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Article

INTEGRATIVE TAXONOMY OF THE MOUNTAIN CAVY *GALEA MUSTELOIDES* MEYEN, 1833, A HIGHLAND NEOTROPICAL CAVIOMORPH RODENT

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ABSTRACT. The mountain cavy *Galea musteloides* Meyen, 1833 is a terrestrial caviomorph rodent with diurnal and colonial habits. It occupies grassland areas and rocky shrub steppes in the arid highlands of the central Andes of western Bolivia, northern Chile, and southeastern Peru. Recent phylogenetic studies based on the analysis of mitochondrial DNA showed that this species has a genealogy geographically structured into two main clades, one encompassing those populations usually referred to *G. m. auceps* (Thomas 1911) and *G. m. musteloides*, and another referable to *G. m. boliviensis* (Waterhouse 1848). Multivariate statistical analysis of 16 craniodental measurements corresponding to seven geographical groups supports this conclusion, allowing us to recognize two subspecies within *musteloides*, for which the names of *musteloides* (including *auceps*) and *boliviensis* (including *G. monasteriensis* Solmsdorff, Kock, Hohoff, & Sachser, 2004) are available. Due to some uncertainties in the original reference, we also restricted the type locality of *G. musteloides* to Pisacoma, Puno, Peru.

RESUMEN. TAXONOMÍA INTEGRATIVA EN EL CUIS DE MONTAÑA *GALEA MUSTELOIDES* MEYEN, 1833, UN ROEDOR CAVIOMORFO DE LAS TIERRAS ALTAS NEOTROPICALES. El cuis de montaña *Galea musteloides* Meyen, 1833 es un roedor caviomorfo terrestre, de hábitos diurnos y coloniales. Ocupa pastizales y estepas arbustivas rocosas en las tierras áridas y altas de los Andes centrales del oeste de Bolivia, norte de Chile y sureste de Perú. Estudios filogenéticos recientes basados en el análisis de ADN mitocondrial mostraron que esta especie tiene una genealogía estructurada geográficamente en dos clados principales, uno que engloba aquellas poblaciones generalmente referidas a *G. m. auceps* (Thomas 1911) y *G. m. musteloides*, y otro atribuible a *G. m. boliviensis* (Waterhouse 1848). El análisis estadístico multivariado de 16 medidas craneodentarias, correspondientes a siete grupos geográficos, respalda esta conclusión, lo que nos permite reconocer dos subespecies dentro de *G. musteloides*, para las cuales los nombres *musteloides* (incluyendo *auceps*) y *boliviensis* (incluyendo *G. monasteriensis* Solmsdorff, Kock, Hohoff & Sachser, 2004) están disponibles. Debido a algunas dudas de la referencia original, también restringimos la localidad tipo de *G. musteloides* a Pisacoma, Puno, Perú.

Key words: Caviidae, Altiplano, subspecies, quantitative morphology.

Palabras clave: Caviidae, Altiplano, subespecies, morfología cuantitativa.

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INTRODUCTION

The genus *Galea* Meyen, 1833 includes five species of terrestrial, medium-sized caviomorph rodents that are widely distributed in both high-elevation and low-elevation grasslands and rocky scrub environments in arid, semiarid, and temperate areas of South America (Dunnum 2015). Species of this genus are mostly diurnal and colonial herbivores that prefer open habitats with good visibility (Dunnum 2015). They can be sorted into two main species groups, *musteloides*, and *spixii*, based on both genetic and morphological evidence (Bezerra 2008; Dunnum & Salazar-Bravo 2010). The *musteloides* group is found in highland and lowland, arid to semiarid and temperate areas from southern Peru, western and central Bolivia, and northernmost Chile to Argentine Patagonia. Four living species are currently included in the *musteloides* group: *G. musteloides* Meyen, 1833; *G. comes* Thomas, 1919; *G. leucoblephara* Burmeister, 1861; and an unnamed form from the mid-elevations of the southern Bolivian Andes (Bezerra 2008; Dunnum & Salazar-Bravo 2010; Ubilla & Rinderknecht 2014). The *spixii* group is distributed in semiarid and savanna environments of Brazil and eastern Bolivia and includes at least two species: *G. flavidens* Brandt, 1835, and *G. spixii* Wagler, 1831 (Dunnum & Salazar-Bravo 2010; but also see Bezerra 2008).

