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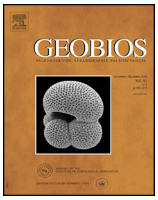

Original article

Comparative analysis of *Galea* (Rodentia, Caviidae) and expanded diagnosis of *Galea ortodonta* Ubilla and Rinderknecht, 2001 (Late Pleistocene, Uruguay)[☆]

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ABSTRACT

The family Caviidae is a diverse group of South American caviomorph rodents with many living and extinct taxa. Paleontological information about the caviid genus *Galea* is scant; only two extinct species have been described from fragmentary material so far. Recently, complete skulls and mandibles of the extinct *Galea ortodonta* have been found (Dolores Fm., Late Pleistocene; Santa Lucía river basin, southern Uruguay). Based on anatomical and quantitative analyses, we provide an expanded diagnosis and description of *G. ortodonta*, which thus becomes the best-known extinct species of the genus, accompanied by a critical assessment of skull, mandible and dental characters at the generic level. The wide intra-specific variability observed in several characters makes difficult to identify exclusive characters at the species level and to describe species based on fragmentary materials or on mandibles alone. *G. ortodonta* is characterized by the following associated features: large size; orthodont upper incisor; latero-external face of the incisors with extended enamel; small and laterally compressed auditory bullae; wide basioccipital; maxillary zygomatic process with apophysis; upper cheek teeth with external primary and secondary folds; palatine wide at the mesopterygoid fossa; and horizontal mandibular crest starting at p4. This character association differs from all other living and extinct species of the genus but resembles the *G. musteloides* species group to some extent. Biostratigraphic information and absolute ages support a Late Pleistocene age for the new material and a correlation with the late phases of Marine Isotope Stage MIS3. *Galea* occupied lowland areas in southern Uruguay during the Late Pleistocene and, like other associated mammals, suggests open or semi-open areas with an arid or semi-arid context, an environmental scenario arguably influenced by the late phases of MIS3.

1. Introduction

The family Caviidae is a diverse group of South American caviomorph rodents, comprising the living cavies of the genera *Cavia*, *Galea* and *Microcavia*; the maras *Dolichotis*; the rock cavies *Kerodon*; the capybaras *Hydrochoerus* (Rowe and Honeycutt, 2002; Woods and Kilpatrick, 2005; Opazo, 2005; Pérez and Pol, 2012); and numerous extinct taxa (Cabrera, 1960; Quintana, 1996, 1998; Vucetich, 1986). Paleontological evidence (Vucetich, 1986; Vucetich and Verzi, 1995; Pérez and Vucetich, 2011) and molecular studies (Rowe and Honeycutt, 2002; Opazo, 2005; Dunnum and Salazar-Bravo, 2010) indicate that the origin and differentiation of caviids occurred during the Miocene, most likely the Middle Miocene (Pérez and Pol, 2012).

The genus *Galea* Meyen, 1832 is placed in the subfamily Caviinae within the family Caviidae (Woods and Kilpatrick, 2005) and is subject to current studies. According to molecular estimates, *Galea* differentiated from *Microcavia* and *Cavia* during Middle Miocene (Opazo, 2005), but Pérez and Pol (2012), using fossil and molecular evidences, proposed a Late Miocene differentiation of the genus. Based on molecular analyses (Dunnum and Salazar-Bravo, 2010), the living representatives of the genus are *Galea spixii* Wagler, 1831 (central and northern Brazil; Alho, 1982; Mares and Ojeda, 1982) and the *G. musteloides* complex. The latter group includes *G. musteloides* Meyen, 1832 (southern Perú, northwestern Bolivia and northeastern Chile), *G. comes* Thomas, 1919 (high Andes of southern Bolivia and northern Argentina), and *G. leucoblephara* Burmeister, 1861 (lowlands of Bolivia and Paraguay to south-central Argentina) (Cabrera, 1960; Woods and Kilpatrick, 2005; Agnolin et al., 2008;

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Fig. 1). This taxonomic arrangement is almost similar to the "*musteloides*" group obtained by Bezerra (2008), who proposed the use of *G. leucoblephara* and *G.* ***comes*** names. Notably, *G. spixii* may be actually a polytypic taxon, the "*spixii*" group, according to the morphometric analysis of Bezerra et al. (2007) and Bezerra (2008), who suggest the *G. spixii* name for populations of the Bahia State only.

Paleontological information about *Galea* is scarce. In light of the variability observed in the living representatives of the genus, it may be inappropriate to describe species based only on fragmentary material. If *Pascualia* Ortega Hinojosa, 1963 is considered a synonym of *Galea*, the genus may be represented in the Pliocene of Argentina. However, *Pascualia* is rarely included in biostratigraphic analyses because of its doubtful stratigraphic provenance (Marshall et al., 1984; Quintana, 2001). The fossil record of *Galea* is mostly based on fragmentary remains from the Pleistocene of Argentina, Bolivia, Brazil and Uruguay (Winge, 1887; Hoffstetter, 1963, 1986; Quintana, 2001; Ubilla and Rinderknecht, 2001; Kerber et al., 2011; Cruz, 2013; Francia et al., 2012) and the Holocene of Argentina, Bolivia, Brazil and probably Chile (Hoffstetter, 1968; Mann Fischer, 1978; Salemme, 1990; Quintana, 2001; Kerber et al., 2011; Coltorti et al., 2012). Only two extinct species have been described so far, both based on fragmentary remains. *G. ortodonta* was described by Ubilla and Rinderknecht (2001) from the Late Pleistocene of Uruguay and the Pleistocene of Bolivia (Fig. 1). *G. tixiensis* was described by Quintana (2001) based on Holocene remains that had accumulated in caves in Argentina (Pampean region; 10,300 to 170 yrs BP), owing to the activity of natural predators and anthropogenic behavior. Recently, Francia et al. (2012) described fragmentary material from open sites in Corrientes (Argentina; Late Pleistocene). This material was doubtfully referred to *G. tixiensis*.

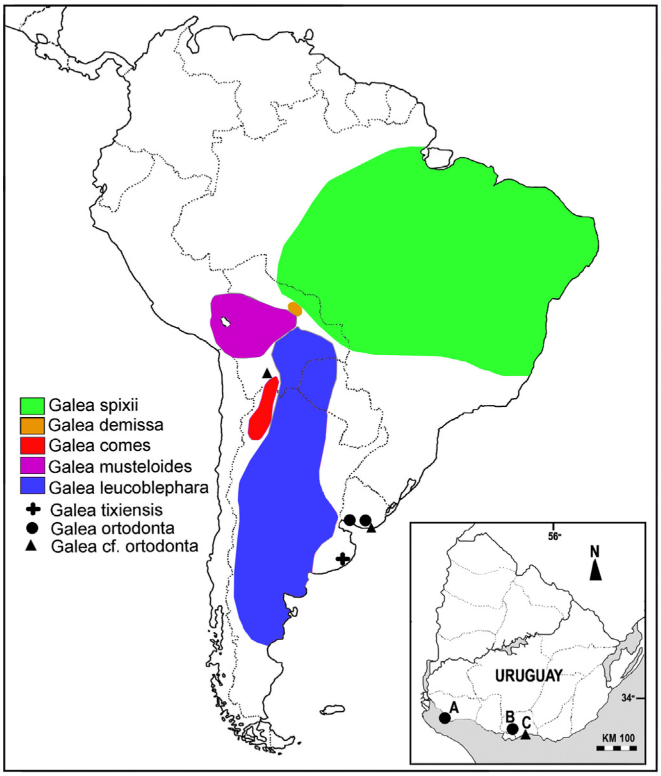

Fig. 1. Geographic location of *Galea ortodonta* (A, B) and *G.* cf. *G. ortodonta* (C) in Uruguay in Bolivia, *G. tixiensis*, and distribution of living members of the genus *Galea*. Based on Mares and Ojeda (1982), Quintana (2001), Ubilla and Rinderknecht (2001), Agnolin et al. (2008), Bezerra (2008), and Dunnum and Salazar-Bravo (2010).

Based on this, the goals of this paper are:

- to provide an expanded diagnosis and description of the extinct *G. ortodonta* based on a well-preserved material (a complete skull, mandibles and postcranial bones) recently found in the Late Pleistocene of Uruguay, making *G. ortodonta* the best-known extinct species of the genus to date;
- to perform a comprehensive anatomical and quantitative comparative analysis, including a large sample of living representatives of the genus, to understand the morphological variability present in *Galea* and to assess the taxonomic usefulness of skull, mandible and tooth characters;
- to discuss the distributional, environmental and climatic significance of the occurrence of this extinct caviid, taking into account the associated fauna and the ecological requirements of its living relatives.

2. Geographical and geological setting

The new material of *Galea* studied here was collected from fossil-bearing deposits that crop out along the Pilatos and Aparicio creeks in the Santa Lucía river basin (from S°34°16′13.3″/W°55°59′34.8″ to S°34°17′25″/W°55°56′5.1″; Southern Uruguay; Fig. 1B). The Pleistocene lithostratigraphic units recognized in this area are the Dolores and Barrancas Formations (Spoturno et al., 2004). According to ongoing field studies, some sedimentary facies are also present that are not referred to any formal stratigraphic unit but that contain remarkable paleontological information (Ubilla et al., 2009, 2011; De Oliveira et al., 2011). In this area, the fossiliferous beds range from Late Pleistocene to Early Holocene in age (30 to 8 ka BP; Ubilla et al., 2011, 2013). The new material was collected from the Dolores Fm. (brown mudstones including occasional sandy levels), which is generally considered a Late Pleistocene continental sedimentary unit based on stratigraphic criteria. Mammalian biostratigraphic information and absolute dating also support a Late Pleistocene age for these fossiliferous beds. Mammals are dominant in the faunal assemblage, which is biostratigraphically correlated with the Lujanian Stage/Age of the Buenos Aires Province (Late Pleistocene–Early Holocene *sensu* Cione and Tonni, 2005) because of the presence in the Dolores Formation of the horse *Equus neogeus*, which is the key diagnostic taxon of this chronostratigraphic unit. Typical extinct South American Pleistocene mammals are also present, with some megafaunal representatives (*Macrauchenia patachonica*, *Toxodon* cf. *T. platensis*, *Catonyx cuvieri*, *Glyptodon clavipes*, *Doedicurus clavicaudatus*, *Panochthus* cf. *P. tuberculatus*, *Pampatherium typum*, *Propraopus* sp., *Hemiauchenia* sp., *Hippidion* sp., *Morenelaphus* sp., *Smilodon populator*, *Myocastor* sp., *Cavia* sp., and others; Ubilla et al., 2009, 2011; Corona et al., 2013). In addition, some mammals are present that are now extinct in this area but still occur in other regions of South America at the generic or specific level (*Microcavia*, *Dolichotis* cf. *D. patagonum*, *Lagostomus* sp., *Chaetophractus villosus*, *Vicugna* sp.; Ubilla, 2008; Ubilla et al., 2009, 2011 and references therein).

