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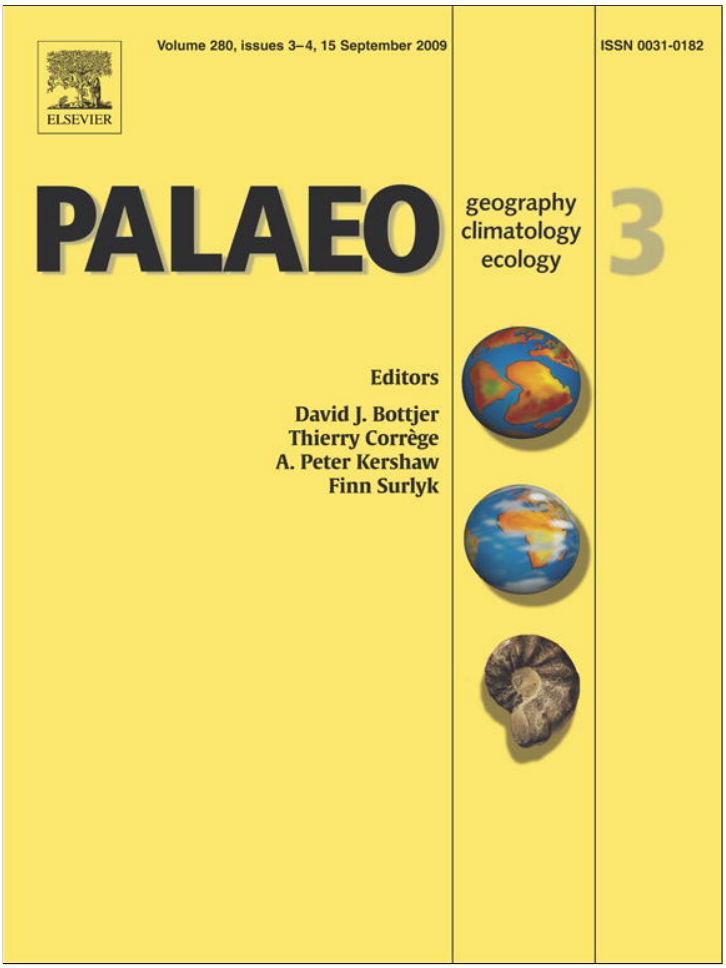

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Comment on "The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): Late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange" by D.H. Verzi and C.I. Montalvo [Palaeogeography, Palaeoclimatology, Palaeoecology 267 (2008) 284–291]

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ABSTRACT

In a recent paper (Verzi, D.H., Montalvo, C.I., 2008. The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange. Palaeogeography, Palaeoclimatology, Palaeoecology 267, 284–291) the potentially oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora) have been reported from a Late Miocene (Huayquerian) assemblage located in central Argentina (Caleufú site, La Pampa province). These findings expand the biochron of these important families in South America 3–4 Ma earlier than previous records. However, several observations prevent us from accepting the validity of these assumptions. In this paper we discuss the age of the Caleufú assemblage, and the assignment of the GHUNLPam 21722 to Mustelidae. The Caleufú assemblage contains a mixture of Pliocene and Late Miocene faunal elements, and has been assigned to the Huayquerian only due to the "stage of evolution" of some rodents. The lack of isotopic or paleomagnetic data coupled with the isolation of this locality and the absence of a local stratigraphic succession inhibit its correlation with other palaeontological comparable sites and a robust inference about its chronology. The "stage of evolution" of a taxon is not a biostratigraphic tool, thus we cannot rule out the possibility that the Caleufú assemblage has an Early Pliocene (Montehermosan) age. The GHUNLPam 21722, a poorly preserved specimen, shows several characters (e.g., 4 lower incisors, mental foramina below the incisors absent, third lower incisor smaller than the first and second ones) that do not match with Mustelidae (or Carnivora) but instead strongly resemble those observed in didelphimorphian marsupials. The discussed caveats regarding Caleufu assemblage chronology and taxonomy indicate that new and detailed studies are needed before the hypotheses advanced by Verzi and Montalvo can be accepted.