Galea musteloides (200-650 g) is a cavy of terrestrial habits, distributed in the Andes of central Bolivia, southeastern Peru, and northernmost Chile (Dunnum 2015). This rodent has been traditionally viewed as a highly polytypic species with a large distributional range, comparable to that presently referred to as the *musteloides* group (e.g., Cabrera 1953). Its current concept was recently established after the recognition of *G. comes* and *G. leucoblephara*, previously considered subspecies of *G. musteloides*, at the species level (Dunnum & Salazar-Bravo 2010). At least three nominal forms are currently included in the synonymy of *G. musteloides* (see **Fig.** 1): *Cavia boliviensis* Waterhouse, 1848, with type locality restricted by Thomas (1911) to “Paratani [= Parotani], close to Cochabamba”; *Kerodon auceps* Thomas, 1911, with type locality at “Guarina (alt. 4000 m.), near the south-east, the Bolivian, end of the lake [Titicaca]” (Thomas 1911); and *Galea monasteriensis* Solmsdorff, Kock, Hohoff, & Sachser, 2004, with type locality at “Valle Hermoso, 2557 m. a.s.l., 66°09’W, 17°23’S, S of Cochabamba, Cordillera Oriental, Province of Cochabamba, Bolivia” (Solmsdorff et al. 2004).

Based on a phylogenetic analysis of DNA sequences, Dunnum & Salazar-Bravo (2010) recognized two main clades and three subspecies within *G. musteloides*, one encompassing those populations referred by Anderson (1997) to *G. m. auceps* (Thomas 1911) and *G. m. musteloides*, and another referable to *G. m. boliviensis* (Waterhouse 1848), this latter including *G. monasteriensis*. However, among previous hypothesis, some authors recognized *auceps* and *musteloides* (including *boliviensis*) as different species (Thomas 1911, 1926), or subsumed *auceps* and *boliviensis* within *G. m. musteloides* (Osgood 1916; Cabrera 1953) or retain *G. m. boliviensis* (including *auceps*) and *G. m. musteloides* as different subspecies (Solmsdorff et al. 2004) (see **Fig.** 1 for a synthesis). Recent contributions used qualitative and quantitative morphological traits to differentiate *G. musteloides* from other closely related species, such as *G. comes* and *G. leucoblephara* (e.g., Ubilla & Rinderknecht 2001; Solmsdorff et al. 2004; Bezerra 2008; Teta et al. 2019). However, no one has evaluated whether there are quantitative morphological differences between the subspecies referred to *G. musteloides* (i.e., *auceps, boliviensis*, and *musteloides*) or the clades recognized by the phylogenetic analyses of Dunnum & Salazar-Bravo (2010).

In this contribution, we studied patterns of quantitative morphological variation in *G. musteloides* from Bolivia and Peru, covering almost entirely its distributional range. Subsequently, these patterns were compared with the available phylogenetic evidence to test previous taxonomic hypotheses (i.e., Dunnum & Salazar-Bravo 2010).

MATERIALS AND METHODS

Sixty-seven specimens (belonging to age classes 3-5 sensu Bezerra 2008), representing 22 collecting localities (**Fig.** 2), form the basis of this report. Studied individuals consist primarily of skins and their associated crania housed at the following biological collections (see Appendix 1): American Museum of Natural History (AMNH, New York, USA), Field Museum of Natural History (FMNH, Chicago, USA), Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN, Buenos Aires, Argentina), Museum für Naturkunde (ZMB, former Zoologische Museum der Alexander von Humboldt Universität, Berlin, Germany), Natural History Museum (BM acronym for specimens, NHM, London, UK), Senckenberg Museum (SMF, Frankfurt am Main, Germany), and United States National Museum of Natural History, Smithsonian Institution (USNM, Washington, DC, USA). The studied samples (see Appendix 1) covered almost entirely the known distributional range of the three subspecies currently included within *G. musteloides* (i.e., *auceps*, *boliviensis*, and *musteloides*). Studied samples include some topotypical specimens and the holotypes of *Cavia boliviensis*, *Galea monasteriensis*, and *Kerodon auceps* (see **Fig.** 3).