Two Optically Stimulated Luminescence (OSL) dates, performed in the Luminescence Dating Research Laboratory of the University of Illinois (UIC) on sandy level samples collected at the base of the outcrops produced ages of 31,160 ± 2285 years (UIC-2826; Aparicio creek, S°34°16′13.3″, W°55°59′34.8″) and 30,855 ± 2370 years (UIC-2822; Pilatos creek, S°34°17′25″, W°55°56′5.1″). Corona et al. (2013) recently provided a congruent OSL age of 32,230 ± 2640 years from the same levels. An AMS ^{14}C age of 22,450 ± 400 years BP (cal BP 25,934–27,436; AA99845, tooth of an undetermined deer from Pilatos creek) is available from an overlying bed (Ubilla et al., 2011 and this paper).

The holotype of *G. ortodonta* was unearthed from Pleistocene sediments referred preliminarily to the Libertad Fm. or Dolores Fm. (Colonia Department, southern Uruguay; Ubilla and Rinderknecht, 2001; Ubilla et al., 2009; Corona et al., 2013 and references therein; Fig. 1A). This site also exhibits a typical Pleistocene mammal fauna in greenish mudstones with sandy and conglomeratic beds (Rinderknecht, 2006; Ubilla et al., 2009). Corona et al. (2013) provided an OSL age of 16,070 ± 930 years for an underlying bed of the holotype of *G. ortodonta*.

3. Material and methods

Institutional abbreviations: **AA**: NSF-Arizona AMS Laboratory; **BAA** and **BRA**: Centro Investigaciones Paleontológicas San Ramón, Andrés Sánchez collection (San Ramón, Uruguay); **BMNH**: Natural History Museum-Mammal Section (London, England); **FC-DPV**: Colección Paleontológica de la Facultad de Ciencias (Montevideo, Uruguay); **MN-RJ**: Museu Nacional, Rio de Janeiro (Brazil); **MNHN**: Museo Nacional de Historia Natural de Montevideo (Uruguay); **MZUSP**: Museu da Zoología da USP (Sao Paulo, Brazil); **MLPV**: Museo de La Plata, Vertebrados (Argentina); **MACN**: Mastozoología, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina); **MNHN-P**: Muséum National d'Histoire Naturelle, Collection de Mastozoologie (Paris, France).

Measurements abbreviations (Fig. 2, Table 1): **TL**: greatest length of skull from anteriormost part of the rostrum (excluding teeth) to the most posterior point of the skull; **UDL**: upper diastema length from alveolar posterior margin of incisor to alveolar anterior margin of P4; **SD**: skull depth from dorsal surface at anterior edge of alveolus of P4; **NL**: nasal length from anteriormost point of nasal bones to posteriormost point; **NW**: nasal width (greatest width across nasals); **RW**: greatest rostral breadth; **IC**: interorbital constriction (least distance between the orbits); **BCW**: greatest breadth between the distal surfaces of the zygomatic arches; **BMW**: mastoid greatest width between mastoids; **PL**: palatal length from posterior edge of incisor alveoli (midpoint) to anteriormost point on posterior edge of palate; **CBL**: condylobasal length from the anterior edge of premaxilla to the posteriormost point of the occipital condyle; **CBrL**: condylobasilar length from the posterior alveolar edge of incisor to the posteriormost point of the occipital condyle; **PW**: palatal breadth at

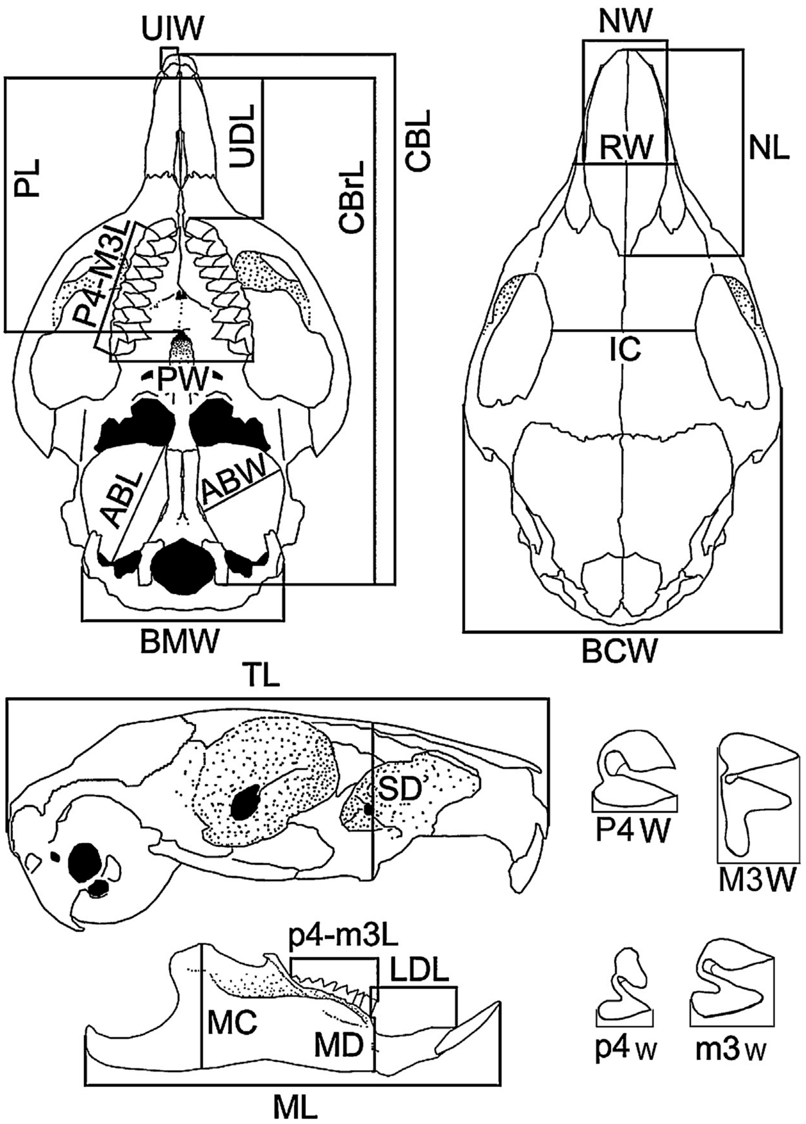

Fig. 2. Measurements used in the comparative analysis. Measurement abbreviations: see Section 3.

Table 1
Measurements (in mm) of the material of *Galea ortodonta* and *G.* cf. G. *ortodonta* from the Pleistocene of Uruguay and Bolivia.

A	TL	UDL	SD	NL	NW	RW	IC	BCW	BMW	PL	CBL	CBrL	PW	P4–M3L	UIW	ABL	ABW	P4W	M3W
Galea ortodonta																			
FC-DPV-900	–	16.4	15.1	23.4	9	9.6	11.4	–	–	27.2	–	–	14.5	14.1	2	–	–	3.1	2.7
Bra-2-655	63.7	18.1	17.4	25.2	9.5	11.8	12.4	37.7	22.8	30.6	58.2	54.8	17	14.5	2.4	14	8.2	3.3	2.6
BAA-2-546	–	–	–	–	–	–	13.2	33.5	21.5	–	–	–	15.5	13	–	14.7	7.7	2.8	2.6
BRA-4-805	–	–	–	–	6.4	–	–	–	–	–	–	–	–	15	2.4	–	–	2.9	3
Galea cf. G. ortodonta																			
TAR-22	–	11.6	–	–	–	8	–	–	–	21.6	–	–	14	12	2	–	–	2.5	2.5

B	ML	LDL	MD	MC	p4–m3l	liw	p4w	m3w
Galea ortodonta								
BRA-2-655	–	–	7	–	–	–	2.5	–
BAA-2-546	47.7	9.3	6.9	14.8	13.1	1.7	2.1	2.6
Galea cf. G. ortodonta								
MNHN-1628	–	11.5	6.6	–	14.8	2.2	2.3	3.4

A: skull and upper dentition; **B**: mandible and lower dentition. Measurement abbreviations: see Section 3.

lateral external alveolar edge of M3; **P4-M3L**: upper p4-m3 crown length; **UIW**: upper incisor width; **ABL**: greatest auditory bulla length from anteriormost point to posteriormost diagonally; **ABW**: greatest auditory bulla breadth from the inner side to lateral side perpendicular to ABL; **P4 W**: upper p4 width; **M3W**: upper m3 width; **ML**: mandible length from the tip of incisor to posteriormost tip of angular ramus; **LDL**: lower diastema length from alveolar posterior margin of incisor to alveolar anterior margin of p4; **MD**: mandible depth anteriorly to the p4; **MC**: mandible depth at condylar level; **p4-m3l**: lower p4-m3 crown length; **liw**: lower incisor width; p4w: lower p4 width; m3w: lower m3 width; **ABW/TL**: auditory bulla-skull length ratio.

All the skull and mandible measurements were taken using a Digimatic-Mitutoyo digital caliper.

Samples for OSL were collected following the requirements of the UIC (Illinois: http://www.uic.edu/labs/ldrl/). The geographic location of the fossil material and samples for dating were recorded using a GPS Garmin etrex VistaHCx. Descriptive statistics and a comparative list of specimens of living *Galea* taxa are included in Tables 2 and 3 and in Appendix A. Our concept of the *G. musteloides* complex follows that of Dunnum and Salazar-Bravo (2010) (see above, Section 1), mostly coincident with Bezerra (2008). *G. spixii* material was grouped according to the following geographic areas, consistently with Bezerra (2008): northeastern Brazil (Pernambuco, Ceará, Alagoas), Bahia, and Minas Gerais. For comparative purposes, *G. demissa* (Bolivia) was considered a separate taxon in agreement with Bezerra (2008). However, since its description by Thomas (1921) as a subspecies of *G. boliviensis*, this entity has received a variety of taxonomic treatments (Ellerman, 1940; Cabrera, 1960; Solmsdorff et al., 2004; Woods and Kilpatrick, 2005; Dunnum and Salazar-Bravo, 2010). Comparative information on the extinct *G. tixiensis* was obtained from Quintana (2001). According to the degree of ossification of the skull bones (Bezerra and Marinho-Filho, 1831) and the unossified epiphyses of the postcranial bones, the *G. ortodonta* specimen BAA-2-546 was characterized as a subadult (Figs. 3G–I and 4A, B). We also

Table 2
Descriptive statistic of living *Galea musteloides* species complex used in the comparative analysis.