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1. Introduction

Twenty years of collection and study plus more than a decade of publications made by Montalvo and collaborators place the paleofauna of the Cerro Azul Formation (La Pampa Province, Central Argentina) within the best known latest Neogene faunistic assemblages in southern South America (see Verzi et al., 2008, and the references therein). In this context, we want to call to attention a single paleontological locality, Caleufú, recently addressed by Verzi and Montalvo in this journal (Verzi and Montalvo, 2008; VM, thereafter). Caleufú faunistic assemblage was claimed as Late Miocene (late Huayquerian) in age and therefore bearing the "oldest" remains of the most diverse subfamily of Neotropical rodents (Cricetidae, Sigmodontinae) and one group of placental carnivores (Mustelidae).

Two main points will be discussed in this contribution: (1) the age of the Caleufú assemblage, and (2) the taxonomic identity of the supposed Carnivora. We present here strong arguments that make the results and interpretations of VM equivocal regarding both issues. Therefore, our interpretation calls into question two fundamental subjects of VM original paper: (1) the biostratigraphy of the Caleufú fauna is weak (therefore, the proposed Late Miocene age for this fauna is arguable), and (2) the taxonomic identification of the poorly preserved mustelid specimen may actually represent an endemic marsupial rather than an early carnivore immigrant (therefore, the biochron of Mustelidae in South America is not increased by 3–4 Ma). Both of the points here discussed are crucial, since they change our knowledge of the calibration of Late Miocene southward dispersal (from North America into South America) during the early phases of the Great American Interchange.

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2. The age of Caleufú assemblage

The Caleufú assemblage emerges as a "rara avis" (from Latin, "rare bird," a rare thing or rarity) within 20 localities, where sediments of Cerro Azul Fm are exposed. This faunal association has yielded unique fossil remains that includes sigmodontines, "mustelids" (but see below), plus a large list of endemic taxa. Most of the rodents present in Caleufú are new species or, at least, specimens slightly different from other known Late Miocene species (either from other Cerro Azul assemblages or from other putative coeval Argentinean northwestern assemblages). The following are some examples: (1) the species of the cavid *Neocavia* from Caleufú is, according to Montalvo and Rocha (2003, p. 504), more derived than *N. lozanoi*, typical of Huayquerian beds; (2) although VM (Table 1) indicates *Neophanomys biplicatus* as one octodontid present in the Caleufú assemblage, this specific status was questioned by Verzi et al. (2008, p. 152) "A new chronomorph of the octodontid *Neophanomys*, more derived than *N. biplicatus*..." (see also VM, p. 287); (3) the octodontid *Xenodontomys* is represented in Caleufú by an exclusive species, *X. elongatus* (see Verzi et al., 2003). In addition to rodents, another well known group of mammals recorded in Caleufú are the armadillos (Dasypodidae) mainly because of the revision of Urrutia et al. (2008; and the references therein). The authors also consolidated the "rara avis" condition of Caleufú with the recognition of *Ringueletia*, a genus previously known from Pliocene Montehermosan?–Marplatan beds (Cione and Tonni, 1996; Cione and Tonni, 2005). Finally, the record of marsupials from the Caleufú assemblage (Abello et al., 2002) is also worth mentioning. The exclusive record of the genus *Argyrolagus* departs from the widespread occurrence of *Microtragulus* in the remaining assemblages of the Cerro Azul Fm (Goin et al., 2000).