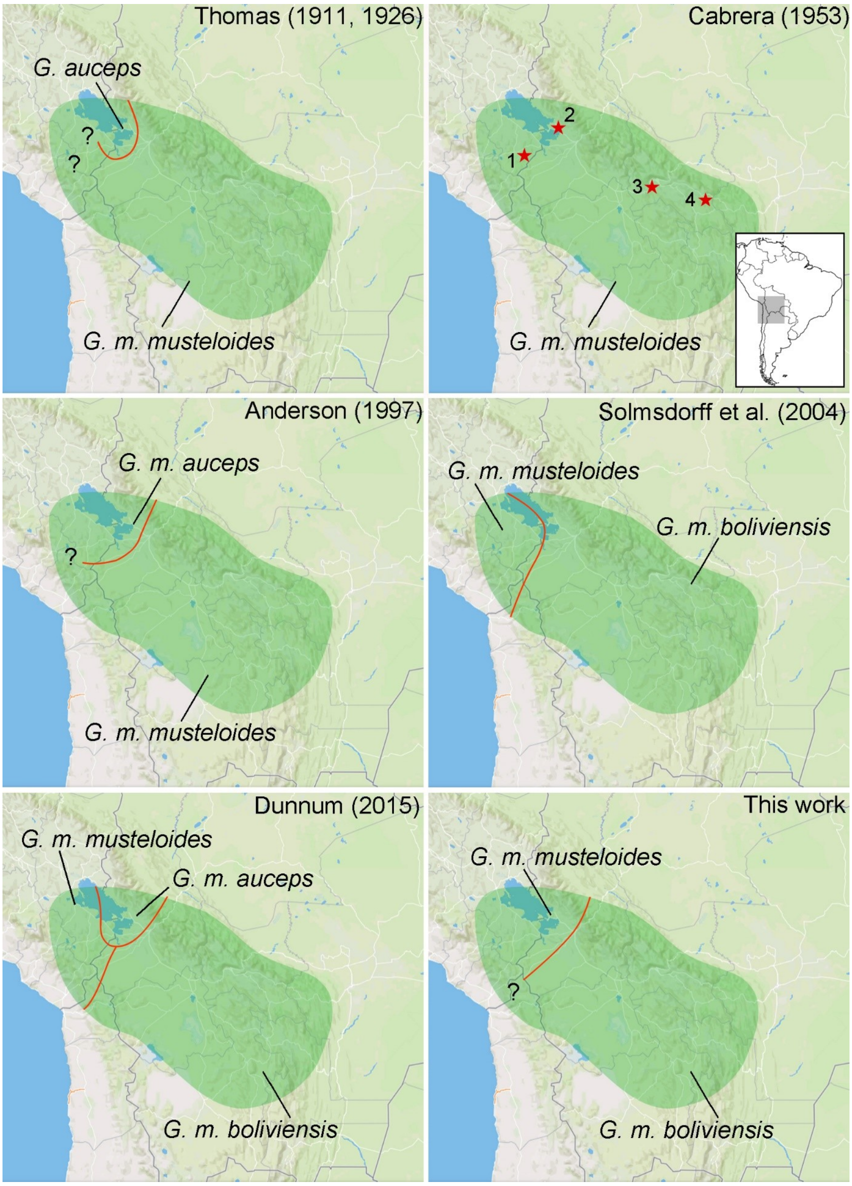

Fig. 1. Main taxonomic hypothesis about the allocation of highland populations of *Galea* from west-central Bolivia, northern Chile, and southeastern Peru. The green shadow area corresponds to the distribution of *Galea musteloides* as currently understood (cf. Bezerra 2008; Dunnum & Salazar-Bravo 2010; Dunnum 2015). Red stars on the second map correspond to the type localities of the nominal forms discussed in the text: 1) *Galea musteloides* Meyen, 1833; 2) *Kerodon auceps* Thomas, 1911; 3) *Cavia boliviensis* Waterhouse, 1848; and 4) *Galea monasteriensis* Solmsdorff, Kock, Hohoff, & Sachser, 2004. Approximate limits between taxa are indicated by red lines; question marks denote uncertainties about the taxonomic identity of some populations or geographical limits between taxa.

Sixteen craniodental measurements were taken from each cranium using a digital caliper accurate to 0.05 mm: TLC, total length of the cranium; CIL, condylo-incisive length; NL, length of nasals; NW, width of nasals; IOC, interorbital constriction; ZW, greatest zygomatic breadth; BB, breadth of braincase; FL, length of frontals; DL, length of the upper diastema; LIF, length of incisive foramina; BIF, breadth of incisive foramina; PL, palatal length; TRL, length of upper toothrow; BPM3, breadth of palate at the level of the upper third molar; BPP, breadth across paraoccipital

