in the taxonomic composition of faunas associated to extinct species of *Galea*, suggest that it corresponds to a new species related to *Galea tixiensis*. The presence of this taxon in the late Pleistocene sediments of Corrientes Province represents a new element to characterize the complex biological dynamics of this region during much of the Pleistocene; in this area, intertropical elements co-occurred with typical Pampean-Patagonian taxa, and conditions could have eventually promoted differentiation of endemic species.

Key words: *Galea*, Pleistocene, Caviidae, Mesopotamian region, paleobiogeography, Lujanian, Argentina.

1. Introduction

The Caviidae (Rodentia) are taxonomically diverse caviomorphs restricted to South America (WOOD 1955; McKENNA & BELL 1997). Their fossil record is abundant and their oldest representatives date back to the middle/late Miocene (MARSHALL et al. 1984; VUCETICH et al. 1999; PÉREZ & VUCETICH 2011). REIG (1986) proposed that the origin of this group was associated to low and humid areas of South America, with subsequent evolution of a progressive adaptation to more

arid regions during the Miocene and Pliocene. Recent phylogenetic studies (based on DNA sequences and morphological data) corroborate the close relationship of Caviidae and Hydrochoeridae (DA SILVA NETO 2000; ROWE & HONEYCUTT 2002; OPAZO 2005; BLANGA-KANFI et al. 2009; PÉREZ 2010).

The genus *Galea* MEYEN, 1833 includes small-sized species distributed exclusively in South America (CABRERA 1953), with a complex taxonomic history. In Argentina, the first record of the genus is from the Ensenadan of Punta Negra, Buenos Aires Province

(VUCETICH & VERZI 1999). The following extant species of the genus have been recognized: *G. flavidens* (BRANDT, 1835), *G. monasteriensis* SOLMSDORFF et al., 2004, *G. mustelooides* MEYEN, 1832, *G. wellsi* (OSGOOD, 1915), *G. saxatilis* (LUND, 1841), and *G. spixii* (WAGLER, 1831). In addition, two extinct species have been described: *G. ortodonta* UBILLA & RINDERKNECHT, 2001 from the Pleistocene of Bolivia and Uruguay, and *G. tixiensis* QUINTANA, 2001 from the Pleistocene-Holocene of Argentina. It is worth mentioning that not all these nominal species have been considered valid: SOLMSDORFF et al. (2004) only included four living species in the genus, whereas BEZERRA (2008), using geometric morphometry, divided the living species of *Galea* into two main groups, “*mustelooides*” and “*spixii*”. On the other hand, DUNNUM & SALAZAR-BRAVO (2010) consider that *G. monasteriensis* is a junior synonym of *G. mustelooides boliviensis* and suggest that the genus is currently composed of *G. spixii*, *G. flavidens* and the species belonging to the *mustelooides* group, in which they recognize *G. mustelooides* (in the Bolivian altiplano, south Peru and extreme northeastern Chile), *G. leucoblephara* BURMEISTER, 1861 (in the plains of eastern Bolivia and part of Paraguay to central Argentina) and *G. comes* THOMAS, 1919 (in the Andes of south Bolivia and north Argentina). However, several studies have shown that poorly characterized species with questionable validity, such as *G. flavidens*, *G. saxatilis* and *G. wellsi*, show no significant anatomical differences with respect to *G. spixii* (see, among others, CABRERA 1961; UBILLA & RINDERKNECHT 2001).

In this paper we describe new *Galea* material from the late Pleistocene of Corrientes Province, Argentina. Its cranio-dental anatomy is analyzed and compared with that of other species both living and extinct. In this context, the paleobiogeographical relevance of its occurrence in Pleistocene deposits of the Argentinian Mesopotamia is discussed taking into account the current geographical distribution of the species of this genus and their respective environmental preferences.

2. Material and methods

The fossil remains studied here are: CTES-PZ 7471, incomplete maxillary with both P4-M3 dental series, anterior portion of both zygomatic arches, and one associated upper left incisor; CTES-PZ 7537, isolated left P4. For descriptions and comparisons, the following cranio-dental materials corresponding to living and extinct species of genus *Galea* were also used:

G. spixii: MN-RJ: 35417, 35337, 35376, 35341, 35410, 35371. *G. mustelooides* group: MACN-Ma: 34.197, 15.324, 15.497, 15.499, 36.419, 47.390, 50.415, 34.189, 29.10, 36.746, 36.756, 50.306, 50.307, 29.18, 34.193, 28.141, 54-134, 54-135; MLP-Ma: 15-X-98-5, 14-IX-98-3, 5-II-49-5, 15-X-98-7. *G. tixiensis*: LARQ: 123, 124, 125, S/N. *G. ortodonta*: FC-DPV-900, TAR-22. *Galea* sp.: MACN-Ma: 14.936, 14.937, 17.352; MLP-Ma: 22-VI-99-4, 738-2.

A total of 21 cranio-dental characters were analyzed, following CONTRERAS (1964), UBILLA & RINDERKNECHT (2001) and QUINTANA (2001): 1. Bizygomatic width at level of P4-M1 contact; 2. Position of anteriormost extreme of mesopterygoid fossa; 3. Shape of mesopterygoid fossa; 4. Position of middle vertex of maxillary-palatine contact; 5. Morphology of palatal surface; 6. Length of P4-M3 prisms; 7. Morphology of zygomatic arch; 8. Position of zygomatic root; 9. P4-M3 length; 10. Outer palatal width at level of external alveolar margin of M3; 11. Transversal width of upper incisor; 12. Anteroposterior width of upper incisor; 13. Width of P4; 14. Length of P4; 15. Proportion between length of P4 and total length of M1-M3 series; 16. Width of M3; 17. Length of M3; 18. Proportion between length of M3 and total length of M1-M3 series; 19. Presence and development of furrows; 20. Angle at union of zygomatic arch and maxillary; 21. Thomas' angle (The angle formed between the chord of the exposed incisor and a line parallel to the occlusal plane of the upper molariforms. Categories of upper-incisor procumbency are defined as: “proodont” for rodents with incisors thrown forward more than 90° to the rostrum, “orthodont” for rodents with incisors at about 90° to the rostrum, and “opisthodont” for rodents with incisors formed an angle of less than 90° with the rostrum).

X-ray images were obtained in lateral and occlusal views to allow better observation for the comparative analysis of those characters that so required (e.g. 20, 21).

Nomenclature of cranio-dental characters follows KRALIEVICH (1940) and CONTRERAS (1964). Quantitative characters were measured using calipers; all measurements are expressed in millimeters. Statistical analyses were made using the software PAST v 1.97 (HAMMER et al. 2001). The goal of the descriptive bivariate analysis is to visualize the spread of data in the space generated from two variables, in order to make quantitative comparisons regarding the existence of size differences between specimens.