	Galea comes						*Galea musteloides*						*Galea leucoblephara*					
	n	X	Min	Max	SE	SD	*n*	X	Min	Max	SE	SD	*n*	X	Min	Max	SE	SD
TL	5	52.76	48.1	54.3	1.18	2.63	9	52.12	50.3	54	0.35	1.2	43	51.6	48	56.6	0.32	2.11
UDL	5	13.52	12	15	0.51	1.14	10	13.44	12.3	14.8	0.24	0.81	43	13.05	10.8	15.5	0.17	1.11
SD	5	13.22	12.0	14	0.33	0.75	11	13.12	11.9	14.7	0.25	0.83	43	13.03	11.6	14.3	0.11	0.75
NL	4	19.7	15.7	21.8	1.23	2.75	11	18.24	11.7	21.1	0.72	2.39	43	17.9	15.4	21.4	0.2	1.31
NW	5	7.32	6.5	8	0.25	0.55	11	7.8	6.8	8.9	0.19	0.62	43	7.3	6	9.1	0.1	0.57
RW	5	8.34	6.6	9.6	0.54	1.21	10	8.67	7.9	9.8	0.15	0.51	43	7.97	6.7	9.5	0.11	0.70
IC	5	10.9	9.9	11.9	0.35	0.78	11	11.05	9.8	11.6	0.19	0.62	43	10.9	9.3	13.1	0.12	0.78
BCW	5	30.8	27.8	32.6	0.81	1.81	11	30.83	27.6	33.1	0.55	1.84	42	29.1	26.6	33	0.21	1.34
BMW	5	19.64	17.3	20.4	0.59	1.32	10	20.01	18.1	21.6	0.31	1.04	43	19.2	18	21.6	0.12	0.78
PL	5	23.34	20.8	24.6	0.67	1.49	9	22.8	21.4	24.2	0.27	0.9	43	21.5	12.9	24.6	0.29	1.9
CBL	5	48.52	43.8	51	1.24	2.78	9	47.25	45.2	50.3	0.45	1.5	41	47.7	43	53.3	0.36	2.35
CBrL	5	45.58	40.5	48.1	1.36	3.05	9	44.12	42.6	47.4	0.45	1.5	43	44.03	40.2	48.1	0.31	2.06
PW	5	13.94	12.1	14.6	0.47	1.04	11	13.74	12	14.6	0.22	0.75	42	12.9	11.3	14.2	0.11	0.71
P4-M3L	5	12.12	10.9	13	0.35	0.79	11	11.8	10.9	12.7	0.14	0.47	42	11.2	9.8	13	0.11	0.7
IUW	5	1.5	1.4	1.6	0.04	0.1	9	1.7	1.6	1.9	0.03	0.1	42	1.5	1.1	1.8	0.03	0.17
ABL	4	15.25	13	16.7	0.71	1.59	10	13.18	12.1	14	0.19	0.63	8	13.7	12.4	14.8	0.13	0.85
ABW	5	8.9	8.6	9.7	0.24	0.53	10	9.01	8	9.8	0.21	0.71	8	8.1	7.7	9	0.07	0.44
P4W	5	2.9	2.7	3.1	0.07	0.16	11	2.78	2.5	3	0.04	0.15	43	2.6	1.8	3.2	0.04	0.29
M3W	5	2.48	2.1	2.8	0.11	0.26	11	2.44	2	2.7	0.07	0.24	42	2.12	1.6	2.6	0.04	0.26
ML	3	45.9	41.8	48.7	2.08	3.61	9	44.9	41	48.4	0.73	2.2	32	44.3	35.8	48.7	0.48	2.27
LDL	5	9.92	8.3	10.9	0.5	1.12	10	9.24	8.1	10.4	0.23	0.74	41	9.17	7.2	10.6	0.14	0.94
MD	5	5.28	4.3	5.8	0.27	0.61	11	5.51	4.4	6.5	0.19	0.64	41	5.47	4	7.5	0.1	0.66
MC	3	13.9	12.7	15.2	0.72	1.25	9	13.94	13.1	14.9	0.19	0.58	35	13.5	11.3	15.5	0.15	0.88
p4-m3l	5	11.62	11	12.4	0.26	0.6	11	11.51	10.7	12.6	0.18	0.59	40	10.98	9.3	12.7	0.1	0.68
liw	5	1.38	1.1	1.6	0.08	0.19	11	1.49	1	1.7	0.07	0.23	40	1.32	0.6	1.6	0.03	0.17
lp4w	5	2.16	1.9	2.4	0.1	0.23	11	2.14	2	2.3	0.04	0.12	41	1.9	1	2.6	0.04	0.27
lm3w	5	2.8	2.6	2.9	0.06	0.14	11	2.72	2.3	3	0.06	0.21	39	2.5	1.8	3	0.04	0.26

n: sample size; X: mean; SE: Standard error; SD: Standard deviation. Measurement abbreviations: see Section 3.

Table 3
Descriptive statistics of living *Galea spixii* used in the comparative analysis.

	Galea spixii (NEB)						*Galea spixii* (B)						*Galea spixii* (MG)					
	N	X	Min	Max	SE	SD	N	X	Min	Max	SE	SD	N	X	Min	Max	SE	SD
TL	121	58.03	50.1	63	0.25	2.8	27	57.7	49.9	62	0.54	2.84	4	56.9	53.5	59.6	1.37	2.74
UDL	122	14.09	11.3	16.3	0.1	1.07	28	13.9	11.3	15.2	0.17	0.9	4	13.4	13	14	0.22	0.43
SD	112	14.7	12.4	16.4	0.07	0.9	28	14.9	12.7	15.8	0.14	0.75	4	14.7	13.3	15.8	0.59	1.17
NL	123	22.5	15.1	27.2	0.18	2.01	26	22.6	18.4	25.2	0.28	1.51	3	19.7	17	22.7	1.43	2.86
NW	123	8.7	7.2	13.8	0.06	0.71	27	8.9	7.4	10	0.12	0.62	3	8.3	7.5	8.9	0.35	0.71
RW	123	10.13	7.2	12	0.08	0.9	27	10.4	8.6	11.8	0.16	0.84	4	9.2	8	9.8	0.41	0.81
IC	122	12.2	10.4	13.7	0.05	0.61	28	12.3	10.7	13.4	0.13	0.7	3	12.7	12	13.4	0.35	0.7
BCW	120	31.1	26.6	34.7	0.15	1.63	26	31.2	28.9	33.2	0.24	1.26	4	31.5	30.5	33.5	0.7	1.4
BMW	121	20.7	17.5	24.4	0.11	1.2	26	20.8	18.7	22.1	0.18	0.95	4	20.05	19.1	21.1	0.41	0.82
PL	122	24.3	19.3	27.3	0.14	1.57	28	24.1	19.9	27.4	0.27	1.44	4	22.7	22.2	23.3	0.29	0.58
CBL	109	51.5	43.5	55.9	0.21	2.4	25	51.8	45.1	55	0.44	2.32	4	51.05	48.3	53.3	1.16	2.32
CBrL	110	48	39.7	52.3	0.22	2.4	25	48	41.1	51.4	0.42	2.23	4	47.6	45.6	49.6	0.97	1.95
PW	117	12.9	11	15	0.07	0.76	27	12.9	11.5	14	0.11	0.6	4	13.3	12.6	14.2	0.33	0.66
P4-M3L	122	12.35	10.6	15	0.07	0.8	28	12.4	10.7	13.4	0.11	0.6	4	12.5	12.2	12.8	0.13	0.25
IUW	121	1.84	1.4	2.3	0.02	0.2	27	1.9	1.4	2.8	0.05	0.26	4	1.9	1.7	2.1	0.09	0.18
ABL	11	13.8	11.7	15.8	0.09	1.05	3	14.7	12.7	16.6	0.37	1.95	–	–	–	–	–	–
ABW	11	8.7	7.6	9.4	0.04	0.5	3	9.7	9.5	9.9	0.04	0.21	–	–	–	–	–	–
P4W	120	2.41	1.2	3.4	0.04	0.44	28	2.4	1.5	3.4	0.1	0.52	3	2.3	2.2	2.5	0.09	0.17
M3W	123	1.78	1	2.8	0.03	0.30	28	1.9	1.3	2.6	0.07	0.36	4	1.9	1.7	2.2	0.11	0.22
ML	112	46.5	52	39	0.26	2.72	24	45.8	38	51	0.6	2.94	2	46.4	45.7	47.2	0.75	1.06
LDL	121	7.95	9.7	6.6	0.06	0.66	24	8.03	6.7	10	0.16	0.79	3	9.2	8.8	9.8	0.3	0.52
MD	122	5.99	7.5	4.3	0.06	0.68	24	5.82	4.8	6.9	0.12	0.58	3	6.43	6	7	0.29	0.51
MC	105	14.8	17	12	0.11	1.12	24	14.9	12.9	17	0.22	1.09	3	14.9	13.6	16	0.69	1.2
p4-m3l	119	12.5	14	11	0.07	0.78	24	12.38	10.8	13	0.11	0.55	3	12.37	11.5	13.4	0.55	0.96
liw	110	1.69	2.2	1.2	0.02	0.25	24	1.71	1.2	2.1	0.05	0.25	3	1.5	1.4	1.6	0.06	0.11
lp4w	119	1.5	2.5	1	0.03	0.38	24	1.64	1.1	2.5	0.09	0.43	3	2.1	2	2.3	0.08	0.15
lm3w	118	2.7	3.4	1.6	0.03	0.32	24	2.68	1.8	3	0.06	0.29	3	2.8	2.5	3	0.16	0.28

n: sample size; X: mean; SE: Standard error; SD: Standard deviation; NEB: northeastern Brazil; B: Bahia; MG: Minas Gerais. Measurement abbreviations: see Section 3.

incorporated relevant information on other caviomorph rodents (Ojasti, 1973; Mones and Ojasti, 1986; Voss and Da Silva, 2001; Lessa and Pessôa, 2005; Cherem and Ferigolo, 2012). The anatomical nomenclature used here follows Ellerman (1940), Contreras (1964), Woods (1972), Woods and Howland (1979), DeBlase and Martin (1974), Cooper and Schiller (1975), and Pérez and Vucetich (2011). The maxillary tooth row was photographed using a Nikon Digital Sight DSFi1 mounted on a Nikon SMZ800 microscope (Fig. 5). Some comparative characters in the skull are illustrated in Fig. 6, including representatives of living taxa of *Galea*.