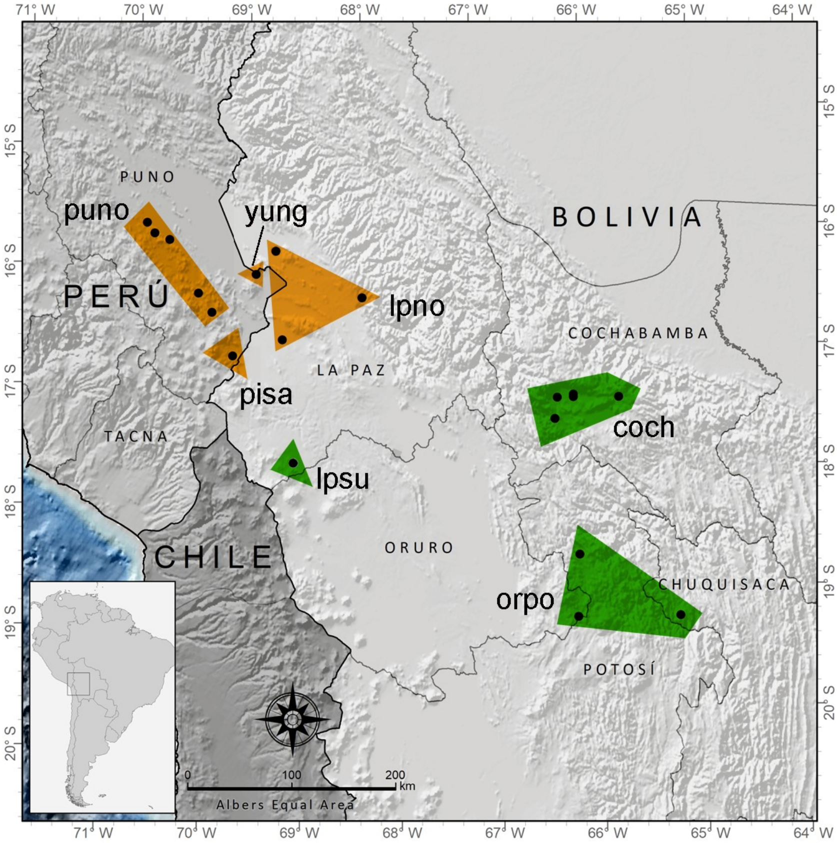

Fig. 2. Map of western Bolivia, northern Chile, and southeastern Peru, depicting the collection localities of the specimens of *Galea musteloides* studied in this work. Green (= *G. m. boliviensis*) and orange (= *G. m. musteloides*) shadows correspond to the two main morphological groups detected by our analysis. For the acronyms, see Materials and Methods.

processes; and TBL, length of tympanic bulla. For the definition of these measurements, we followed Contreras & Contreras (1984), Ubilla & Rinderknecht (2014), and Teta et al. (2017). Anatomical terminology for the cranium and dental features followsCherem & Ferigolo (2012).

The studied specimens were grouped into seven geographical groups (**Fig**. 2), considering the geographical proximity between localities, the absence of major geographic barriers among localities, and the lack of obvious discrepancy in size or morphology among individuals (see examples of this approach in Bezerra & Oliveira 2010; Brennand et al. 2013; Chiquito et al. 2014; Libardi & Percequillo 2016). The constituted groups were: Bolivia: coch, Cochabamba Department (N = 25); lpsu, southern La Paz Department (N = 5); lpno, northern La Paz Department (N = 5); and orpo, Chuquisaca, Oruro and Potosí Departments (N = 3). Peru: pisa, Pisacoma, southern Puno Department (N = 9); puno, northern Puno Department (N = 17); and yung, Yunguyo, southeastern Puno Department (N = 3).

Principal component analysis and discriminant functions were computed using the sixteen craniodental measurements of all specimens, all of which were previously transformed to log10. In addition, we also calculated the squared Mahalanobis (D2) distances among geographical samples, depicting these results in a dendrogram based on the unweighted pair-group method by using arithmetic averages (UPGMA; Sneath & Sokal 1973). Standard descriptive statistics (range, mean, and standard deviation) were derived from each resulting morphometric group. As previous authors did not detect differences between sexes (Bezerra 2008), males and females were combined in morphometric analyses. All statistical analyses were conducted with the software PAST v. 2.17 (Hammer et al. 2001).

RESULTS

Studied specimens are remarkably homogeneous in most external and cranial features (e.g., **Fig**. 4), although they depict some quantitative differences (see results of PCA, DFA, and UPGMA below).

The first two PCs together accounted for 63.5% of the total variance (**Fig**. 5A; **Table** 1). Plots of specimen scores were moderately overlapped in the

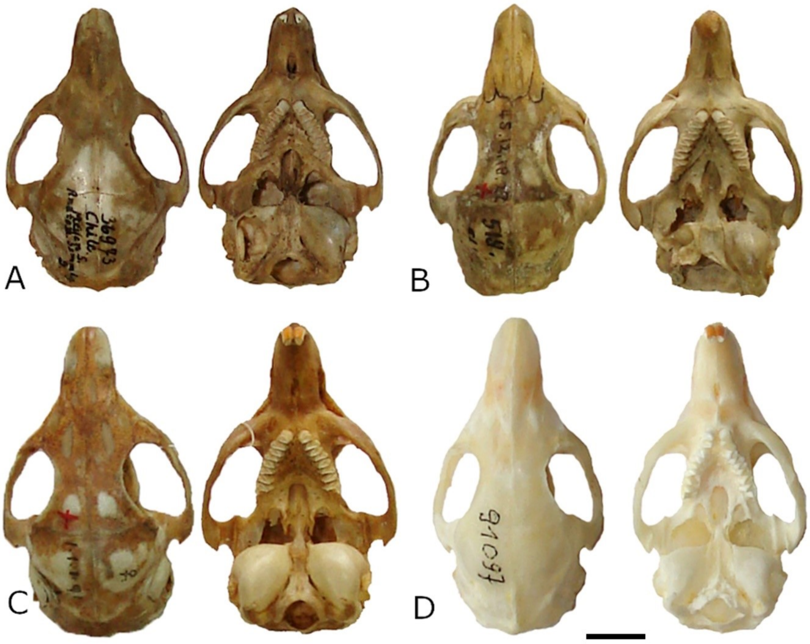

Fig. 3. Dorsal and ventral views of the crania of the lectotype of *Galea musteloides musteloides* (A; ZMB 36973) and the holotypes of *Cavia boliviensis* (B; BM 45.12.18.22), *Kerodon auceps* (C; BM 1.1.1.91), and *Galea monasteriensis* (D; SMF 91097). Scale = 5 mm.

