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Occurrence of *Dicolpomys* (Echimyidae) in the late Holocene of Argentina: The most recently extinct South American caviomorph genus

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ABSTRACT

Echimyidae is an ancient, widely diversified hystricomorph clade whose evolutionary history is linked to the Neotropical forested areas. Its fossil record, mostly from southern South America, shows temporal stages concurrent with Cenozoic climatic trends. Fossils from the late Oligocene to middle Miocene are related to living arboreal species, whereas those known since the late Miocene are restricted to lineages currently inhabiting the Chacoan diagonal of open vegetation in eastern South America. Since the late Quaternary, echimyid faunas were already composed of currently living genera, with the only exception of *Dicolpomys*. Here we report the discovery of a mandibular fragment of *Dicolpomys* in the late Holocene of Argentina. In accordance with phylogenetic affinities, geographic distribution, and fossorial adaptations, the new record, like those of the late Miocene–Pleistocene echimyids of Argentina, can be interpreted as a southward expansion of open-adapted Brazilian lineages through the Chacoan corridor. This supports a previously proposed pattern of changes of the southern boundary of these Chacoan faunas linked to Cenozoic paleoclimatic fluctuations. The occurrence of *Dicolpomys* in the late Holocene represents the most recent record of an extinct South American caviomorph genus. Since the phylogenetic pattern of echimyids among Octodontoidea supports the hypothesis of the survival of lineages at lower latitudes after their extinction at higher latitudes, the absence of *Dicolpomys* in Brazilian sites contemporaneous with, or younger than the new Argentinian site, is here interpreted as a case of taphonomic or sampling bias.

1. Introduction

Echimyidae is a very diversified clade of Neotropical hystricomorph rodents ('caviomorphs') currently distributed mainly in northern South America, occupying Andean, Amazonian, and coastal tropical forests and occasionally more open, xeric habitats of the Cerrado and Caatinga (Emmons and Feer, 1997; Eisenberg and Redford, 1999; Fabre et al., 2013, 2016; Emmons et al., 2015; Upham and Patterson, 2015; Álvarez et al., 2017). As an exception, *Myocastor* is the only extant representative that inhabits the steppes of southern South America, among other habitats (Patton, 2015).

Tertiary fossils of this family are known mainly from Argentina (late Oligocene–Pliocene), and are less frequently recorded in Chile (early–middle Miocene), Brazil (late Miocene), and Peru (late Miocene) (Sant'Anna-Filho, 1994; Campbell et al., 2006; Flynn et al., 2008;

Olivares et al., 2017); the more modern, late Pleistocene–Holocene paleontological and archaeological records come essentially from Brazil (e.g., Winge, 1887; Roth et al., 2008; Hadler et al., 2008, 2016; Ferreira et al., 2012, 2016). Whereas the Tertiary–early Quaternary fossils belong to extinct genera, with the single exception of *Myocastor* (Candela and Noriega, 2004), the late Quaternary echimyid faunas already consisted of genera that exist at present (Ferreira et al., 2016, table 1). †*Dicolpomys* is the only extinct genus recorded among these modern, late Pleistocene–Holocene echimyids. This is a monotypic genus, its single species, †*D. fossor*, being a small echimyid with craniodental specializations for burrowing (Winge, 1887; Hadler et al., 2008). It was originally described through five mandibles collected by Lund from the Quaternary caves of Lagoa Santa, in Minas Gerais, southeastern Brazil (Winge, 1887); more recently, abundant samples have been recovered from late Pleistocene–Holocene archaeological sites in Rio Grande do

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Sul, southern Brazil (Roth et al., 2008; Hadler et al., 2008, 2016). Here we report the discovery of a mandibular fragment of †*Dicolpomys fossor* in the late Holocene of Argentina, which represents the most recent record of an extinct South American caviomorph genus. We discuss the contribution of this finding to the understanding of the evolutionary patterns of southern fossil echimyids and their climatic context. In addition, we provide an interpretation of this record in the context of the hypothesis of survival of lineages in lower latitudes.

2. Material and methods

Revised extant and fossil echimyids are housed in the paleontological and mammalogical collections of MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; MAMA, Museo Arqueológico Manuel Almeida, Gualeguaychú, Argentina; MARSUL, Museu Arqueológico do Rio Grande do Sul, Taquara, Brasil; MN-UFRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil; UFRGS, Setor de Arqueologia da Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil; UnB, Universidade de Brasília, Brasil; UNISC, Centro de Ensino e Pesquisas Arqueológicas da Universidade de Santa Cruz do Sul, Santa Cruz do Sul, Brasil. Winge’s type series was revised through photographs provided by Z.M.K., Zoologisk Museum, Københavns Universitet, Danmark.

The new specimen, MAMA-SPL-S1-5-1, comes from the Sambaquí de Puerto Landa archaeological site, 500 m from the western margin of

Uruguay river (Entre Ríos Province, 33° 19′ 25″ S, 58° 27′ 13″ W; Fig. 1A). The site is a mound lying in a NE–SW line, at 3.0 m above the flatland and with a maximum diameter of 80 m and a minimum of 38 m (Greslebin, 1931; Krapovickas, 1957; Castro and Del Papa, 2015; Castro, 2017). An exploratory test pit was excavated in the NE extreme (grid square 1). Excavation was set up using a 1 × 1 m grid system, and the removal of sediment followed 5 cm thick artificial layers to control the vertical resolution of the remains, through a depth of 70 cm. The sediment was screened through a 3 mm mesh. The mandible of †*Dicolpomys* was recovered from level 5, at a depth of 20–25 cm.

Radiocarbon dates were obtained in the Laboratorio de Tritio y Radiocarbono, Centro de Investigaciones Geológicas CONICET- UNLP, La Plata, Argentina. According to ¹⁴C dating of the freshwater mussel *Diplodon* from the †*Dicolpomys*-bearing level, the archaeological site corresponds to the late Holocene, 1100 ± 60 radiocarbon yr. BP (LP 3290), which, when calibrated as Southern Hemisphere calendar years (Hogg et al., 2013) with a 1σ range, matches the 1056–997 yr BP (894–953 CE) lapse. A previous radiocarbon dating of human remains yielded an age of 630 ± 50 yr BP (LP 2828; Castro and Del Papa, 2015). However, it is not possible to establish a univocal relationship between this date and the age of the site, because the human skeleton was collected from a burial site within the sector but without precise provenance data. The assemblage of archaeological materials collected at grid squared 1 includes lithic and ceramic artifacts, animal and human skeletal remains, bone tools, coals, mineral pigments and baked