Our anatomical comparisons and quantitative analyses used 215 specimens of living members of *Galea* (*G. musteloides* species group: 59; *G. spixii*: 155; *G. demissa*: 1). Statistical analyses were performed using PAST (Hammer et al., 2011). The quantitative analyses included univariate, bivariate and principal component analysis (PCA). In the univariate analysis, we computed the sample size, mean and observed range of each character. When the *G. ortodonta* specimens fell within the observed range of a given comparative sample of *Galea*, we calculated the 95% confidence interval for the mean of this taxon using two error types following Sokal and Rohlf (1981) (Figs. 7, S1). The univariate and bivariate analyses (Figs. 8, S2) were chosen to compare both the complete remains and the fragmentary material of *G. ortodonta* (the holotype FC-DPV-900 and the BAA-2-546 specimens) and *Galea* cf. *G. ortodonta* (the TAR-22 specimen from Tarija) with the comparative sample. The *G. spixii* specimens include both adult and subadult specimens to facilitate comparison with the subadult *G. ortodonta* specimen. Two distinct PCAs were performed using the skull and upper dentition measurements. To minimize the effect of missing data, only the complete material of *G. ortodonta* was included (Fig. 9). Eigenvalues and eigenvectors (Appendix A) were obtained using a variance-covariance matrix; factor loadings for the first three principal components are included in (Appendix A). The PCAs included 17 descriptors and involved the complete *G. ortodonta* specimen (BRA-2-655), the living *G. musteloides* species group, *G. spixii* and *G. demissa* (Fig. 9). This matrix had some missing data for the living taxa that were imputed using the iterative algorithm implemented in PAST.

4. Results

4.1. Systematic paleontology

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Family CAVIIDAE Fischer von Waldheim, 1817
Genus ***Galea*** Meyen, 1832
Galea ortodonta Ubilla and Rinderknecht, 2001
Figs. 3, 4A, B, 5A–D

Type material: FC-DPV-900: an incomplete skull with incisors, rostral region, a complete left P4-M3 series and incomplete right series lacking most of M3; lacking the braincase and most of the zygomatic arches (Figs. 3A–C, 5A).

Type locality: Colonia Department, southwestern Uruguay (S 34°25′, W 57°55′); Libertad or Dolores Formation (Late Pleistocene).

Referred material: BRA-2-655: a complete skull with left and right mandibular fragments, both with part of the diastema and p4–m1; the origin of the horizontal crest; 8 thoracic vertebrae associated with 11 ribs; the proximal epiphysis of the left ulna and the distal epiphysis of the right humerus of an adult specimen (Figs. 3D–F, 5B). BAA-2-546: an almost complete skeleton including a skull lacking the rostral region; right and left mandibles; and most of the axial and apendicular bones of a subadult specimen (Figs. 3G–I, 4A and B, 5C). BAA-2-805: an incomplete and distorted skull with the anterior region including the incisors, diastema, maxillary tooth rows and maxillary portion of the right zygomatic arch (Fig. 5D).

Geographic and stratigraphic location: BRA-2-655: Canelones Department, southern Uruguay, Pilatos creek (S 34°17′25″,

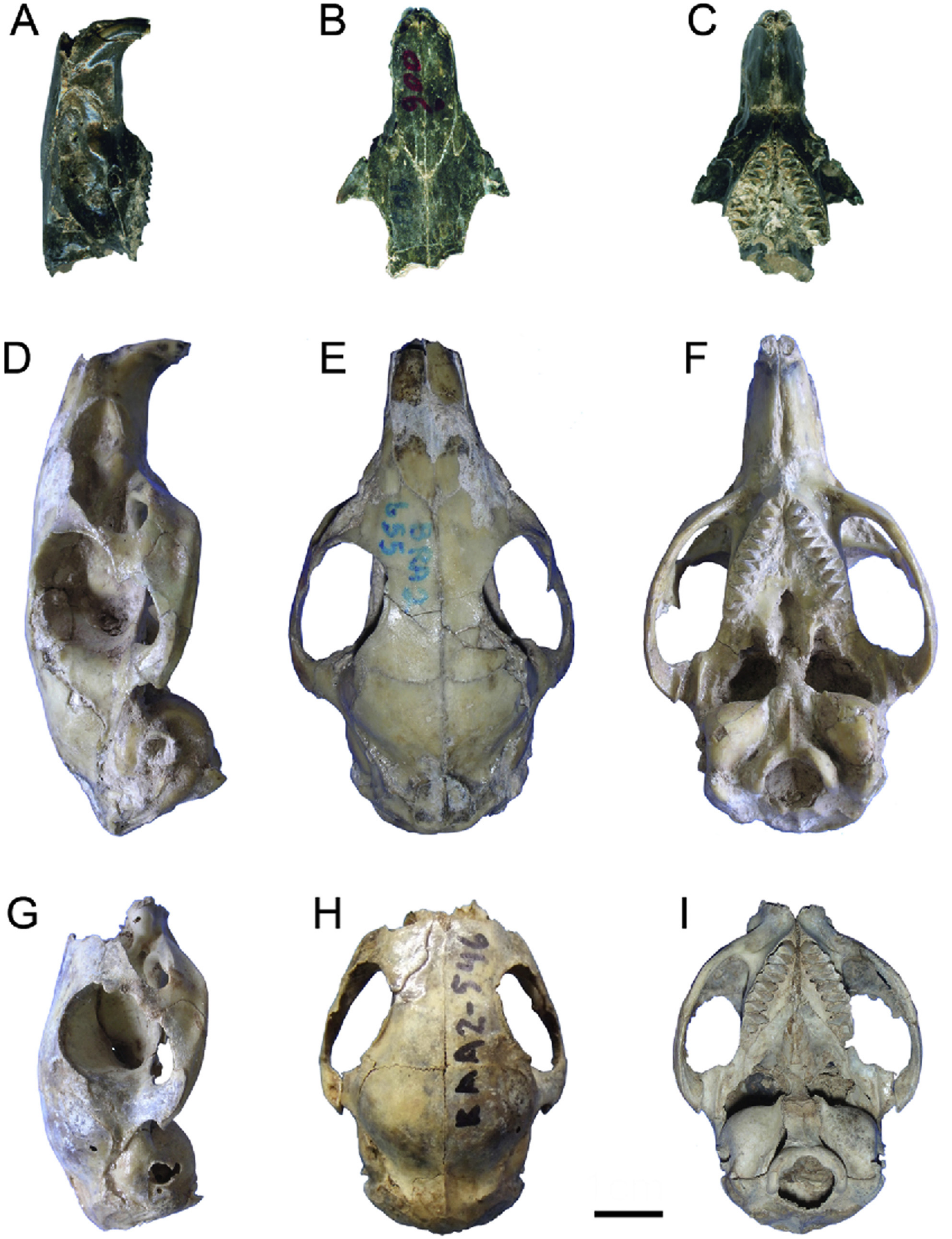

Fig. 3. Skulls of *Galea ortodonta*. **A–C**. FC-DPV-900 (Holotype); **D–F**. BRA-2-655; **G–I**. BAA-2-546. From left to right: lateral, dorsal and palatal view. Scale bar: 1 cm.

W 55°56′5.1″), Dolores Fm. BAA-2-546: Canelones Department, southern Uruguay, Aparicio creek (S 34°16′13.3″, W 55°59′34.8″), Dolores Fm. BAA-2-805: Canelones Department, southern Uruguay, Pilatos creek (S 34°17′17.25″, W 55°55′5.07″), Dolores Fm.

Expanded diagnosis: A large-bodied species of the genus *Galea*, similar to or larger than the largest specimens of *G. spixii* (northeastern Brazil sample); differing from living and extinct species of the genus in having an orthodont rather than

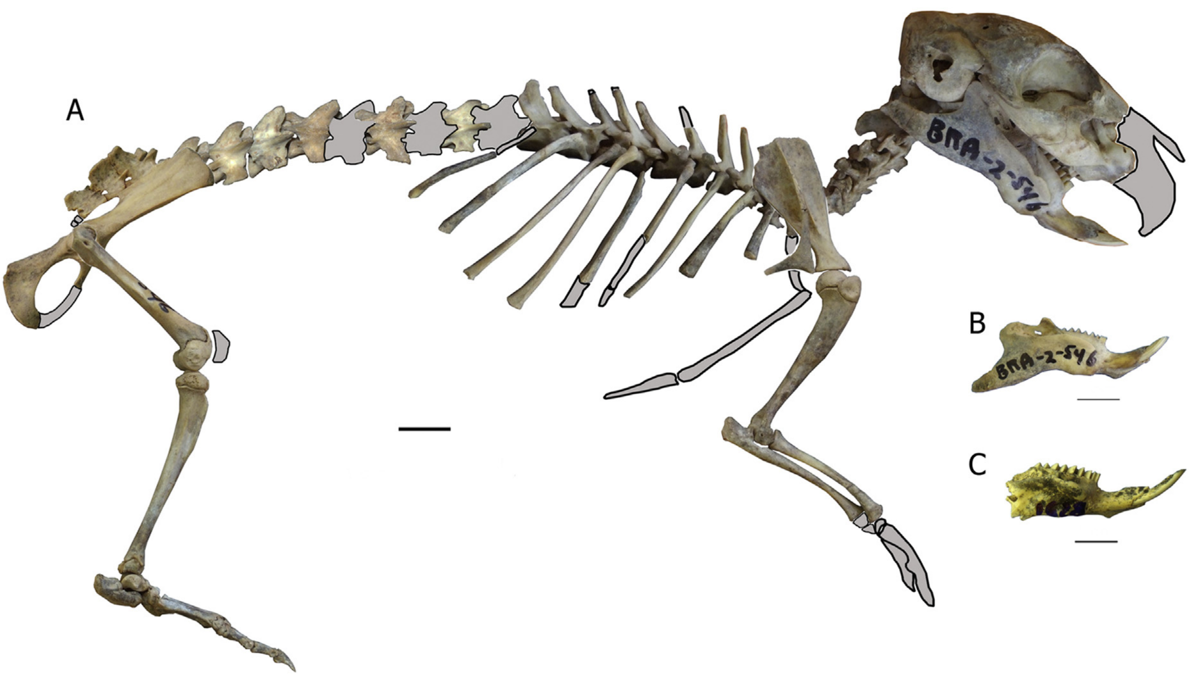

Fig. 4. A and **B**. Lateral view of the articulated skeleton of *G. ortodonta* and its right mandible (BRA-2-546). Pelvis and scapula are inverted images from left. Missing bones in gray. **C**. Lateral view of the mandible of *Galea* cf. *G. ortodonta* (MNHN-1628). Scale bars: 1 cm.

opisthodont upper incisor; a more extended enamel covering of the lateroexternal face of the upper and lower incisors; proportionally small and laterally compressed auditory bullae, differing from *G. comes* and *G. musteloides*, which have large bullae relative to their small skulls; a wide basioccipital, differing from *G. musteloides*; the zygomatic process of the maxilla yielding an apophysis, which is absent in *G. spixii* and *G. demissa*; external primary and secondary folds in the labial face of the upper cheek teeth, comparable to the *G. musteloides* species group, *G. demissa* and *G. tixiensis;* a wide palatine at the mesopterygoid fossa level, differing from *G. spixii* in which it is narrow; and a horizontal mandibular crest starting at the level of p4, as found in the *G. musteloides* species group and *G. demissa*.