The crucial issue is the reference of Caleufú assemblage to the Late Miocene (late Huayquerian). VM supported this conclusion by developing a biochronological scheme based on the grade of evolution of two octodontid lineages, *Chasichimys–Xenodontomys–Actenomys* and *Neophanomys*. Tacitly in VM and several other contributions (e.g., Verzi et al., 2003, 2008), the genus *Actenomys* (widespread during Neogene times in Central Argentina) seems to be indicative of post-Huayquerian beds, while *Chasichimys–Xenodontomys* from Chasicoan–Huayquerian levels. But in a specific paper devoted to the taxonomy of *Xenodontomys*, Verzi et al. (2003) considered (a) the difficulty to separate larger *Xenodontomys* species (like *elongatus*) from smaller *Actenomys* species (like *priscus*), and (b) the high degree of variance represented in *X. elongatus* measurements (see Verzi et al., 2003, Figs. 7–8). These two elements clearly tackled the potential value of *X. elongatus* as a chronological indicator. According to our view, the weakest point of the biochronology proposed by Verzi and collaborators is the lack of stratigraphic succession of, at least, two putative successional chronomorphs of the line *Chasichimys–Xenodontomys–Actenomys*. Following the authors: "Since there is no stratigraphic superposition among the studied levels, the following scheme of biostratigraphic and biochronological correlation among the bearing units is based on the stage of evolution of octodontoid rodents…" (Verzi et al., 2008, p. 150). None of the 20 paleontological localities of the Cerro Azul Fm permits comparison of their stratigraphical columns, the change from one form into another. In other words, their biochronology is based on findings from isolated localities linked and "arranged" by a presumptive evolutionary order of the octodontid lineage. In this context, the possibility of circular reasoning is very high, leading to their hypotheses being weakly supported.

The interpretation of the chronological order of these localities based on the "stage of evolution" of some taxa stated by VM clearly does not constitute a biostratigraphic argument (e.g. Hedberg, 1980; Código Argentino de Estratigrafía, 1992; Woodburne, 2004), and, in the absence of other kind of information, it is not possible to ascertain the relative age of each locality. Thus, to be a biostratigraphic tool, the "biochronological" schema of the rodents studied by VM must be based on a sequence where the superposition of each stratum with rodents in different "stages" of evolution could be observed, or on isotopic dates or paleomagnetic analysis. In consequence, this biochronological interpretation is not a robust argument to expand the earliest occurrence of cricetids and "mustelids" in South America.

The issue is, in addition, related to the chronological position of the "Irenean". In this regard, VM (see also Verzi et al., 2008, p. 151–152) unequivocally positioned the "Irenean" in the Late Miocene (late Huayquerian) and considered this bed in part to be older than the Caleufú assemblage. The authors based this inference on the occurrence of *Xenodontomys ellipticus*, a more "primitive" species than *X. elongatus* present in Caleufú, but younger than the Barranca de Sarmiento and Cantera Seminario sites because it is a more "derived" *X. ellipticus* "chronomorph" than the one present in the latter localities (Verzi et al., 2008, p. 152). This "derived" *X. ellipticus* "chronomorph" is present only in some exposures of the Irene Formation (Arroyo Indio Rico, Irene, Paso del Médano and Oriente, Verzi et al., 2008, p. 151–512). If this schema is correct, the time span represented by the Caleufú fauna is not represented in the Irene Formation, where post-Huayquerian rodents (*Actenomys*) were recovered in some localities (i.e. Cascada Grande, see below) or older Huayquerian rodents (*Xenodontomys ellipticus*) from others (see below).

In order to reinforce this point, a brief historical review of this faunistic unit is presented here. The term "Irenean" ("Irenense" in Spanish) was introduced by Kraglievich (1934) to characterise a group of poorly known paleofaunas collected from isolated outcrops from south-central Buenos Aires Province, mainly exposed in or near the Quequén Salado River and one of its tributaries, the Indio Rico Creek. Fidalgo et al. (1975) introduced for the first time the term Irene Formation to refer to these deposits. The principal paleontological locality is Cascada Grande (= Cascada Cifuentes or Cascada Aldaya) along the sides of the Quequén Salado River. The sedimentary exposures achieve a thickness of eight meters and are arranged in several tabular banks (Mignone, 1949). Other fossiliferous localities along this river are restricted to isolated and patchily distributed riverine cliffs, no larger than 300 m long and less than three meters thick, the best known of which is Paso del Médano (in the place locally known as Cueva del Tigre), ca. 11 km above the mouth of the Quequén Salado River (e.g., Reig, 1955; Pascual and Herrera, 1973; Goin et al., 1994). Early paleontological material considered by Kraglievich (1934) to define the "Irenean" came from Irene, Oriente, and Indio Rico localities. These localities were never revisited because the exact position of the deposits is unknown and the collections lack associated stratigraphical data. Despite that, VM used the presence of *Xenodontomys ellipticus* in these historical collections to position the "Irenean" in the Late Miocene, older than the Caleufú assemblage. An internal contradiction of this statement – overlooked by VM – is that if the "Irenean" of Paso del Médano is older than Caleufú, then the cricetid remain recovered there (see Pascual and Herrera, 1973, p. 48) is older than the presumed "oldest" Cricetidae from Caleufú.

