



A Late Pleistocene Guloninae (Carnivora, Mustelidae) from South America (Argentina, Entre Ríos province), biogeographic implications



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ABSTRACT

The record of Guloninae presents mainly a Holarctic distribution, with only *Eira barbara* occurring in South America (SA). This lineage immigrated from Central America at least in the Pleistocene. The fossil record of Guloninae for SA is limited to a few known specimens of *Eira* from Late Pleistocene of Brazil. We report a new specimen of *E. barbara* (an upper carnassial) from Late Pleistocene of Entre Ríos, Argentina. We also discuss the taxonomic assignment of this new fossil and its paleoenvironmental relevance using Species Distribution Modeling (SDM). The new material comes from Ensenada Creek, Salto Ander Egg Formation, from the Late Pleistocene between 120 and 60 ky BP. The locality is farther south than its recent distribution, and SDM shows low suitability values for such area, which also indicates that the species is absent from this area in present time. The P4 is bigger and the protocone has a more anterior position relative to the paracone than that of recent specimens of *E. barbara*. This new fossil indicates that *E. barbara* had a wider distribution over the Late Pleistocene and, if our interpretation is correct, it has been present in SA at least since 120–60 ky BP. The presence of *E. barbara* in such a southern locality, together with other taxa recorded in this site and the associated geological and paleoenvironmental evidences, indicates warmer and more humid conditions, compared with the current conditions, which might have allowed a southern displacement of taxa more related to forested and tropical environments.

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1. Introduction

South American carnivorans (Mammalia: Carnivora) are quite recent due to the long isolation of the continent throughout the Tertiary (Patterson and Pascual, 1972; Reig, 1981; Marshall et al., 1984). Most carnivorans arrived after the Panamian Isthmus was completed, which allowed the Great American Biotic Interchange (GABI), around 3 Ma (Marshall et al., 1982; Webb, 1985; Pascual, 2006). However, today it is well known that some carnivorans arrived before the GABI, in particular Procyonidae belonging to *Cyonasua*, from the Huayquerian Stage/Age (late Miocene, around

7–8 Ma) and *Chapalmalania*, from the Chapalmalalan Stage/Age (Pliocene, around 3.3 Ma), both found in Argentina and northern South America (Colombia and Venezuela; Soibelzon and Prevosti, 2007; Prevosti and Soibelzon, 2012; Forasiepi et al., 2014 and references therein). Immigration of carnivorans in South America might have occurred in a “step-like” pattern, with procyonids arriving in late Miocene, Canidae and Ictonychinae (Mustelidae) at late Pliocene (Vorohuean Stage/Age, ca. 2.6–2.9 Ma), and Felidae, Ursidae, Lutrinae (Mustelidae), and Mephitidae in early-Middle Pleistocene (Ensenadan Stage/Age, around 1.8 Ma) or later (see Marshall et al., 1984; Cione and Tonni, 1995; Prevosti et al., 2006; Soibelzon and Prevosti, 2007; Prevosti and Soibelzon, 2012).

Three groups of Mustelidae fossils are present in South America during the Pleistocene:

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- 1 Ictonychinae Pocock, 1922, with three genera and several species of weasels. The oldest Ictonychinae belongs to *Galictis sorgentinii* Reig, 1957, from the late Pliocene (Vorohuean Stage/Age, around 2.8 Ma) in Chapadmalal area (Buenos Aires, Argentina). There are also records of *Stipanicia pettoruti* Reig, 1956 from the late Pliocene-early Pleistocene of southeast Buenos Aires province, and *Lyncodon bosei* Pascual, 1958 from the Ensenadan Stage/Age in the northeast of Buenos Aires province (Reig, 1957; Pascual, 1958; Berman, 1994). The three species are extinct members of the South American carnivoran fauna. The extant ones are only related species, such as *G. cuja* (Molina, 1782), *G. vittata* (Schreber, 1776) and *L. patagonicus* (de Blainville, 1842).
- 2 Lutrinae Bonaparte, 1838 with two species, *Lontra longicaudis* (Olfers, 1818), whose oldest record dates from the early Pleistocene (Ensenadan Stage/Age) in Buenos Aires province, Argentina (Rusconi, 1932; Berman, 1994) and *Pteronura brasiliensis* (Gmelin, 1788) from the Late Pleistocene in Entre Ríos province, Argentina, and the Late Pleistocene in Bahía, Brazil (Cartelle, 1999; Prevosti and Ferrero, 2008).
- 3 Guloninae Gray, 1825, represented by the tayra *Eira barbara* (Linnaeus, 1758), which has records in the Late Pleistocene in Bahía (Lund, 1843; Cartelle, 1999; Lessa et al., 1998; Castro et al., 2014), Minas Gerais (Lund, 1843; Cartelle, 1999), Ceará (Gomide, 1989, but see below) and western Amazon region (Rancy, 1991, 1999). Other fossil records of *Eira* from “Ensenadan” in Bolivia have been assigned to *Galera barbara* (= *Eira barbara*, Hoffstetter, 1963), and two others from North America have also been erroneously assigned to this taxa (see Presley, 2000; Ruiz-García et al., 2013). Thus, *E. barbara* is only known as a fossil from a few sparse localities within a wide geographic range. This species has been previously assigned to Galictinae Reig 1956, together with South American weasels such as *Galictis*, *Lyncodon* and *Stipanicia*. However, recent phylogenetic analyses support a clade formed by *Eira* plus other Holarctic mustelids: *Martes* Pinel, 1792, *Gulo* Pallas, 1780, and *Pekania* Gray, 1865, named Guloninae Gray, 1825; so *E. barbara* is the only South American member of this subfamily (Koepfli et al., 2008; Yu et al., 2011; Sato et al., 2012; Li et al., 2014).

