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HISTORIA EVOLUTIVA Y PALEOBIOGEOGRÁFICA DE LOS VERTEBRADOS DE AMÉRICA DEL SUR

Evolutionary history of South American Paucituberculata (Mammalia: Marsupialia)

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Abstract: *Historia evolutiva de los Paucituberculata (Mammalia: Marsupialia) de América del Sur*. Paucituberculatan marsupials are a group of Metatheria with a long evolutionary history (early Eocene-Recent) exclusively recorded in South America. This contribution presents a synthetic overview of the knowledge on their evolution, paleoecology and paleobiogeography. It is offered the current view of their phylogenetic origin and changes in their taxonomic diversity through time, emphasizing the main steps in their evolution. The paleoecological inferences for species, considering locomotion, diets and body masses, are noted; likewise, some aspects of the historical biogeography of the main paucituberculatan clades, taking into account their geographical ranges during the Cenozoic, are remarked. Finally, the main perspectives to be addressed in the study of paucituberculatans are highlighted.

Key words: Caenolestidae, Palaeothentidae, Abderitidae, Palaeoecology, Paleobiogeography.

Resumen: *Evolutionary history of South American Paucituberculata (Mammalia: Marsupialia)*. Los marsupiales Paucituberculata constituyen un grupo de Metatheria con una larga historia evolutiva (Eoceno temprano- Reciente) registrada exclusivamente en América del Sur. Esta contribución presenta una síntesis del conocimiento de este grupo en cuanto a su evolución, paleoecología y paleobiogeografía. Se ofrece la visión actual sobre su origen filogenético y cambios en su diversidad taxonómica a través del tiempo, poniendo énfasis en las principales etapas de su evolución. Se menciona la ecología de las especies extintas, en términos de locomoción, dietas y masas corporales inferidas y se comentan aspectos de la biogeografía histórica de los principales clados de paucituberculados, teniendo en cuenta sus distribuciones geográficas a lo largo del Cenozoico. Finalmente, se resaltan las principales perspectivas a desarrollar en el estudio de los paucituberculados.

Palabras Clave: Caenolestidae, Palaeothentidae, Abderitidae, Palaeoecología, Paleobiogeogeografía.

INTRODUCTION

Geographic isolation of South America occurred during an important part of the Cenozoic (early-middle Eocene-Pliocene), promoting the evolution of many endemic therian groups (Wilf *et al*., 2013). Among them are the paucituberculatan marsupials which, along with the Didelphimorphia, Microbiotheria, Polydolopimorphia, and Sparassodonta, are one of the major clades of metatherians that have evolved in this continental area. Paucituberculatans, didelphimorphs, and microbiotherians are the only South American Metaherian groups that have survived up to the present. The evolutionary history of paucituberculatans spans at least 50 Ma (early Eocene-Recent; see below), and their paleontological record shows that, in contrast with the restricted Andean distribution of the extant forms, they were more widely distributed. Their fossil record includes species coming from Paleogene sites of Peru, Bolivia, Brazil and Argentina, and Neogene sites of Colombia, Bolivia, Chile and Argentina (Abello, 2013: table1). Taking into account these geographic and temporal ranges, the evolution of paucituberculatans is expected to have been shaped by the deep paleogeographic and climatic-environmental changes happened during the Cenozoic in South America (Ortiz-Jaureguizar & Cladela, 2006; Woodburne *et al*., 2014b).

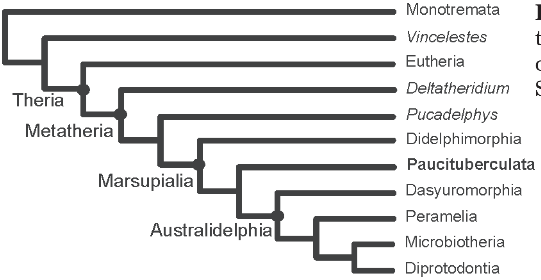

Figure 1. Phylogenetic tree showing the relationships of living marsupial orders (modified from Horovitz & Sanchez-Villagra, 2003).

In the following it is offered a synthetic overview of the current knowledge about evolution, paleoecology and paleobiogeography of paucituberculatans. In addition, the main perspectives to be addressed in their study are highlighted.