Summarizing the facts mentioned above, the chronology of the Caleufú assemblage is, at least, controversial, and its assignment to post-Huayquerian stages (early Pliocene, as was suggested in several studies previous to VM; see, e.g., Montalvo et al., 2000) cannot be ruled out without more solid arguments (e.g., stratigraphy, radiometric dates). The difficulties to unequivocally assessing the antiquity of Caleufú are in line with other Central and Western Mio-Pliocene paleofaunas of Argentina (see Tauber, 2000, 2005). In order to explore this important issue, a promising way could be a revisionary work of the Quequén Salado river beds and its fossils. We and our collaborators made extensive collections in Cascada Grande, Paso del Médano, and other small riverine cliffs along the Quequén Salado river, during the years 1991–1998. These collections, including thousands of fossil remains with precise stratigraphical provenance, are housed in La Plata Museum but have remained basically unstudied. A preliminary

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stratigraphical scheme, based on our field notes, seems to indicate that the outcroppings placed along the Quequén Salado River could be useful to adequately contrast against part of the biochronology proposed by VM and Verzi et al. (2008). At least in Cascada Grande, the successive sedimentary beds show, from bottom to top, an increment on the *Actenomys* frequency and the first record of Cricetidae in the uppermost levels. In addition, our field work indicates that there is no *Xenodontomys* nor *Actenomys* in Paso del Médano outcrops, but the former is present in a single level of a sedimentary sequence, exposed about 1 km upstream from this locality, and informally called as Paso de la Tufa. The sudden occurrence of this genus plus the absence of *Xenodontomys* within the rich collection made in Cascada Grande, preliminary suggest an erratic pattern of appearance that deserve more detailed studies and more samples with stratigraphic control prior to establishing *Xenodontomys* species as useful biostratigraphic tools.

3. The oldest South American mustelids?

The second topic we want to discuss here is the taxonomic hypothesis advanced by VM regarding a small mandible fragment [GHUNLPam 21722] from the Caleufú assemblage, which they interpreted as an unidentified Mustelidae (see VM, Fig. 4). We will analyze the identification and review some misinterpretations made by VM about the oldest record of placental carnivores (Order Carnivora) in South America.

Placental carnivores are relatively young immigrants in South America, with the first records as old as late Miocene (Huayquerian), older than 6 Ma, and represented by the Procyonidae (see Marshall et al., 1979; Yrigoyen, 1994; Soibelzon and Prevosti, 2007). First appearances of other families of Carnivora occurred in the Late Pliocene (Marplatan Age, Vorohuean subage,≈3-2.5 Ma, see Woodburne et al., 2006) when canids (*Dusicyon cultridens*) and Mustelidae (*Galictis sorgentinii*) are recorded and later during the Pleistocene, when unequivocal fossils of Felidae, Lutrinae, and Ursidae are recovered (Prevosti, 2006; Prevosti et al., 2006; Soibelzon and Prevosti, 2007). The age of *Conepatus altiramus* is still uncertain (see Cione and Tonni, 1995; Woodburne et al., 2006), and the older Mephitidae (mephitids are not mustelids, see Flynn et al., 2000, 2005; Sato et al., 2004, 2006; Delisle and Strobeck, 2005; Fulton and Strobeck, 2006, 2007; Árnason et al., 2007; Yonezawa et al., 2007; Yu et al., 2008; and references therein), with adequate data of provenance, coming from Early Pleistocene levels. If the reference of the GHUNLPam 21722 to an unidentified mustelid is accepted and the age of the Caleufú assemblage as Late Miocene (Huayquerian) is supported, then the biochron of the family in South America has to be expanded by more than 2 Ma. This is an important point about the biochronological ramifications of a poorly preserved specimen. But the putative Huayquerian mustelid of Caleufú is clearly not the oldest South American carnivoran as VM claimed (p. 289) since several procyonid remains come from older beds (>6 Ma according to Marshall et al., 1979; see also Yrigoyen, 1994).