Although five to seven subspecies of *Eira barbara* were traditionally recognized based on pelage coloration patterns (see Thomas, 1900; Cabrera, 1958), a recent analysis using mitochondrial DNA supports only two valid subspecies (Ruiz-García et al., 2013). Today, *E. barbara* is a common Neotropical mesopredator, found from southern Mexico to northern Argentina (Presley, 2000). It is a generalist feeder, which usually inhabits tropical and subtropical forests (Emmons and Freer, 1990; Presley, 2000) and, although it is also found in grasslands, it is usually assumed to be moving from one forest to another (Defler, 1980).

In this work, we report a new fossil specimen from Entre Ríos province, Argentina, assigned to *Eira* cf. *Eira barbara* and we also discuss its relevance for the Guloninae fossil record. We also analyze extant distribution with Species Distribution Modeling (SDM), with the aim to infer habitat suitability from the fossil locality in current times and its relevance to paleoenvironmental reconstructions.

2. Materials and methods

2.1. Measurements

LMPr, total length between the mesial border of the parastyle and the distal border of the protocone. **LP4Pr**, total length of upper fourth premolar from mesial border of the protocone to the distal edge of metastyle. **MW**, maximum width at the base of metastyle,

excluding protocone. **MWPr**, maximum width including protocone. **TLP4**, total length of upper fourth premolar from its mesial most border to the distal edge of metastyle (Fig. 1).

2.2. Institutions

AMNH, American Museum of Natural History, New York, USA. **CICYTP-PV**, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción de Diamante, Argentina. **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina.

2.3. Morphological and morphometric analysis

The fossil remain described herein is housed at the paleontological collections of the Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción de Diamante, Argentina (CICYTP-PV). The comparative samples included all the specimens available from AMNH and MACN mammal collections of *Eira barbara*. A total of 99 adult specimens assigned to *Eira barbara* with P4 were analyzed. P4 was linearly measured (see above) with digital caliper. The Coefficient of Variation (CV) was calculated for each measure. The dimensionless index is used for characterizing the range of individual variation in one trait (Yablokov, 1974). Dental morphology was analyzed using the pattern and disposition of cusps and crests, following Van Valen (1994) nomenclature.

Mosimann's variables were created from the linear measurements described above, by dividing each specimen measurements by the geometric mean of the measurements of all the specimens (Mosimann, 1970, a similar methodology was used in Meachen-Samuels and Van Valkenburgh, 2009; Morales and Giannini, 2010). This way, shape variables (independent of size) were created and used for Principal Component Analysis (PCA), performed on the covariance matrix, using InfoStat v.2010 software (Di Rienzo et al., 2010).

We followed the biostratigraphic/chronostratigraphic scheme of Cione and Tonni (2005), modified by Cione et al. (2015).

2.4. Species distribution modeling

We performed Species Distribution Modeling (SDM) to analyze the potential distribution and its relationship with fossil record locality for CICYTP-PV-M-2-406. Occurrence points were obtained from analyzed specimens of museum collections (AMNH, MACN) and published references. All the localities recorded were georeferenced using gazetteers and reference maps and plotted in QGIS 2.8.1-Wien (QGIS Development Team, 2015). The 139 localities obtained (without duplicates, see Supplementary Data Table S1) were analyzed with Moran's I to detect the existence of spatial autocorrelation, and confidence intervals (95%) were obtained with 1999 permutations in SAM v. 4.0 (Rangel et al., 2010). As spatial autocorrelation was present (maximum I = -0.408 between intervals), 75% ($n = 104$), 50% ($n = 69$) and 25% ($n = 39$) the recorded localities were randomly selected in QGIS (QGIS Development Team, 2015) and analyzed with Moran's I. Only the dataset of 25% of the localities did not show spatial autocorrelation (i.e., all values near I = 0.1 and inside confidence interval) and was thus used to perform SDM (see Supplementary Data Table S1).

SDMs were performed with MaxEnt v. 3.3.k (Phillips et al., 2006) and Worldclim (Hijmans et al., 2005) database at a spatial resolution of 1 km² as predictor/environmental variables. Two different datasets of environmental variables were tested in SDM: (1) using all layers (i.e., predictors) and (2) using only non-correlated layers (i.e., correlation analysis was performed between environmental layers and layers with $r > 0.7$ were eliminated). The areas not