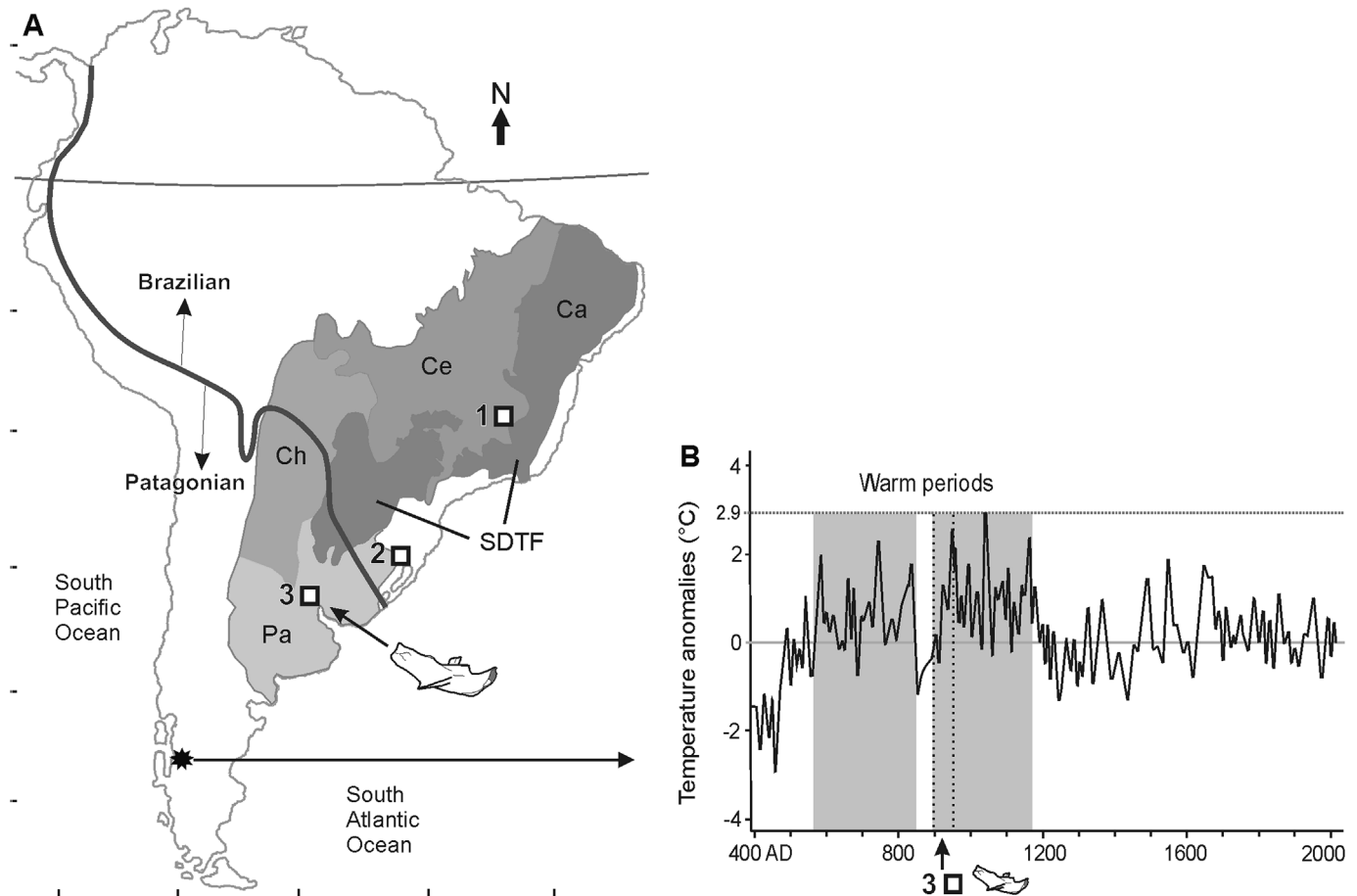


Fig. 1. A, †*Dicolpomys*-bearing localities. 1, Lagoa Santa caves, Minas Gerais, Brazil; 2, Sangão, Garivaldino, Pilger and Deobaldino Marques sites, Rio Grande do Sul, Brazil; 3, Sambaquí de Puerto Landa, Entre Ríos, Argentina. Gray shaded areas indicate the biogeographic Provinces of Chacoan Dominion. Abbreviations: Ca, Caatinga; Ce, Cerrado; Ch, Chaco; Pa, Pampa; SDF, Seasonally Dry Tropical Forests (after Pennington et al., 2004; Morrone, 2014). Solid gray line denotes the boundary between Brazilian and Patagonian Subregions (sensu Hershkovitz, 1958). B, Reconstructed annual temperature anomalies for Laguna Escondida, Región Aysén, Chile (asterisk in A), after Elbert et al. (2013). The reconstruction shows warm periods between ca. 550 CE and 1150 (gray shaded areas). The time calibrated record of †*Dicolpomys fossor* from Argentina is between dotted lines.

clay lumps. Remains of the following mammal species were recovered from the same level: *Blastocerus dichotomus*, *Ozotoceros bezoarticus* (Cervidae), *Hydrochoerus hydrochaeris*, *Cavia aperea* (Caviidae), *Myocastor coypus* (Echimyidae), *Euphractus sexcinctus* (Dasypodidae). Some elements of the archaeofaunal assemblage show clear evidences of man-made handling, such as cut marks, negative impact marks and thermal alteration (Castro, 2017). In addition, small rodents (Sigmodontinae) show evidences of predation by barn owls. Although it was not possible to determine how the single mandible of †*Dicolpomys* reached the site, this assemblage lacks allochthonous taxa resulting from transport but includes species currently extinct in the deposit area (*O. bezoarticus*; see Politis et al., 2011). Thus, we consider that *Dicolpomys* occurred naturally in the area.

3. Systematic paleontology

Order Rodentia Bowdich, 1821.

Suborder Hystricomorpha Brandt, 1855.

Superfamily Octodontoidea Waterhouse, 1839.

Family Echimyidae Gray, 1825.

Subfamily Euryzygomatomyinae Emmons, 2005.

†*Dicolpomys* Winge, 1887.

Type Species. – †*Dicolpomys fossor* Winge, 1887.

Included Species. – Only the type species.

†*Dicolpomys fossor* Winge, 1887.

Figs. 2 and 4.

Syntypes. – Five mandibles labelled Z.M.K. 1/1845:13344 (Lund's numbers 1–5; Fig. 2B–F; Winge, 1887:pl. VIII, fig. 10).

Material. – The syntypes and 220 specimens from the Holocene of Brazil (see Roth et al., 2008; Hadler et al., 2008, 2016); the new specimen, MAMA-SPL-S1-5-1, a right hemimandible with m1, part of the masseteric crest, and base of the condyle and coronoid process, from the late Holocene of Argentina (Fig. 2A).

Stratigraphic and Geographic range. – The type series comes from Lapa da Escrivania Nr. 5, Lagoa Santa, Minas Gerais, Brazil (Late Pleistocene–Holocene). Samples from the Holocene of Rio Grande do Sul, Brazil, come from the sites Garivaldino (from < 7250 to > 8290 yr BP), Sangão (from < 3730 to > 7390 yr BP), Pilger (from < 3000 to > 8010 yr BP), and Deobaldino Marques (Holocene). MAMA-SPL-S1-5-1 come from the late Holocene of Sambaquí de Puerto Landa archaeological site, Entre Ríos, eastern Argentina (1056–997 yr BP; 894–953 CE).

Remarks. – Description of †*Dicolpomys fossor* can be found in Winge (1887) and Hadler et al. (2008). Here we provide complementary comparative data on its mandibular and dental morphology (Figs. 2–4).

The mandible of †*Dicolpomys* (Fig. 2) differs from that of the euryzygomatomyines *Clyomys laticeps*, †*Clyomys riograndensis*, †*Euryzygomatomys mordax*, *Euryzygomatomys spinosus*, and *Carterodon sulcidens* by having the chin process (i.e. the ventral tip of the symphysis in the sagittal plane) anterior with respect to the dp4 location (cp, Figs. 2 and 3). The notch for the tendon of the infraorbital part of medial masseter muscle (nm; preserved in the new material) is longer than that of *C. laticeps* and *E. spinosus*. The condyle is lower than in *C. laticeps* and †*C. riograndensis*; it is larger and more posteriorly extending than in *C. laticeps*, *E. spinosus*, and *C. sulcidens*.