Although the GHUNLPam 21722 is very fragmentary and lacks many diagnostic traits, the significance of this fossil invites further exploration beyond the brief description provided by VM and the restricted set of comparisons with presumptive related taxa made by those authors. VM made the taxonomic assignment by highlighting that "the position of preserved roots and alveoli shows similarities with those of living Lutrinae" (p. 287). It must be noted that this anatomical portion does not bear the characters commonly used to diagnose Carnivora and/or Mustelidae (e.g. Bryant et al., 1993; Wolsan, 1993; Baskin, 1998; Wesley-Hunt and Flynn, 2005). In contrast, a detailed study of the evidence published by VM plus direct inspection of the GHUNLPam 21722, and its comparison with recent and fossil specimens housed at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) allows us to propose a different conclusion. The GHUNLPam 21722 displays several traits that do not agree with a mustelid: (1) the symphysis is very low and long, and reaches the "p3" (could be also a p2, see below; see VM, Fig. 4; Fig. 1A), with a very flat anterior face of the mandible that is in angle with the lateral border of the horizontal ramus; (2) a mental foramen is not visible in the anterior face of the mandible (below the incisors); (3) the distal alveolus of the "p2" is smaller than the mesial alveolus of the "p3" (Fig. 1B); (4) the root of the "i3" (i4 in our interpretation) is smaller than the "i1–i2" roots (i2-i3 in our interpretation, see Fig. 1B, C) (see Bjork, 1970; Ewer, 1973; Hershkovitz, 1995).

On the other hand, several of the traits observed in the GHUNLPam 21722 are present in different clades of marsupials (i.e., Sparassodonta, Didelphimorphia). Some sparassodonts have three (crowded) incisors with a well-defined "staggered" pattern (Marshall, 1978; Hershkovitz, 1995). Specially, the GHUNLPam 21722 shares several features and similar size with some species of Didelphimorphia (e.g. *Sparassocynus*, *Thylatheridium*, *Hyperdidelphys*, and *Thylophorops*; see Goin et al., 2000 for the record of these taxa in Cerro Azul Fm) that occur in the Late Miocene–Pliocene of South America: the first premolar (p1) is obliquely implanted, with the first root slightly smaller and more labial than the distal one (Fig. 1E); the symphysis is very low and long, and the anterior face of the mandible is flat and in angle with the lateral one (Fig. 1D, F); the distal root of the p1 is smaller than the mesial root of the p2; lack the mental foramina on the anterior face of the mandible.

If these similarities are correctly interpreted, then the GHUNLPam 21722 could belong to a didelphimorphian, and the roots of the premolar must be interpreted as a p1 (the two more mesial ones) and the mesial root of the p2 (the distal one).