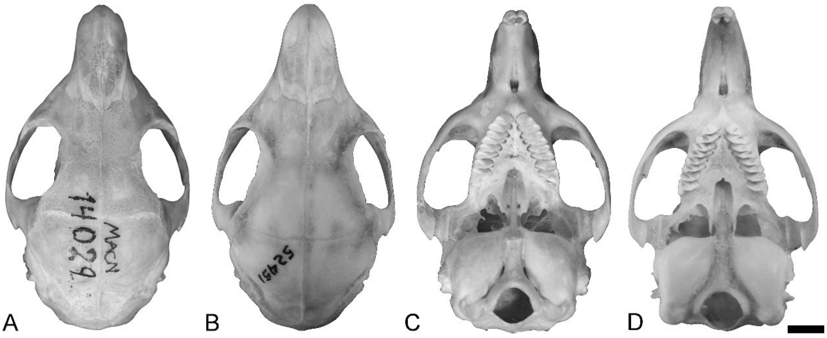

Fig. 4. Dorsal and ventral views of the crania of *Galea musteloides boliviensis* (A, C; MACN-Ma 14029), and *G. m. musteloides* (B, D; FMNH 52451; topotype). Scale = 5 mm.

multivariate space, although they showed primary segregation of the geographical groups into two principal clusters (**Fig.** 5A) along the first PC. One cluster is composed of those groups southerly distributed in Bolivia (i.e., coch, lpsu, and orpo; **Fig.** 2), while the second encompasses those groups northerly distributed in Bolivia and Peru (i.e., lpno, pisa, puno, and yung; **Fig.** 2). The highest absolute weights on PC1 and PC2 corresponded to variables BPM3 and ZB and LIF and BIF, respectively (**Fig.** 5A; **Table** 1).

As in the PCA, the DFA also revealed a major separation between the southern (i.e., coch, lpsu, and orpo) and northern geographical groups (i.e., lpno, pisa, puno, and yung) of *Galea musteloides* (**Fig.** 5B). Among the first group (i.e., southern), there is a segregation between coch + lpsu and orpo along the second axis. The first and second axes of DFA explained 90.61% of the total variance (**Table** 2). Variables BIF, BPM3, IOC, and ZW were relevant

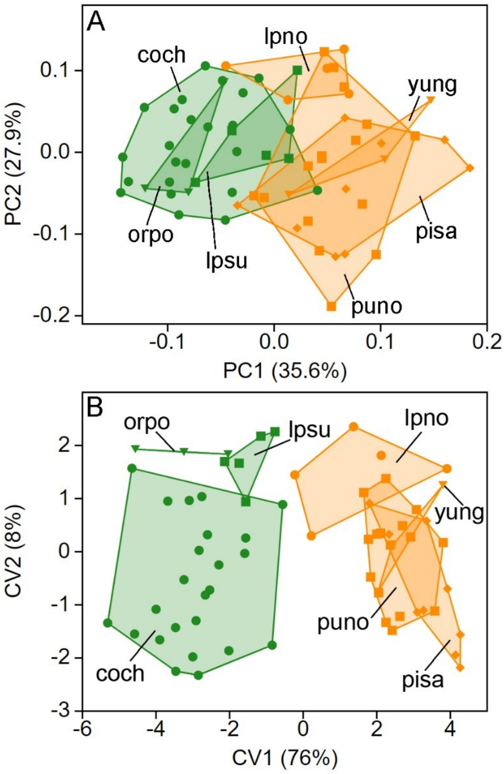

Fig. 5. Results of principal components analysis (above) and seven-group discriminant function analysis (below) based on 16 log-transformed craniodental measurements for adult individuals of *Galea m. musteloides* (orange symbols) and *G. m. boliviensis* (green symbols). Symbols are the same for the two figures. For the acronyms, see Materials and Methods.

for discrimination on the first axis and BIF, BPM3, LIF, and CIL on the second (**Table** 1).

The unweighted pair-group method (UPGMA) also underscores the phenetic separation of the geographical groups into the two same clusters recovered by the above-mentioned analysis (i.e., PCA, DFA) (**Fig**. 6).

For the three analyses (i.e., PCA, DFA, UPGMA), within the first cluster (i.e, coch, lpsu and orpo) there is included a large sample of topotypes of *Cavia boliviensis* (AMNH 38728, 38270, 40795, 40798, 40799, 40804; FMNH 21561, 21562, 21566, 21567, 21570), while as part of the second cluster there are nine topotypes of *Galea musteloides* (FMNH 52441, 52442, 52444, 52446, 52447, 52448, 52449, 52450, 52451) and two nearly topotypes of *Kerodon auceps* (USNM 271396, 271397).

Basic descriptive statistics for the two recognized morphometric groups, including mean, SD, range (min. and max.), and sample sizes (n), are summarized in Table 2.