The lower incisor of †*Dicolpomys* is more deeply inserted than that of extant euryzygomatomyines, as in †*C. riograndensis* and †*E. mordax*. It is less recurved (i.e. with higher radius of curvature) and consequently more procumbent than that of the extant and extinct taxa above-mentioned. Its base is oriented towards the condyle and the mandibular foramen (mf, Figs. 2 and 3) is ventral to it; in the other above-mentioned taxa, the base of the incisor (bi) is oriented toward, or located within the sigmoid notch (sn), and the foramen is posterior to it.

The new material from Sambaquí de Puerto Landa, in Argentina, can be confidently assigned to †*Dicolpomys fossor* based on: its figure-eight shaped, anteroposteriorly compressed m1; long and procumbent

diastema; chin process anterior to the dp4 level; lower incisor moderately recurved, and with its base and accompanying mandibular foramen reaching the base of the condylar process (condyle was not preserved); mandibular foramen ventral (not posterior) to base of the incisor. The ontogenetic state of the m1 of MAMA-SPL-S1-5-1 is very similar to that of the syntype Z.M.K. 1/1845:13344 (Lund's number 1), and corresponds to a subadult or adult, non-senile individual (Fig. 4F and G).

The simplified molars of †*Dicolpomys fossor*, superficially similar to those of Octodontidae, led Winge (1887) to relate this species to extant members of that family. Unlike octodontids, however, the mesoflexid closes earlier than the metaflexid in †*Dicolpomys*, as in the equally simplified †*Reigechimys* and the remaining Echimyidae (Verzi et al., 1994).

The material assigned to †*Dicolpomys* by Ameghino (1907:64, figs. 2 and 3) from the Caves of Iporanga, Sao Pablo, Brazil, does not belong to this genus and could correspond to the living Echimyidae *Trinomys*.

3.1. Paleoclimatic context

Radiocarbon dating indicates that the bearing levels of †*Dicolpomys* at the Sambaquí de Puerto Landa site correspond to the Medieval Warm Period (MWP). This global climate event (also known as Medieval Climate Anomaly) was associated to warmer temperatures during ca 800–1300 CE (Ljungqvist, 2010; Elbert et al., 2013; Rosenthal et al., 2013; Danladi and Akçer-Ön, 2017; Tonni, 2017). In southern South America, a sustained warm lapse between ca 700 CE and 1200 is supported by several sources of evidence (Fig. 1B; Iriondo, 1999; Cioccale, 1999; Favier-Dubois, 2007; Quattrocchio et al., 2008; Del Puerto et al., 2013; Elbert et al., 2013 and literature therein). This warm period is largely associated to humid conditions (although see Mauquoy et al., 2003; Perez et al., 2016; Ponce et al., 2017); in this case, however, local climate data based on the genesis of the sediments and terrestrial mollusk assemblage at the site Aldea Valle María, located ca. 200 km northwest from Sambaquí de Puerto Landa and nearly contemporary with the latter (895–1162 CE), suggest an arid to semiarid episode (Tonni et al., 2001; Compagnucci and Tonni, 2006).

4. Discussion

4.1. The significance of †*Dicolpomys* in the fossil record of South American echimyids

Echimyidae is an ancient clade of hystricomorphs whose evolutionary history is linked to forested areas of South America. Throughout the Cenozoic environmental changes (including diastrophic events), they mostly tracked their original habitats. Thus, extant representatives primarily inhabit Amazonian and Atlantic forests whereas only a few lineages have colonised the open areas of eastern and southern South America (Pascual, 1967; Hoffstetter, 1986; Verzi et al., 1994; Upham and Patterson, 2012; Olivares et al., 2012; Fabre et al., 2013; Patton et al., 2015). The fossil record of Echimyidae is poor when compared to the current high diversity of the family. This paucity is not unexpected, primarily because this record is not geographically coincident with the area where the main radiation of the group would have taken place. Due to the biased distribution of both fossil beds and paleontological collecting (Marshall et al., 1983; Hoffstetter, 1986; MacFadden, 2006), Oligocene to Pliocene echimyids are known essentially from southern South America (Flynn et al., 2008; Vucetich et al., 2015; Verzi et al., 2016, appendix table 2). In this context, fossil echimyids from southern locations have been interpreted as representing an impoverished marginal sample of the outstanding diversity achieved by the clade in the Brazilian Subregion (sensu Hershkovitz, 1958, Fig. 1A) of northern South America (Verzi et al., 2016; Olivares et al., 2017). Undisputed Amazonian fossil echimyids are exceptionally recorded in the late Miocene Acre region (Brazil and Peru; Sant'Anna-Filho, 1994; Campbell



Fig. 2. Lateral, medial, and occlusal views of right hemimandibles of †*Dicolpomys fossor*. A, MAMA-SPL-S1-5-1, Sambaquí de Puerto Landa, Entre Ríos, Argentina; B–F, Z.M.K. 1/1845:13344 (Lund's numbers 1 to 5), Lagoa Santa, Minas Gerais, Brazil (syntypes); G, UNISC 1757-14, Garivaldino site, Rio Grande do Sul, Brazil. E, F and G, reversed left hemimandibles. Scale bar equals 5 mm. Abbreviations: bi, base of the lower incisor; c, condyle; cp, chin process; mf, mandibular foramen; nm, mandibular notch.

et al., 2006).

The taxonomic composition of the echimyid fossil record at latitudes corresponding to the current Patagonian Subregion (sensu Hershkovitz; Fig. 1A) shows temporal stages which are concurrent with local and global Cenozoic climatic trends (Fig. 5; Verzi et al., 2015; see Denton, 1999; Zachos et al., 2001; Le Roux, 2012). Early fossils, late Oligocene to middle Miocene in age, are related to living arboreal tree-rats and bamboo-rats (Echimyini sensu Fabre et al., 2017), which agrees with the persistence of forests with tropical elements as far as southern Argentina in this period (Fig. 5A; Palazzesi and Barreda, 2007). From the late Miocene on, southern echimyid faunas no longer include lineages related to living species from Amazonian or Atlantic forests;

rather, they are limited to lineages of terrestrial and fossorial Euryzomatomyinae and Myocastorini (sensu Fabre et al., 2017) that currently inhabit open, shrubby to grasslands environments, and dry forests of the Chacoan Dominion (sensu Morrone, 2014) (Fig. 5B; Verzi et al., 1994, 2004, 2015, 2016; Vucetich et al., 1997; Olivares et al., 2012, 2017; Olivares and Verzi, 2015; see Patton et al., 2015; Fabre et al., 2016). Although these lineages originated earlier (Upham and Patterson, 2012, 2015; Álvarez et al., 2017), they acquired their identity during the late Miocene concurrently with the establishment of the diagonal of open vegetation biomes or Chacoan corridor in eastern South America (Nascimento et al., 2013; Olivares et al., 2017 and literature therein). Currently, this Chacoan Dominion comprises