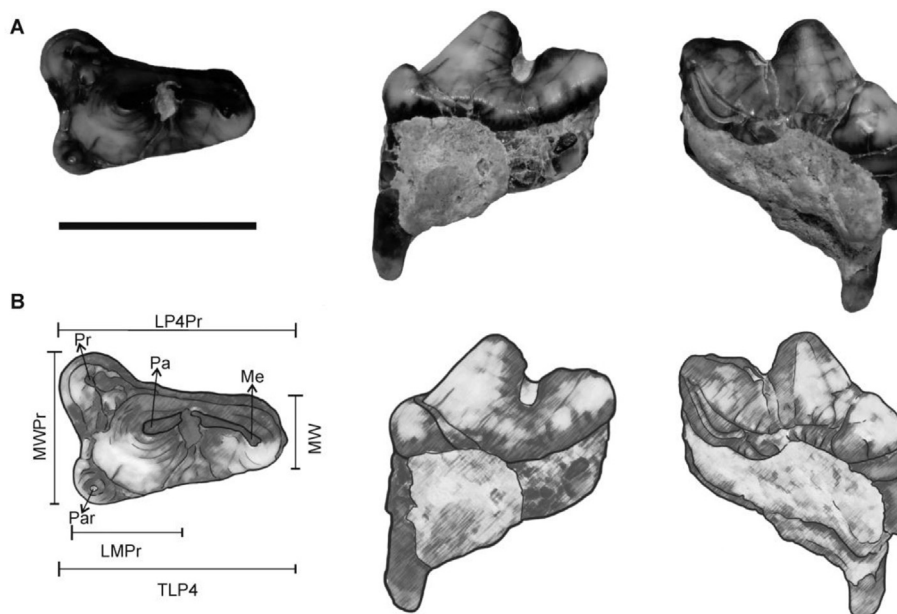


Fig. 1. (A) Right upper fourth premolar of *Eira* cf. *Eira barbara* CICYTTP-PV-M-2-406, in occlusal, lingual and labial views, respectively from left to right; (B) Linear measurements taken to the specimens (see abbreviations in Materials and Methods). Scale bar equals 10 mm. Pa: Paracone, Me: Metastyle, Pr: Protocone, Par: Parastyle.

inhabited by *E. barbara* were excluded from the total extent of environmental layers in order to prevent the model to compare between presence and background areas not accessible for the species, and then projected into a complete map of South and Central America.

2.4.1. Model fitting and validation

Models were performed using 25% of the localities recorded as test data, (and 75% as training data), random seed, 10 000 background points and auto features (but only linear and quadratic features were selected). To avoid overfitting, MaxEnt models were calibrated using different values, from 1 to 5, (see Merow et al., 2013; Radosavljevic and Anderson, 2014), to regularize parameter β (which controls the strength of the penalties for complex models). Ten SDMs were analyzed with Akaike Information Criterion (Akaike, 1973) corrected for sample size (AICc, see Burnham and Anderson, 2004) in ENMTools v. 1.4 (Warren et al., 2010): models 1 to 5, using different β values (1, 2, 3, 4, 5) and selected predictor variables (i.e., non-correlated), and models 6–10 using different β values (1, 2, 3, 4, 5) and all predictor variables. A similar methodology, using AICc for β selection, was used in Nori et al. (2011), Isaac et al. (2014) and Gallardo et al. (2015). The SDM with the lowest AICc was re-done using ten replicates and cumulative output, and the assigned suitability values were 100–76 (black, high prediction), 75–51 (dark gray, high-medium prediction), 50–26 (gray, medium prediction), 25–10 (light gray, low prediction) and 9–0 (white, very low-null prediction). The average of 10 replicates of this model is here presented. SDM was evaluated with a threshold-dependent test, using True Skill Statistic (Allouche et al., 2006) and binary maps were created (presence/absence) with 10th percentile threshold. Variable contribution to SDM was evaluated with MaxEnt's Jackknife test. Distribution of *E. barbara* was analyzed according to the ecoregions biogeographic scheme of Olson et al. (2001).

2.5. Paleoenvironmental relevance of other taxa recorded in the lower section of the Ensenada Creek site

Other records of relevant taxa present at Late Pleistocene levels

in the Ensenada Creek (Entre Ríos province, Argentina) are: the tropical turtle *Chelonoidis denticulata* (Linnaeus, 1766) (see Manzano et al., 2009), the giant river otter *Pteronura brasiliensis* (see Prevosti and Ferrero, 2008) and the tapir *Tapirus terrestris* (Linnaeus, 1758) (although it was recorded in Arroyo Perucho Verna, near Villa Elisa and not in Ensenada Creek, it is the same latitude; Tonni, 1992; Holanda and Ferrero, 2013). We included *T. terrestris* in this analysis because it was found in similar latitudes and at similar age in the same province, whereas *Tapirus mesopotamicus* Ferrero and Noriega, 2007, an extinct species that is the sister taxon of the living *T. terrestris* (Holanda and Ferrero, 2013), was recovered in the Ensenada Creek site. Thus, we think that this living taxon is a good model to understand the distribution of the extinct tapir. Data about present distribution of these species was obtained from Global Biodiversity Information Facility (GBIF, accessed from www.gbif.org). SDMs were created for each species following the methodology explained above (see Supplementary Data Table S2 for the complete citation of each dataset).

We then identified the overlapping area of high suitability values (>75%) from SDMs for the four species (*E. barbara*, *Ch. denticulata*, *P. brasiliensis*, *T. terrestris*) and enclosed it within a polygon in QGIS (QGIS Development Team, 2015). Then, we extracted climatic values from 1000 random points created within the polygon (annual mean temperature, temperature annual range, annual precipitation and precipitation seasonality). This allowed us to compare the climatic values from the overlapping area for the four species with current climate in Ensenada Creek. As the four species were present at the same locality at the same time, it might also give us insights to reconstruct paleoclimatological conditions in the Late Pleistocene in Entre Ríos province, Argentina.

