



BIOSTRATIGRAPHIC REASSIGNMENT OF THE NEOGENE CAENOLESTINES (MARSUPIALIA) OF THE PAMPEAN REGION: THE CASE OF *PLIOLESTES TRIPOTAMICUS* REIG, 1955

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Recibido: 12 de mayo de 2017 - **Aceptado:** 29 de junio de 2017

Para citar este artículo: Cecilia M. Deschamps, Germán M. Gasparini, Elisa Beilinson, Marcelo A. Zárate, and Rodrigo L. Tomassini (2017). Biostratigraphic reassignment of the Neogene Caenolestines (Marsupialia) of the Pampean Region: the case of *Pliolestes tripotamicus* Reig, 1955. *Publicación Electrónica de la Asociación Paleontológica Argentina* 17 (1): 24–30.

Link a este artículo: <http://dx.doi.org/10.5710/PEAPA.29.06.2017.243>

DESPLAZARSE HACIA ABAJO PARA ACCEDER AL ARTÍCULO

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Abstract. The stratigraphic reinterpretation of a controversial paleontological site such as the Quequén Salado River banks allowed refinement of the biochron of the caenolestine marsupial *Pliolestes tripotamicus* Reig. Two fossil bearing units were proposed for these exposures: a lower one, AUA (Huayquerian) and an upper one, AUB (Montehermosan). *P. tripotamicus* is found in AUA, but not in AUB or in typical Montehermosan and Chapadmalalan localities, which suggests that this taxon was not part of the Montehermosan–Chapadmalalan assemblages. The other species, *P. venetus* Goin *et al.* (Huayquerian), and Caenolestidae n. sp. aff. *P. tripotamicus* (Chasicuan) indicate the genus was restricted to the Chasicuan–Huayquerian stages/ages. The retraction of the caenolestines toward the Andean Region (where they live today) would have taken place at the beginning of the Pliocene, probably more related to environmental changes than to competence with cricetid rodents as first proposed.

Key words. Huayquerian. Montehermosan. Chapadmalalan. Quequén Salado River. Buenos Aires Province. *Pliolestes*.

Resumen. REASIGNACIÓN BIOESTRATIGRÁFICA DE LOS CENOLESTINOS NEÓGENOS (MARSUPIALIA) DE LA REGIÓN PAMPEANA: EL CASO DE *PLIOLESTES TRIPOTAMICUS* REIG, 1955. La reinterpretación estratigráfica de un sitio paleontológico controvertido, como las barrancas del río Quequén Salado, permitió ajustar el biocrón del marsupial cenolestino *Pliolestes tripotamicus* Reig. En estos afloramientos se identificaron dos unidades fosilíferas: una inferior, AUA (Huayqueriense), y una superior, AUB (Montehermosense). *P. tripotamicus* fue hallado en la unidad AUA, pero no en la AUB ni en localidades típicamente montehermosenses o chapadmalalenses. Esto sugiere que el taxón no fue parte de los elencos montehermosenses–chapadmalalenses. La otra especie, *P. venetus* Goin *et al.* (Huayqueriense), y Caenolestidae n. sp. aff. *P. tripotamicus* (Chasiquense) indican que el género se restringe a los pisos/edades Chasiquense–Huayqueriense. La retracción de los cenolestinos hacia la Región Andina, donde habitan actualmente, habría tenido lugar a comienzos del Plioceno, posiblemente más relacionada con cambios ambientales que con la competencia con roedores cricétidos como se había propuesto.

Palabras clave. Huayqueriense. Montehermosense. Chapadmalalense. Río Quequén Salado. Provincia de Buenos Aires. *Pliolestes*.

Acronyms. GHUNLPam, Geología Histórica Universidad Nacional de La Pampa, Santa Rosa, Argentina; MACN-Pv, Museo Argentino de Ciencias Naturales “B. Rivadavia”, Paleontología Vertebrados, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales “L. Scaglia”, Mar del Plata, Argentina.