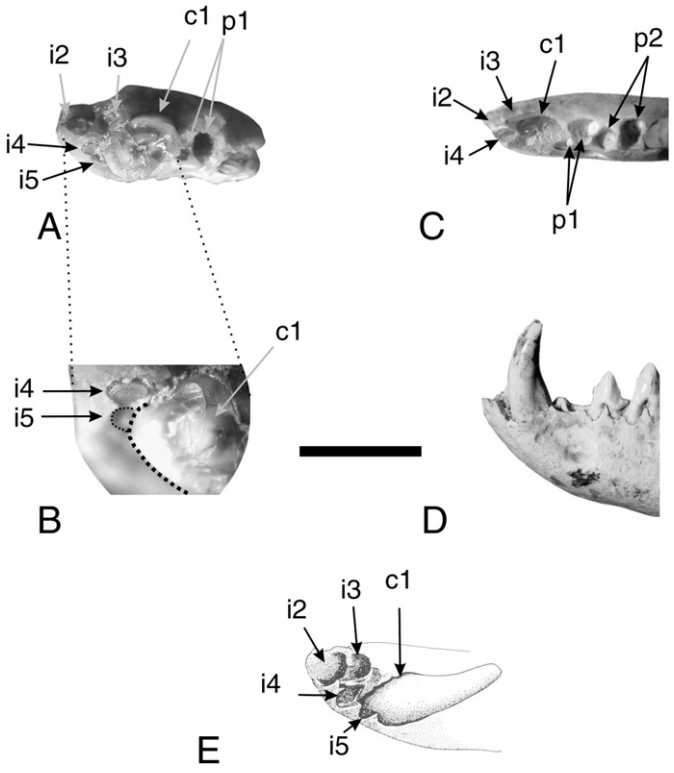

Fig. 1. Comparison between the mandible fragment of Caleufú (A–B, GHUNLPam 21722) and *Thylatheridium* sp. (C: MACN M 16719; D: MACN M 17758). A, mandible in dorsal view; B, magnification of the anterior border of the mandible in dorsal view; C, mandible anterior portion in dorsal view; D, mandible anterior portion in labial view; E: schematic draw of a recent marsupial (*Philander opossum*) showing the staggered pattern of the incisors (Modified from Hershkovitz, 1995, fig. 2A). Abbreviations: i = root/alveolus of the incisors; c1 = root/alveolus of the canine; p = roots/alveoli of the premolars. Scale = 0.5 cm.

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With regard to the incisor count, the authors (VM) originally considered that the GHUNLPam 21722 has three elements, nevertheless, a revision of the material revealed that there are four incisors. One interesting feature worth mentioning that can be seen in Fig. 4A of VM, is a small depression between distal part of the i4 and the mesiolabial border of the c1 (Fig. 1B, C). This depression is separated from the i4 by an internal expansion of the external bone, and is smaller than the i3 root, and matches very well in position, size, and morphology the expected alveolus of a fifth incisor (i5) according to our taxonomic interpretation (see Fig. 1G). Marsupials, such as most metatherians, are characterized by having the root of i3 placed lingual to the roots of the i2–i4 ("staggered" pattern following Hershkovitz, 1995), and four lower incisors (i2–i5). This pattern is more evident in the extinct didelphimorphians *Thylophorops* (MACN M 18917) and *Thylatheridium* (MACN M 16719; Fig. 1E). This staggered pattern is widely distributed in marsupials (see Hershkovitz, 1995). The absence of the i5 alveolus in some didelphimorphians occurs because the alveolus of the i5 is shallower than the remainder alveolus and has a very thin labial, easily broken wall (as can be seen in many recent specimens of *Didelphis* too). The GHUNLPam 21722 clearly shares this pattern.

In conclusion, the GHUNLPam 21722 lacks diagnostic features that can be identified as representing a mustelid or even a carnivoran, and displays trenchant differences with the representatives of Mustelidae and Carnivora. Conversely, this material shows strong similarities with comparable parts of several fossil didelphimorphians. The claim of VM that the GHUNLPam 21722 is a mustelid is not supported and therefore the oldest unequivocally record of Mustelidae in South America remains that of *Galictis sorgentinii* from the Late Pliocene (Marplatan Age, *Vorohuean subage*).

Clearly, the efforts of Montalvo, Verzi, and several collaborators greatly expand our knowledge about faunal and environmental evolution during Mio-Pliocene times in central Argentina. But in order to avoid the potential implications arising from poorly-supported chronological and taxonomical hypotheses (for instance, the use of Caleufú records of Cricetidae and "mustelid" as late Miocene to calibrate molecular clocks), we contend here that (1) an Early Pliocene age for the Caleufú fauna could not be discarded, and the chronology of this locality has to be revised; and (2) the supposed mustelid could instead correspond to a didelphimorphian marsupial.

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