3. Systematic paleontology

Order Carnivora Bowdich, 1821.
 Suborder Caniformia Kretzoi, 1938.
 Family Mustelidae Fischer, 1817.
 Subfamily Guloninae Gray, 1825.
 Genus *Eira* Smith, 1842
Eira cf. *Eira barbara* (Linnaeus, 1758)

Mustela barbara Linnaeus, 1758: 46.
Galera barbata (Linnaeus, 1758) Browne, 1789: 495.
Tayra barbara (Linnaeus, 1758) Oken, 1816: 377.
Gulo barbatus (Linnaeus, 1758) Desmarest, 1820: 174.
Galictis barbara (Linnaeus, 1758) Bell, 1826: 551; Lund, 1842: 198, 202–203; 1843: 78, 80; 1845: 82, 91; Ameghino, 1889: 321, 325; Winge, 1895: 37–38.
Galictis aff. *barbarae* Lund, 1842: 198; 1843: 78; 1845: 82; Gervais and Ameghino, 1880: 32–33 (lapsus pro *Galictis barbara* (Linnaeus, 1758)).
Eira barbara (Linnaeus, 1758) Smith, 1842: 201; Reig, 1957: 40, 46; Lessa et al., 1998: 162; Cartelle, 1999: 32; Rancy, 1999: 24; Soibelzon and Prevosti, 2007: 57–58; Prevosti and Soibelzon, 2012: 102, 115; Castro et al., 2014: 7–9.
Galera barbara (Linnaeus, 1758) Gray, 1843: 67; Burmeister, 1879: 157; Hoffstetter, 1963: 198.

3.1. Studied material

A nearly complete right upper fourth premolar (P4), CICYTTP-PV-M-2-406.

3.2. Age, stratigraphy and locality

The CICYTTP-PV-M-2-406 comes from Ensenada Creek, Entre Ríos province, Argentina (60°32'59"W, 32°04'10"S). Although the specimen was collected without having accurate information about its stratigraphic provenance, the fossiliferous horizons outcropping at the locality correspond to the Salto Ander Egg Formation (SAEF). In addition, taphonomic evidences indicate that the specimen came from the lower levels of the SAEF, which typically has a matrix of carbonate pebbles, thus reinforcing its purported provenance.

The Salto Ander Egg Formation is a geologic unit exposed at the southern Mesopotamia in Argentina, particularly at the southwest of Entre Ríos province. This formation is composed of complex fluvial deposits containing a heterogeneous collection of sub-environmental sequences with geochronological dates ranging from 120 to 60 ky BP (Brunetto et al., 2015).

The clast supported gravel facies containing sparse boulders indicate high flow during a humid climate. The large and middle-scale architectures of fluvial sedimentary bodies evidence the relationship between the sediment accommodation and the sea level oscillations. Three sub-sequences (SS1–SS3) identified in the succession suggest a transgressive trend over the MIS5e, a high-stand stage over MIS5c, and a minor transgressive cycle over MIS3 (Brunetto et al., 2015).

The lower sections of the depositional sequences (SS1) contain a faunistic association of the typical Late Pleistocene elements for Argentina, together with several taxa nowadays distributed within tropical regions of South America (*Pteronura brasiliensis* and *Chelonoidis denticulata*) and other extinct taxa whose tropical affinities are inferred (*Tapirus mesopotamicus* and *Holmesina paulacoutoi*, see Ferrero and Noriega, 2007; DeSantis and MacFadden, 2007; Prevosti and Ferrero, 2008; Manzano et al., 2009). Inferences based on sedimentological data indicate that these basal levels of the SAEF were deposited under wet and warm climatic conditions within tropical or subtropical paleoenvironments. Such conditions, characteristic of the maximum of the last interglacial stage (MIS5e), show a signal stronger than that of the current interglacial stage (Brunetto et al., 2015).

3.3. Description and comparison

The P4 (CICYTTP-PV-M-2-406) presents grey color with black

carbonates attached. It seems to belong to an adult specimen (i.e., a completed erupted teeth), with slight wear. The paracone constitutes the highest cusp of the teeth and is wider on the base than it is on the tip. A small parastyle is visible on the mesial and labial edge. The v-shaped centrocrista communicates the paracone with a well-marked but short metastyle, which is lower than that of the paracone. The protocone is well developed, has a rounded shape and is directed on an almost 90° angle to the paracone–metastyle plane. It is surrounded by a cingulum connected with a mesial cingulum that reaches the parastyle, and with a straight lingual cingulum that reaches the linguodistal end of the metastyle.

3.4. Morphometric analysis

The analysis of dental measurements shows that, with the exception of LMP_r, CICYTTP-PV-M-2-406 is larger than recent specimens of *E. barbara* (Table 1). The inclusion of CICYTTP-PV-M-2-406 in the sample of recent specimens increases the coefficient of variation (except for LMP_r) up to 9.96% in MW (Table 1).

Principal Component Analysis using Mosimann's variables shows segregation in morphospace between the fossil and recent specimens, particularly in PC3 (Fig. 2). The PC3 explains 11.6% of the variation and was mainly related to positive values of LP4_r and negative values of LMP_r. Segregation between CICYTTP-PV-M-2-406 and recent specimens was seen on PC1 vs PC3, PC1 vs PC4 and PC2 vs PC3 (Supplementary Data Figure S1, Table S3, Table S4).