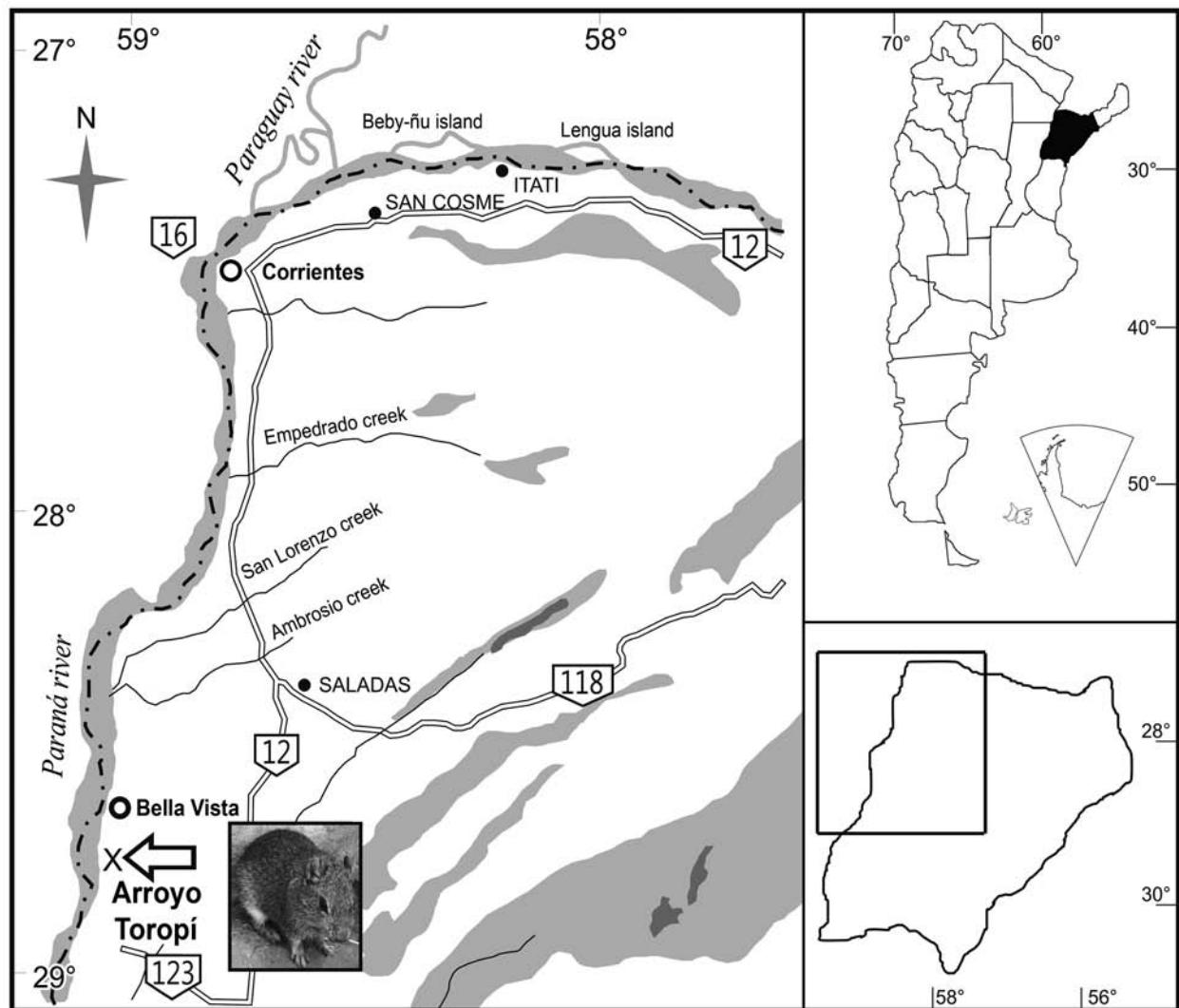


Fig. 1. Map showing location of the paleontological site.

Abbreviations: CTES-PZ, Facultad de Ciencias Exactas y Naturales y Agrimensura de la Universidad Nacional del Nordeste, Colección Paleozoológica, Corrientes, Argentina; FC-DPV, Facultad de Ciencias, Paleontología de Vertebrados, Montevideo, Uruguay; LARQ, Colección Científica del Laboratorio de Arqueología, Facultad de Humanidades, Universidad Nacional de Mar del Plata, Argentina; MACN-Ma, Museo Argentino de Ciencias Naturales, Colección de Mastozoología, Buenos Aires, Argentina; MLP-Ma, Museo de La Plata, Colección de Mastozoología, La Plata, Argentina; MN-RJ, Museu Nacional de Rio de Janeiro, Brazil; TAR, Muséum National d'Histoire Naturelle, France; Hy, hypoflexus; II, upper incisor; Ka, thousand years; M, up-

per molar; Ma, million years; Mx, maxillary; OIS, Oxygen Isotope Stages; OSL, Optically Stimulated Luminescence; P, upper premolar; PrI, first prism; PrII, second prism; Za, zygomatic arch.

3. Geology and stratigraphy

The materials studied here were collected from Quaternary outcrops in the Arroyo Toropí valley (28°36' S and 59°02' W), located about 10 km south from the town of Bella Vista, in Bella Vista Department, Corrientes Province, Argentina (Fig. 1).

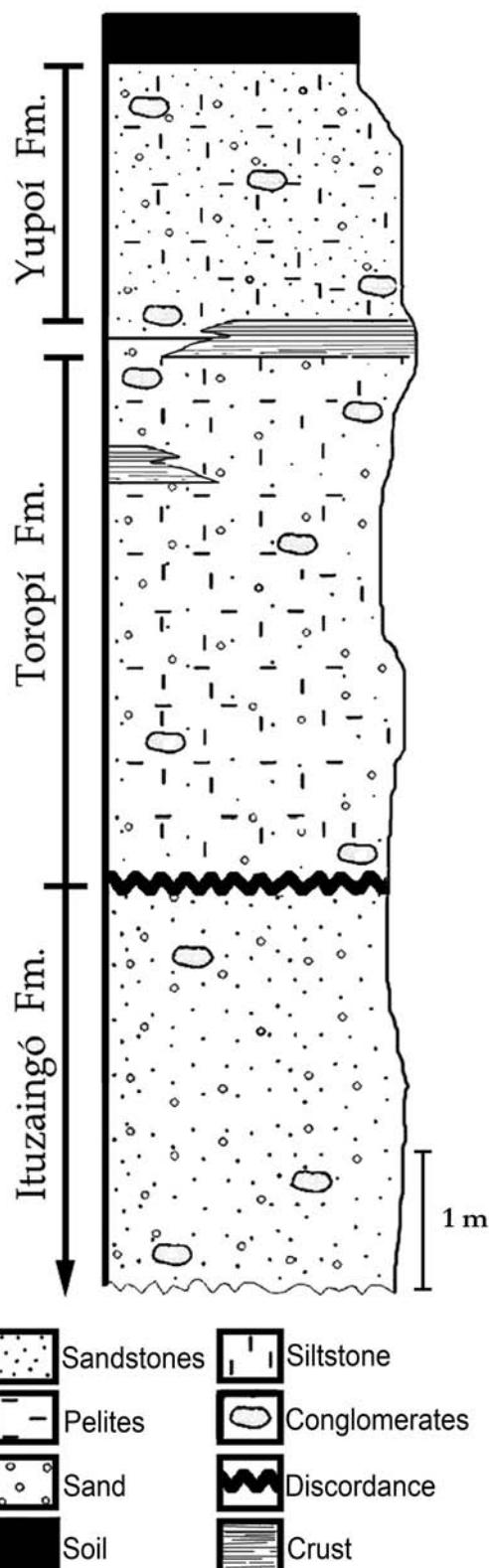


Fig. 2. Lithostratigraphic profile of Toropí/Yupoí Formations (Corrientes Province).