DISCUSSION

Our morphological assessment of the largest sample of *Galea musteloides* to date strongly suggests that this taxon includes at least two morphologically distinctive groups. As we were unable to find qualitative differences in their craniodental traits (P. Teta & A. Bezerra, pers. obs.), and considering the low level of genetic divergence between them (cf. Dunnum & Salazar-Bravo 2010), we prefer to preliminarily regard these groups at the subspecies level, under the names *G. m. musteloides* (including *auceps*) and *G. m. boliviensis* (including *G. monasteriensis*). Overall, the samples referred to *G. m. musteloides* have smaller crania with proportionally larger frontals and palates, while *G. m. boliviensis* is characterized by larger crania with proportionally broader nasals and zygomatic arches (see **Figs**. 4 and 5). In coincidence with our results, the supposed type (see discussion below) of *G. m. musteloides* and the holotype of *Kerodon auceps* have broader zygomatic arches in dorsal view (**Fig**. 3), while the holotypes of *Cavia boliviensis* and *Galea monasteriensis* have a more elongated profile (**Fig**. 3). Our findings (**Fig**. 1) are in partial accordance with those of Dunnum & Salazar-Bravo (2010), which identified an unresolved trichotomy within *G. musteloides* that they tentatively subdivide into 2 subclades (referred as A and B; Dunnum & Salazar-Bravo 2010: **Fig**. 2). As in our study, one of these subclades was southerly distributed, including populations from the Bolivian departments of Oruro, Cochabamba, and Santa Cruz (subclade A), while the other occurs in northern Bolivia and southern Peru (subclade B), with populations in the departments of La Paz and Puno, respectively (cf. Dunnum & Salazar-Bravo 2010).

Dunnum & Salazar-Bravo (2010) and Dunnum (2015) recognized two subspecies within the northern subclade of *G. musteloides* (referred by these authors as subclade A; see **Fig**. 1), maintaining *G. m. musteloides* as different from *G. m. auceps* based on the pale, yellowish coloration of *auceps* in contrast to the supposed darker coloration of the nominate subspecies. According to their results, there was at least one locality ("La Paz, 11.5 km W San Andres de Machaca, 3.800 m") where both *G. m. musteloides* and *G. m. auceps* are found in sympatry (Dunnum & Salazar-Bravo 2010: **Fig**. 2). In contrast to these results, we were unable to find

Table 1

Loadings of principal components analysis and seven-group discriminant function analysis based on 16 log10-transformed cranial and dental measurements for adult individuals (N = 67) of *Galea musteloides*.

	PC 1	PC 2	CV1	CV2
TLC	0.1515	0.1408	0.0023	−0.0001
CIL	0.1610	0.1548	0.0025	−0.0078
NL	0.2466	0.1902	0.0048	−0.0014
NW	0.0985	0.2179	−0.0002	0.0026
IOC	0.2572	0.0053	0.0068	−0.0023
ZW	0.3213	0.1218	0.0080	0.0053
BB	0.1832	0.0858	0.0045	0.0050
FL	0.1939	0.0617	0.0044	0.0018
DL	0.2398	0.1857	0.0050	0.0023
LIF	0.2438	0.3640	0.0031	0.0147
BIF	−0.5396	0.7790	−0.0153	0.0143
PL	0.1921	0.1436	0.0037	0.0001
TRL	0.1095	0.1586	0.0002	0.0035
BPM3	0.3448	0.0654	0.0083	0.0100
BPP	0.2110	0.0992	0.0053	−0.0002
TBL	0.1397	0.1133	0.0033	0.0026
% Variance	35.62	27.87	76.03	8.05
Eigenvalue	0.006	0.005	8.267	0.873

qualitative or quantitative differences in the cranial anatomy between our samples of *G. m. musteloides* (pisa, puno, and yung) and those referable to *auceps* (i.e., lpno). Although we did not explore objectively the existence of differences in the hair color, the inspection of large samples of individuals allowed us to sort them into two main groups that match well with the groups detected by the multivariate analysis: one composed of brownish and darker colored individuals from southern Bolivia (i.e., coch, lpsu, orpo) and another of much paler and yellowish ones (as was described for *auceps*) from northern Bolivia (e.g., USNM 271396, 271397) and Peru, in which are included some topotypes of *musteloides*. However, contrary to this overall pattern, two specimens from northern Bolivia, housed at the MACN (MACN 33.77, 33.78), have a brownish coloration.

When Thomas (1911) described *auceps*, he used an individual from Sajama, Bolivia, which is located ca. 170 km SW of the itinerary followed by Meyen (cf. Weberbauer 1911), as an example of a "true" *musteloides*. However, according to our results, it seems more likely that the Sajama populations (near lpsu sample from southern La Paz) correspond to *G. m. boliviensis*. Therefore, it was not entirely surprising that some years later Thomas (1926); (see also Osgood 1916) itself synonymized *boliviensis* under *musteloides*, since those samples from Parotani (where Thomas restricted the type locality of *boliviensis*) and Sajama likely belong to the same taxon (**Fig**. 1; this work). On the contrary, Thomas (1911) recognized *auceps* as the form occurring at the southern end of the Titicaca Lake, referring to its specimens from both La Paz (Bolivia) and Puno (Peru) (**Fig**. 1). In his description of *auceps*, Thomas (1911) discussed that this taxon has a broader cranium with more widely expanded zygomata and larger tympanic bullae than *boliviensis* or those individuals from Sajama that he identified as *musteloides* (cf. **Fig**. 3). Coincidentally, our samples from southern Peru (pisa, puno, yung) and northern Bolivia (lpno), here referred to *G. m. musteloides*, are characterized by larger values for BB, BPM3, TBL and ZB (**Table** 1 and 2).