THE BOUNDARIES of Neogene continental stratigraphic units in the central region of Argentina, as well as the associated vertebrate fauna, have been long debated from a geologic and biostratigraphic standpoint. The understanding of the stratigraphy and chronology of complex or controversial paleontological sites is essential for establishing the tempo-

ral and geographic ranges of the involved taxa. In turn, the taxonomy of the Neogene mammals is in constant progress, which forces the biostratigraphy to be continuously updated. However, the stratigraphic reinterpretations and taxonomic updates have often remained unnoticed and not taken into account in related papers. These two issues are

directly involved in the correlation of the South American Land Mammal Ages (Pascual *et al.*, 1965) or stages/ages (Cione and Tonni, 2005 and literature therein) to the global scale, which has changed with increasing knowledge and, mostly, when numerical ages became available.

Among others, the boundary between Huayquerian and Montehermosan stages/ages is one of the most controversial. When Pascual *et al.* (1965) proposed the scheme of South American Land Mammal Ages, this boundary was assigned to the base of the late Pliocene; it was later extended back into the late Miocene (*e.g.*, Cione and Tonni, 1995; Flynn and Swisher, 1995), and recently into the earliest Pliocene (Deschamps *et al.*, 2013; Tomassini *et al.*, 2013). The southeastern Buenos Aires Province is an outstanding area for the study of this interval because many reference localities, whose mammal associations are the basis for the construction of the biochronological sequence from South America, are located here.

In the area of the Quequén Salado River (Fig. 1), Neo-

gene deposits assigned to the “Irenean” (“Irenense”, Kraglievich, 1934) crop out. The “Irenean”, considered a single unit, was first correlated to the Montehermosan (Reig, 1955) and afterwards to the Chapadmalalan Age (Fidalgo *et al.*, 1975; Marshall *et al.*, 1983; Goin *et al.*, 1994). However, Verzi *et al.* (2008) suggested that at least those levels bearing the octodontid rodent *Xenodontomys ellipticus* Kraglievich, 1927 could be referred to the Huayquerian. In the last 20 years, the knowledge of the evolutionary lineages of several taxa, some of them represented in the Quequén Salado River valley, increased largely, *e.g.*, the octodontid rodents of the lineage *Chasichimys-Xenodontomys-Actenomys* (Verzi *et al.*, 2015 and literature therein). In addition, the new interpretation of the origin of the “Irenense” sediments (Beilinson *et al.*, 2015, 2017) supplied essential information for the understanding of the mammal fauna recorded in the banks of the Quequén Salado River.

On the basis of the stratigraphic reinterpretations (Beilinson *et al.*, 2017) and the improvement of the knowledge