The Arroyo Toropí runs in ES-WN direction, almost perpendicular to the Paraná river into which it flows. It extends for about 3 km, with a maximum width of its valley of approximately 500 m (ÁLVAREZ 1974). Traditionally, two lithostratigraphic units have been recognized for the late Quaternary of Corrientes Province: Toropí Formation and Yupoí Formation (HERBST & ÁLVAREZ 1977; HERBST & SANTA CRUZ 1999) (Fig. 2). However, Iriondo (1996) proposed the unification of both units in what he called the Toropí/Yupoí Formation, correlating it with the Hernandarias Formation (middle Pleistocene, between 1.3 and 0.8 Ma) that outcrops on the left margin of Paraná river, in Entre Ríos Province. From a lithological perspective, both units are very similar, with a composition of “areniscas bastante pelíticas hasta pelitas bastante arenosas, con proporciones variables de ambos componentes... sin una estratificación visible” [“rather pelitic sandstone to rather sandy pelites, with variable proportions of both components... without visible stratification”] (HERBST & SANTA CRUZ 1999: 43). Regarding the age of the bearing sediments, SCILLATO-YANÉ et al. (1998), based on the study of fossil mammals in the area, attributed an age referable to the Lujanian s.l. (middle Pleistocene – early Holocene; CIONE & TONNI 1995) to the sequence (Toropí Fm./Yupoí Fm.). Lastly, datings of the bearing sediments by means of OSL analyses have yielded ages between 52 ka and 36 ka BP, corresponding to the Lujanian s.st. (late Pleistocene; TONNI et al. 2005).

4. Systematic paleontology

Class Mammalia LINNAEUS, 1758

Order Rodentia BOWDICH, 1821

Suborder Hystricomorpha BRANDT 1955

Family Caviidae FISCHER DE WALDHEIM, 1817

Subfamily Caviinae FISCHER DE WALDHEIM, 1817

Genus *Galea* MEYEN, 1833

Galea aff. *G. tixiensis* QUINTANA, 2001

Figs. 3A, 4

Referred material: CTES-PZ 7471, incomplete maxillary, with both complete P4-M3 series, anterior portion of both zygomatic arches and one associated upper left incisor. CTES-PZ 7537, isolated left P4.

Geographic and stratigraphic provenance: The studied material was exhumed 300 m west from the headwaters of the Arroyo Toropí (28°36' S and 59°02' W), 10 km south from Bella Vista, Bella Vista Department, Corrientes, Argentina. Toropí Formation (late Pleistocene; ca. 52 ka, TONNI et al. 2005) (Figs. 1-2).

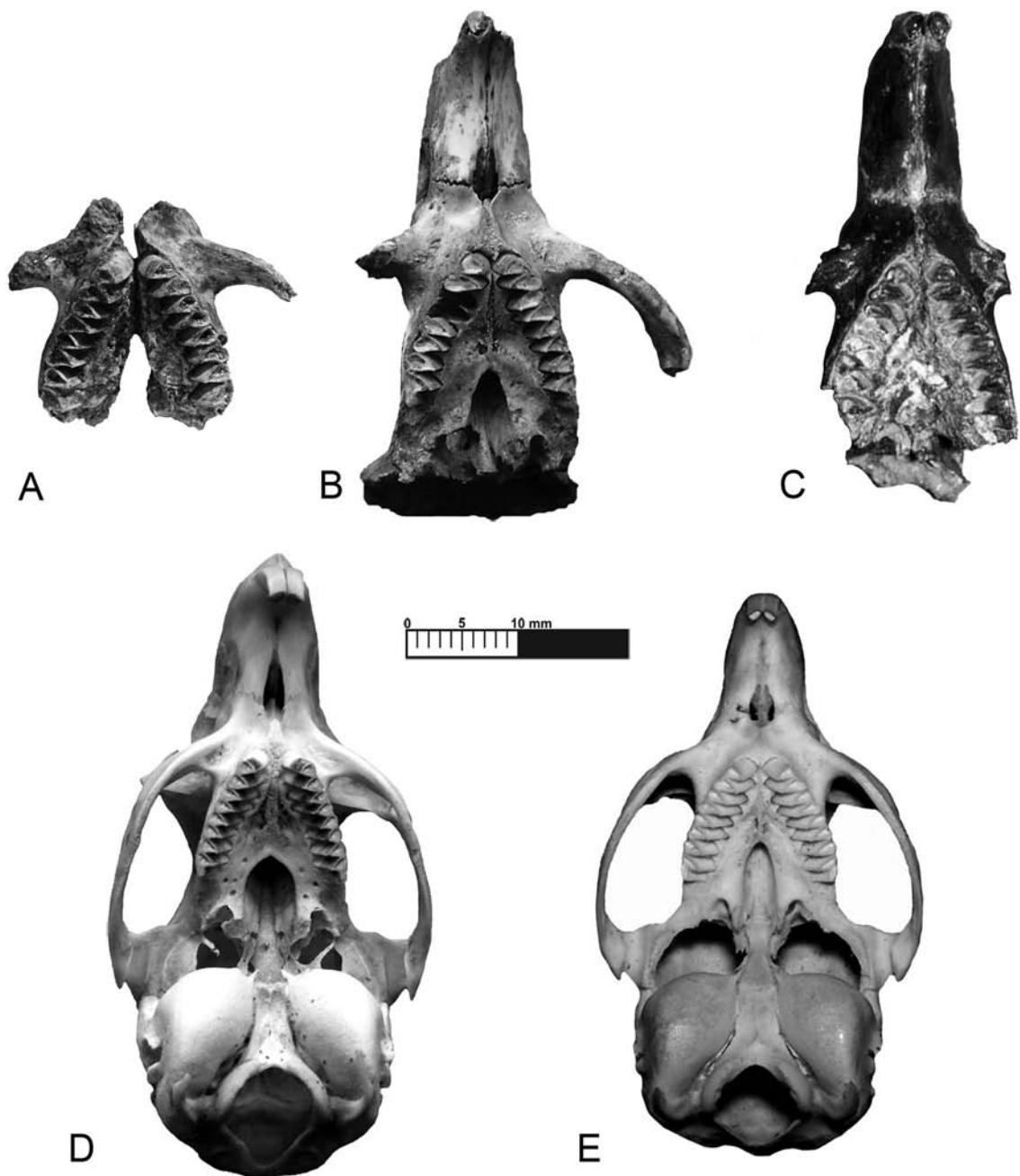


Fig. 3. Palatal views of *Galea*. **A** – *Galea* aff *G. tixiensis* (CTES-PZ 7471). **B** – *G. tixiensis* (LARQ 123). **C** – *G. ortodonta* (FC-DPV 900). **D** – *G. spixii* (MN-RJ 35337). **E** – *G. mustelooides* (MACN 54-134). Scale bar = 20 mm.