ORIGIN, EVOLUTION AND DIVERSITY

Most phylogenies indicate that paucituberculatans are the sister-group of the Australidelphia (i.e., Microbiotheria + Australasian marsupials, Szalay, 1982a; e.g., Beck, 2008; Horovitz and Sanchez Villagra 2003; Figure 1). However, there is also certain support for the Ameridelphia hypothesis (i.e., Didelphimorphia + Paucituberculata; e.g., Burk *et al.*, 1999) as well as for a sister-group relationship between Paucituberculata and Peramelia (Ladevèze & Muizon, 2010) or between Paucituberculata and the remaining marsupials (May Collado *et al.*, 2015). While time-calibrated molecular phylogenies push their origin back into the upper Cretaceous (76.5 Ma; Beck 2008; 71–86 Ma Meredith et al., 2008), the fossil record can be traced back only up to the early Eocene (about 53 – 50 Ma; Woodburne *et al.*, 2014a). The first paucituberculatans are registered in the early Eocene of Brazil and Patagonia where they are represented by the basal taxa *Riolestes* and *Bardalestes* (Goin *et al.*, 2009), respectively. Then, about the early–middle Eocene, two clades were differentiated, Caenolestoidea and Palaeothentoidea, representing the major cladogenetic event in the whole group (Figure 2, nodes 1 and 2). Caenolestoids (Figure 2, node 1) include seven extant species, which are grouped in the genera *Lestoros*, *Rhyncholestes* and *Caenolestes* (Ojala-Barbour *et al.*, 2013), and six extinct species (Abello, 2007). This clade has a long ghost lineage from their early–middle Eocene origin up to their first fossil record in the early Miocene (Colhuehuapian age) from Patagonia. At that time, extinct caenolestoids shows their highest diversity with three genera and species, and the lineages leading to modern caenolestids and to *Pliolestes*. On the other hand, Palaeothentoids (Figure 2, node 2) are the most specious paucituberculatan clade. It includes 41 species, 18 genera, and three main groupings: Pichipilidae (Figure 2, node 3), Palaeothentidae (Figure 2, node 7) and Abderitidae (Figure 2, node 6) (Abello, 2013; Rincon *et al.*, 2015). The major diversity of palaeothentoids occurred in the early Miocene (Coulhuehuapian to Santacrucian ages). However, the radiation that gives rise to most of non-Pichipilidae palaeothentoids (NPP; e.g., *Pilchenia* clade, palaeothentids and abderitids; Figure 2, node 4) is inferred to have occurred near the Eocene–Oligocene boundary (EOB; Goin *et al.*, 2010; Abello, 2013). This evolutionary process seems to have been linked to the climatic-environmental changes occurred at the EOB, which had strongly affected the metatherian assemblages of South America (Goin *et al.*, 2010; Goin *et al.*, 2015). Among paucituberculatans not only new lineages emerged, but morphological disparity appears to have increased as well (see below). During the early to middle Miocene (Colhuehuapian to Friasian ages) paucituberculatans have their highest diversity being represented by all the