Description:

Skull: The skull is larger in total length, zygomatic breadth and depth than those of members of the *G. musteloides* species group; wider at the zygomatic arch than *G. spixii*; and similar or larger in total length and depth than those of the largest individuals of *G. spixii.* In lateral view, the skull roof is slightly convex. In dorsal view, the rostrum is larger than those of the *G. musteloides* species

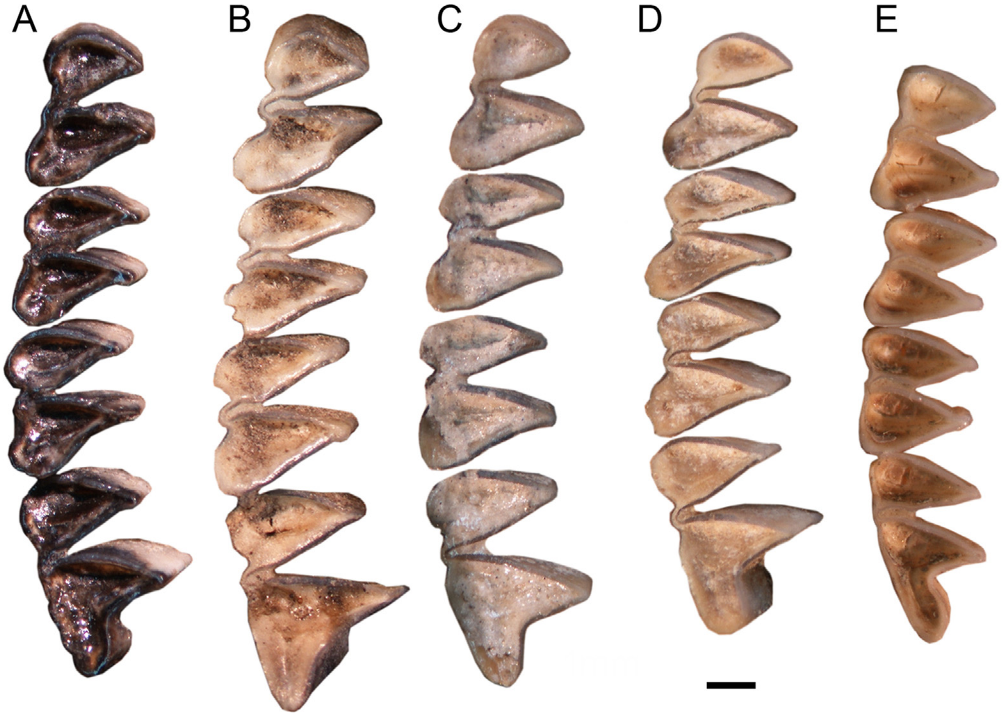

Fig. 5. Occlusal surfaces of right P4-M3. **A–D**. *Galea ortodonta*; A: FC-DPV-900 (holotype). B. BRA-2-655. C. BAA-2-546. D. BAA-2-805. **E**. *G. spixii*. Scale bar: 1 mm.

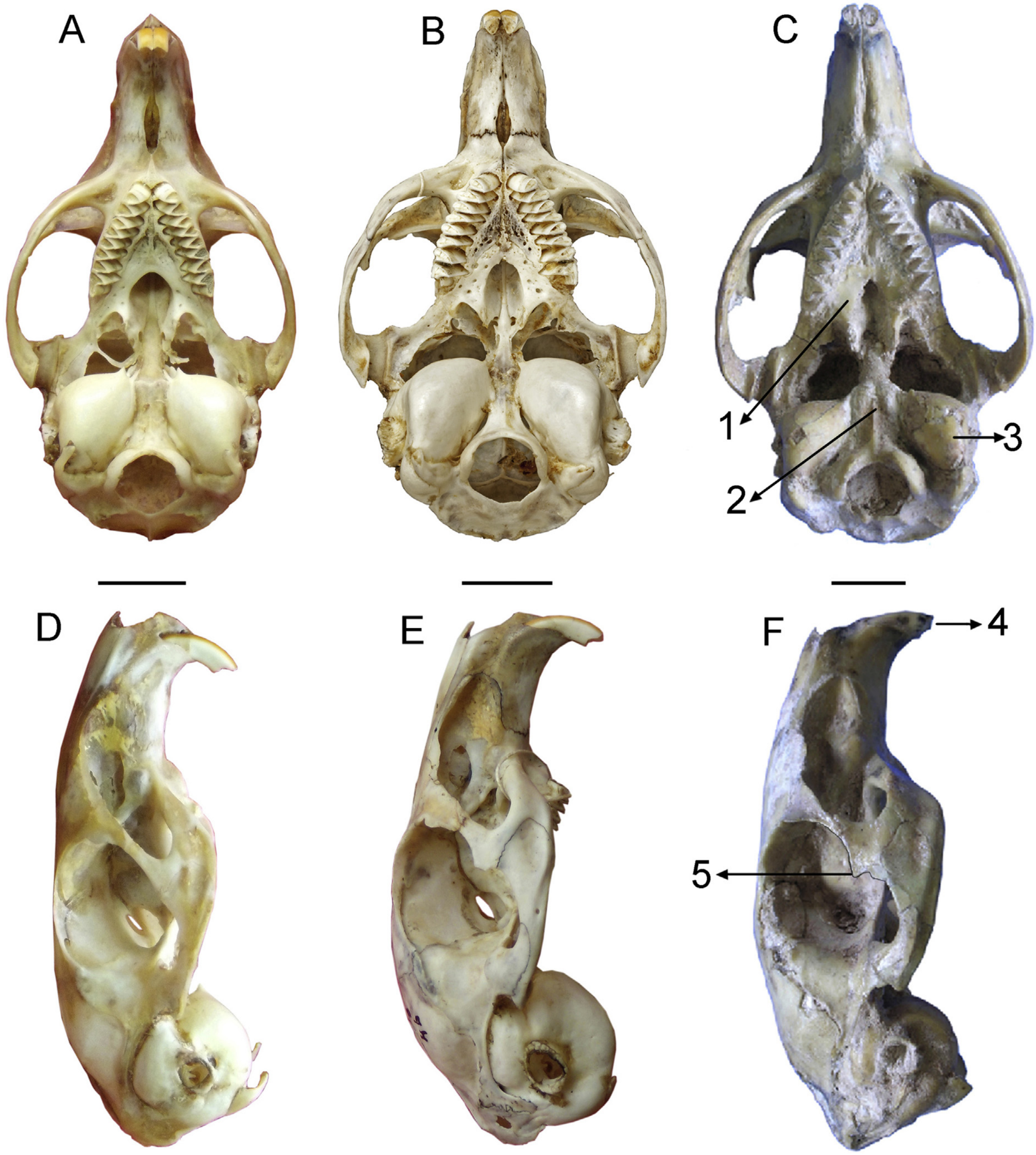

Fig. 6. Palatal (upper) and lateral (lower) views of the skulls of selected representatives of *Galea*. **A** and **D**. *Galea spixii*; **B** and **E**. *Galea musteloides* (BMNH.97.10.3.46); **C** and **F**. *Galea ortodonta*, including some morphological comparative characters: 1: palatine width, 2: basioccipital width, 3: auditory bulla size, 4: orthodont incisor, 5: maxillary zygomatic process with apophysis. Scale bars: 1 cm.

group and *G. demissa*. The external borders of the nasals are subparallel and posteriorly tapered. The coronal (frontoparietal) suture in the adult develops two anteroposterior concavities, resembling *G. leucoblephara* and differing from the mostly straight sutures of *G. spixii*, *G. demissa*, *G. comes* and *G. musteloides*. An interparietal is visible, best delimited in the subadult. As in all members of the genus *Galea*, the maxilla has a lateral projection forming a roof above the infraorbital foramen. In lateral view, this foramen is subcircular. In the subadult, it is more dorsoventrally compressed and more elliptical in shape, like those of the other compared taxa. The zygomatic arch is stouter than that of *G. spixii*, with the vertical ramus constrained in its central portion (it is thicker in the subadult). The zygomatic process of the maxilla is stout and yields an apophysis, as observed in the *G. musteloides* species group and *G. tixiensis*. As in all members of the genus *Galea*, the lacrimal bone is intercalated between the frontal and maxillary bones, forming part of the vertical ramus of the zygomatic arch. The jugal is high in its anterior portion, with a well-developed crest for the insertion of the masseter lateralis profundus muscle; it can reach the anterior border of the zygomatic vertical ramus. In *G. tixiensis* and *G. demissa*, the jugal is located anterior to this border. The Hill foramen is absent, whereas it is large in *G. tixiensis* and variable in recent taxa. The incisive foramen is short and rhomboidal, similar to those of *G. tixiensis* and *G. demissa*. Unlike *G. spixii* and *G. comes*, in which the mesopterygoid fossa is mostly U-shaped, *G. ortodonta* has a V-shaped mesopterygoid fossa. The borders of this structure are anteroposteriorly divergent from the midline, differing from *G. tixiensis*, in which they are mostly

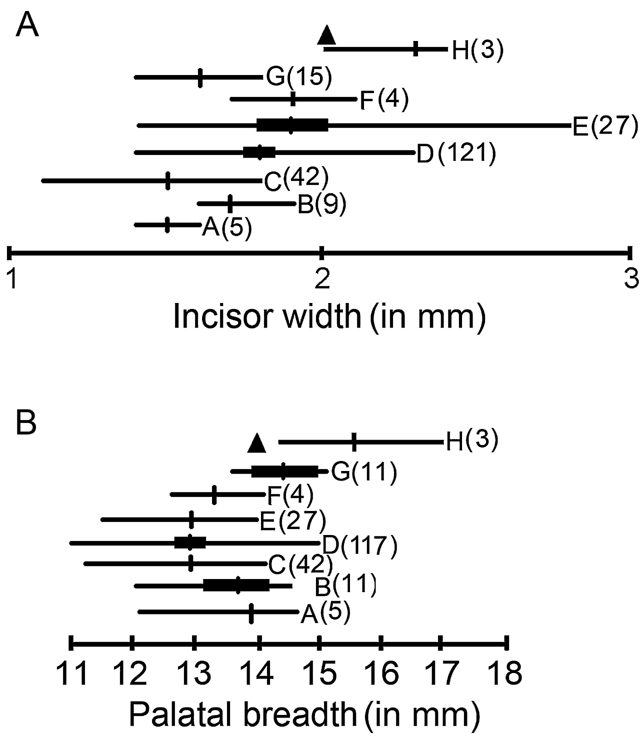

Fig. 7. Univariate analysis of upper incisor width (**A**) and palatal breadth (**B**) in living and extinct species of the genus *Galea*. A. *Galea comes*. B. *G. musteloides*. C. *G. leucoblephara*. D. *G. spixii* (northeastern Brazil samples). E. *G. spixii* (Bahia samples). F. *G. spixii* (Minas Gerais sample). G. *G. tixiensis*. H. *Galea ortodonta*. Black triangle: *G.* cf. *G. ortodonta* (TAR-22). Numbers between brackets: sample size.

parallel. This structure is also narrow compared with those of living forms and starts at the anterior prism of M3. The palate is flat, barely larger than those of *G. tixiensis* and the largest individuals of *G. spixii*. The palatine is wide at the mesopterygoid fossa, occupying most of the palate, differing from that of *G. spixii*, which is narrow. The basioccipital is wide, differing from the narrow basioccipital of *G. musteloides*. The auditory bulla is proportionally small relative to the large skull, longer than wide and rounded in lateral view. It differs from those of *G. comes* and *G. musteloides*, which have large bullae. The paroccipital process is short and anteroposteriorly wide (thinner in the subadult), unlike in living forms, in which it is slender. The subadult has a globose braincase; the interfrontal, coronal, sagittal and parietal-interparietal sutures are loosely attached, and the supraoccipital, interparietal and parietals are closed. The suture between the jugal and the zygomatic ramus of the squamosal is slightly open. In ventral view, the maxilla-palatine, basioccipital-basisphenoid and basisphenoid-presphenoid sutures are visible. The occipital and sagittal crests are not yet developed.