Description and comparison: In palatal view the maxillary is short, the maxillary root of the zygomatic arch is robust as in *G. tixiensis* and located at level of P4, extending to hypoflexus of M1; the flat area for insertion of anterior portion of lateral masseter muscle is very large, more so than in *G.*

tixiensis (Fig. 3B). The palatal surface is broad as in *G. tixiensis* and different from *G. spixii*, which has a narrower and less concave palate. The bizygomatic width is greater than in *G. spixii* and the *G. mustelooides* group, and somewhat lesser than in *G. tixiensis* (Table 1). The limits of the mesopterygoid

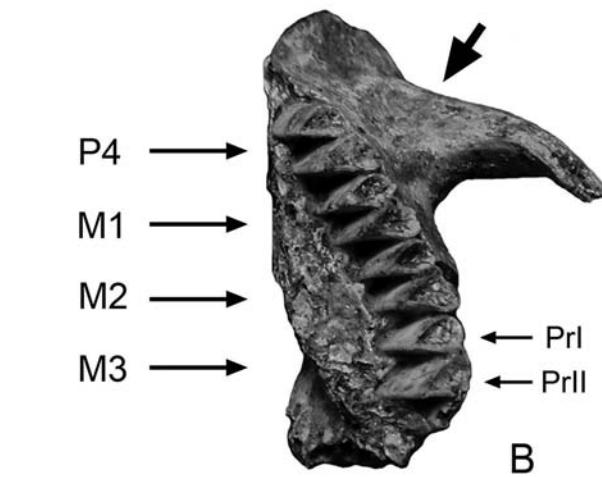
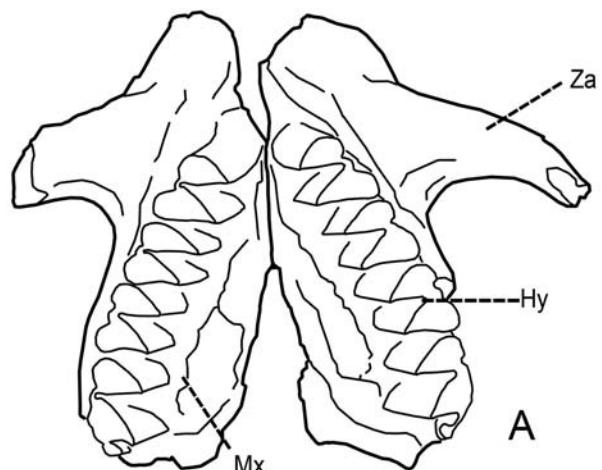


Fig. 4. Palatal views of *Galea* aff *G. tixiensis* (CTES-PZ 7471). **A** – Line drawing of palatal view of the maxillary and **B** – left hemimaxillary showing the dental series and the flat area for insertion of the anterior portion of the lateral masseter muscle. Abbreviations: Hy, hypoflexus; M, upper molar; Mx, maxillary; P, upper premolar; PrI, first prism; PrII, second prism; Za, zygomatic arch.

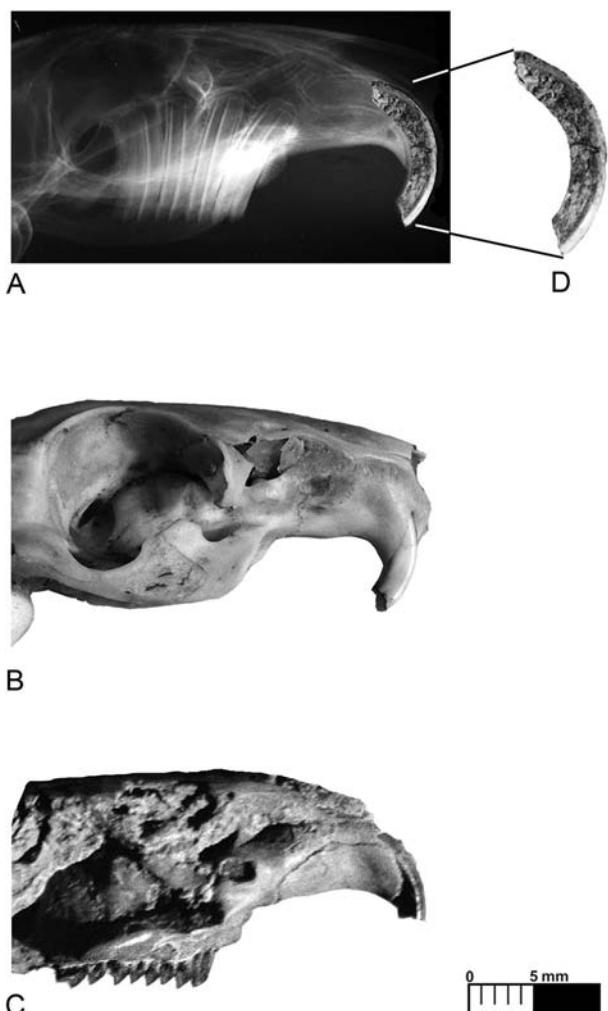


Fig. 5. Right lateral view of rostral region of: **A** – *G. spixii* (MN-RJ 35376), **B** – *G. spixii* (MN-RJ 35337), **C** – *G. ortodonta* (TAR-22). **D** – Lateral view of the upper right incisor of *Galea* aff. *G. tixiensis* (CTES-PZ 7471). Scale bar = 10 mm.

fossa cannot be precisely determined due to the preservation of the material; however, its morphology appears to be rather narrow and V-shaped, as in all examined specimens of *G. tixiensis* and *G. ortodonta* (Fig. 3C). This condition differs from that observed in *G. spixii* specimens, in which this fossa is wide and has rounded margins (Fig. 3D). On the other hand, in the *G. mustelooides* group and in contrast with the uniformity observed in the remaining species, the shape of the meopterygoid fossa is a highly variable character (Fig. 3E).

In specimen CTES-PZ 7471, the P4-M3 series form an pointed arch-shaped dental arch, with M3 slightly displaced

toward the sagittal plane. The molariforms are proportionally large, with both prisms subtriangular in section; the prisms are separated lingually by a deep hypoflexus partially filled with cement, and labially by two shallower furrows; a primary and secondary external furrow are always present. The posterior prisms are equal or larger in size than the anterior ones and present a variably-developed posterior extension on the labial face. This extension is maximally developed in M3, where it forms an additional prolongation of the posterior prism, defined lingually by a secondary internal furrow. The anterior prisms of P4-M3 are narrower