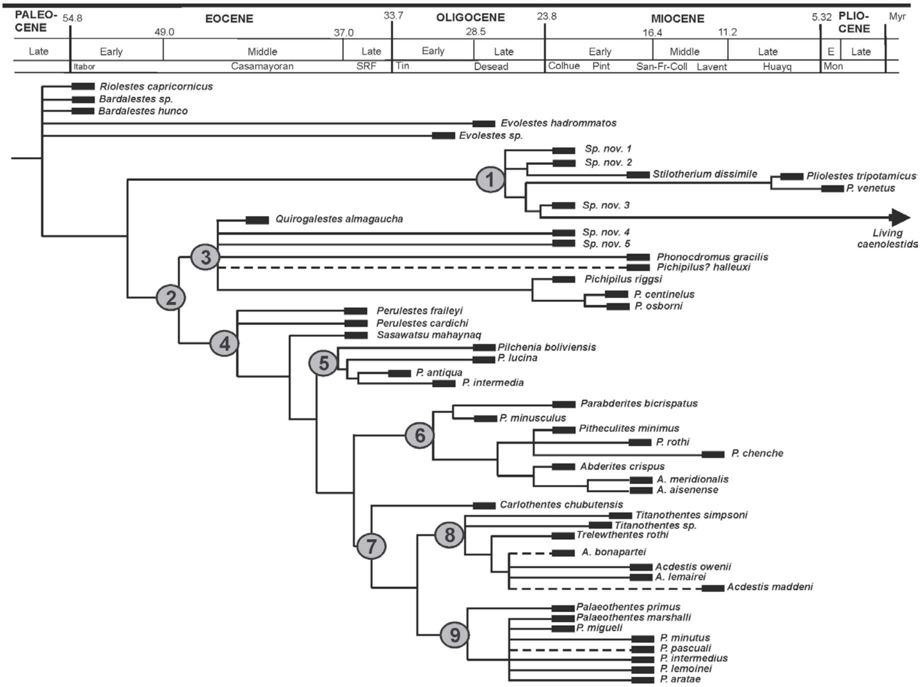

Figure 2. Time-calibrated phylogeny of Paucituberculata based on relationships recovered in the strict consensus tree produced by the analysis of the reduced matrix under implied weights, after STR, performed by Abello (2013). Taxonomic equivalents are included following the methodology of Wilkinson (1995; 2001). Heavy lines = known temporal ranges; thin lines = missing ranges; dashed lines = expected origin of taxonomic equivalents. Main paucituberculatan clades mentioned in the text: 1- Caenolestoidea, 2- Palaeothentoidea, 3- Pichipilidae, 4- non-Pichipilidae palaeothentoids (NPP), 5- *Pilchenia*, 6- Abderitidae, 7- Palaeothentidae, 8- Acdestinae; 9, Palaeothentinae. Geochronological units, mammal ages, and faunas: Itabor, Itaboraian; SRF, Santa Rosa Fauna; Tinguir, Tinguirirican; Desead, Deseadan; Colhue, Colhuehuapian; Pint, Pinturan Fauna; Sant–Fr–Coll, Santacrucian, Friasian, and Colloncuran; Lavent, Laventan; Huay, Huayquerian; Mon, Montermosan.

major groups (caenolestids, pichipilids, palaeothentids and abderitids). Species diversity drops markedly from the middle Miocene, time of the last records of pichipilids (*Pichipilus*? *haleuxi*, Friasian age from Chile), palaeothentids (*Acdestis* and *Hondathentes* Laventan age from Bolivia and Colombia, respectively) and abderitids (*Pitheculites* Laventan age from Colombia). During the late Miocene only the caenolestids persisted, represented by *Pliolestes* (late Miocene-Pliocene from Central Argentina) and the lineage leading to extant paucituberculatans.

PALEOECOLOGY

The knowledge about the ecology of extinct paucituberculatans mainly comes from the study of dental morphology, since to date most of species are only known by dental remains. Relatively complete cranial remains are scarce and only three postcrania are known, which were referred to two palaeothentid species (*Palaeothentes minutus* and *P. lemoinei*; Abello & Candela, 2010; Forasiepi *et al*., 2014). Morphofunctional studies carried out indicate that these palaeothentid species were agile curso-saltatorial forms, like the extant caenolestid *Caenolestes* and the didelphid *Metachirus* (Abello

& Candela 2010; Forasiepi *et al.*, 2014). From the analysis of molar morphology, estimations of body mass and dietary inferences were made for a large variety of paucituberculatans (Dumont *et al.*, 2000; Abello *et al.*, 2012, Zimics, 2012). Taking both ecological parameters, caenolestids and pichipilids were reconstructed as small insectivorous and insectivore-frugivore species with body masses ranging from 8g to 120g. In contrast, for palaeothentids and abderitids a wider ecological diversity of species was inferred, with body masses ranging from 25g to 1,271 g and diets that include insectivory, insectivory-frugivory and frugivory (Dumont *et al.*, 2000; Zimics, 2012; Abello *et al.*, 2012; Abello *et al.*, 2015).

A recent analysis of paucituberculatan body mass evolution evidenced that caenolestids and pichipilids were small (8-120g) during all of their evolutionary history. In contrast, this analysis showed that NPP (e.g. *Pilchenia*, Abderitidae and Palaeothentidae) developed, from a medium size ancestor (400g), a wider body mass spectrum, with estimations ranging from 35g to 1,271g (Abello *et al.*, 2015). This increase of body mass disparity happened during the diversification of NPP posterior to EOB. It was suggested that this represents an adaptive radiation that could have been triggered by climatic-environmental changes and the demise of other small potentially competing metatherian groups (e.g. polydolopids and basal "Ameridelphia") (Abello et al., 2015).