Mandible: The horizontal crest begins at the level of p4, as seen in the *G. musteloides* species group and *G. demissa*, with a strongly developed notch for the insertion of the tendon of the masseter medialis pars anterior muscle. In *G. spixii*, the horizontal crest is variable and can begin at m1. The coronoid process is larger than those of living forms, extending up to or slightly above the condyle. As in all members of *Galea*, the lunar notch is shallow because of a conspicuous lamina that extends from the coronoid process to the condyle.

Dentition: The incisors are subcircular in cross-section, whereas those of other *Galea* are cordiform; the external lateral face is more extensively covered by enamel. The incisors are wider than those of the *G. musteloides* species group and *G. tixiensis*. The upper incisors are orthodont rather than opisthodont, as observed in the other examined representatives of *Galea*. The cheek teeth have discontinuous enamel on the labial face of prisms in upper teeth and in the lingual face in lower ones. An internal primary fold separates the upper prisms and includes cementum at the base; a deep external primary fold is present between the lower anterior and posterior prisms. The P4-M3 length is greater than that of the *G. musteloides* species group and similar to that of large *G. spixii* individuals. As in the *G. musteloides* species group, *G. demissa* and *G. tixiensis*, the upper cheek teeth of *G. ortodonta* have external primary and secondary folds on the labial face of the prisms. M3 is wide, as in *G. comes*, *G. musteloides* and large *G. spixii* individuals, with a short additional projection on the posterior prism that is anteroposteriorly oriented and delimited by a wide and shallow fold.

Postcranial: The appendicular bones are robust, with well-developed muscular crests. The humerus has well-developed proximal tuberosities, and the distal epiphysis has a well-rounded articular surface for the radius. The femur has a large head, and the tibia has a well-developed tibial crest. The metatarsals and phalanges of the hind foot are short and wide.

Galea cf. *G. ortodonta*
Fig. 4C

Referred Material: TAR-22: a fragmentary skull with incisors, diastema, both maxillary tooth rows and nasofrontal area partially preserved; lacking most of the postorbital region. MNHN-1628: a nearly complete right mandible with incisor, diastema and tooth row, lacking the angular region (Fig. 4C), and some postcranial bones (left humerus, ulna and radius; left femur and tibial diaphysis; two thoracic vertebrae; all materials belong to the same individual).

Geographic and stratigraphic location: TAR-22: Tarija (Pueblo Viejo), Bolivia; Tarija Formation (Late Pleistocene in part *sensu* Tonni et al., 2009; Coltorti et al., 2007). MNHN-1628: Canelones, San Luis, Uruguay (S 34°49′, W 55°40″); Libertad Fm. (Pleistocene).

Description: TAR-22 has orthodont incisors like those of *G. ortodonta*, wider than those of the *G. musteloides* species group and similar in width to those of *G. spixii* and *G. ortodonta*. The diastema is shorter than those of the other examined taxa, including *G. ortodonta*. M3 is wide, as in the *G. musteloides* species group and the largest *G. spixii* specimens. The mandible of MNHN-1628 is similar in morphology to that of the subadult *G. ortodonta*, with the horizontal crest beginning at p4. The external lateral face of the incisor is more extensively covered by enamel, similar to *G. ortodonta*. The diastema is larger than those of the subadult *G. ortodonta* and the living taxa; it is similar to that of *G. tixiensis*. The p4-m3 length is also greater than those of the living taxa and the subadult *G. ortodonta*. The appendicular bones are large and robust, larger than those of *G. leucoblephara* and *G. spixii*.

Remarks: TAR-22 was previously designated as a paratype of *G. ortodonta* by Ubilla and Rinderknecht (2001). MNHN-1628 was treated as *Galea* sp.

4.2. Morphological comparisons

Living representatives of *Galea* show intra- and inter-population variability in several skull, jaw and teeth characters. The nasals vary in shape, with subparallel to anteroposteriorly convergent external borders, and in their contact with the frontal (straight to pointed). The Hill foramen may be present or absent. The coronal suture may be straight or concave. The anterior border of the mesopterygoid fossa may be located at the anterior or posterior prism of M3 and may be continuous or notched. Few characters are shared by all members of the genus (living and extinct). In the skull, the roof above the infraorbital foramen and the lacrimal intercalated between the frontal and the maxilla (Figs. 3 and 6). A

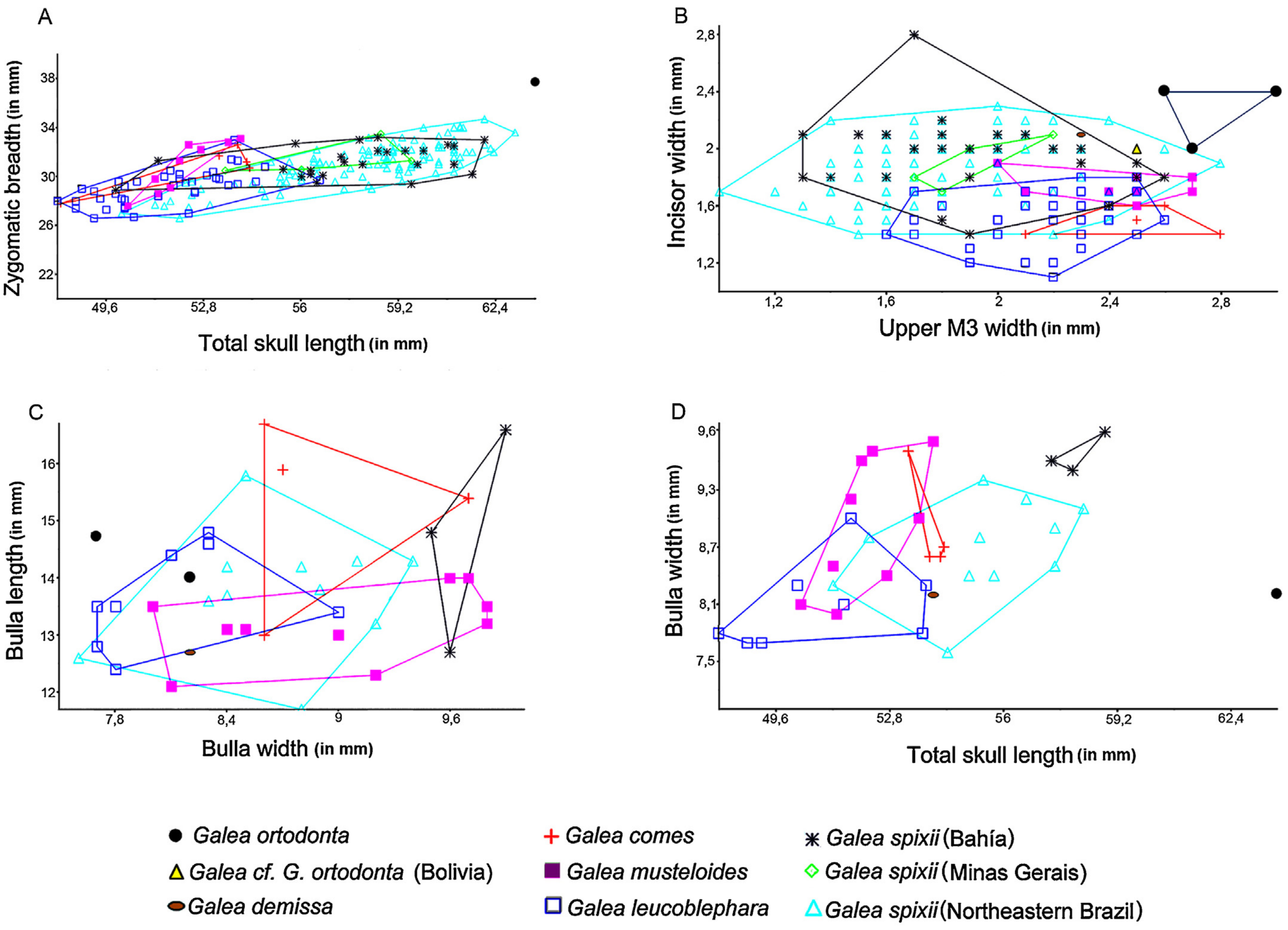

Fig. 8. Bivariate analysis of selected characters of skull and upper teeth in living and extinct taxa of the genus *Galea*.

shallow lunar notch is the only one mandibular character that appears to be constant in all members of *Galea*. Certain characters are shared by some members of the genus:

- an apophysis in the posterior margin of the maxillary zygomatic process (*G. ortodonta*, the *G. musteloides* species group and *G. tixiensis*; Figs. 3D, G and 6);
- the horizontal crest beginning at the level of p4 (*G. musteloides* species group, *G. demissa* and *G. ortodonta*; in *G. spixii*, it varies in position from p4 to m1; in the latter case, the horizontal crest is shorter);
- external folds in prisms of the upper molars (*G. musteloides* species group, *G. demissa*, *G. tixiensis* and *G. ortodonta*) (Contreras, 1964; Quintana, 2001; Ubilla and Rinderknecht, 2001; Fig. 5). In contrast, these folds are absent or poorly developed in *G. spixii*, whose occlusal surfaces are more similar to those of *Microcavia* (Fig. 5E). This fact was already observed by Ubilla and Rinderknecht (2001) and is corroborated by the larger comparative sample in this paper;
- the mesopterygoid fossa anteriorly narrowed into a V-shaped notch (*G. ortodonta G. tixiensis*, *G. demissa* and most of the *G. musteloides* species group; Figs. 3F, I and 6; see also Quintana, 2001). The notch in the anterior margin described by Thomas (1919) for *G. comes* also occurs in some members of *G. musteloides* and *G. leucoblephara*, and according to Bezerra (2008) in some populations of Minas Gerais of *G. spixii*;
- a wide palatine at the mesopterygoid fossa (*G. ortodonta*, *G. demissa*, *G. tixiensis* and the *G. musteloides* species group), which is narrow in *G. spixii* (see also Quintana, 2001) (Figs. 3F, I and 6).