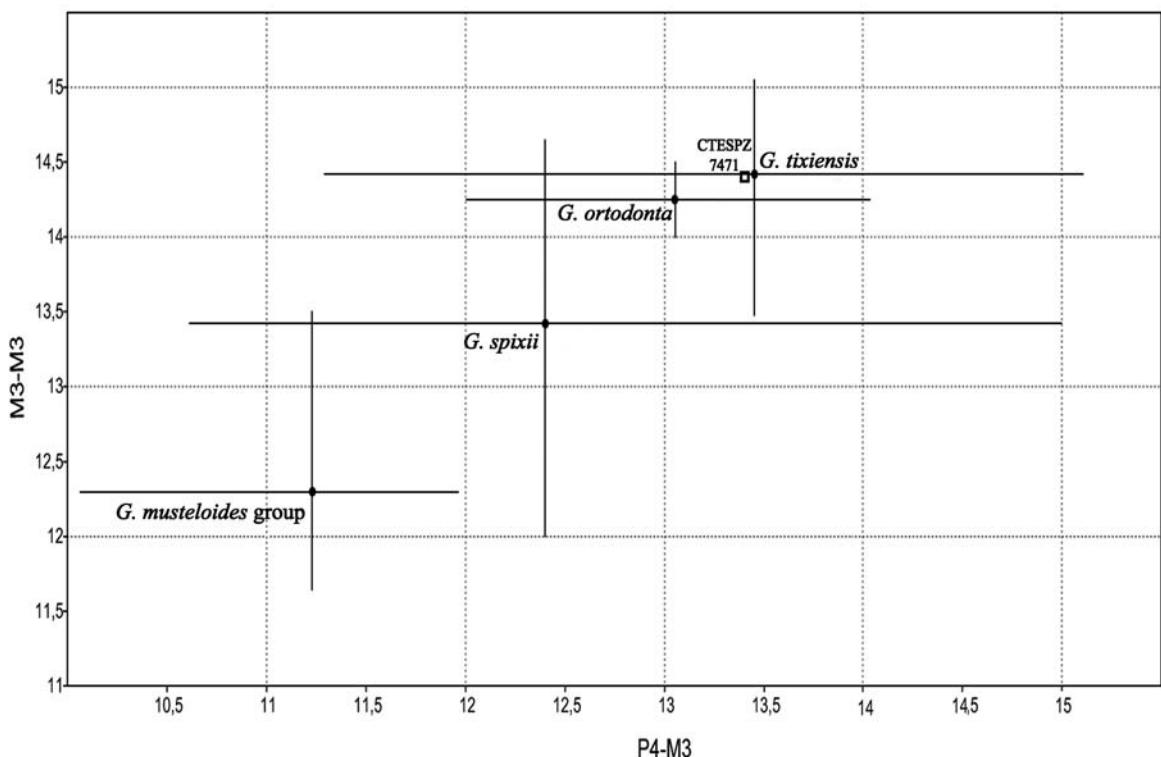


Fig. 6. Bivariate diagram of P4-M3 length (X) vs. external palatal width at external alveolar margin of M3 (M3-M3) (Y) based on the range and mean for each *Galea* species.

anteroposteriorly than the posterior ones, and their transversal diameter is always lesser than that of the posterior prism (Fig. 4).

II is separate from the skull; however, its wear facet and degree of curvature indicate that its morphology would correspond to the opistodont condition (see LANDRY 1957), as in all the species analyzed with the exception of *G. ortodonta* (Fig. 5). According to its measurements, the II is smaller than in *G. ortodonta* and intermediate in size between the values observed in *G. spixii* and *G. tixiensis* (Table 1). Although one of the diagnostic characters indicated for *G. tixiensis* is that the II would be narrower in this species than in *G. spixii*, the individuals analyzed here presented overlapping values for this character, and the measurements for specimen CTES PZ 7471 fell within the recorded range. Lastly, the isolated P4 (CTES-PZ 7537) is formed by two subtriangular prisms separated by a hypoflex whose base is filled with cement. On the basis of its size and prism morphology, it can also be assigned to *Galea* aff. *G. tixiensis*.

The results of the descriptive bivariate analysis indicate considerable intraspecific variation in several craniodental characters considered for the interspecific comparison (Fig. 6). It seems clear that the material from Corrientes shows

the diagnostic characters of the genus: (a) teeth formed by two prisms with the base of the hypoflexus filled with interprismatic cement (UBILLA & RINDERKNECHT 2001; SOLMS-DORFF et al. 2004), (b) upper molariforms with primary and secondary external furrows of variable configuration (UBILLA & RINDERKNECHT 2001), and (c) palatines clearly exposed in a relatively shallow palate (UBILLA & RINDERKNECHT 2001). Nevertheless, we prefer to leave the species assignation open because of the nature of this remain and its state of preservation. The inclusion of these remains in the most recent published phylogenetic analyses (e.g. QUINTANA 1998; PÉREZ 2010; PÉREZ & VUCETICH 2011) conducted to poorer results with poliomorphies due to the large number of missing entries, and did not contribute to any additional information.

On the other hand, the quantitative comparisons made here reinforce this tentative assignation (Fig. 6). In this sense, the values for the metric variables analyzed in the materials assigned to *G. aff. G. tixiensis* are higher than the means observed in the *G. musteloides* group and *G. spixii*, and mostly coincide with the value ranges observed in *G. tixiensis* and *G. ortodonta* (Table 1).

Table 1. Craniodental measurements (in mm) of CTES-PZ 7471, *G. tixiensis*, *G. ortodonta*, *G. musteloides* group y *G. spixii*. 1) Bonygomatic width, 2) P4-M3 length, 3) External palatal width at external alveolar margin of M3, 4) Antero-posterior width of upper incisor, 5) Transverse width of upper incisor, 6) Width of P4, 7) Length of P4, 8) Width of M3, 9) Length of M3. *Taken from QUINTANA (2001). *Taken from UBILLA & RINDERKNECHT (2001).

	CTESPZ 7471			<i>G. tixiensis</i>			<i>G. ortodonta</i>			<i>G. musteloides</i> group			<i>G. spixii</i>		
	Mean	Range	n	Mean	Range	n	Mean	Range	n	Mean	Range	n	Mean	Range	n
1	23.4	-	1	26.5	24 - 30	4	-	-	-	20.65	20 - 21	4	18.6	18 - 19.2	4
2	13.4	-	1	13.45	11.3 - 15.3	5	13.05*	12 - 14.1	2	11.23	10.1 - 11.9	10	12.4*	10.6 - 15	141
3	14.4	-	1	14.42°	13.6 - 15.1	11	14.25*	14 - 14.5	2	12.3°	11.3 - 13.5	8	13.42°	12 - 14.7	18
4	2.55	-	1	2.09°	1.6 - 2.4	15	-	-	-	2	1.8 - 2.2	3	2.4	2.3 - 2.6	4
5	1.8	-	1	1.59°	1.4 - 1.8	15	2*	2	2	1.76	1.5 - 1.8	3	1.8*	1.4 - 2.8	139
6	3	-	1	-	-	-	2.8*	2.5 - 3.1	2	2.3*	1.8 - 3.2	9	2.32	2.1 - 2.5	4
7	3.6	-	1	3.22	2.7 - 3.6	5	-	-	-	2.8	2.5 - 3.1	4	2.95	2.8 - 3.2	4
8	2.7	-	1	-	-	-	2.6*	2.5 - 2.7	2	1.8*	1.6 - 2.4	8	1.7*	1.4 - 3.4	142
9	4.4	-	1	4.34	3.3 - 4.8	5	-	-	-	3.96	3.85 - 4.2	4	3.68	3.5 - 4	4

5. Discussion

Specimen CTES-PZ 7471 was previously listed by SCILLATO-YANÉ et al. (1998) as *Galea* sp., and here it is described, compared and interpreted as belonging to a taxon related to *G. tixiensis*, mainly because its metric characters fall within the range of variation of this latter species, and also due to similarities in the morphology of the palatal surface and the mesopterygoid fossa, and the shared opistodonty. However, given the morphology of its zygomatic root and of the flat area for insertion of the anterior portion of the lateral masseter muscle (see Fig. 4B), the hypothesis that the studied material may represent a new extinct species of *Galea* with clear affinities to *G. tixiensis* cannot be dismissed. Morphological testing of this hypothesis depends on the finding of new specimens that allow a more thorough comparison.

From a paleozoogeographical and zoogeographical viewpoint, the record of *Galea* shows variations between its former and current geographical range (UBILLA & RINDERKNECHT 2001; KERBER et al. 2011a). The same pattern is also observed in other rodents (see ÁLVAREZ 1974; UBILLA et al. 2008; KERBER et al. 2011a, b).