During the Miocene, when paucituberculatans were highly diverse, they constituted an important component in the micromammal assemblages. At this time, they coexisted with other small non-carnivorous metatherians as microbiotheriids and, at limited localities, with polydolopimorphian argyrolagids and didelphimorph didelphoids (e.g., Goin *et al.*, 2000). The study of an association of non-carnivorous metatherians from the Santacrucian of Patagonia (late-early Miocene; Abello *et al.*, 2012), suggested that the ecological diversity of paucituberculatans and microbiotherids was probably correlated with the habitat complexity. Among paucituberculatans small-to medium-sized insectivorous, small-to medium-sized insectivorous-frugivorous, and medium-to large sized frugivorous, were reconstructed. As the vertical heterogeneity offers an additional dimension for niche partitioning, it was suggested that along the curso-saltatorial locomotion inferred for palaeothentid species, scansorial and/or arboreal habits could have developed among the coexisting paucituberculatans in order to exploit the available resources in the vertical space.

PALEOBIOGEOGRAPHY

Differently to other metatherians as microbiotherians, polydolopimorphians and "didelphimorphians", paucituberculatans were not registered in Antarctica or North America (Case *et al.*, 2004; Goin *et al.* 1999; Chornogubsky *et al.*, 2009). This stands the idea that, at least from the geographic range of extinct and extant species, paucituberculatans are endemic to South America. However, as dating molecular phylogenies push their origin back into the late Cretaceous (Campanian), and no paucituberculatans are known for the Cretaceous or Paleocene from South America, it was suggested that they could have originated in Laurasia (Beck, 2008). In this biogeographic scene, paucituberculatans could have dispersed to South America in the latest Cretaceous–earliest Paleocene as assumed did other mammalian groups (Woodburne *et al.*, 2014b).

The oldest paucituberculatan records from the early Eocene sites of Brazil and Patagonia, show an early wide latitudinal distribution of the group. With the exception of the Pichipilidae, which had a fossil record restricted to Patagonia, a relatively widespread distribution is also apparent for the less inclusive Palaeothentoid clade. By the middle Eocene, probably shortly after its origin (early-middle Eocene, see above), palaeothentoids are recorded in middle Eocene deposits of Patagonia (*Quirogalestes*; Goin & Candela, 1998) and late Eocene deposits of Peru (e.g. *Perulestes*; Goin & Candela, 2004; Antoine *et al*, 2016). During the Oligocene and Miocene the main NPP groups (*Pilchenia*, Abderitidae, Paleothentinae and Acdestinae; Figure 2, nodes 5, 6, 8 and 9, respectively) appears widely distributed with records in Oligocene sites of Bolivia, Peru, and Patagonia (*Pilchenia*, palaeothentids, and abderitids; Abello, 2007; Rincon *et al*., 2015; Antoine *et al*., 2016) and Miocene sites of Patagonia, Bolivia and Colombia (e.g. abderitids and palaeothentids, Abello, 2007). It appears that, from their origin up to their extinction, palaeothentoids were widely distributed throughout South America.

In contrast to palaeothentoids, the early history of the caenolestoids (early–middle Eocene to early Miocene) is still unknown. Since no caenolestoids are recognized in well-known Paleogene mammal assemblages, as those from Patagonia and Peru (e.g., Goin & Candela, 2004; Goin *et al*., 2010; Antoine *et al*., 2016), it was suggested that it could have occurred in areas with yet under sampled Paleogene levels (Abello, 2013). Extinct caenolestids have their fossil record restricted to Patagonia and central Argentina (Goin *et al*., 2000; Abello, 2007) while extant species are distributed discontinuously in the Andes from Venezuela to southern Argentina and Chile (Brown, 2004; Martin, 2011; Ojala-Barbour *et al*., 2013). A study of the historical biogeography of caenolestids found that the changing paleogeography of South America, from the late Oligocene to the present, can explain the observed distribution patterns (Abello *et al*., 2010). Among the inferred geological events promoting vicariance, were the successive Atlantic transgressions during the late Oligocene–early Miocene in Patagonia (Malumian & Nañez, 2011), and during the middle to late Miocene in extensive areas of South America (Hernández *et al*., 2005). In addition, uplifting of the Andes in the middle Miocene (Quechua Phase of the Andean Orogeny), was proposed as the geological event driving cladogenesis within the clade of extant caenolestids, as xeric conditions were then developed in the Andes (Abello *et al*., 2010).