In *G. ortodonta*, the lateral external face of the incisors is more extensively covered by enamel than in living forms. The comprehensive comparative analysis presented here supports the following:

- the orthodont condition of the upper incisors (Fig. 6F) is verified by the new, more complete *G. ortodonta* material from Uruguay;
- the opisthodont condition (Fig. 6D, E) is present in all specimens of the *G. musteloides* species group, *G. demissa*, *G. spixii* and, according to Quintana (2001), *G. tixiensis*;
- in addition to the orthodont incisors, other skull features characterize *G. ortodonta*;
- in light of the intra- and inter-population variability in living forms, which may exhibit the same characters in different taxa, the specimen TAR-22 is more appropriately treated as *G.* cf. *G. ortodonta* rather than as a paratype of *G. ortodonta*, as originally proposed by Ubilla and Rinderknecht (2001). A specific determination would require more complete skull material from Tarija, with the postorbital portion intact.

The almost complete postcranial skeleton (Fig. 4A) makes it possible to compare some skeletal features. Unfortunately, postcranial comparative material of living *Galea* species is scarce in collections. Indeed, the fossil postcranial material of *G. ortodonta*

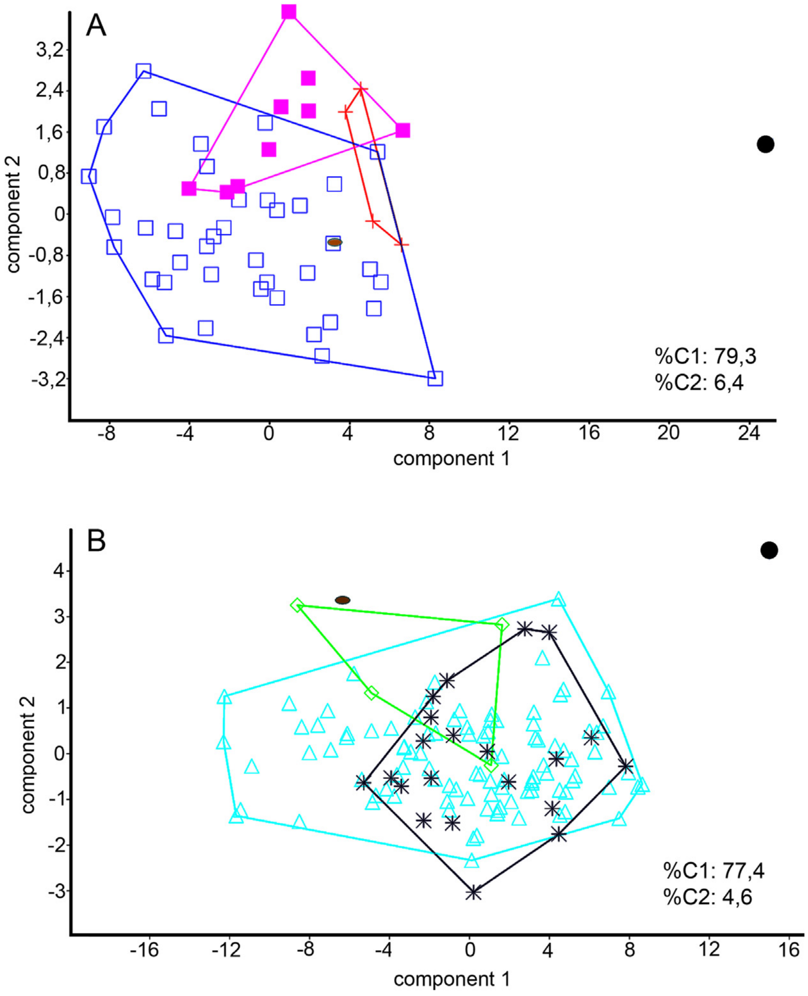

Fig. 9. Principal component analysis: projection of first two principal components (Component 1 and Component 2) based on skull and upper dental measurements. **A**. PCA involving the *Galea musteloides* species group, *G. demissa* and *G. ortodonta* (BRA-2-655). **B**. PCA involving *G. spixii*, *G. demissa* and *G. ortodonta* (BRA-2-655). See Fig. 8 for symbols; %C: percentage of variance explained by each principal component.

is more complete than the compared specimens of living *Galea* species. A preliminary comparison with one adult *G. spixii* specimen shows remarkable differences, with a more robust fossil specimen. This difference is particularly evident in the hind foot, which has shorter and wider metatarsals and phalanges. Compared to one specimen of *G. leucoblephara*, the hind foot of *G. ortodonta* appears to be more similar in proportions but larger and more robust. Nevertheless, caution must be taken in any postcranial characterization because of the subadult condition of the fossil specimen.

4.3. Quantitative analysis

The univariate analysis shows that *G. ortodonta* is larger than the *G. musteloides* species group and *G. spixii* in several skull characters and falls within the upper end of the observed range of most characters for *G. spixii* (Tables 1–3; Figs. 7, S1). The extinct *G. tixiensis* differs from *G. ortodonta* in having narrower upper incisors and palatal wide. The specimen TAR-22 (Tarija) is smaller than the material from Uruguay in several characters. The p4-m3 length is larger than that of the *G. musteloides* species group.

The bivariate analysis (Figs. 8, S2) shows that *G. ortodonta* has the largest skull in length and breadth. Its auditory bulla is intermediate in length but is laterally compressed; those of the Bahia members of *G. spixii*, *G. comes* and *G. musteloides* are widest, whereas that of *G. musteloides* is also shorter. The auditory bulla of *G. ortodonta* is narrow relative to its large skull, while those of *G. musteloides* and *G. comes* are wide despite their short skulls, which is also corroborated by the lower ABW/TL ratio (0.12) of *G. ortodonta* compared with those of *G. musteloides* and *G. comes* (0.17). The incisor width relative to the M3 width allow for the analysis of more fossil specimens of *G. ortodonta* and differentiates G. *ortodonta* from *G. leucoblephara* and the *G. spixii* samples from Bahia, Minas Gerais and, to some extent, northeastern Brazil. The specimen TAR-22 (Tarija) is more similar to the *G. musteloides* species group and to *G. spixii* from northeastern Brazil (Figs. 8B, S2). The *G.* cf. *G. ortodonta* specimen (MNHN-1628) is distinguished by its large size with respect to the total sample (Fig. S2).

In the first PCA (Fig. 9A), including the *G. musteloides* species group, *G. demissa* and *G. ortodonta* (BRA-2-655), the complete *G. ortodonta* skull is successfully differentiated from the *G. musteloides* species group along PC1 and partly differentiated from *G. leucoblephara* along PC2. The members of the *G. musteloides* species group are mostly separated along PC2 (in particular *G. leucoblephara* and *G. musteloides*), and *G. demissa* is included in *G. leucoblephara*. The first three PCs account for 90% of the total variation (Appendix A). The skull, condylobasal, condylobasilar, palatal and nasal lengths and zygomatic breadth have the greatest effect on PC1; the zygomatic and rostral breadths, and condylobasal and P4–M3 lengths have the greatest effect on PC2; and the palatinal length has the greatest effect on PC3. In the second PCA (Fig. 9B), including *G. spixii*, *G. demissa* and *G. ortodonta* (BRA-2-655), the first two components strongly differentiate *G. ortodonta*. The Bahia and Minas Gerais *G. spixii* samples and *G. demissa* are differentiated along PC2. The first three PCs account for 85.5% of the total variation (Appendix A). The skull, condylobasal, condylobasilar and nasal lengths have the greatest influence on PC1; the nasal, skull and condylobasal lengths and zygomatic breadth have the greatest influence on PC2; and the nasal and skull lengths, and zygomatic and palatal breadths have the greatest influence on PC3.

5. Discussion

5.1. Comparative analysis and taxonomy

On the basis of a large comparative sample of living forms, we observed intra-population and intra-specific variability in several skull, mandible and teeth characters (see above, Section 4.2). Part of this variability was observed within *G. leucoblephara* populations in the prism shapes and the configuration of the flexus and flexids of the upper and lower teeth (Kraglievich, 1930; Contreras, 1964; Quintana, 2001). Similar variability occurs in *G. spixii* (Ubilla and Rinderknecht, 2001). These variations can occur among individuals of the same species or population. Thus, it is difficult to find exclusive characters at the specific level, and it may be risky to define species based on fragmentary material. Describing species based solely on mandible remains is also inadvisable because few or no useful characters were detected. On the contrary, associations of characters that vary among taxa are needed to characterize species. Some characters (e.g., the roof above the infraorbital foramen, the lacrimal intercalated between the frontal and the maxilla, the shallow lunar notch in the mandible) were initially described by Kraglievich (1930) for members of the *G. musteloides* species complex, but can now be confidently extended to the whole genus. When Ubilla and Rinderknecht (2001) described the extinct *G. ortodonta*, they emphasized that the orthodont condition of the upper incisors was the most important character differentiating this species from other known taxa. This character was observed in the holotype (FC-DPV-900) and in the specimen designated as a paratype (TAR-22), both fragmentary skulls. But, in the light of the described variability, it is more appropriate to characterize *G. ortodonta* by a set of associated characters including those of postorbital region, pending the discovery of complete cranial remains the determination at species level of the material from Tarija. The character association seen in *G. ortodonta* differs in many respects from the other living and extinct species of the genus. Nevertheless, this species resembles the *G. musteloides* species group and *G. tixiensis* in some respects, including the external folds in the labial faces of the upper teeth, the apophysis in the vertical ramus of the zygomatic arch, the wide palatines and the horizontal mandibular crest beginning at p4.