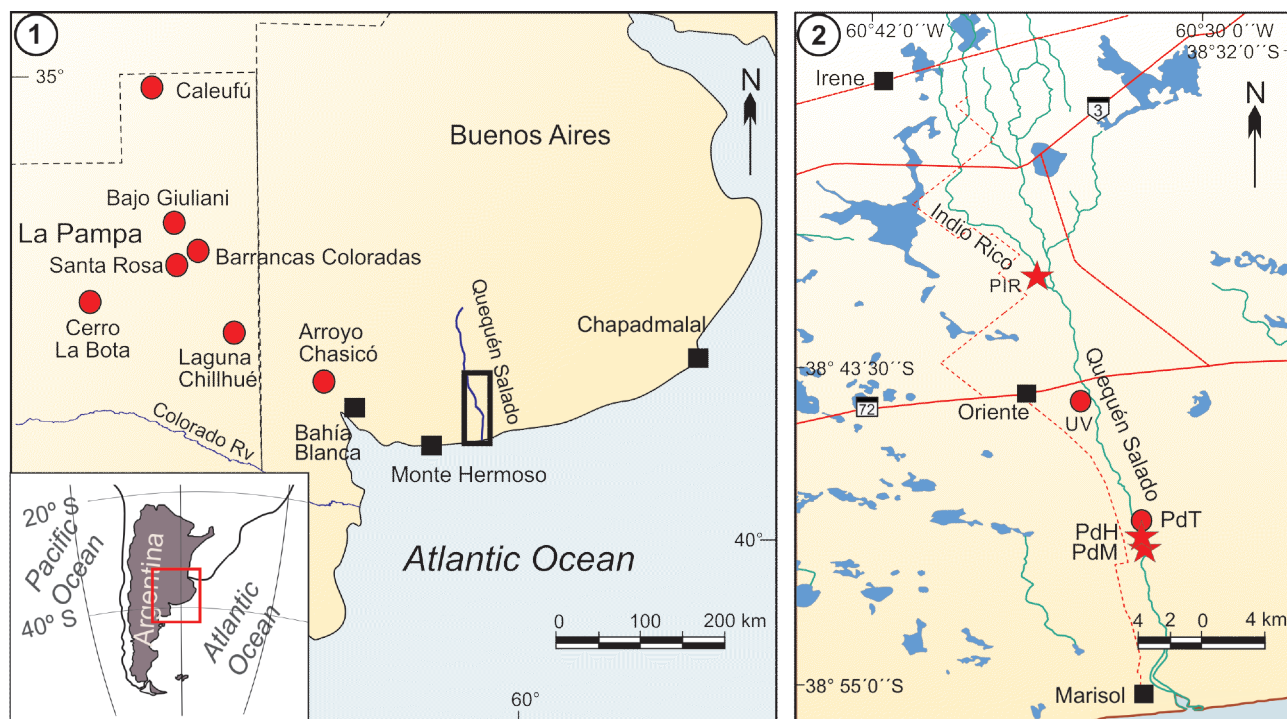


Figure 1. 1, Location map showing the paleontological sites mentioned in this contribution (red circles) and the area of Quequén Salado River. 2, Detail of the localities at the Quequén Salado River. PdH, Paso del Halcón; PdM, Paso del Médano; PdT, Paso de la Tufa; PIR, Paso del Indio Rico; Rv, River; UV, Usina Vieja. Red stars, localities in which *P. tripotamicus* was found.

of some lineages of rodents, the biostratigraphic distribution of the marsupial caenolestine *Pliolestes tripotamicus* Reig, 1955, and hence that of the whole genus, is presented herein. This Argentinean caenolestid is included in the Subfamily Caenolestinae (Goin *et al.*, 2009), Patagonian in origin, whose living representatives (*Caenolestes* Thomas, 1895 and *Rhyncholestes* Osgood, 1924) are restricted to cold and wet environments of the Andes from western Venezuela to southern Chile (Ojala-Barbour *et al.*, 2013).

Reig (1955, p. 67) defined *P. tripotamicus* based on the specimen MACN-Pv 9971 (Fig. 2.1–2) found in the Pliocene exposures of the Quequén Salado River banks, near Oriente Station of the Coronel Dorrego County, Buenos Aires Province (“...afloramientos pliocenos de las márgenes del río Quequén Salado, en las proximidades de la estación Oriente del Partido de Coronel Dorrego de la Provincia de Buenos Aires.”). These data are not precise enough to establish the type locality of this taxon. Two other specimens were found in Paso del Médano (see below), but Pardiñas *et al.* (in press) also mention other two from Paso del Halcón and El Paso (here known as Paso del Indio Rico), so the provenance of the type specimen can hardly be unraveled (see discussion in Pardiñas *et al.*, op. cit.). With respect to its stratigraphic origin, according to Reig (1955), the holotype was recovered from levels of the Irene “Formation” (“Irenense” *sensu* Kraglievich, 1927, 1934), considered at that moment as Montehermosan in age, which was conventionally assigned to the Upper Pliocene (“edad Montehermosiana, Plioceno superior”; *sic* Reig, 1955, p. 67).