FINAL REMARKS

Knowledge about the extinct Paucituberculata goes back to the prominent work of Carlos and Florentino Ameghino of the end of 19th century and beginnings of 20th century (e.g, Ameghino, 1887; Ameghino, 1900–1902). Since then, diverse contributions have increased our understanding of their taxonomic diversity, phylogenetic relationships, and paleobiology (e.g., Marshall, 1980; for a review see Abello, 2007 and Abello, in preparation). Despite this bulk of knowledge, studies are still needed in relation to several aspects of their evolution. Among the most notable are those about their origin and early history. Considering their phylogenetic origin, several hypotheses of their closest phylogenetic relationships within Metatheria were proposed. Most phylogenetic analysis, based on morphological and/or molecular data, favor a sister-group relationship with Australidelphia. However, this and other hypotheses were still poorly explored in more inclusive analyses of metatherians, e.g., those including most extinct South American lineages (Ladevèze & de Muizon, 2010; Beck, 2012). Thus, the phylogenetic position of the Paucituberculata among Metatheria is still contentious. On the other hand, their poorly-known earliest history would be due to the scarce Paleogene fossil record. If their Cretaceous origin were correct (see above), then a gap of about 27 M.a. (Campanian–early Eocene) is evident in the paucituberculatan fossil record. An equivalent gap (early–middle Eocene- early Miocene, see above) is also apparent in the fossil record of the caenolestoids. Thereby, to the extent that more knowledge of the South American

Paleogene mammal assemblages is produced, it is expected that the earliest steps in the paucituberculatan evolution could be elucidated.

In relation to the paucituberculatan paleobiology, there have been major advances in the reconstruction of their ecological niches and in the analysis of their ecological evolution in the context of the climatic-environmental changes occurred during the Cenozoic (Dumont, 2000; Abello & Candela, 2010; Zimics, 2012; Abello *et al*., 2012; Abello *et al*., 2015; Goin *et al*., 2015; Goin *et al*., in press). Future studies should be extensive to the whole recognized extinct species, as well as, ecological studies should move forward considering phylogenetic information (Abello & Ortiz Jaureguizar, 2009: Abello *et al*., 2010; Abello *et al*., 2015).

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REFERENCES

Abello, M.A. 2007. Sistemática y bioestratigrafía de los Paucituberculata (Mammalia, Marsupialia) del Cenozoico de América del Sur. Thesis, Universidad Nacional de La Plata. Available at: http://naturalis.fcnym.unlp.edu.ar/id/ 20120126000025

Abello, M.A. 2013. Analysis of dental homologies and phylogeny of Paucituberculata (Mammalia: Marsupialia). *Biological Journal of the Linnean Society* 109: 441-465.

Abello, M.A. & A.M. Candela 2010. Postcranial skeleton of the Miocene marsupial *Palaeothentes* (Paucituberculata, Palaeothentidae): paleobiology and phylogeny. *Journal of Vertebrate Paleontology* 30: 1515-1527.

Abello, M.A. & E. Ortiz Jaureguizar. 2009. Climatic environmental changes and body mass evolution in South American mammals: the Abderitidae's case (Marsupialia: Paucituberculata). *X International Mammalogical Congress, Actas* 331A-332A.

Abello, M.A., P. Posadas & E. Ortiz-Jaureguizar. 2010. Biogeografía histórica de los Caenolestidae (Marsupialia, Paucituberculata) del Cenozoico de América del Sur. *X Congreso Argentino de Paleontología y Bioestratigrafía y VII Congreso Latinoamericano de Paleontología, Actas* R189: 128.

Abello, M.A., E. Ortiz-Jaureguizar & A.M. Candela. 2012. Paleoecology of the Paucituberculata and Microbiotheria (Mammalia, Marsupialia) from the late early Miocene of Patagonia. In: Kay R., Vizcaíno, S. & S. Bargo, (eds.), *Paleobiology in Patagonia. Reconstructing a high-latitude paleocommunity in the early miocene climatic optimum*. Cambridge: Cambridge University Press, 156-172.

Abello, M.A., N. Toledo & E. Ortiz-Jaureguizar. 2015. Evolución del tamaño corporal y radiación evolutiva de los Paucituberculata (Mammalia: Marsupialia) durante el Cenozoico de America del Sur. Reunión de Comunicaciones de la Asociación Paleontológica Argentina (RCAPA 2015), Mar del Plata. Resúmenes: 10.

Abello, M.A. in preparation. Paucituberculata, In: F.J. Goin & A. Forasiepi (eds.) *New World Marsupials and their Extinct Relatives: One Hundred Million Years of Metatherian Evolution*. Springer, Berlin.