The extant species of *Galea* are characteristic of open environments and occur from the altiplano of Peru and Bolivia, parts of Brazil, Chile and Paraguay to the Province of Santa Cruz in Argentina (MARES & OJEDA 1982; UBILLA & RINDERKNECHT 2001; AGNOLIN et al. 2008). Particularly, *G. spixii* occurs in central-east South America (central, north and northeast Brazil and eastern Bolivia) (MARES & OJEDA 1982), whereas the

species of the *G. musteloides* group are known from Peru, Bolivia, northeast Chile and Argentina (DUNNUM & SALAZAR-BRAVO 2010). In the latter territory, this species complex is typical of the Monte phytogeographical Province and has also been reported for the Patagonian phytogeographic Province (AGNOLIN et al. 2008).

It is worth noting that the distribution of each of the abovementioned species is tightly linked to characteristics of their respective habitats, since none of them appear to have evident plasticity. Despite the ample latitudinal ranges of some of the species, their occurrence within such ranges is associated with the existence of similar biomes. In this sense, consideration of the geographical and stratigraphical distribution of these taxa, the accompanying fauna reported for extinct *Galea* species, and the poor plasticity of extant species, opens an additional angle for discussion. The records of *G. tixiensis* are restricted to late Pleistocene-early Holocene deposits distributed throughout the stratigraphic profile of the archaeological sites Cueva Tixi and Cueva El Abra (Balcarce Formation) of the hill system La Vigilancia, in General Alvarado (37°50'26" S; 58°3'57" W), Buenos Aires Province (Argentina), which span a lapse of radiocarbon dates between 10,300 and 170 years BP (QUINTANA 2001). The taxa associated with those deposits include: *Lestodelphys halli*, *Lynchailurus pajeros*, *Dolichotis patagonum*, *Canis avus*, *Eutatus seguini*, *Monodelphis*, *Akodon azarae*, *Calomys*, *Necromys obscurus*, *Cavia aperea*, *Ctenomys talarum*, *Lagostomus maximus*, *Conepatus chinga*, *Lycalopex gymnocercus*, *Puma concolor*, *Chaetophractus villosus*, *Dasyurus hybridus*, *Zaedyus*

pichiy, *Lama guanicoe*, *Ozotoceros bezoarticus*, *Clelia rustica*, and *Rhea americana*, an association primarily linked to open and transitional environments, with bushes, scrubland and grasslands, and with primarily temperate-cold to cold, arid and semiarid climate. On the other hand, *G. ortodontia* is known from Pleistocene deposits of Uruguay and Bolivia (UBILLA & RINDERKNECHT 2001), from four different geographical localities: 1) El Caño (Colonia Department, Uruguay), whose sediments have been tentatively assigned to Libertad Fm.; 2) San Luis (Canelones Department, Uruguay), with sediments also tentatively assigned to Libertad Fm.; the fossil remains found here have allowed linking it to the Ensenadan Age-Stage (Goso AGUILAR 2006); 3) Arroyo Malo (Tacuarembó Department, Uruguay), whose sediments have been assigned to Sopas Fm. and, according to C^{14} datings of *Diploodon peraeformis* (Mollusca) shells, yield ages >43,000 years BP (UBILLA & RINDERKNECHT 2001; UBILLA et al. 2004; 4) Pueblo Viejo (Tarija, Bolivia), in Tarija Fm. (Ensenadan Age-Stage, early-middle Pleistocene, according to UBILLA & RINDERKNECHT 2001, although recently TONNI et al. (2009) discuss a younger age and COLTORTI et al. (2007) consider it as late Pleistocene. Recently, KERBER et al. (2011a) reported the first record of *Galea* sp. in the late Pleistocene of Rio Grande do Sul State, Southern Brazil. This specimen comes from Ponte Velha I locality in Touro Passo Creek (Touro Passo Formation) and the associated taxa include typical South American Pleistocene mammals (see OLIVEIRA 1999; KERBER & OLIVEIRA 2008; KERBER et al. 2011a, b).

Regarding the faunal association present in the Quaternary deposits of Corrientes Province, it comprises a group of taxa with clear intertropical affinities together with others typical of the Pampean Region (CARLINI et al. 2004, 2008; FRANCIA & CARLINI 2009). The paleoclimatic-environmental interpretation of the faunal diversity occurring in these sediments is consistent with an area characterized by alternation of colder, arid or semiarid pulses (evidenced by the presence of *Dolichotis* sp., *Pampatherium typum*, *Neosclerocalyptus paskoensis*, *Glyptodon reticulatus*, *Chelonoidis?* sp., etc.), with other more humid, warmer periods (indicated by the presence of *Holmesina paulacoutoi*, *Tapirus* sp., *Tayassu pecari*, *Panthera onca*, *Boa constrictor*, etc.). Consequently, these deposits cannot be assigned to a single, uniform paleoenvironment, but rather to a dynamic one typical of ecotonal areas readily affected by changes in the most relevant paleoclimatic variables (e.g. tempera-

ture and humidity). Similar scenarios have been interpreted in faunas from other parts of the world (LUNDELIUS 1983; UBILLA 2004; UBILLA et al. 2004; TAMBUSI et al. 2005; OLIVEIRA & PEREIRA 2009 and references cited therein) for equivalent lapses and latitudes. In any case, and considering its peculiarities and range, the fauna recorded in Corrientes for the late Pleistocene is not taxonomically equivalent to the one that accompanies *Galea tixiensis*, especially with respect to highly significant taxa (e.g. *Lestodelphys halli*). In this sense, there are noteworthy differences between the faunal associations recognized in Corrientes and in SW Buenos Aires, which add to the temporal differences that apparently exist between the deposits in Uruguay and Bolivia and their counterparts in Corrientes. Therefore, the possible assignation to a new species would be supported not only by the abovementioned anatomical differences, but also by temporal and latitudinal differences and by the widely different taxonomic composition of the accompanying faunas of these extinct *Galea* species. Although this hypothesis cannot be dismissed, the finding of additional remains is necessary to provide more solid anatomical support to propose a new morphospecies.

Lastly, the presence of *Galea* in the Pleistocene of Corrientes Province where there are no extant representatives of the genus, provides other evidence to support the hypothesis of a complex, dynamic paleoclimatic-environmental scenario for the late Pleistocene of the Mesopotamian Region (ERRA et al. 2011), which includes the occurrence of colder, more arid pulses that would have favored the sporadic entrance of faunal elements of central-pampean (or related) provenance, and other warmer, more humid pulses that allowed the entrance of brasiliac taxa. It should be noted that this agrees with the paleoclimatic-environmental development proposed for the OIS 3 (65-28 ka), a lapse characterized by alternance of relatively humid tropical climates with cold, arid or semiarid periods (IRIONDO 1999), which could have eventually promoted the differentiation of endemic species.

Acknowledgements

The authors thank Dr. QUINTANA of Universidad Nacional de Mar del Plata, for granting access to the scientific collection of the Archaeology Department and for his invaluable help. Dr. ALVES DE OLIVEIRA and Dr. S. FRANCO, of Museu Nacional-UFRJ, Dr. Flores of the Mammalogy Collection of Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” and Dr. I. OLIVARES of the Mammalogy Collection of Museo de La Plata, for their assistance

and permission to access the collections under their care. Dr. ÚBILLA of the Facultad de Ciencias de Montevideo, for providing us with photographs and pertinent bibliographical materials. Dr. CIANCIO for a critical reading and comments on the manuscript, Dr. C. MORGAN for improving the English version, the editor of *Neues Jahrbuch für Geologie und Paläontologie* and the reviewers Dr. M.E. PÉREZ and an anonymous referee. This work is a contribution to projects PICTO-UNNE 164 and PI 011/2008.