3.5. Species distribution modeling

Eira barbara extends from northern Mexico to southern Brazil and northern Argentina, across Central and South America. The northernmost recorded locality was in central Mexico (21°N, Sierra Gorda Biosphere Reserve, record 106 in Supplementary Data Table S1) and the southernmost in southern Brazil (29°S, Parque nacional dos Aparados da Serra, record 95 in Supplementary Data Table S1). Mean annual temperature for the 139 localities recorded was 23.5° (6.4–28.2 °C), with an annual mean range of 14.5 °C, and a mean annual precipitation of 1917 mm (40–4377 mm).

The model with the lowest AICc includes a β of 4 and all predictors (AICc = 1313.28). Two other models show a similar support (depicted by a Δ AIC lower than 2, see Burnham and Anderson, 2004), including β of 4 and 5, respectively, and the predictor variables selected. However, the distribution extents for these models are highly similar to that of the former, thus they are not presented in this work. SDM shows high accuracy, with a 0.794 TSS value.

Although the distribution of *E. barbara* extends over 14 million km² (see Supplementary Data Figure S2), SDM shows the highest suitability values on forested habitats, such as the Central American, Andean and Amazon basin forests (sensu lato). Particularly high values (76–100%) were found on Central American Atlantic Moist Forests (Nicaragua, Honduras), Isthmian Atlantic Moist Forests (Costa Rica, Panama) Magdalena Valley Montane Forests

Table 1

Linear measurements (in mm) of CICYTTP-PV-M-2-406 and recent specimens of *Eira barbara*. Mean = Mean of 99 recent specimens. SD= Standard Deviation of recent specimens. CV= Coefficient of variation of recent specimens. CV* = Coefficient of variation of recent specimens plus CICYTTP-PV-M-2-406.

Specimens	TLP4	LMP _r	LP4 _r	MWP _r	MW
CICYTTP-PV-M-2-406	11.11	6.45	13.19	8.01	4.34
Mean	9.27	6.57	10.14	6.97	3.79
SD	0.55	0.53	0.68	0.47	0.38
CV	5.91	8.07	6.74	6.76	9.92
CV*	6.19	8.03	7.32	6.88	9.96

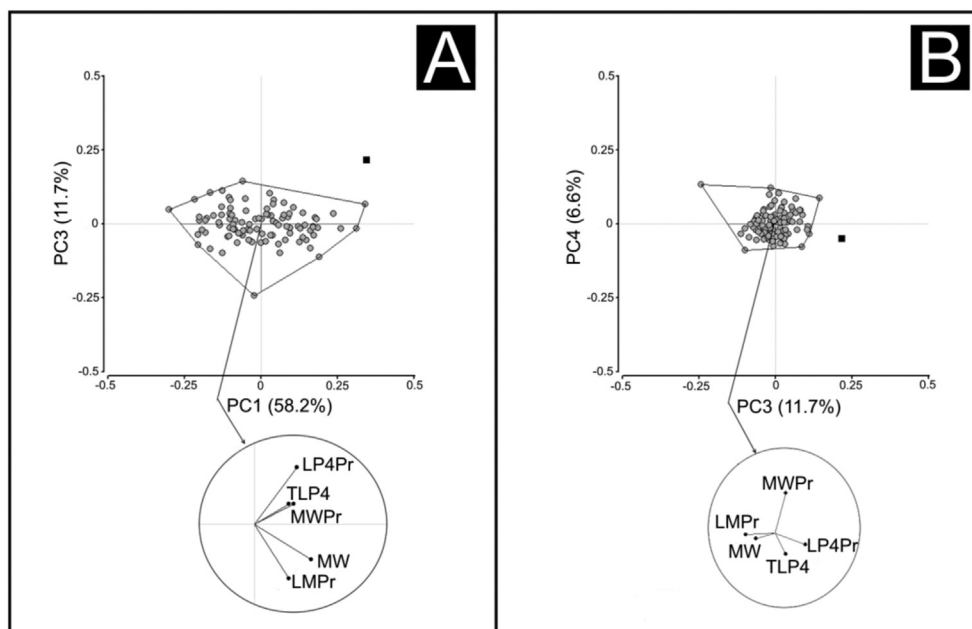


Fig. 2. (A) Scatterplot of PC1 vs. PC3; (B) scatterplot of PC3 vs. PC4 from PCA between 99 adults specimens of *E. barbara* (gray dots) and CICYTTP-PV-M-2-406 (black square) using Mosimann's variables.

(Colombia), Guianan Moist Forests (Venezuela, Guyana, Suriname), Napo Moist Forests (Ecuador, Peru), Purus Varzea and Japurá-Solimoes–Negro Moist Forests (Brazil), Bahia Costal Forests (Brazil) sensu Olson et al. (2001, Fig. 3). Low suitability values (0–25%) were found in the arid diagonal in Brazil, particularly in Cerrado (sensu Olson et al., 2001). Both northern (Veracruz Moist Forests in Mexico) and southern (Southern Andean Yungas in Argentina) distribution limits showed low suitability values (0–10%) (Fig. 3). The record site for CICYTTP-PV-M-2-406 in Entre Ríos province in Argentina also shows the lowest values in SDM (Fig. 3).