The type locality of *Galea musteloides* was implicitly, although vaguely, defined by Meyen (1833:598) when he referred to this species for "Sie bewohnen die Hochebenen der westlichen Cordillerenkette, auf dera Passe von Tacna nach dem Alpensee von Titicaca. Das Plateau von Tacora, besonders der Kamm desselben, zwischen dem Bolivianschen Indianerdorfe Morocallo, und dem Peruanschen Kirchdorfe Pisacoma…" (= They inhabit the plateaus of the western Cordillera, on the pass from Tacna to the Alpine Titicaca Lake. The Tacora plateau, especially the ridge of the same, between the Bolivian Indian village of Morocallo and the Peruvian church village of Pisacoma… [the translation is ours]).

Table 2

Summary statistics (mean, SD, range [min-max]) of the craniodental measurements (in mm) of adult individuals (N) of *Galea musteloides boliviensis* and *G. m. musteloides.*

	Galea musteloides boliviensis					*Galea musteloides musteloides*				
	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.
TLC	25	50.21	2.25	45.70	55.16	42	51.33	1.97	47	55.13
CIL	25	45.09	2.11	41.15	50.48	42	46.22	1.97	42.19	49.74
NL	25	17.63	1.43	13.55	19.79	42	18.5	1.15	16.84	21.20
NW	25	7.80	0.43	6.84	8.63	42	7.68	0.49	6.69	8.75
IOC	25	10.87	0.58	9.86	11.98	42	11.56	0.75	10.11	13.73
ZW	25	28.01	2.06	21.01	32.92	42	30.43	1.62	27.1	33.34
BB	25	21.19	0.94	19.59	24.09	42	22.05	0.92	19.87	23.71
FL	25	15.93	0.93	13.37	18.06	42	16.37	0.95	14.09	18.27
DL	25	13.16	0.88	11.48	15.37	42	13.64	0.83	11.94	15.22
BIF	25	1.25	0.19	0.87	1.72	42	1.32	0.14	1.02	1.72
LIF	25	4.67	0.48	3.89	5.58	42	4.03	0.66	2.75	5.43
PL	25	21.41	1.05	19.48	23.53	42	22.16	1.13	19.63	24.54
TRL	25	11.91	0.65	10.97	13.44	42	12.04	0.60	11.05	13.02
BPM3	25	12.63	0.88	11.25	15.44	42	13.76	0.77	11.84	14.9
BPP	25	16.25	1.00	14.00	17.91	42	17.13	0.83	15.72	18.61
TBL	25	11.55	0.64	10.34	12.64	42	11.98	0.61	11.22	13.52

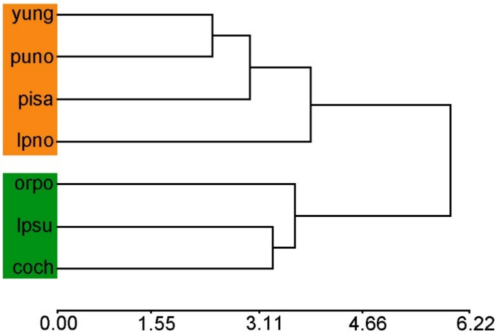

Fig. 6. UPGMA clustering of Mahalanobis distances computed on 16 log-transformed craniodental measurements of 7 geographical groups of adult samples of *Galea musteloides* (colors are as in Fig. 2). For the acronyms, see Materials and Methods.

Solmsdorff et al. (2004) identified one specimen housed at the Zoologische Museum der Alexander von Humbolt Universitat (ZMB 36973, previously cataloged in the Anatomical Collection as AN 7215, preserved as cranium) as the holotype of *Galea musteloides.* These authors considered this individual as the type by "original designation" which is erroneous, as Meyen (1833) did not designate any type material for *musteloides.* According to its tag, the specimen ZMB 36973 was caught at "zw. Morocallo u. Pisacoma, Chile" (= between Morocallo and Pisacoma, Chile [the translation is ours]). Although this individual lacks data about its collector or collection date, it is assumed that it was collected by Meyen itself (see the discussion in Bezerra 2008). Based on these facts, we can safely restrict the type locality of *Galea musteloides* to the village of Pisacoma (16°54'S, 69°23'W, Puno, Peru), which was certainly visited by Meyen during his travel. In addition, we think that individual ZMB 36973 should be more appropriately considered a lectotype of *G. musteloides* (Fig. 3). The reference to Chile in the tag is erroneous (also observed by Bezerra 2008), since Meyen traveled mostly across southern Peru, from the coastal city of Arica (that by this time belonged to Peru) to Chucuicito, on the southern margin of the Titicaca Lake, visiting among others the villages of Tacna, Tacora, and Pisacoma (Weberbauer 1911).