References

- ÁLVAREZ, B.B. (1974): Los mamíferos fósiles del Cuaternario de Arroyo Toropí, Corrientes, Argentina. – *Ameghiniana*, **11** (3): 295-311.
- AGNOLIN, F.L., LUCERO, S.O. & BOGAN, S. (2008): *Galea musteloides* en la provincia de Santa Cruz, Argentina. – *Mastozoología Neotropical*, **15** (1): 113-115.
- BEZERRA, A.M.R. (2008): Revisão taxonômica do gênero *Galea* MEYEN (1832) (Rodentia, Caviidae, Caviinae). – Unpublish PhD Thesis, Universidade de Brasília, Brazil. – 125 pp.
- CABRERA, A. (1953): Los roedores argentinos de la familia Caviidae. – *Publicaciónes de la Escuela de Veterinaria*, **7**: 1-93.
- CABRERA, A. (1961): Catálogo de los mamíferos de América del Sur. – *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” e Instituto Nacional de Investigación de las Ciencias Naturales, Ciencias Zoológicas*, **4**: 309-732.
- CARLINI, A.A., ZURITA, A.E., GASPARINI, G.M. & NORIEGA, J.I. (2004): Los mamíferos del Pleistoceno de la Mesopotamia argentina y su relación tanto con aquellos del Centro-Norte de la Argentina, Paraguay, sur de Bolivia, como con los del sur de Brasil y oeste de Uruguay: Paleobiogeografía y Paleoambientes. – *Revista del Instituto Superior de Correlación Geológica (Misceláneas)*, **12**: 5-12.
- CARLINI, A.A., ZURITA, A.E. & MIÑO-BOILINI, A.R. (2008): Reseña paleobiogeográfica de los Xenarthra (Mammalia) del Pleistoceno tardío de la región Mesopotámica (Argentina). – In: ACEÑOLAZA, F.G. (Ed.): Temas de la Biodiversidad del Litoral fluvial argentino III. – *Revista del Instituto Superior de Correlación Geológica (INSUGEO)*, **17** (2): 259-270.
- CIONE, A.L. & TONNI, E.P. (1995): Chronostratigraphy and land-mammal ages in the Cenozoic of Southern South America: principles, practices, and the Uquian problem. – *Journal of Paleontology*, **69** (1): 135-159.
- COLTORTI, M., ABBAZZI, L., FERRETI, M., LACUMIN, P., PAREDES RÍOS, F., PELLEGRINI, M., PIERUCCINI, P., RUSTIONI, M., TITO, G. & ROOK, L. (2007): Last glacial mammals in South America: a new scenario from the Tarija Basin (Bolivia). – *Naturwissenschaften*, **94**: 288-299.
- CONTRERAS, J.R. (1964): Datos acerca de la variación intrapoblacional de la morfología de los molares de entidades de los géneros *Galea* y *Microcavia* (Rodentia, Caviidae). – *Ameghiniana*, **3**: 235-255.
- DA SILVA NETO, E.J. (2000): Morphology of the regions ethmoidalis and orbitotemporalis in *Galea musteloides* MEYEN, 1832 and *Kerodon rupestris* (WIED-NEUWIED, 1820) (Rodentia: Caviidae) with comments on the phylogenetic systematic of the Caviidae. – *Journal of Zoological Systematics and Evolutionary Research*, **38**: 219-229.
- DUNNUM, J.L. & SALAZAR-BRAVO, J. (2010): Phylogeny, evolution, and systematics of the *Galea musteloides* complex (Rodentia: Caviidae). – *Journal of Mammalogy*, **91** (1): 243-259.
- ERRA, G., OSTERRIETH, M., ZURITA, A.E., FRANCIA, A. & CARLINI, A.A. (2011): Paleoambientes alternantes en el Pleistoceno de Corrientes. Una perspectiva fitolítica. – *33º Jornadas Argentinas de Botánica*, Misiones, Argentina. 2011.
- FRANCIA, A. & CARLINI, A.A. (2009): La fauna del Pleistoceno tardío de Corrientes (Mesopotamia, Argentina), su relevancia paleobiogeográfica. – *III Jornadas de Jóvenes Investigadores*, La Plata, Bs. As. Libro de resúmenes en CD:12. ISBN: 978-950-34-0593-2.
- GOSO AGUILAR, C. (2006): Aspectos sedimentológicos y estratigráficos de los depósitos cuaternarios de la costa platense del departamento de Canelones (Uruguay). – *Latin American Journal of Sedimentology and Basin Analysis*, **13** (1): 77-89.
- HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. (2001): PAST: Paleontological Statistics Software Package for Education and Data Analysis. – *Palaeontologia Electronica*, **4** (1): 9 pp.
- HERBST, R. & ÁLVAREZ, B.B. (1977): Nota sobre dos formaciones del Cuaternario de Corrientes, República Argentina. – *Facena*, **1**: 7-17.
- HERBST, R. & SANTA CRUZ, J.N. (1999): Mapa litoestratigráfico de la provincia de Corrientes. – *D’Orbigniana*, **2**: 1-69.
- IRIONDO, M. (1996): Estratigrafía del Cuaternario de la cuenca del río Uruguay. – *Actas XIII Congreso Geológico Argentino y III de Exploración de Hidrocarburos*, **4**: 15-25.
- IRIONDO, M. (1999): Climatic changes in the South American plains: Records of a continent-scale oscillation. – *Quaternary International*, **57/58**: 93-112.
- KERBER, L. & OLIVEIRA, E.V. (2008): Fósseis de vertebrados da Formação Touro Passo (Pleistoceno Superior), Rio Grande do Sul, Brasil: atualização dos dados e novas contribuições. – *GAEA, Journal of Geoscience*, **4**: 49-64.
- KERBER, L., RIBEIRO, A.M. & OLIVEIRA, E.V. (2011a): The first record of *Galea* MEYEN, 1932 (Rodentia, Hystriognathidae, Caviidae) in the late Pleistocene of southern Brazil and its paleobiogeographic implications. – *Alcheringa*, **35**: 445-475.
- KERBER, L., PEREIRA LOPEZ, R., VUCETICH, M.G., RIBEIRO, A.M. & PEREIRA, J. (2011b): Chinchillidae and Dolichotinae rodents (Rodentia: Hystriognathidae: Caviomorpha) from the late Pleistocene of Southern Brazil. – *Revista Brasileira de Paleontologia*, **14** (3): 229-238.
- KRAGLIEVICH, L. (1930): Diagnosis osteológico-dentaria de los géneros vivientes de la subfamilia Caviinae. – *Anales del Museo Nacional de Historia Natural de Buenos Aires*, **36**: 59-96.
- KRAGLIEVICH, L. (1940): Morfología normal y morfogéne-