Our quantitative analyses enabled us to better understand the variability in living *Galea* species and provided useful clues for the interpretation of characters seen in the extinct forms. The results tend to corroborate in some extent the major arrangement proposal for living forms of *Galea* by Bezerra (2008), despite the fact that our measurement set differs in some characters from those of Bezerra (2008). Although the *G. musteloides* species group includes the smallest representatives of the genus, the skulls of its members are proportionally wide and are thus small but stout, particularly *G. musteloides* and *G. comes*; *G. spixii* has a proportionally narrower skull and palate despite having a longer skull. *G. ortodonta* clearly appears to possess a large skull, perhaps the largest among the studied taxa, in terms of its anteroposterior length relative to its zygomatic, palatal and mastoid breadths. However, taking into account the observed variability within living *Galea* species, it is more parsimonious to assume that *G. ortodonta* was similar to or slightly larger in size than the largest *G. spixii* individuals (those from northeastern Brazil). The medium-sized, narrow auditory bulla of *G. ortodonta* is a remarkable character, apparently differentiating *G. ortodonta* from the Bahia specimens of *G. spixii*, *G. musteloides* and *G. comes*, which have proportionally wider auditory bullae. Notably, the auditory bulla is narrow in the subadult *G. ortodonta*; thus, this structure likely reaches the observed size early in its ontogenetic development. The tooth-size character in fragmentary remains should be treated with caution at the species level. Although the members of the *G. musteloides* species group are the smallest representatives of the genus, *G. comes* and *G. musteloides* possess a large M3, similar in size to those of *G. ortodonta* and the largest individuals of *G. spixii* (S1). Although fewer characters are available from the extinct *G. tixiensis*, our analysis shows that *G. ortodonta* differs from *G. tixiensis* in having a wider upper incisor and palate. In terms of robustness, the mandible of *G. ortodonta* is clearly separated from the *G. musteloides* species group (in particular specimens of *G. musteloides* and *G. comes* have lower mandibles), resembling the largest *G. spixii* specimens (those from northeastern Brazil). The partially preserved mandible of a presumed adult specimen (MNHN-1628; Fig. 4C) is referred to *G.* cf. *G. ortodonta* because it is not associated with a skull. Nevertheless, this specimen provides interesting information because it may represent an adult *G. ortodonta* mandible. It is notably differentiated by its size and by the robustness of the horizontal ramus, being similar to *G. tixiensis* in the lower diastema length. The PCA successfully differentiated *G. ortodonta* from the *G. musteloides* species group, *G. spixii* and *G. demissa*. Both size (PC1) and shape (PC2) differentiate *G. ortodonta* from *G. spixii* and *G. demissa*, but *G. ortodonta* apparently resembles the *G. musteloides* species complex in shape. This conclusion is reinforced by some qualitative characters discussed above.

5.2. Biogeographic and environmental considerations

The living representatives of the genus *Galea* are broadly distributed in the Neotropical Region *sensu* Hershkovitz (1972), particularly in the Neotropical and Transitional Regions and part of the Andean Region *sensu* Morrone (2001, 2004), ranging from the lowlands to the highlands above 4000 m in elevation (Mares and Ojeda, 1982; Fig. 1). *G. leucoblephara* occupies predominantly lowland areas (below 1000 m) in Argentina, Bolivia and Paraguay, but some populations can reach up to 4000 m in Argentina. *G. comes* inhabits highlands up to 4500 m in northern Argentina and Bolivia. *G. musteloides* is adapted to live between 2000 and 3800 m in southeastern Perú and the Bolivian Andes (Olrog and Lucero, 1981; Bezerra, 2008; Dunnum and Salazar-Bravo, 2010). *G. spixii* populations are widespread in most parts of Brazil (central, northern and northeastern areas), predominantly from sea level to 1000 m in elevation (Alho, 1982; Mares and Ojeda, 1982). *G. spixii* and the *G. musteloides* species group show a disjunct distribution that can arguably be modeled by tectonic-climatic and environmental processes, particularly those associated with the Andean evolution during the Miocene and Pliocene (Bezerra, 2008; Garzione et al., 2008). A phylogeographic analysis of living *Galea* species by Dunnum and Salazar-Bravo (2010) supports the hypothesis that a vicariant process split the ancestral area of *Galea*, resulting in the differentiation of the *G. spixii* clade from the *G. musteloides* species group. According to these authors, most of the evolution of the latter clade occurred in the Prepuna region. In the Prepuna and surrounding areas, the Andes underwent a punctuated uplift, reaching 2000 m during the Miocene and 4000 m in the Late Miocene and Pliocene (Garzione et al., 2008). Some members of the *G. musteloides* clade may have spread into the lowlands of central and southern South America during the

Late Pliocene and Pleistocene (Dunnum and Salazar-Bravo, 2010). *G. ortodonta*, which exhibits morphological similarities in its skull and teeth with the *G. musteloides* species group, probably reflects this general process and demonstrates the occupation of lowland areas in southern Uruguay during the Late Pleistocene. Nevertheless, this hypothesis needs to be tested by phylogenetic analysis. The *G.* cf. *G. tixiensis* specimen from the Mesopotamian area of Argentina similarly reflects this process (Francia et al., 2012).

Galea species are adapted to live in open and semi-open areas. In particular, the *G. musteloides* species group is mostly found in grassland, savanna and scrub communities in both highlands and lowlands. In Salta, Argentina, *G. leucoblephara* is common in moist areas, such as stream edges and croplands (Eisenberg and Redford, 1999; Mares et al., 1981; Mares and Ojeda, 1982). *G. spixii* can inhabit semi-deciduous Amazonian forest, or "cerrado"; open sections of the Atlantic forest; and arid environments, such as the caatinga of northeastern Brazil (Lacher, 1981; Alho, 1982; Mares and Ojeda, 1982). The large to very large auditory bulla in small skulls seems to be an adaptation to arid environments of some epigeous and fossorial rodents of South America (Ojeda et al., 1999; Gallardo et al., 2009; Traba et al., 2010 and references therein). It can explain the pattern observed in *G. musteloides* and *G. comes*, which are arid environment inhabitant and epigeic rodents. Although the auditory bulla pattern just described for *G. ortodonta* does not reflect such arid conditions (that could be explained because rodents with large skull tends to develop small auditory bullae), there are some mammals as *Microcavia criolloensis*, *Dolichotis* cf. *D. patagonum* and *Lagostomus* sp. collected in the same beds as *G. ortodonta* in the Santa Lucía Basin, suggesting an open to semi-open vegetation and an arid to semi-arid context (Ubilla et al., 2009). The presence of the caviine *G. ortodonta* during the Late Pleistocene (30 ka BP) does not refute this proposal. The absolute ages are correlated with the end of Marine Isotope Stage 3 (MIS3), which spans 60–27 ka BP (Van Meerbeeck et al., 2009). MIS3 implies abruptly alternating warm and cold cycles at a millennial scale during the Last Glacial Cycle in the northern hemisphere (Van Meerbeeck et al., 2009, 2011), and to a lesser degree in the southern hemisphere (Tonni et al., 2010; Buiron et al., 2012). The environmental scenario described above may have been influenced by the last phases of MIS3 in continental environments at this latitude, where the tree cover may have been sparse (Van Meerbeeck et al., 2009). We concur with Francia et al. (2012) concerning the effect of this climatic process.

Sympatry has been observed in living forms of some Caviinae rodents (Carmignotto et al., 2012; Bonvicino et al., 2008; Rood, 1967, 1970, 1972). Indeed, *Galea* and *Microcavia* occur sympatrically in northwestern and central Argentina, and *Galea* and *Cavia* occur sympatrically in part of Brazil and in the southernmost portion of the distribution. Although closely related sympatric species are expected to have different ecological roles, behavioral differences can help to lessen competition (Rood, 1972). This phenomenon may occur among these Caviine genera (Rood, 1970, 1972). The presence of three Caviinae taxa (the extinct *Microcavia criolloensis*, the extinct *G. ortodonta* and an undetermined *Cavia* sp.) in the same stratigraphic beds from the Late Pleistocene in southern Uruguay suggests that this distributional pattern and perhaps a similar behavioral pattern were developed by extinct members of these genera. The records of *Galea* from Uruguay, Mesopotamian Argentina and southern Brazil (Francia et al., 2012; Kerber et al., 2011 and references therein; this paper) indicate that the geographic distribution of the genus during the Late Pleistocene differed from the current pattern. During the Recent, this caviomorph rodent does not occur in the mammal communities of Uruguay, southern Brazil and most of Mesopotamian Argentina. It is difficult to explain why *Galea* disappeared from this area. The climatic processes that occurred during the Late Pleistocene and Early Holocene may have modified its habitat and caused distributional changes. Similarly, the habitat of the related caviine *Microcavia* may have been modified, leading to the disappearance of this genus from Uruguay and southern Brazil (Ubilla, 2008; Ubilla et al., 2008). The persistence of *Cavia*, which is presently common in this area, remains to be explained. The factor that may be considered is that *Cavia* can swim, which allows it to spread and survive in tropical and subtropical moist areas of South America (Rood, 1972).

6. Conclusions

The study of a large comparative sample of living and fossil forms of *Galea* reveals a high intra-population and intra-specific variability in skull, mandible and teeth characters. Exclusive characters at the specific level are hard to find, making risky to define species based on a fragmentary material. On the contrary, associations of characters that vary among taxa are needed to characterize species. The living *G. musteloides*, *G. leucoblephara* and *G. comes* seem to be recognizable species of the genus on the basis of skull characters and quantitative analysis, which is in agreement with recent molecular and morphological studies. This species group includes the smallest representatives of the genus. By and large, the skulls of its members are proportionally wide and are thus small but stout, particularly *G. musteloides* and *G. comes*. On the contrary, *G. spixii* has a proportionally narrower skull and palate despite having a longer skull.

Based on a comprehensive qualitative and quantitative comparative analysis, it has been possible to provide an expanded diagnosis and description of the extinct *G. ortodonta* from the Late Pleistocene of Uruguay (30 ka BP). The very well-preserved material makes *G. ortodonta* the best-known extinct species of the genus. This species is characterized by a unique combination of features including rostral and postorbital region of the skull, which seems to be similar or slightly larger than the largest member of the genus (northeastern Brazil population of the living *G. spixii*). The fragmentary remains from the Pleistocene of Tarija (Bolivia) are assigned here to *Galea* cf. *G. ortodonta*, waiting for more complete skull material.

According to our analysis, some characters should not be considered isolated or in fragmentary material at the species level. In addition to the aforementioned skull breadth, the tooth-size character, frequently used in fossils, should be treated with caution. Indeed, the small *G. comes* and *G. musteloides* possess a large M3, which is similar to the largest member of the genus. In the same way, the auditory bulla is proportionally very large in the smallest species of the genus. These characters seem to be non-predictive and further studies should analyze these patterns in terms of functional or ecological constraints. Finally, describing *Galea* species based solely on mandible remains is inadvisable because few or no useful characters were detected.

Taking into account the environmental adaptations of the living representatives of *Galea*, the record of *G. ortodonta* in Uruguay, which is accompanied by some mammals suggesting an open to semi-open vegetation and an arid to semi-arid context, seems to indicate that this type of environments were prevalent at ~30 ka BP at these latitudes of South America. Local extinction or shifting range of the genus *Galea* in the Mesopotamia Argentina, Uruguay and Southern Brazil, where it does not occur in the extant mammal communities, was likely favored by environmental changes during the latest Pleistocene and Early Holocene, implying the reduction of arid and semi-arid contexts.

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Appendix A. Supplementary data

Supplementary information (list of extant comparative materials, supplementary univariate and bivariate analyses, details of the multivariate analysis, and Figs. S1, S2) associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.geobios.2014.06.001.

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