The most important variable to explain *E. barbara* SDM was temperature annual range (Bio7) with a 29.8% contribution, followed by temperature seasonality (Bio4) with a 24.4%, precipitation in the driest month (Bio14, 17.8%), precipitation of the driest quarter (Bio17, 16.2%) and precipitation seasonality (Bio15, 4.8%). However, as Bio7–Bio4, and also Bio14–Bio17 are correlated variables ($r > 0.7$), *E. barbara* distribution seems to be mainly related to temperature seasonality, precipitation of the driest periods and precipitation seasonality.

3.6. Paleoenvironmental relevance of other taxa recorded in the lower section of the Ensenada Creek site

The overlapping area of the highest suitability values for the SDMs for the four species was in northern South America (4°N to 6°S, and 77°W to 64°W, including small areas of Brazil, Colombia, Ecuador, Peru and Venezuela). Mean annual temperature was 26 °C (23–27.8 °C), with an 11.2 °C temperature annual range; 2940 mm (2267–3720 mm) annual precipitation, and with a 26 CV precipitation seasonality. Nowadays, climate in Ensenada Creek shows an 18 °C mean annual temperature, a 25.6 °C temperature annual range of; and 992 mm annual precipitation with a 45 CV. This relates the presence of the four species (in the Late Pleistocene in Entre Ríos) with warmer and more humid climate than the current in Ensenada Creek.

4. Discussion

The CICYTTP-PV-M-2-406 differs from other South American

mustelids in several morphological characters. The absence of lingual shelf and the presence of a round protocone separate it from *Lutrinae* Bonaparte (1838) and *Mustela* Linnaeus, 1758. Both species of *Lyncodon* (*L. patagonicus* and *L. bosei*), *Stipanicia pettoruti* and recent species of *Galictis* (*G. vittata* and *G. cuja*) also display a more developed lingual shelf, which includes the protocone and gives the P4 a much less round look (i.e., more triangular, see Reig, 1957; Pascual, 1958; Berman, 1994; Prevosti and Pardiñas, 2001). Besides, the position of the protocone in CICYTTP-PV-M-2-406 seems to be much more displaced to lingual than it is in *Galictis* and *Lyncodon*. The CICYTTP-PV-M-2-406 displays a morphology much more similar to that of the other Guloninae (see Supplementary Data Figure S3). However, P4s of *Gulo gulo* (Linnaeus, 1758) and *Pekania pennanti* (Erxleben, 1777) are larger and display a smaller protocone and a more extended centrocrist with a more developed metastyle (e.g., more adapted to feed on vertebrate flesh). The species of *Martes* Pinel, 1792 display a morphology similar to CICYTTP-PV-M-2-406, particularly for the position of the protocone regarding the paracone-metastyle plane (i.e., an almost 90° angle), but with a more developed metastyle. *Martes martes* (Linnaeus, 1758) and *M. americana* (Turton, 1806) seem to have smaller protocones, whereas *M. flavigula* (Boddaert, 1785) and *M. foina* (Erxleben, 1777) display a constriction at the beginning of the protocone shelf. Finally, *M. melampus* (Wagner, 1840) and *M. zibellina* (Linnaeus, 1758) seem to present sharper paracones, compared to CICYTTP-PV-M-2-406, which displays a more robust and blunt paracone (see Supplementary Data Figure S3). It must also be stated that no fossil or recent record of any of these species have been found in South America.

The combination of size and the morphological features mentioned above (e.g., large and rounded protocone, short metastyle, absence of lingual shelf) for CICYTTP-PV-M-2-406 is shared with *Eira barbara*, but there are some morphological differences between them. The presence of the parastyle seems to be a variable character, given that although present in most extant specimens, it is also absent in others (e.g., AMNH 15471, AMNH 36507, AMNH 38095, MACN 32.1, MACN 32.110). Other differences observed for the protocone are that it is more anteriorly placed regarding the parastyle, and the larger size of the tooth in general. Size decrease