- sis de los molares de los carpinchos y caracteres filogenéticos de este grupo de roedores. – In: TORCELLI, A.J. & MORELLI, C.A. (Eds.): Obras de Geología y Paleontología 3 (Obras completas y trabajos científicos inéditos), 438-484; Buenos Aires (Ministerio de Obras Públicas de la Provincia de Buenos Aires).
- LANDRY, S.O. (1957): Factors affecting the procumbency of rodent upper incisors. – *Journal of Mammalogy*, **38** (2): 223-234.
- LUNDELius, E. (1983): Climatic implications of Late Pleistocene and Holocene faunal associations in Australia. – *Alcheringa*, **7**: 125-149.
- MARES, M.A. & OJEDA, R.A. (1982): Patterns of diversity and adaptation in South American hystricognath rodents. – In: MARES, M.A. & GENOWAYS, H.H. (Eds.): *Mammalian biology of South America*. – Pymatuning Laboratory of Ecology, University of Pittsburgh, Special Publications, **6**: 393-432.
- MARSHALL, L., BERTA, A., HOFFSTETTER, R., PASCUAL, R., REIG, R., BOMBIN, M. & MONES, A. (1984): Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. – *Palaearctovertébrata, Mémoire Extraordinaire*, 1-76.
- MCKENNA, M.C. & BELL, S.K. (1997): Classification of mammals, above the species level. – 631 pp.; New York (Columbia University Press).
- OLIVEIRA, E.V. (1999): Quaternary vertebrates and climates from Southern Brazil. – *Quaternary of South America and Antarctic Peninsula*, **12**: 61-73.
- OLIVEIRA, E.V. & PEREIRA OPAZO, J.C. (2009): Intertropical cingulates (Mammalia, Xenarthra) from the Quaternary of southern Brazil: systematic and paleobiogeographical aspects. – *Revista Brasileira de Paleontología*, **12** (3): 167-178.
- OPAZO, M. (2005): A molecular timescale for caviomorph rodents (Mammalia, Hystricognathi). – *Molecular Phylogenetics and Evolution*, **37**: 932-937.
- PÉREZ, M.E. (2010): A new rodent (Cavioidae, Hystricognathi) from the middle Miocene of Patagonia, mandibular homologies, and the origin of the crown group Cavioidae sensu stricto. – *Journal of Vertebrate Paleontology*, **30** (6): 1848-1859.
- PÉREZ, M.E. & VUCETICH, M.G. (2011): A new extinct genus of Cavioidae (Rodentia, Hystricognathi) from the Miocene of Patagonia (Argentina) and the evolution of cavioid mandibular morphology. – *Journal of Mammal Evolution*, **18** (3): 163-183.
- QUINTANA, C. (1998): Relaciones filogenéticas de roedores Caviinae (Caviomorpha, Caviidae), de América del Sur. – *Boletín de la Real Sociedad Española de Historia Natural*, **94** (3-4): 125-134.
- QUINTANA, C. (2001): *Galea* (Rodentia, Caviidae) del Pleistoceno Superior y Holoceno de las sierras de Tandilia oriental, provincia de Buenos Aires, Argentina. – *Ameghiniana*, **38** (4): 399-407.
- REIG, O.A. (1986): Diversity patterns and differentiation of high Andean rodents. – In: VUILLEUMIER, F. & MONASTERIO, M. (Eds.): High altitude tropical biogeography, 404-439; New York & Oxford (Oxford University Press).
- ROWE, D. & HONEYCUTT, R. (2002): Phylogenetic relationships, ecological correlates, and molecular evolution within the Cavioidae (Mammalia, Rodentia). – *Molecular Biology and Evolution*, **19**: 263-277.
- SCILLATO-YANÉ, G.J., TONNI, E.P., CARLINI, A.A. & NORIEGA, J.I. (1998): Nuevos Hallazgos de Mamíferos del Cuaternario en el Arroyo Toropí, Corrientes, Argentina. Aspectos Bioestratigráficos, Paleoambiental y Paleogeográficos. – *10º Congreso Latinoamericano de Geología y 6º Congreso Nacional de Geología Económica, Actas*, **1**: 263-268.
- SOLMSDORFF, K., KOCH, D., HOHOFF, C. & SACHSER, N. (2004): Comments on the genus *Galea* MEYEN, 1833 with description of *Galea monasteriensis* n. sp. from Bolivia (Mammalia, Rodentia, Caviidae). – *Senckenbergiana Biologica*, **84**: 1-20.
- TAMBUSSI, C., UBILLA, M., HOSPITALECHE, C.A. & PEREA, D. (2005): Fossil records and palaeoenvironmental implications of *Chloephaga picta* (GMELIN, 1789) (Magellan Goose) and *Cariama cristata* (LINNAEUS, 1766) (Seriemá) from the Late Pleistocene of Uruguay. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2005**: 257-268.
- TONNI, E.P., CARLINI, A.A., ZURITA, A.E., FRECHEN, M., GASPARINI, G., BUDZIAK, D. & KRUCK, W. (2005): Cronología y Bioestratigrafía de la Unidades del Pleistoceno aflorantes en el Arroyo Toropí, provincia de Corrientes, Argentina. – *19º Congreso Brasileiro de Paleontología y 6º Congreso Latino-American de Paleontología, Edición electrónica de resúmenes*.
- TONNI, E.P., SOIBELZON, E., CIONE, A.L., CARLINI, A.A., SCILLATO YANÉ, G.J., ZURITA, A.E. & PAREDES RÍOS, F. (2009): Preliminary correlation of the Pleistocene sequences of the Tarija valley (Bolivia) with the Pampean chronological standard. – *Quaternary International*, **210**: 57-65.
- UBILLA, M. (2004): Mammalian biostratigraphy of Pleistocene fluvial deposits in northern Uruguay, South America. – *Proceedings of Geologists' Association*, **115**: 347-357.
- UBILLA, M. & RINDERKNECHT, A. (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., PEREA, D., GOSO AGUILAR, C. & LORENZO, N. (2004): Late Pleistocene vertebrates from northern Uruguay: tools for biostratigraphic, climatic and environmental reconstruction. – *Quaternary International*, **114**: 129-142.
- UBILLA, M., OLIVEIRA, E.V., RINDERKNECHT, A. & PEREIRA, J.C. (2008): The hystricognath rodent *Microcavia* in the late Pleistocene of Brazil (Rio Grande do Sul, South America) (Mammalia: Caviidae): biogeographic and paleoenvironmental implications. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **247**: 15-21.
- VUCETICH, M.G., VERZI, D.H., HARTENBERGER, J.L. (1999): Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia). – *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes*, **329**: 763-769.
- WOOD, C.A. (1955): A revised classification of the Rodents. – *Journal of Mammalogy*, **36** (2): 165-187.

Manuscript received: April 23rd, 2012.

Revised version accepted by the Stuttgart editor: July 16th,
2012.

Addresses of the authors:

FRANCIA, A., CARLINI, A.A., División Paleontología de Vertebrados, Museo de La Plata, Universidad Nacional de La Plata. Paseo del Bosque, s/n (1900) La Plata, Buenos Aires, Argentina & Consejo Nacional de Investigaciones Científicas y Técnicas;
e-mails: analiafrancia@yahoo.com.ar,
acarlini@museo.fcnym.unlp.edu.ar

ZURITA, A.E., Centro de Ecología Aplicada del Litoral (CE-COAL-CONICET). Ruta 5, km. 2,5. CC 128 (3400) Corrientes, Argentina;
e-mail: aezurita74@yahoo.com.ar

VERZI, D.H., División Zoología de Vertebrados, Museo de La Plata. Universidad Nacional de La Plata. Paseo del Bosque, s/n (1900) La Plata, Buenos Aires, Argentina & Consejo Nacional de Investigaciones Científicas y Técnicas;
e-mail: dverzi@fcnym.unlp.edu.ar