The morphological differences here documented between *G. m. musteloides* and *G. m. boliviensis* are remarkable, especially considering that the level of morphological differentiation between other well-established species of this genus, even when accessed through multivariate statistical analysis, was moderate to low (e.g., Bezerra 2008; Teta et al. 2019). As we evaluated only quantitative craniodental traits, we believe that our taxonomic hypothesis is preliminary; supplementary samples are much needed to better understand patterns of intra- and interspecific variability in *Galea musteloides.* For example, there is a large information gap between those records in Puno (Peru) and La Paz (Bolivia) and the most southerly records distributed in the Bolivian departments of Potosi and Cochabamba. Specifically, additional fieldwork in northernmost Chile (i.e., Arica) and western Bolivia (i.e., La Paz, Oruro) is essential to cover the entire distributional range of *G. musteloides*. We also have no information about possible contact areas between *G. musteloides* and other species of the genus, such as *Galea comes* in the highlands to the south or *Galea leucoblephara* in the lowlands to the east. Finally, objective descriptions of other character traits (e.g., pelage coloration) are also desirable. Future contributions must also attempt to clarify the distributional boundaries between subspecies or the existence of gradients of clinal variation between them. In general, continuing with the taxonomic studies of the genus *Galea* will help us not just to better understand the systematics, evolution, and biogeography of Caviidae but also to delimit meaningful taxonomic units as a first step to conserving them.

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APPENDIX 1

List of studied specimens and their collection localities. Acronyms for museums and collections are as follows: American Museum of Natural History (AMNH, New York, USA), Field Museum of Natural History (FMNH, Chicago, USA), Museum für Naturkunde (ZMB, Berlin, Germany), Museo Argentino de Ciencias Naturales (MACN, Buenos Aires, Argentina), Natural History Museum (BM acronym for specimens, London, UK), Senckenberg Museum (SMF, Frankfurt am Main, Germany), and United States National Museum of Natural History, Smithsonian Institution (USNM, Washington, DC, USA). Please note that individuals BM 1.1.1.91, BM 45.12.18.22, ZMB 36973, and SMF 91097 were not included in the quantitative analysis.

Galea musteloides musteloides (n = 37): Bolivia: "Guarina (alt. 4000 m.), near the southeast, the Bolivian, end of the lake [Titicaca]", (BM 1.1.1.91 [holotype of *Kerodon auceps*]); La Paz, 4 km by road SW of San Andrés de Machaca 3850 m (AMNH 263001); La Paz, 5 km W Achacachi (USNM 271396, 271397); La Paz, Nuestra Señora de La Paz (MACN 33.77, 33.78). Peru: Puno, 6 mi S of Yunguyo (FMNH 51304, 51306, 51308); Puno, 8 mi NW Puno, 1300 ft. (AMNH 213465); Puno, Callacama (FMNH 52452, 52453, 52454, 52455, 52456, 52457); Puno, Chucuicito (FMNH 52458, 52459, 52460, 52461); Puno, Hacienda Colllacachi (FMNH 49447, 49450), Puno, Pichipichuni (FMNH 52475); Puno, Paso de Tcana, between Marocallo and Pisacoma (ZMB 36973, specimen erroneously considered holotype of *Galea musteloides*); Puno, Pisacoma (FMNH 52441, 52442, 52444, 52446, 52447, 52448, 52449, 52450, 52451 [topotypes of *Galea musteloides*]); Puno, Puno (FMNH 51305, 51307); Puno, Sorapa (AMNH 91600).

Galea musteloides boliviensis (n = 34): Bolivia: Cochabamba, Cochabamba (MACN 13035, 50.307; AMNH 38714, 38738); Cochabamba, Cercado (MACN 13031, 13032, 13033, 13034); Cochabamba, Parotani (BM 45.12.18.22 [holotype of *Cavia boliviensis*]; AMNH 38728, 38270, 40795, 40798, 40799, 40804; FMNH 21561, 21562, 21566, 21567, 21570 [topotypes of *Cavia boliviensis*]); Cochabamba, Tiraque (USNM 259639); Cochabamba, Valle Hermoso (SMF 91097 [holotype of *Galea monasteriensis*]); Cochabamba, Vinto (AMNH 36743, 38239, 38740, 38751); Chuquisaca, Pulce (AMNH 38977); La Paz, Esperanza, Pacajes (MACN 14029, 50.305; FMNH 53645, 53646. 53647); Oruro, 7 km S and E of Cruce Ventanilla 3450 m (AMNH 262993); Potosi, 3 km SE of Pocoata 3370 m (AMNH 256006).