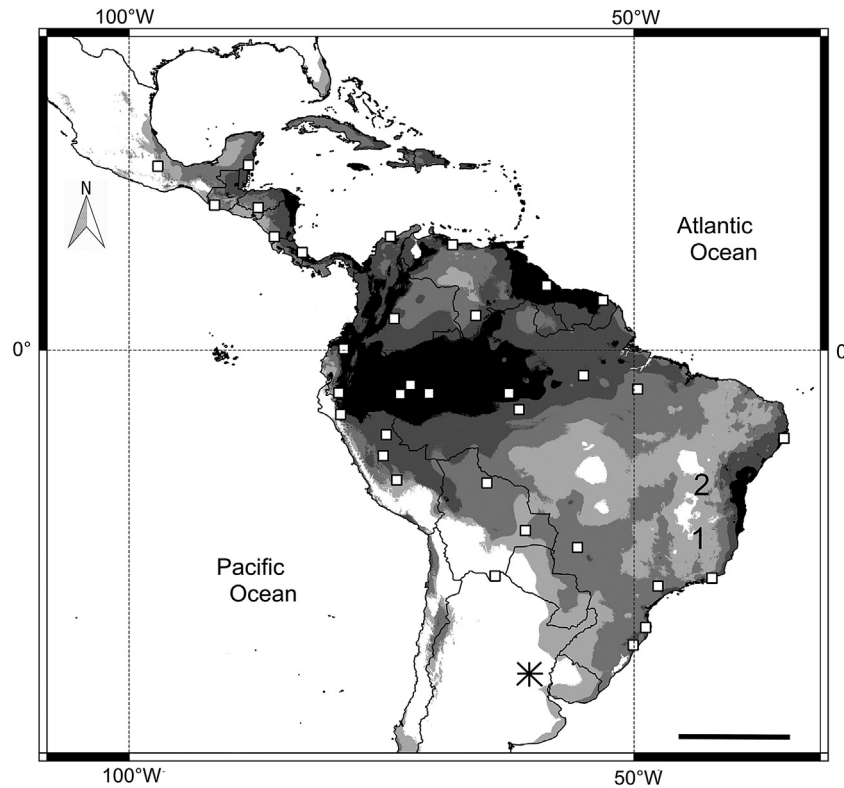


Fig. 3. Fossil record locality for CICYTTP-PV-M-2-406 (black asterisk) and SDM for *Eira barbara*, using 25% of recorded localities (white squares). Climate suitability values are 100–76 (black, high prediction), 75–51 (dark gray, high-medium prediction), 50–26 (gray, medium prediction), 25–10 (light gray, low prediction) and 9–0 (white, very low-null prediction). 1. Late Pleistocene records for Lagoa Santa, Minas Gerais (Lund, 1843); 2: Late Pleistocene records for Bahía state (Lessa et al., 1998; Castro et al., 2014). Scale (black bar) equals 1000 km.

in lineages (i.e., dwarfism, a significant decrease in mean body size of a lineage occurring in a short period of time, Marshall and Corruccini, 1978) has been widely documented, particularly for the Late Pleistocene lineages, with several hypothetical explanations which could explain size differences, such as competition, predator-prey interactions, changes in resource availability, and temperature changes among others (Kurtén, 1958, 1965; Marshall and Corruccini, 1978; Davis, 1981). The Coefficient of Variation including CICYTTP-PV-M-2-406 is very close to or lies within the mean CV values for P4 of 31 species of Mustelidae (6.72, Meiri et al., 2005), and for P4s of other South American Musteloidea [5–13 for *Galictis cuja*, *G. vittata*, *Lontra longicaudis*, *Lyncodon patagonicus*, *Conepatus chinga* (Molina, 1782), M. Schiaffini, pers. obs.], something that could suggest that the difference between the fossil and living specimens are part of the intraspecific variation of *E. barbara*. Another possible explanation for differences between CICYTTP-PV-M-2-406 and recent specimens of *E. barbara*, if dwarfism were not the case in this lineage, is that CICYTTP-PV-M-2-406 is actually a different species of *Eira*. However, as only a P4 was available and the differences are not large, we prefer to determine this fossil as *Eira* cf. *E. barbara*, at least until having more evidence.

The Guloninae are assumed to be separated from other Mustelidae at 10–14 Ma in middle or late Miocene (Koepfli et al., 2008; Sato et al., 2012). Fossils are known from Asia, Europe, Africa, North and South America, with the oldest well dated fossil belonging to *Pekania occulta* Samuels and Cavin, 2013 from the New World in Oregon (USA) in 7.05 Ma (Samuels and Cavin, 2013). However, as *Pekania* might have evolved somewhere in Eurasia, *P. occulta* might represent an early immigrant (Samuels and Cavin, 2013). Regarding the Old World members, the genus *Plesiogulo* Zdansky, 1924 might have originated in Asia and migrated into

North America around 6.5–7 Ma (Harrison, 1981) and into Africa at the end of Miocene around 5.5 Ma (Haile-Selassie et al., 2005). Several specimens of the genus have been recorded from middle Miocene to upper Pliocene of Europe (see Viret, 1939; Schmidt-Kittler, 1976; Montoya et al., 2011). Although *Plesiogulo* has often been referred to as the ancestor of *Gulo* (Kurtén and Anderson, 1980; Pasitschniak-Arts and Larivière, 1995), several authors stated against this hypothesis or mentioned a closer relationship with *Mellivora* Storr, 1780, within the subfamily Mellivorinae (see Hendey, 1978; Sotnikova, 1995; Haile-Selassie et al., 2005). The first records of *Gulo* are from the Pliocene (3.3–3.8 Ma) in Russia (Sato et al., 2003 and references therein); whereas they are recorded since Middle Pleistocene in USA in the New World (Kurtén and Anderson, 1980; Pasitschniak-Arts and Larivière, 1995; Tomasik and Cook, 2005). The genus *Martes* extends from late Miocene to recent times. It possibly had an Eurasian origin (Koepfli et al., 2008), and spread into the New World through the Bering land bridge in the late Miocene (Powell, 1981; Clark et al., 1987; Stone and Cook, 2002). To our knowledge, the oldest *Martes* species is *Martes ginsburgi* Montoya et al., 2011, which has been recorded in the late Miocene (6 Ma) in Spain (Montoya et al., 2011), as the early Miocene *Martes laevidens* Dehm, 1950 was disregarded as a congeneric of *Martes* (see Sato et al., 2003).