So far, in addition to the holotype, there are four other specimens of this species. MLP 57-VII-23-49 (Fig. 2.3–4) was found by Pascual and Herrera (1973) in the right margin of the Quequén Salado River, at Paso del Médano. Goin *et al.* (1994, p. 17) described the specimen MLP 91-VII-2-1 (Fig. 2.5) also recovered from Paso del Médano (“... a unos 11 km aguas abajo del puente Copetonas-Oriente...”). The latter was first referred as *Pliolestes* cf. *P. tripotamicus*, and Abello (2007) confirmed it as *P. tripotamicus*. The third specimen (MLP 94-II-1-120) was referred by Abello (op. cit.) as coming from Paso de la Tufa, but this was rectified by Pardiñas *et al.* (in press) as coming from Paso del Halcón (Fig. 1). In addition, these authors reported a fourth specimen, yet unstudied, from El Paso (=Paso del Indio Rico).

Pliolestes venetus Goin *et al.*, 2000 is another species of the genus identified on the basis of two specimens (the holotype, GHUNLPam 2339, and GHUNLPam 5458) from Bajo Giuliani and Laguna Chillhué, respectively, La Pampa Province (Fig. 1), in outcrops of the Cerro Azul Formation (late Miocene, Huayquerian). According to Goin *et al.* (2000), this species is more generalized than *P. tripotamicus*.

Finally, Pascual and Herrera (1973) reported *Pliolestes* sp. (MMP 975M) from the Arroyo Chasicó Formation at its type locality (Fig. 1), Chasicóan Age, “conventionally lower Pliocene” *sensu* Pascual and Herrera (1973) and currently late Miocene (Cione and Tonni, 2005; Verzi *et al.*, 2008). Abello (2007, p. 155) stated that this specimen from Arroyo Chasicó had a unique combination of characters that suggests this is a new species related to the genus *Pliolestes*, but different, and referred to it as *Caenolestidae* n. sp. aff. *Pliolestes tripotamicus*.

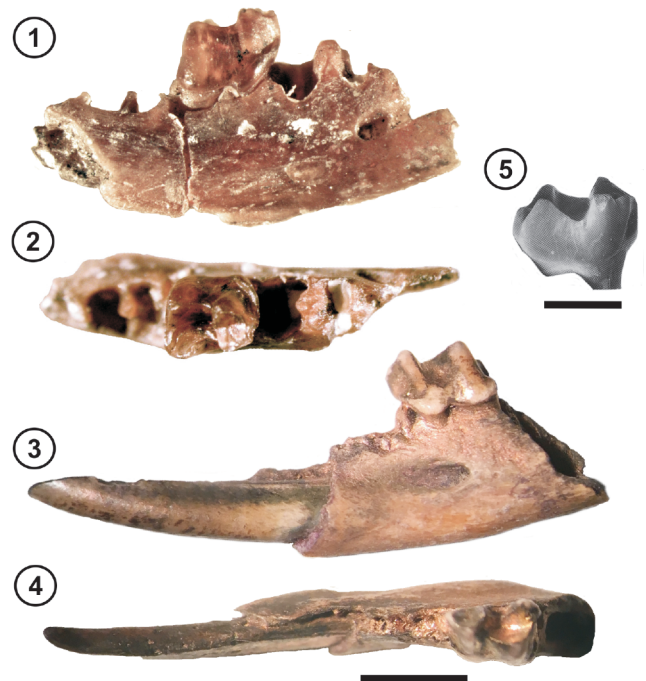


Figure 2. 1–4, *Pliolestes tripotamicus*. 1–2, holotype MACN-Pv 9971, left mandible with m2; 1, labial view; 2, occlusal view. 3–4, MLP 57-VII-23-49, left mandible with i1, p3-m1; 3, labial view; 4, occlusal view. 5, *Pliolestes* cf. *P. tripotamicus*, MLP 91-VII-2-1, left m3 in lingual view (modified from Goin *et al.*, 1994). Scale equals 2.5 mm (1–4) and 1 mm (5).