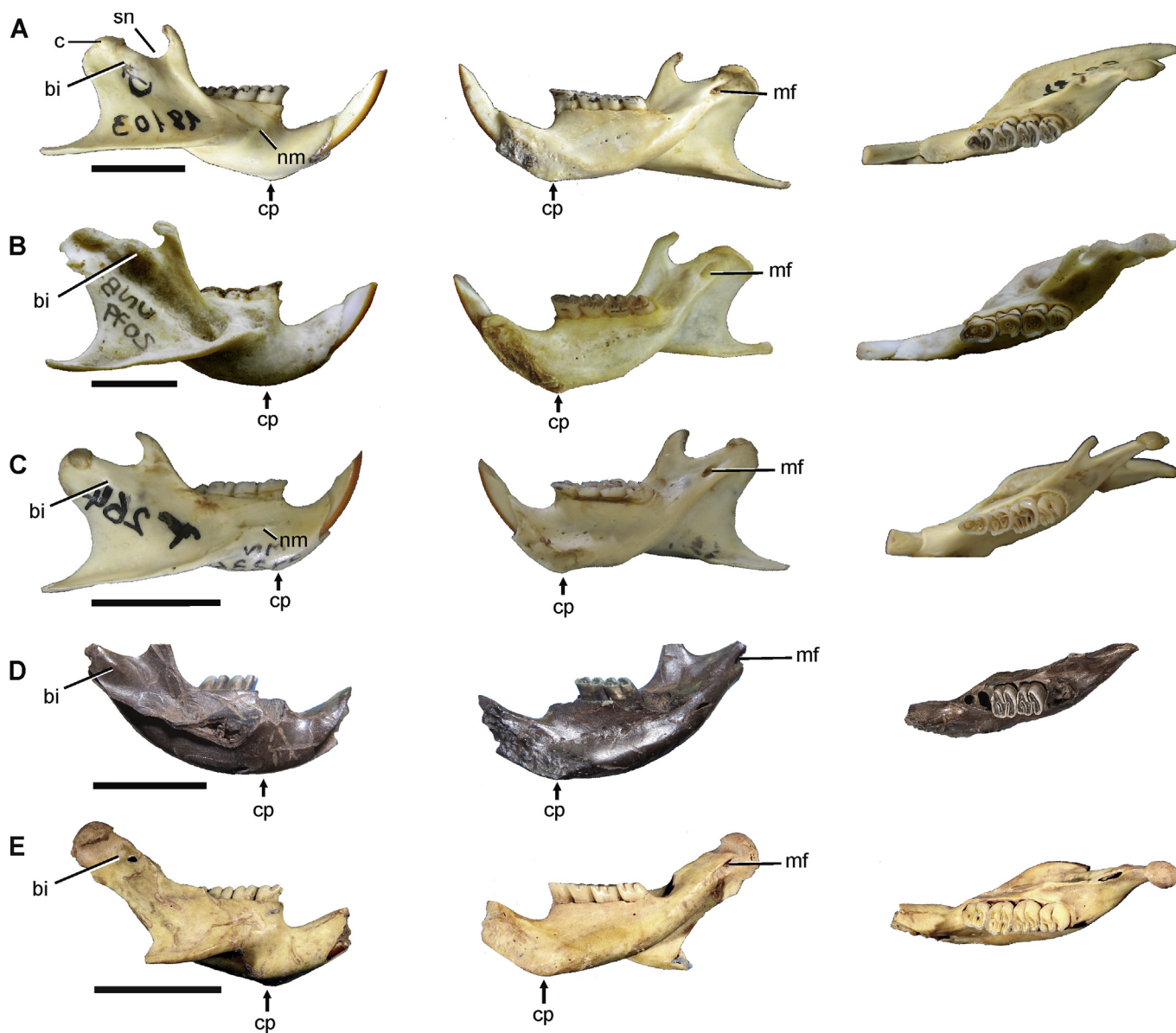


Fig. 3. Lateral, medial, and occlusal views of right hemimandibles of A, *Euryzygomatomys spinosus* MACN 18103 (left reversed); B, *Clyomys laticeps* UnB 2079; C, *Carterodon sulcidens* MN-UFRJ 24230 (left reversed); D, †*Euryzygomatomys mordax* UNISC 1759-3; E, †*Clyomys riograndensis* UNISC 1700-1. Scale bar equals 10 mm. Abbreviations: bi, base of the lower incisor; c, condyle; cp, chin process; mf, mandibular foramen; nm, mandibular notch; sn, sigmoid notch.

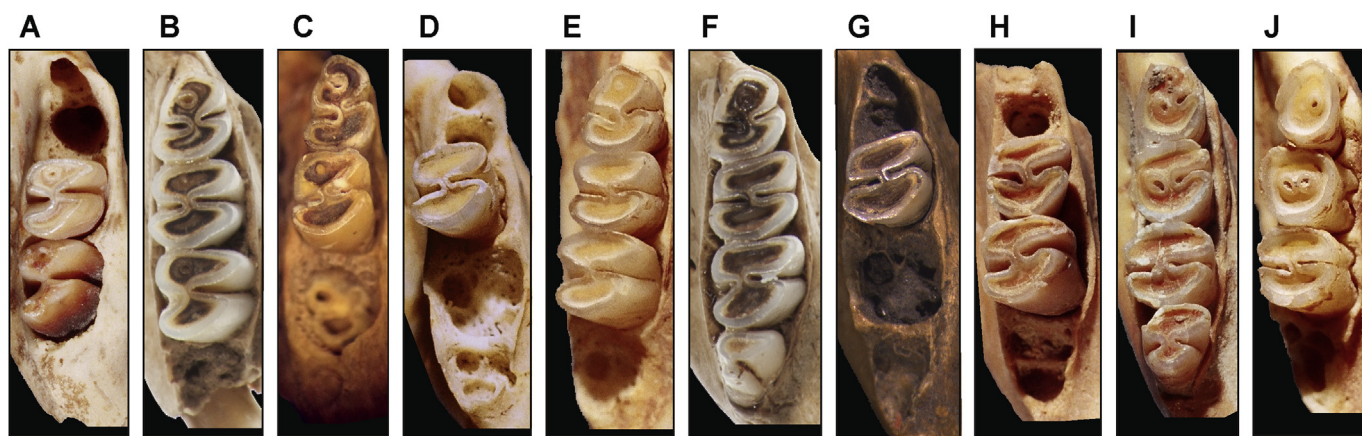


Fig. 4. Occlusal view of lower right molars of †*Dicolpomys fossor*. A, m1-2 UNISC 1756-18 (left reversed); B, dp4-m2 Z.M.K. 1/1845:13344 (Lund's number 4; left reversed); C, dp4-m1 UFRGS 135-2; D, m1 UNISC 1757-14 (left reversed); E, dp4-m2 UNISC 1764-2; F, dp4-m3 Z.M.K. 1/1845:13344 (Lund's number 1); G, m1 MAMA-SPL-S1-5-1; H, m1-2 UNISC 1690-13 (left reversed); I, dp4-m3 UNISC 1699-3 (left reversed); J, dp4-m2 UNISC 1764-3. Not in scale.