A recent study shows that diversification process in *Eira barbara* might have occurred 7–8.2 Ma ago (Ruiz-García et al., 2013). This period is around 4 Ma, before the Panamian Isthmus was completed, although recent studies stated that the land bridge could be present by middle Miocene (13–15 Ma, Montes et al., 2015; Bacon et al., 2016). Thus, *E. barbara* might have entered South America before the GABI by the land bridge and then differentiated there, or might have differentiated in Central

America and immigrated to South America later, as suggested by its young and limited fossil record. Unfortunately, South American Guloninae are not common in the fossil record, and they are only known as locality records coming from Brazil (Rancy, 1991, 1999; Cartelle, 1999), without good chronological constraints, and they are referred to be Late Pleistocene s.l. (e.g., Auler et al., 2006; Prevosti and Soibelzon, 2012). Even more, some of the materials presented in Lund (1843) analyzed in Cartelle (1999) do not seem to be from Pleistocene in Age, but to be actually recent or holocene specimens (L. Kasper, pers. comm.) as Lessa et al. (1998) previously mentioned. The material analyzed in Rancy (1991, 1999) is a broken mandible with only a p3 that has some morphological differences with *E. barbara* (i.e., lower and different ventral border of horizontal ramus, different extension of masseteric fossa, different position and development of p3), that suggest to belong to other genera. Another remains of *E. barbara* mentioned in the literature is an unpublished master thesis about the Late Pleistocene mammals of Itapipoca (Céara, Brazil; Gomide, 1989; Lessa et al., 1998) and a partial skull from Bahia (Castro et al., 2014). However, the reference for Eira in Ceará state (Gomide, 1989) is possibly wrong, and should not be taken into account (G. Lessa, pers. comm.). If our interpretation about the geological provenance of the CICYTTP-PV-M-2-406 is correct, *Eira* would be present in South American at least since 120–60 ky BP during the last interglacial. Although this is not enough to indicate the place of origin for the genus, this record indicates that ca. 120–60 ky BP *Eira* geographic distribution was more expanded in the south than it is in present times, in agreement with recent ecological requirements and the paleoclimatic conditions inferred for the region (Manzano et al., 2009; Brunetto et al., 2015; see below).

Species Distribution Modeling indicates that *Eira* has a marked preference for forested environments, with open and arid environments displaying low suitability values. As mentioned above, CICYTTP-PV-M-2-406 was found farther south than extant distribution of *E. barbara*, extending 1000 km southwest from the southernmost record (Parque nacional dos Aparados da Serra, record 77 in Supplementary Data Table S1) in Brazil, and 1000 km south of the closest Argentine record (Yuto, Jujuy, record 52 in Supplementary Data Table S1). Thus, a strong climatic change is needed to explain its past distribution if we accept our systematic assignment and the conservatism of its niche. Variable contribution analysis shows that temperature and precipitation seasonality were important variables to explain *E. barbara* distribution. It is important to notice that forested tropical environments usually display a temperature and rainfall seasonality lower than that of arid and/or open environments (Noy-Meir, 1973; Deblauwe et al., 2008). This is in agreement with paleoenvironmental reconstructions for Ensenada Creek, which suggest the existence of warmer and more humid conditions over the last Interglacial period, with subtropical savannahs alternating with humid forest (see Manzano et al., 2009; Brunetto et al., 2015), at least during some brief pulses (see Góis et al., 2015). Even more, the expansion of gallery forests related to wetter conditions (de Oliveira et al., 1999) along main water courses (e.g., Paraná and Uruguay rivers) might have acted as a corridor for *E. barbara* dispersal. The climatic conditions suitable for the tayra are also corroborated by the presence of other tropical (or sub-tropical) recorded taxa, as the giant river otter *Pteronura brasiliensis* (although antropic pressure cannot be discarded as a retraction cause of its distribution, see Prevosti and Ferrero, 2008), a tapir *Tapirus mesopotamicus* (Ferrero and Noriega, 2007) and a tropical tortoise *Chelonoidis denticulata* (see Manzano et al., 2009) among others. In this regard, SDMs show that the presence of the four species in the same area was related with tropical climates (high temperatures and high precipitations with low seasonality). The combination of these taxa and the SDM clearly supports

previous interpretations, and suggests that the climate of the region was warmer and wetter ca. 60–120 ka BP, in agreement with a global situation that corresponds to the Last Interglacial Stage (130–85 Ka BP; see Pedoja et al., 2011 and references therein). However, the current climate in Ensenada Creek region displays lower temperatures with higher seasonality, compared to the mean values recorded for the current distribution of *E. barbara* and for the overlapping area for the four species, which indicates more arid conditions which would probably explain the retraction in distribution of *E. barbara* since Late Pleistocene.

5. Conclusions

Most Guloninae fossils are known from the late Miocene in Eurasia, Africa and North America. South American Guloninae, instead, have been recorded only since the Late Pleistocene s.l. in the northern part of the continent. We present new fossil material assigned to *Eira* cf. *E. barbara* from the beginning of the Late Pleistocene, from a site that is farther than 1000 km south to its recent location, indicating that at this time the tayra was well extended across South America. Morphological patterns show that the new material can be clearly assigned to Guloninae, with marked differences from other South American Mustelidae. Although there exist some morphometric differences between the new fossil specimen (which is larger) and recent specimens of *E. barbara*, we decided to assign it to this species at least until new material can be found.

We identified the main patterns of distribution of *E. barbara* which are related to forested environments with high precipitations, medium-high temperatures and low seasonality. This way, open/arid environments are recognized as low suitability habitats. The presence of *E. barbara*, together with other taxa of recent tropical distribution from the early Late Pleistocene in Ensenada Creek, allows inferring warmer and much more humid climatic conditions in the last interglacial stage than Recent.

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Appendix A. Supplementary data

Supplementary data related to this chapter can be found at <http://dx.doi.org/10.1016/j.jsames.2017.06.006>.

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