Taking into account the temporal assignment of the bearing levels of *P. tripotamicus*, it was considered that the last record of caenolestines in the Pampean Region reached the late Pliocene (Abello, 2013), suggesting interesting evolutionary and paleobiogeographic issues (Pascual and Herrera, 1973; Goin *et al.*, 1994).

DISCUSSION

The Neogene sedimentary succession exposed at the Quequén Salado River valley is 10 m thick, mainly made up of fine to medium sandstones, silty sandstones, and siltstones; silty claystones are scarce. Beilinson *et al.* (2017) divided the sedimentary record into two allostratigraphic units informally named AUA (lower) and AUB (upper), bounded by a stratigraphic discontinuity exposed at Paso del Indio Rico.

AUA is exposed at Paso del Indio Rico, Usina Vieja (2 km downstream of the old electric factory), Paso de la Tufa, Paso del Halcón, and Paso del Médano (Fig. 1). This unit yielded remains of *Xenodontomys ellipticus*, *Lagostomus* sp., *Pliolestes tripotamicus*, *Argyrolagus* sp., and *Paedotherium minor* Cabrera, 1937, among others. The record of *X. ellipticus* allows correlation with the late Huayquerian (Verzi *et al.*, 2008). This taxon is part of a late Miocene biochronological succession of the Pampean Region (Fig. 3), constrained by paleomagnetic data and numerical ages (Deschamps, 2005; Verzi *et al.*, 2008; Tomassini *et al.*, 2013; Deschamps and Tomassini, 2016). This rodent was found in Cantera Vialidad (Bahía Blanca), among other localities, where the bearing level is constrained by a dating of 5.28 ± 0.04 Ma (Schultz *et al.*, 2006; Folguera and Zárate, 2009; see Deschamps and Tomassini, 2016, and Beilinson *et al.*, 2017 for updating data on rodent record correlations and stratigraphic interpretations).

AUB was recognized in several localities of the Quequén Salado River (Beilinson *et al.*, 2017). In this unit, numerous taxa were found, such as *Eumysops laeviplicatus* Ameghino, 1888, *Paramyocastor diligens* (Ameghino, 1888), *Actenomys priscus* (Owen, 1840), *Lagostomus incisus* Ameghino, 1888, *Pseudoplateomys* sp., *Orthomyctera* sp., Phyllotini indet., *Paedotherium bonaerense* Ameghino, 1887, *Proscelidodon patrius* Ameghino, 1889, and *Parahyaenodon argentinus* Ameghino, 1904, among others. This assemblage, especially the record

of *E. laeviplicatus*, suggests a Montehermosan age. Reig (1958) reported *Phugatherium catacliticum* Ameghino, 1887 from Paso del Indio Rico, which is a key taxon for the Montehermosan, but this specimen has no precise stratigraphic provenance (Deschamps *et al.*, 2013; Vucetich *et al.*, 2014).

Pliolestes tripotamicus was recorded at Paso del Médano (Pascual and Herrera, 1973; Goin *et al.*, 1994), Paso del Halcón, and Paso del Indio Rico (Pardiñas *et al.*, in press). In turn, *Xenodontomys ellipticus* was recorded at Paso del Médano (Verzi *et al.*, 2008), Paso del Halcón, Paso de la Tufa (Pardiñas *et al.*, in press), and Paso del Indio Rico (Verzi *et al.*, 2008; Beilinson *et al.*, 2017). *P. tripotamicus* has not been recorded either in AUB or in the type localities of the Montehermosan and Chapalmalalan, both with large collections of mammals. In support of discarding a bias in the record because of the small size of caenolestines, it can be argued that a large amount of small mammal remains has been found in both Montehermosan and Chapadmalalan collections.