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia austral. Boletín del Museo de La Plata 1: 1-26.

Ameghino, F. 1900-1902. L'âge des formations sédimentaires de Patagonia. *Anales de la Sociedad Científica Argentina* L: 109-130, 145-165, 209-229 (1900); LI: 20-39, 65-91 (1901); LII: 189-197, 244-250 (1901); LIV: 161-180, 220-249, 283- 342 (1902).

Antoine, P.O., Abello, M.A., Adnet, S., Sierra, A.J.A, Baby, P., Billet, G., Boivin, M., Calderon, Y., Candela, M.A., Chabain, J., Corfu, F., Croft, D.D., Ganerød, M., Jaramillo, C., Klaus, S., Marivaux, L., Navarrete, R.E., Orliac, M.J. & F. Parra. 2016. A 60-million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Research*

31: 30-59.
Beck, R.M.D. 2008. A dated phylogeny of marsupials using a molecular supermatrix and multiple fossil constraints. *Journal of Mammalogy* 89: 175-189.
Beck, R.M.D. 2012. An 'ameridelphian' marsupial from the early Eocene of Australia supports a complex model of Southern Hemisphere marsupial biogeography. *Die Naturwissenschaften* 99: 715-729
Brown, B.E. 2004. Atlas of New World Marsupials. *Fieldiana Zoology*, new series 102, 308 pp.
Burk, A., M. Westerman, D.J. Kao, J.R. Kavanagh & M.S. Springer. 1999. An Analysis of Marsupial Intraordinal Relationships Based on 12S rRNA, tRNA Valine, 16S rRNA, and Cytocrome *b* Sequences. *Journal of Mammalian Evolution* 6(4): 317-334.
Case, J.A., F.J. Goin & M.O. Woodburne. 2004. "South American" marsupials from the Late Cretaceous of North America and the origin of marsupial cohorts. *Journal of Mammalian Evolution* 11(3-4): 223-255.
Chornogubsky, L., F.J. Goin & M. Reguero. 2009. A reassessment of Antarctic polydolopid marsupials (Middle Eocene, La Meseta Formation). *Antarctic Sciences* 21(3):285-297.
Dumont, E.R., S.G. Strait & A.R. Friscia. 2000. Abderitid marsupials from the Miocene of Patagonia: an assessment of form, function, and evolution. *Journal of Paleontology* 74: 1161-1172.
Goin F.J. & A.M. Candela. 1998. Dos nuevos marsupiales 'Pseudodiprotodontes' del Eoceno de Patagonia, Argentina. *Asociación Paleontológica Argentina. Publicación Especial Paleógeno de América del Sur y de la Península Antártica* 5: 30-12.
Goin F.J., & A.M. Candela. 2004. New Paleogene Marsupials from the Amazon Basin of Eastern Perú. In: Campbell Jr. K.E. (ed.) *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru*, Natural History Museum of Los Angeles County, sciences series, 40. Los Angeles: Natural History Museum of Los Angeles County, 15-60.
Goin, F.J., J.A. Case, M.O. Woodburne, S.F. Vizcaíno & M.A. Reguero. 1999. New discoveries of "opposum-like" marsupials from Antarctica (Seymour Island, Medial Eocene). *Journal of Mammalian Evolution* 6(4): 335-365.
Goin F.J., C.I. Montalvo & G. Visconti. 2000. Marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (provincia de La Pampa, Argentina). *Estudios Geológicos* 56: 101-126.
Goin F.J., A.M. Candela, M.A. Abello & E.V. Oliveira. 2009. Earliest South American paucituberculatans and their significance in the understanding of 'pseudodiprotodont' marsupial radiations. *Zoological Journal of the Linnean Society* 155: 867-884.
Goin F.J., M.A. Abello & L. Chornogubsky. 2010. Middle Tertiary Marsupials from Central Patagonia (Early Oligocene of Gran Barranca): understanding South America's Grande Coupure. In: Madden R., Carlini F., Vucetich G. & Kay R. (eds) *The paleontology of Gran Barranca: evolution and environmental change through the middle Cenozoic of Patagonia*. Cambridge: Cambridge University Press, 69-105.
Goin F.J., M.O. Woodburne, A.N. Zimicz, G.M. Martin, & L. Chornogubsky. 2015. *A Brief History of South American Metatherians: Evolutionary Contexts and Intercontinental Dispersals*. Springer Earth System Sciences, Springer, New York, 237 pp.
Goin F.J., N. Zimicz, A.M. Forasiepi, L.C. Chornogubsky & M.A. Abello. In press. The rise and fall of South American metatherians: contexts, adaptations, radiations, and extinctions. In: Rosenberger A.L. & Tejedor M.F. (eds.) *Origins and evolution of Cenozoic South American mammals*. Springer, New York.
Hernández R.M., T.E. Jordan, A.D. Farjat, L. Echavarría, B.D. Idleman & J.H. Reynolds. 2005. Age, distribution, tectonics, and eustatic controls of the Paranense and Caribbean marine transgressions in southern Bolivia and Argentina. *Journal of South American Earth Sciences* 19(4): 495-512.
Forasiepi, A.M., M.R. Sánchez-Villagra, T. Schmelzle, S. Ladevèze & R.F. Kay. 2014. An exceptionally well-preserved skeleton of *Palaeothentes* from the Early Miocene of Patagonia, Argentina: new insights into the anatomy of extinct paucituberculatan marsupials. *Swiss Journal of Palaeontology* 133(1): 1-21.
Horovitz, I. & M.R. Sánchez-Villagra. 2003. A morphological analysis of marsupial higher-level phylogenetic relationships. *Cladistics* 19: 181-212.
Ladevèze, S. & C. de Muizón. 2010. Evidence of early evolution of Australidelphia (Metatheria, Mammalia) in South America: phylogenetic relationships of the metatherians from the