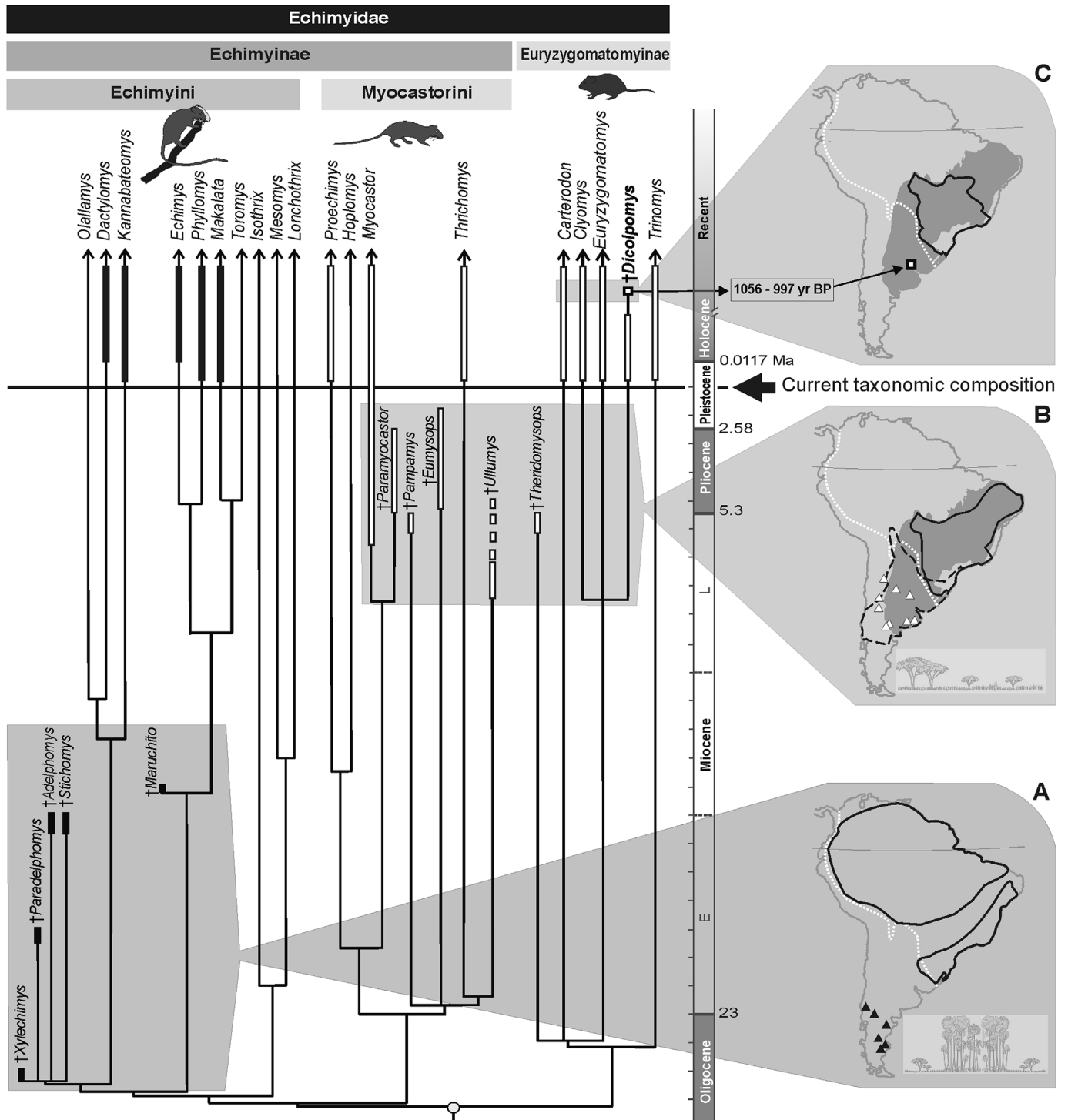


Fig. 5. Biochrons of Echimyidae in a combined molecular and morphological phylogeny of the family (after Olivares et al., 2017; time calibrated after Álvarez et al., 2017). Maps A-C show the distribution of the living (solid and dotted black lines) and extinct representatives (triangles and squares) of the shaded lineages. Dotted black line in B indicates the distribution of the Patagonian *Myocastor*; white dotted line indicates the boundary between the Brazilian and Patagonian Subregions; dark gray shading in B and C denotes the distribution of the Chacoan Dominion (see Fig. 1).

Seasonally Dry Tropical Forests (including the Caatinga in its northern portion) and the Cerrado, Chaco, and Pampa biomes (Figs. 1A and 5; Morrone and Coscarón, 1998; Pennington et al., 2004; Werneck, 2011; Morrone, 2014). These and other widespread open biomes of South America postdated the withdrawal of the middle-late Paranense marine transgression and the main diastrophic phases that gave rise to the Andes, both events representing the onset of the current biogeographical situation (Pascual, 1984; Pascual and Ortiz Jaureguizar,

1990; Webb, 1995; Hernández et al., 2005; see Carmignotto et al., 2012, pp. 330).

Fossils indicate that the southernmost distribution of open-adapted echimyids has changed over the time. Thus, the late Miocene-Pleistocene echimyids from Argentina have been interpreted as being part of episodes of southward drift distribution (sensu Vrba, 1992) from the Brazilian Subregion through the Chacoan corridor (Verzi, 2002; Olivares et al., 2017). In the Quaternary, one of these events is detected

for the middle Pleistocene OIS 11 warm episode, and involves the presence of the euryzygomatomyine †aff. *Clyomys* in central Argentina (Vucetich et al., 1997; Verzi et al., 2004; Tonni, 2009).

The record of †*Dicolpomys* in the Holocene of Argentina agrees with this scenario. In recent phylogenies, †*D. fossor* nested within Euryzygomatomyinae, and was more closely related to the living fossorial *Clyomys*, *Euryzygomatomys*, and *Carterodon* that inhabit the Seasonally Dry Tropical Forests, the Cerrado, and grasslands in the Atlantic Forest (Fig. 5C; Verzi et al., 2016; Olivares et al., 2017). In addition, †*Dicolpomys*, along with the extinct †*Clyomys riograndensis* and †*Euryzygomatomys mordax*, show the most deeply inserted lower incisors among echimyids, which is a clear fossorial specialization (Winge, 1887; Verzi and Olivares, 2006; Hadler et al., 2008). Its geographic distribution, together with its presumptive ecological features and phylogenetic affinities, indicate that †*Dicolpomys* inhabited open environments in the Chacoan partition of the Brazilian Subregion; in some cases, possibly areas in a Chacoan-Atlantic Forest ecotone (see De Queiroz and De Carvalho, 2008; Werneck, 2011; Carmignotto et al., 2012) as suggested by the presence of the arboreal echimyine *Phyllomys* in the same Holocene levels from Rio Grande do Sul (Hadler et al., 2008; *Phyllomys* is still part of the extant fauna in Rio Grande do Sul). Thus, the archaeological record of †*Dicolpomys* from Argentina reported here can also be interpreted as a southern expansion of the distribution of this echimyid, coinciding with both the MWP and synchronous locally semiarid conditions. This supports a possible pattern of changes in the southern boundary of Brazilian faunas, within the Chacoan Dominion, linked to paleoclimatic trends (see Quattrocchio et al., 2008; Tonni, 2017).

4.2. Recent generic extinction among South American caviomorph rodents

The current taxonomic composition of Echimyidae has been established since the late Pleistocene (Fig. 5; Ferreira et al., 2016: table 1). Moreover, the present-day composition of the South American caviomorph fauna had been attained by that time (Vucetich and Verzi, 1999). Interestingly, the scarce subsequent generic extinctions are recorded in the late Pleistocene – Holocene of the Brazilian Subregion; i.e. the chinchilloids †*Niedemys* and †*Tetrastylus* in addition to †*Dicolpomys* (Winge, 1887; Ferreira et al., 2016; Kerber et al., 2016). On this basis, Vucetich et al. (2015, pp. 32) highlighted the survival of lineages at lower latitudes after their extinction at higher latitudes. At first, †*Dicolpomys* seems to defy this interpretation. Its southern late Holocene record reported here is more recent than those from Brazilian sites and represents the most recent extinction at genus level among South American caviomorphs (an even more recent extinction of caviomorph genera, especially capromyids, is recorded only at the West Indies as part of a widespread loss of mammalian diversity extending into the post-AD 1500 historical era; Cooke et al., 2017; Turvey et al., 2017; Upham, 2017). Nevertheless, biases of the fossil record make it difficult to establish a direct link between extinction and latitude on the basis of paleontological evidence only. If the proposal is accepted that echimyids tracked their original habitats as an evolutionary response to environmental changes (Pascual, 1967; Verzi et al., 2014, 2015, 2016), the absence of †*Dicolpomys* in Brazilian sites that are contemporaneous with, or younger than that of Sambaquí de Puerto Landa would be a case of taphonomic or sampling bias. In fact, greater climatic stability predicts fewer extinctions in tropical areas with respect to temperate ones (Fine, 2015; Marin and Hedges, 2016). The phylogenetic structure of Octodontoidea is consistent with this hypothesis, with the familial clades Abrocomidae, Octodontidae, and Ctenomyidae from temperate regions showing younger crown groups when compared to the essentially tropical Echimyidae (Verzi et al., 2015, 2016).