According to the correlation proposed above, the bearing levels of *P. tripotamicus* can be assigned to the late Huayquerian (latest Miocene–earliest Pliocene). From a biostratigraphic point of view, the caenolestines would have been represented in the Pampean Region by Caenolestidae n. sp. aff. *Pliolestes tripotamicus* (Abello, 2007) in the Chasican, and by *P. venetus* and *P. tripotamicus* in deposits correlated with the Huayquerian, with no other fossil record since the Montehermosan (see Abello, 2013: tab. 1). Therefore, *P. tripotamicus* would be the youngest representative and the last record of caenolestines in the Pampean Region (Fig. 3). Since that moment, their fossil record shows a gap until their current presence in the Andean Region, where they live in cold and wet environments from Venezuela to southern Chile. This geographic retraction has been explained by competence with Holarctic immigrants, such as cricetid rodents (Pascual and Herrera, 1973), or related to paleoclimatic events triggered by the uplift of the Andes (Abello, 2013 and literature therein). Concerning the competence proposal, the oldest cricetids so far recorded in the Pampean Region are those from the Cerro Azul Formation exposed in La Pampa Province at Caleufú (Verzi and Montalvo, 2008) and Santa Rosa (Laguna Don Tomás; Montalvo *et al.*, 2009), both localities temporarily close and assigned to the latest Huayquerian Age (Fig. 3), where *Pliolestes* is not