Late Palaeocene of Itaboraí (Brazil) based on teeth and petrosal bones. *Zoological Journal of the Linnean Society* 159: 746-784.

Malumian, N., & C. Nañez. 2011. The Late Cretaceous-Cenozoic transgressions in Patagonia and the Fuegian Andes: foraminifera, palaeoecology, and palaeogeography. *Biological Journal of the Linnean Society*, *103*(2), 269-288.

Marshall L.G. 1980. Systematics of the South American marsupial family Caenolestidae. *Fieldiana: Geology (New Series)* 5: 1-145.

Martin, G.M. 2011. Geographic distribution of *Rhyncholestes raphanurus* Osgood, 1924 (Paucituberculata : Caenolestidae), an endemic marsupial of the Valdivian Temperate Rainforest. Australian Journal of Zoology, 59, 118-126.

May-Collado, L.J., C.W. Kilpatrick & I. Agnarsson. 2015. Mammals from 'down under': a multi-gene species-level phylogeny of marsupial mammals (Mammalia, Metatheria). *PeerJ*, *3*, e805.

Meredith, R.W., M. Westerman, J.A. Case & M.S. Springer. 2008. A Phylogeny and timescale for marsupial evolution based on sequences for five nuclear genes. *Journal of Mammalian Evolution* 15: 1-36.

Ojala-Barbour, R., C.M. Pinto, J. Brito, L. Albuja, T.E. Lee Jr & B.D. Patterson. 2013. A new species of shrew-opossum (Paucituberculata: Caenolestidae) with a phylogeny of extant caenolestids. *Journal of Mammalogy* 94(5): 967-982.

Ortiz-Jaureguizar, E. & G.A. Cladera. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments* 66(3): 498-532.

Szalay, F.S. 1982. A new appraisal of marsupial phylogeny and classification. In: Archer M. (ed.) *Carnivorous marsupials*, 2. Sydney: Royal Zoological Society of New South Wales, 621-640.

Wilf, P., N.R. Cúneo, I.H. Escapa, D. Pol & M.O. Woodburne. 2013. Splendid and seldom isolated: the paleobiogeography of Patagonia. *Annual Review of Earth and Planetary Sciences* 41(1): 561-603.

Woodburne, M.O., F.J. Goin, M.S. Raigemborn, M. Heizler, J.N. Gelfo & E.V. Oliveira. 2014a. Revised timing of the South American early Paleogene land mammal ages. *Journal of South American Earth Sciences* 54: 109-119.

Woodburne, M.O., F.J. Goin, M. Bond, A.A. Carlini, J.N. Gelfo, G.M. López, A. Iglesias, & A.N Zimicz. 2014b. Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. *Journal of Mammalian Evolution* 21(1): 1-73.

Zimicz, A.N. 2012. *Ecomorfología de los marsupiales paleógenos de América del Sur*. Unpublished PhD. thesis, Universidad Nacional La Plata.