Thus, †*Dicolpomys fossor* could have occurred at even more recent times in open Brazilian biomes. Its last occurrence, together with those of †*Euryzygomatomys mordax* and †*Clyomys riograndensis*, suggests that fossorial euryzygomatomyines affected by the Quaternary extinctions

were those with greater specialization for burrowing, a pattern that remains to be contrasted in a comparative phylogenetic context.

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References

- Álvarez, A., Moyers Arévalo, R.L., Verzi, D.H., 2017. Diversification patterns and size evolution in caviomorph rodents. *Biol. J. Linn. Soc.* 121, 907–922.
- Ameghino, F., 1907. Notas sobre una pequeña colección de huesos de mamíferos procedentes de las grutas calcáreas de Iporanga en el Estado de São Paulo, Brazil. *Rev. Mus. Paul.* 7, 59–124.
- Bowdich, T.E., 1821. An Analysis of the Natural Classifications of Mammalia, for the Use of Students and Travelers. J. Smith, Paris.
- Brandt, J.F., 1855. Beiträge zur nähern Kenntniss der Säugethiere Russland's. *Mem. Acad. Sci. St. Petersburg.* 7, 1–365.
- Carmignotto, A.P., Vivo, M., Langguth, A., 2012. Mammals of the Cerrado and Caatinga: distribution patterns of the tropical open biomes of central South America. In: Patterson, B.D., Costa, L.P. (Eds.), *Bones, Clones, and Biomes: the History and Geography of Recent Neotropical Mammals*. The University of Chicago Press, Chicago, pp. 307–350.
- Compagnucci, R.H., Tonni, E.P., 2006. Climatic change of the Argentina in the last 1000 years: a multiproxy analysis. In: *Proceedings of the International Symposium. Reconstructing Past Regional Climate Variations in South America over the Late Holocene: a New PAGES Initiative*. Malargüe, Argentina, pp. 87.
- Campbell Jr., K.E., Frailey, C.D., Romero-Pittman, L., 2006. The Pan-Amazonian ucayali peneplain, late neogene sedimentation in amazonia, and the birth of the modern amazon river system. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 239, 166–219.
- Candela, A.M., Noriega, J.L., 2004. Los coipos (Rodentia, Caviomorpha, Myocastoridae) del “Mesopotamiense” (Mioceno tardío; Formación Ituzaingó) de la provincia de Entre Ríos. vol. 12. *INSUGEO, Miscelánea*, Argentina, pp. 77–82.
- Castro, J.C., 2017. Investigaciones arqueológicas en la cuenca media e inferior del río Uruguay (provincia de Entre Ríos). Unpublished Ph.D. dissertation. Universidad Nacional de La Plata, La Plata 536 pp.
- Castro, J.C., Del Papa, M.C., 2015. La estructura del registro bioarqueológico del río Uruguay inferior. Análisis de la colección osteológica humana del Museo Arqueológico Manuel Almeida (Gualeguaychú, Entre Ríos). *Intersecc. Antropol.* 16, 195–205.
- Gioccale, A., 1999. Climatic fluctuations in the central region of Argentina in the last 1000 years. *Quat. Int.* 62, 35–47.
- Cooke, S.B., Dávalos, L.M., Mychajliw, A.M., Turvey, S.T., Upham, N.S., 2017. Anthropogenic extinction dominates Holocene declines of West Indian mammals. *Annu. Rev. Ecol. Syst.* 48, 301–327.
- Danladi, I.B., Akçer-Ön, S., 2017. Solar forcing and climate variability during the past millennium as recorded in a high altitude lake: lake Salda (SW Anatolia). *Quat. Int.* <http://dx.doi.org/10.1016/j.quaint.2017.08.068>. (in press).
- Denton, G.H., 1999. Cenozoic climate change. In: Bromage, T.G., Schrenk, F. (Eds.), *African Biogeography, Climate Change, and Human Evolution*. Oxford University Press, New York, pp. 94–114.
- De Queiroz, A.N., De Carvalho, O.A., 2008. Problems in the interpretation of Brazilian archaeofaunas: different contexts and the important role of taphonomy. *Quat. Int.* 180, 75–89.
- Del Puerto, L., Bracco, R., Inda, H., Gutiérrez, O., Panario, D., García-Rodríguez, F., 2013. Assessing links between late Holocene climate change and paleolimnological development of Peña Lagoon using opal phytoliths, physical, and geochemical proxies. *Quat. Int.* 287, 89–100.
- Eisenberg, J.F., Redford, K.H., 1999. *Mammals of the Neotropics. The Central Neotropics: Ecuador, Peru, Bolivia, Brazil*. The University of Chicago Press, Chicago.
- Elbert, J., Wartenburger, R., von Gunten, L., Urrutia, R., Fischer, D., Fajak, M., Hamann, Y., Greber, N.D., Grosjean, M., 2013. Late Holocene air temperature variability reconstructed from the sediments of Laguna Escondida, Patagonia, Chile (45°30'S). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 369, 482–492.
- Emmons, L.H., 2005. A revision of the genera of arboreal Echimyidae (Rodentia: Echimyidae, Echimyinae), with descriptions of two new genera. In: Lacey, E.A., Myers, P. (Eds.), *Mammalian Diversification: from Chromosomes to Phylogeography (A Celebration of the Career of James L. Patton)*. University of California Press, Berkeley, pp. 247–309.
- Emmons, L.H., Feer, F., 1997. *Neotropical Rainforest Mammals: a Field Guide*. The