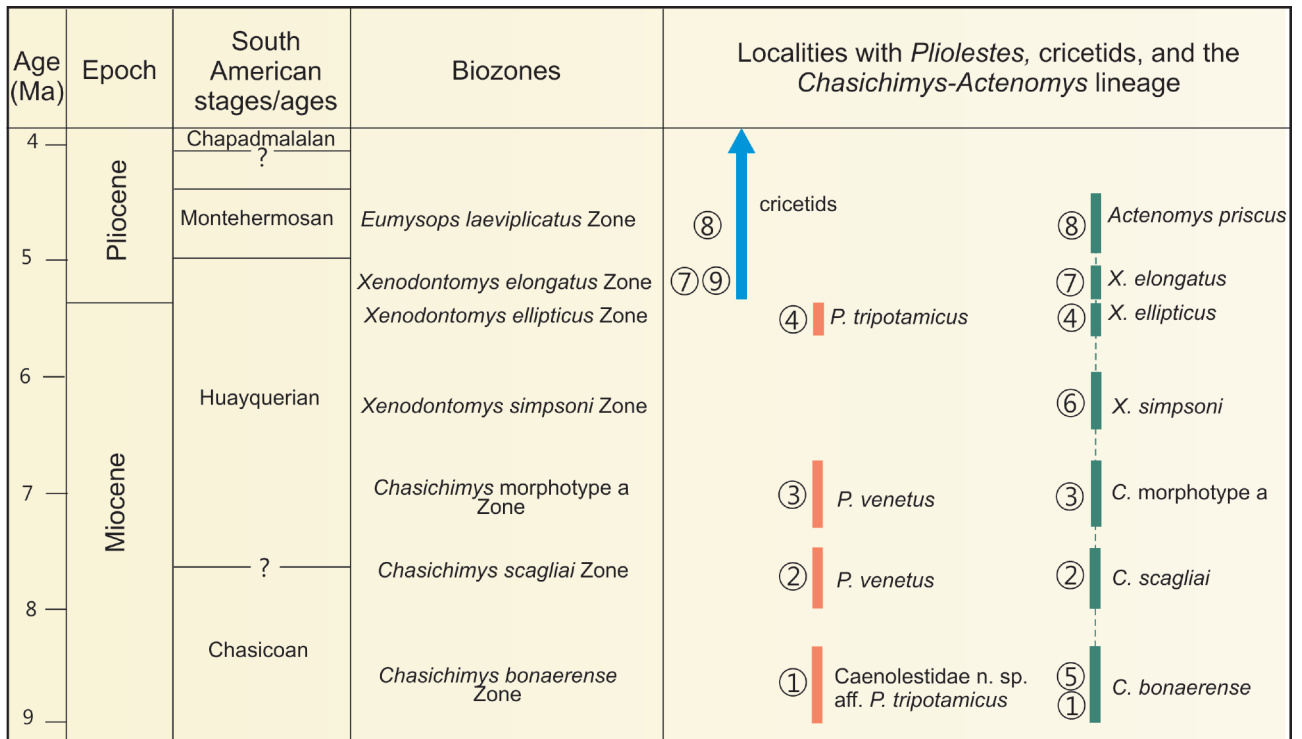


Figure 3. Biostratigraphic chart with the record of *Pliolestes* and the *Chasichimys-Actenomys* lineage. 1, Arroyo Chasicó Formation; 2, Laguna Chillhué; 3, Bajo Giuliani; 4, AUA at the Quequén Salado River; 5, Cerro La Bota; 6, Barrancas Coloradas; 7, Caleufú; 8, Monte Hermoso Formation; 9, Laguna Don Tomás, Santa Rosa. 2–3 and 5–7, Cerro Azul Formation. Note: *X. ellipticus* is also found in other localities near Bahía Blanca (see Deschamps and Tomassini, 2016), *A. priscus* is a common taxon in Pliocene sediments, and cricetids are well recorded since the late Pliocene. South American stages/ages follow Beilinson *et al.* (2017 and literature therein).

present. The age of Caleufú, based on the record of *X. elongatus*, was debated by Prevosti and Pardiñas (2009, p. 543) who stated "...the possibility that the Caleufú assemblage has an Early Pliocene (Montehermosan) age." Caleufú (where *X. elongatus* Range Zone was defined; Fig. 3) may be Pliocene in age considering the dating of Cantera Vialidad (5.24 ± 0.04 Ma) associated with *X. ellipticus*; however, the assemblage suggests a Huayquerian rather than a Montehermosan age (see discussion in Deschamps and Tomassini, 2016). Cricetids then became abundant and diversified, with a first radiation pulse (Barbiere *et al.*, 2016), when *Pliolestes* is no longer present in the region (Fig. 3) according to the current records. So far, there is no evidence suggesting coexistence of caenolestines and cricetids.

Regarding the paleoclimatic events, Abello *et al.* (2010) mentioned the increasing aridity resulting from the uplift of the Andes to explain the biogeographic distribution of the caenolestines. This aridization was also inferred for the late

Miocene of the Pampean Region (Chasicoan–Huayquerian) through the analysis of the hypsodonty of octodontid rodents (Verzi, 1999; Verzi *et al.*, 2008).

The western retraction of caenolestines toward the Andes would have taken place at the end of the Miocene or the beginning of the Pliocene and not at the end of the Pliocene, as previously thought (Montehermosan *sensu* Pascual and Herrera, 1973; Chapadmalalan *sensu* Goin *et al.*, 1994; Abello, 2013).

The approach of a detailed stratigraphic analysis together with taxonomic updates of the involved taxa at a complex site such as the exposures of the Quequén Salado River valley allowed refining the temporal and geographic ranges of caenolestines of the Pampean Region. Therefore, future studies can deepen the previous proposals and explore alternative working hypotheses on the causes of their absence in the fossil record since the early Pliocene.

ACKNOWLEDGEMENTS

The authors thank M. Reguero for access to material housed in the Museo de La Plata; L. Cruz for providing the photograph of MACN-PV 9971; two anonymous reviewers and the editors for comments that contributed to improve the manuscript. This paper was partially funded by Grant PIP 0496 (Consejo Nacional de Investigaciones Científicas y Técnicas).

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Doi: 10.5710/PEAPA.29.06.2017.243

Recibido: 12 de mayo 2017

Aceptado: 29 de junio 2017