- University of Chicago Press, Chicago.
- Emmons, L.H., Leite, Y.L.R., Patton, J.L., 2015. Family Echimyidae. In: In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), *Mammals of South America*, vol. 2. Rodents. The University of Chicago Press, Chicago, pp. 877–880.
- Fabre, P.-H., Galewski, T., Tilak, M., Douzery, E., 2013. Diversification of South American spiny rats (Echimyidae): a multigene phylogenetic approach. *Zool. Scr.* 42, 117–134.
- Fabre, P.-H., Patton, J.L., Leite, Y.L.R., 2016. Family Echimyidae. In: In: Wilson, D.E., Lacher Jr.T.E., Mittermeier, R.A. (Eds.), *Handbook of the Mammals of the World*, vol. 6. Lagomorphs and Rodents I. Lynx Edicions, Barcelona, Spain, pp. 552–641.
- Fabre, P.-H., Upham, N.S., Emmons, L.H., Justy, F., Leite, Y.L.R., Loss, A.C., Orlando, L., Tilak, M.-K., Patterson, B.D., Douzery, E.J.P., 2017. Mitogenomic phylogeny, diversification, and biogeography of South American spiny rats. *Mol. Biol. Evol.* 34, 613–633.
- Favier-Dubois, C.M., 2007. Soil genesis related to medieval climatic fluctuations in southern Patagonia and Tierra del Fuego (Argentina): chronological and paleoclimatic considerations. *Quat. Int.* 162/163, 158–165.
- Ferreira, D., Silva, A.K.B., Matos, C.H.C., Hadler, P., Hsiou, A.S., 2012. Assembléia holocênica de vertebrados de pequeno porte do sítio Alcoçaba, Estado de Pernambuco, Brasil. *Rev. Bras. Paleontol.* 15, 359–370.
- Ferreira, T.M.F., Olivares, A.I., Kerber, L., Parisi Dutra, R., Santos Avilla, L., 2016. Late Pleistocene echimid rodents (Rodentia, hystricognathi) from northern Brazil. *An. Acad. Bras. Cienc.* 88, 829–845.
- Fine, P.V.A., 2015. Ecological and evolutionary drivers of geographic variation in species diversity. *Annu. Rev. Ecol. Syst.* 46, 369–392.
- Flynn, J.J., Charrier, R., Croft, D.A., Gans, P.B., Herriott, T.M., Wertheim, J.A., Wyss, A.R., 2008. Chronologic implications of new Miocene mammals from the Cura-Mallín and Trapa Trapa formations, Laguna del Laja area, south central Chile. *J. South Am. Earth Sci.* 26, 412–423.
- Greslebin, H.R., 1931. La estructura de los túmulos indígenas prehispánicos del departamento de Gualaguaychú provincia de Entre Ríos, República Argentina. *Rev. Soc. Amigos Arqueol.* 5, 5–51.
- Gray, J.E., 1825. An outline of an attempt at the disposition of the Mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. *Ann. Philos.*, new Ser. 10, 337–344.
- Hadler, P., Cherem, J.J., Turbay, R., Alberti, A., Pardiñas, U.F.J., 2016. Diversidade de pequenos mamíferos (Didelphimorphia e Rodentia) do Holoceno do nordeste do estado do Rio Grande do Sul, Brasil: implicações taxonômicas e paleoambientais. *Rev. Bras. Paleontol.* 19, 127–144.
- Hadler, P., Verzi, D.H., Vucetich, M.G., Ferigolo, J., Ribeiro, A.M., 2008. Caviomorphs (mammalia, Rodentia) from the Holocene of Rio Grande do Sul state, Brazil: systematics and paleoenvironmental context. *Rev. Bras. Paleontol.* 11, 97–116.
- Hernández, R.M., Jordan, T.E., Dalenz Farjat, A., Echavarría, L., Idelman, B.D., Reynolds, J.H., 2005. Age, distribution, tectonics, and eustatic controls of the Paranense and Caribbean marine transgressions in southern Bolivia and Argentina. *J. South Am. Earth Sci.* 19, 495–512.
- Hershkovitz, P., 1958. A geographic classification of Neotropical mammals. *Fieldiana Zool.* 36, 581–620.
- Hoffstetter, R., 1986. High andean mammalian faunas during the plio-pleistocene. In: Vuilleumier, F., Monasterio, M. (Eds.), *High Altitude Tropical Biogeography*. Oxford University Press, Oxford, pp. 218–245.
- Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Zimmerman, S.R., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* 55, 1889–1903.
- Iriondo, M., 1999. Climatic changes in the South American plains: records of a continent-scale oscillation. *Quat. Int.* 57/58, 93–112.
- Kerber, L., Mayer, E.L., Ribeiro, A.M., Vucetich, M.G., 2016. Late Quaternary caviomorph rodents (Rodentia: hystricognathi) from the Serra da Capivara, northeastern Brazil, with description of a new taxon. *Hist. Biol.* 28, 439–458.
- Krapovickas, P., 1957. Excursión arqueológica a Rincón de Landa. *Rev. Geogr. Am.* 12, 149–156.
- Le Roux, J.P., 2012. A review of Tertiary climate changes in southern South America and the Antarctic Peninsula. Part 2: continental conditions. *Sediment. Geol.* 247–248, 21–38.
- Ljungqvist, F.C., 2010. A new reconstruction of temperature variability in the extra-tropical northern hemisphere during the last two millennia. *Geogr. Ann.* 92, 339–351.
- MacFadden, B.J., 2006. Extinct mammalian biodiversity of the ancient New World tropics. *Trends Ecol. Evol.* 21, 157–165.
- Marin, J., Hedges, S.B., 2016. Time best explains global variation in species richness of amphibians, birds and mammals. *J. Biogeogr.* 43, 1069–1079.
- Marshall, L.G., Hoffstetter, R., Pascual, R., 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. *Palaeovertabrata, Mém. Extraordin.* 1–93.
- Mauquoy, D., Blaauw, M., van Geel, B., Borromei, A., Quattrocchio, M., Chambers, F.M., Possnert, G., 2003. Late Holocene climatic changes in Tierra del Fuego based on multiproxy analyses of peat deposits. *Quat. Res.* 61, 148–158.
- Morrone, J.J., 2014. Cladistic biogeography of the Neotropical region: identifying the main events in the diversification of the terrestrial biota. *Cladistics* 30, 202–214.
- Morrone, J.J., Coscarón, M.C., 1998. Cladistics and biogeography of the assassin bug genus *rasahus* amyot & serville (heteroptera: reduviidae: peiratinae). *Zool. Med. Genid.* 72, 73–87.
- Nascimento, F.F., Lazar, A., Menezes, A.N., Durans, A.M., Moreira, J.C., Salazar-Bravo, J., D'Andrea, P.S., Bonvicino, C.R., 2013. The role of historical barriers in the diversification processes in open vegetation formations during the Miocene/Pliocene using an ancient rodent lineage as a model. *PLoS One* 8, e61924.
- Olivares, A.I., Verzi, D.H., 2015. Systematics, phylogeny and evolutionary pattern of the hystricognath rodent *Eumysops* (Echimyidae) from the Plio-Pleistocene of southern South America. *Hist. Biol.* 27, 1042–1061.
- Olivares, A.I., Verzi, D.H., Vucetich, M.G., 2012. Definición del género *Eumysops* Ameghino, 1888 (Rodentia, Echimyidae) y revisión de las especies del Plioceno temprano de Argentina central. *Ameghiniana* 49, 198–216.
- Olivares, A.I., Verzi, D.H., Contreras, V.H., Pessôa, L.M., 2017. A new Echimyidae (Rodentia, Hystricomorpha) from the late Miocene of southern South America. *J. Vert. Paleontol.* 37 e1239204.
- Palazzesi, L., Barreda, V., 2007. Major vegetation trends in the Tertiary of Patagonia (Argentina): a qualitative paleoclimatic approach based on palynological evidence. *Flora* 202, 328–337.
- Pascual, R., 1967. Los roedores Octodontoidea (Caviomorpha) de la Formación Arroyo Chasicó (Plioceno inferior) de la provincia de Buenos Aires. *Rev. Mus. La Plata, Paleontol.* 5, 259–282.
- Pascual, R., 1984. Late Tertiary mammals of southern South America as indicators of climatic deterioration. *Quat. S. Am.* A 2, 1–30.
- Pascual, R., Ortiz Jaureguizar, E., 1990. Evolving climates and mammal faunas in Cenozoic South America. *J. Hum. Evol.* 19, 23–60.
- Perez, L., García-Rodríguez, F., Hanebuth, T.J.J., 2016. Variability in terrigenous sediment supply offshore of the Rio de la Plata (Uruguay) recording the continental climatic history over the past 1200 years. *Clim. Past.* 12, 623–634.
- Politis, G.G., Prates, L., Merino, M.L., Tognelli, M.F., 2011. Distribution parameters of guanaco (*Lama guanicoe*), pampas deer (*Ozotoceros bezoarcticus*) and marsh deer (*Blastocerus dichotomus*) in central Argentina: archaeological and paleoenvironmental implications. *J. Archaeol. Sci.* 38, 1405–1416.
- Ponce, J.F., Borromei, A.M., Menounos, B., Rabassa, J., 2017. Late-Holocene and Little Ice Age paleoenvironmental change inferred from pollen analysis, Isla de los Estados, Argentina. *Quat. Int.* 442, 26–34.
- Patton, J.L., 2015. Subfamily myocastorinae. In: In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), *Mammals of South America*, vol. 2. Rodents. The University of Chicago Press, Chicago, pp. 1019–1022.
- Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), 2015. *Mammals of South America*, vol. 2. Rodents. The University of Chicago Press, Chicago.
- Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K., Butterworth, C.A., 2004. Historical climate change and speciation: Neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philos. Trans. R. Soc. B* 359, 515–537.
- Quattrocchio, M.E., Borromei, A.M., Deschamps, C.M., Grill, S.C., Zavala, C.A., 2008. Landscape evolution and climate changes in the Late Pleistocene–Holocene, southern Pampa (Argentina): evidence from palynology, mammals and sedimentology. *Quat. Int.* 181, 123–138.
- Roth, P.R.O., Jung, D.M.H., Christoff, A.U., 2008. Identificação de remanescentes de roedores de um abrigo sob rocha do Nordeste do RS: implicações paleoambientais. *Rev. Iniciação Científica ULBRA* 7, 71–82.
- Rosenthal, Y., Linsley, B.K., Oppo, D.W., 2013. Pacific Ocean heat content during the past 10,000 years. *Science* 342, 617–621.
- Sant'Anna-Filho, M.J., 1994. *Roedores Do Neógeno Do Alto Juruá, Estado Do Acre, Brasil*. Unpublished M.S. thesis. Universidade Federal do Rio Grande do Sul, Porto Alegre 167 pp.
- Tonni, E.P., 2009. Los mamíferos del Cuaternario de la región pampeana de Buenos Aires, Argentina. In: Ribeiro, A.M., Bauermann, S.G., Cherer, C.S. (Eds.), *Quaternario Do Rio Grande Do Sul: Integrando Conocimientos*. Monografías da Sociedade Brasileira de Paleontologia, Porto Alegre, Brazil, pp. 193–205.
- Tonni, E.P., 2017. Cambios climáticos en la región pampeana oriental durante los últimos 1000 años. Una síntesis con énfasis en la información zoogeográfica. *Rev. Mus. La Plata* 2, 1–11.
- Tonni, E.P., Cione, A.L., Fignini, A.J., Noriega, J.I., Carlini, A., Miquel, S., 2001. Extensión del período árido del Holoceno hasta los siglos X a XIII basada en el registro de moluscos terrestres en Entre Ríos (Argentina). In: *Proceedings of the XI Congreso Latinoamericano y III Congreso Uruguayo de Geología*, pp. 1–7 Montevideo, Uruguay.
- Turvey, S.T., Kennerley, R.J., Nuñez-Miño, J.M., Young, R.P., 2017. The last survivors: current status and conservation of the non-volant land mammals of the insular Caribbean. *J. Mammal.* 98, 918–936.
- Upham, N.S., 2017. Past and present of insular Caribbean mammals: understanding Holocene extinctions to inform modern biodiversity conservation. *J. Mammal.* 98, 913–917.
- Upham, N.S., Patterson, B.D., 2012. Diversification and biogeography of the neotropical caviomorph lineage Octodontoidea (Rodentia: hystricognathi). *Mol. Phylogenet. Evol.* 63, 417–429.
- Upham, N.S., Patterson, B.D., 2015. Evolution of caviomorph rodents: a complete phylogeny and timetree for living genera. In: Vassallo, A.L., Antenucci, D. (Eds.), *Biology of Caviomorph Rodents: Diversity and Evolution*. SAREM Series a. Mammalogical Research, Buenos Aires, pp. 63–120.
- Verzi, D.H., 2002. Patrones de evolución morfológica en Ctenomyiinae (Rodentia, Octodontidae). *Mastozool. Neotrop* 9, 309–328.
- Verzi, D.H., Olivares, A.I., 2006. Craniomandibular joint in South American burrowing rodents (Ctenomyiidae): adaptations and constraints related to a specialised mandibular position in digging. *J. Zool.* 270, 488–501.
- Verzi, D.H., Deschamps, C.M., Tonni, E.P., 2004. Biostratigraphic and palaeoclimatic meaning of the middle Pleistocene South American rodent *Ctenomys kraglievichi* (caviomorpha, Octodontidae). *Palaeoogeogr. Palaoclimatol. Palaeoecol.* 212, 315–329.
- Verzi, D.H., Morgan, C.C., Olivares, A.I., 2015. The history of South American octodontoid rodents and its contribution to evolutionary generalisations. In: Cox, P., Hautier, L. (Eds.), *Evolution of the Rodents*. Advances in Phylogeny, Functional Morphology, and Development. Cambridge Studies in Morphology and Molecules:

- New Paradigms in Evolutionary Biology. Cambridge University Press, Cambridge, pp. 139–163.
- Verzi, D.H., Olivares, A.I., Morgan, C.C., 2014. Phylogeny and evolutionary patterns of South American octodontoid rodents. *Acta Palaeontol. Pol.* 59, 757–769.
- Verzi, D.H., Vucetich, M.G., Montalvo, C.I., 1994. Octodontid-like Echimyidae (Rodentia): an upper Miocene episode in the radiation of the family. *Palaeovertebrata* 23, 199–210.
- Verzi, D.H., Olivares, A.I., Morgan, C.C., Alvarez, A., 2016. Contrasting phylogenetic and diversity patterns in octodontoid rodents and a new definition of the family Abrocomidae. *J. Mamm. Evol.* 23, 93–115.
- Vrba, E.S., 1992. Mammals as a key to evolutionary theory. *J. Mammal.* 73, 1–28.
- Vucetich, M.G., Verzi, D.H., 1999. Changes in diversity and distribution of the caviomorph rodents during the Late Cenozoic in southern South America. *Quat. S. Am. A* 12, 207–223.
- Vucetich, M.G., Verzi, D.H., Tonni, E.P., 1997. Paleoclimatic implications of the presence of *Clyomys* (Rodentia, Echimyidae) in the Pleistocene of central Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 128, 207–214.
- Vucetich, M.G., Arnal, M., Deschamps, C.M., Pérez, M.E., Vieytes, E.C., 2015. A brief history of caviomorph rodents as told by the fossil record. In: Vassallo, A.I., Antenucci, D. (Eds.), *Biology of Caviomorph Rodents: Diversity and Evolution*. SAREM Series a. Mammalogical Research, Buenos Aires, pp. 11–62.
- Waterhouse, G.R., 1839. *Mammalia*. In: Darwin, C. (Ed.), *The Zoology of the Voyage of the H.M.S. Beagle under the Command of Captain Fitz Roy, R. N., during the Years 1832–1836, Fascicle 10*. vols. vols. ii–ix. Smith, Elder and Co, London, pp. 49–97.
- Webb, S.D., 1995. Biological implications of the middle Miocene amazon seaway. *Science* 269, 361–362.
- Werneck, F.P., 2011. The diversification of eastern South American open vegetation biomes: historical biogeography and perspectives. *Quat. Sci. Rev.* 30, 1630–1648.
- Winge, H., 1887. *Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien: med udsigt over gnavernes indbyrdes slaegtskab*. E Mus. Lundii 1, 1–178.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.