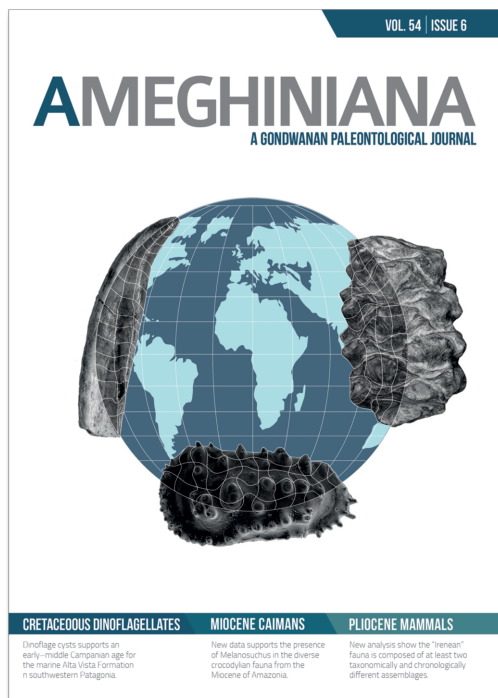




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THE PRESENCE OF *LEPIDOBATRACHUS* (ANURA, CERATOPHRYIDAE) IN THE NEOGENE OF THE LA PAMPA PROVINCE, ARGENTINA

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THE PRESENCE OF *LEPIDOBATRACHUS* (ANURA, CERATOPHRYIDAE) IN THE NEOGENE OF THE LA PAMPA PROVINCE, ARGENTINA

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Key words. Cerro Azul Fm. Quehué locality. Huayquerian SALMA.

Palabras clave. Cerro Azul Fm. Localidad Quehué. Huayqueriense SALMA.

INTENSIVE paleontological prospection in the Neogene beds referred to the Cerro Azul Formation carried out by Montalvo and collaborators throughout the last twenty years has produced one of the most important collections of Neogene vertebrate remains from South America. The assemblage includes mainly mammals but birds, squamates, and anurans are also represented (Goin *et al.*, 2000; Verzi *et al.*, 2008; Cenizo *et al.*, 2012; Albino *et al.*, 2013; Sostillo *et al.*, 2014; Scanferla and Agnolin, 2015 and references therein). The only known anuran remain (GHUNLPam 8633) consists of an incomplete maxilla that was recently assigned to *Ceratophrys*, a genus of South American horned frogs, by Scanferla and Agnolin (2015). This identification, however, was based on characters that are not exclusive of *Ceratophrys* and, thus, a revision of its taxonomic placement is pertinent.

Institutional acronyms. FML, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina; GHUNLPam, Facultad de Ciencias Exactas y Naturales, Universidad de La Pampa, Santa Rosa, La Pampa, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina. Additional institutional abbreviations in the supplementary information follow Sabaj Pérez (2014).

STRATIGRAPHIC PROVENANCE AND AGE

The specimen GHUNLPam 8633 was collected in sediments attributed to the Cerro Azul Formation that crops out

in the Quehué locality, La Pampa province, Argentina. This unit includes continental beds exposed in numerous discontinuous outcrops in the La Pampa and Buenos Aires provinces (Goin *et al.*, 2000; Folguera and Zárate, 2009; Visconti *et al.*, 2010) that belong to a major Neogene cycle of sedimentation that occurred after the regression of the Miocene Paranean sea in the extra Andean foreland region of central Argentina (Folguera and Zárate, 2009). These deposits are characterized by their lithological uniformity and therefore correlations have been traditionally based on paleontological evidence (Verzi *et al.*, 2008; Folguera and Zárate, 2009). Radiometric dates of the Cerro Azul Formation are not available and therefore the age of this unit has also been inferred on the basis of its paleontological content.

The mammalian assemblage recovered from these sediments has been traditionally considered equivalent to that of the Huayquerías Formation (Mendoza province, Argentina; Cabrera, 1939; Pascual and Bocchino, 1963), which formed the basis of the Huayquerian South American Land Mammal Age (SALMA; Rovereto, 1914; Kraglievich, 1934; Rusconi, 1939; Simpson, 1940). Thenceforth, the Cerro Azul Fm. has been repeatedly assigned to the Huayquerian Age (*e.g.*, Pascual *et al.*, 1965; Ortega Hinojosa, 1967; Montalvo and Casadío, 1988; Goin *et al.*, 2000). Forasiepi *et al.* (2016), however, recently noted that the evidence for the faunal and temporal correlations of the mammalian assemblage from

the Cerro Azul Fm. with the Huayquerian SALMA as presently understood is notably slim. Similarly, the biochronological scheme for the Cerro Azul Fm. proposed on the basis of the “stage of evolution” of octodontid rodents (Verzi *et al.*, 2008) was also questioned (Prevosti and Pardiñas, 2009). In summary, currently there is no unambiguous evidence on the age of the Cerro Azul Fm. and on the stratigraphic correlations among the different outcrops or with other units.

The specific faunal assemblage recovered in the Quehué locality, however, includes several taxa also recorded in other units radiometrically dated as late Miocene (*i.e.*, the El Jarillal Member of the Chiquimil Formation and the Arroyo Chasicó Formation, see details in the Supplementary Online Information), suggesting that the sediments in the Quehué locality would have been deposited during this time. This hypothesis, however, is still tentative and must be used

with caution for supporting evolutionary or biogeographic scenarios. Its use as temporal evidence for molecular clock analysis, for example, would require taking into account the large uncertainty in the age of the beds.

SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813

NEOBATRACHIA Reig, 1958

CERATOPHYRIDAE Tschudi, 1838

Lepidobatrachus Budgett, 1899

Type species. *Lepidobatrachus asper* Budgett, 1899. Extant taxon, Chacoan distribution.

Lepidobatrachus sp.

Figures 1.1–2; 2

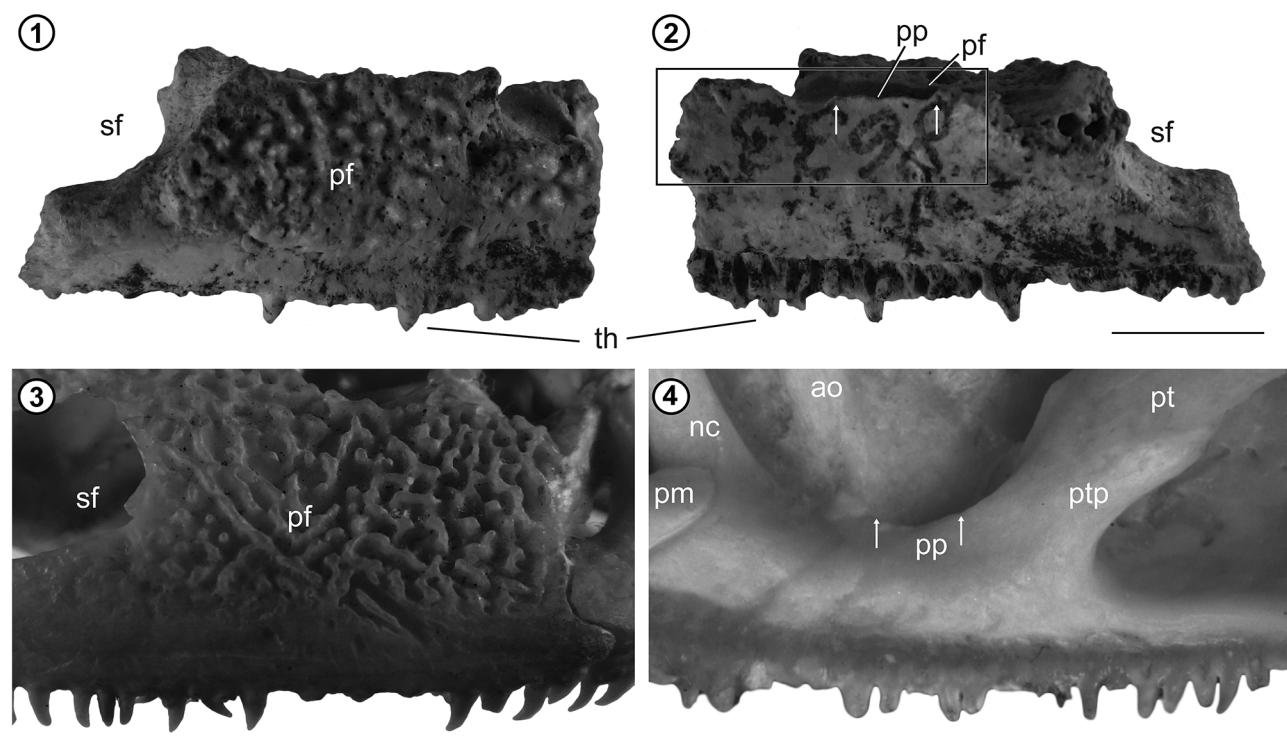


Figure 1.1–2, Partial maxilla from Quehué (GHUNLPam 8633) referred to *Lepidobatrachus*; 3–4, detail of the of the right maxilla of extant *Lepidobatrachus* (3, *L. laevis* FML 13703; 4, *L. asper* FML 5470); 1, 3, labial view; 2, 4, lingual view; the arrows over the fossil show the anterior and posterior limits of the entire margin of the *pars palatina*, the same area is denoted in the extant specimen; the rectangle indicates the area showed in detail in Fig. 2. Abbreviations: **ao**, ossifications of the planum antorbitale; **nc**, ossifications of the nasal cartilages; **pf**, pars facialis; **pm**, premaxilla; **pp**, pars palatina; **pt**, pterygoid; **ptp**, pterygoid process; **sf**, subtemporal fenestra; **th**, teeth. Scale bar= 5 mm.

Referred specimen. GHUNLPam 8633, incomplete right maxilla (Fig. 1.1–2).

Locality and age. Quehué locality, La Pampa province, Argentina. Neogene (?late Miocene, see above).

Description. GHUNLPam 8633 is an incomplete right maxilla, which lacks the medial portion as well as most of the anterior and posterior regions (Fig. 1.1–2). The preserved portion of the bone is large (about 19 mm) and robust, demonstrating that it belonged to a large (and presumably adult) individual. A high *pars facialis* with conspicuous ornamentation is evident in labial view (Fig. 1.1). This ornamentation consists of low tubercles interconnected by ridges, forming a reticulum. The *pars facialis* is not projected over the subtemporal fenestra. The *pars palatina* is markedly dorsally directed and a groove between the preserved portions of the *pars palatina* and *pars facialis* is visible in dorsal aspect (Figs. 1.2, 2). The distal margin of the preserved *pars palatina* is evidently broken at the anterior and posterior regions, suggesting its articulation with the surrounding bones: presumably with the ossified nasal cartilages and the *planum antorbitale*, anteriorly, and with the pterygoid, posteriorly. In the central region of the preserved maxilla, the distal margin of the *pars palatina* seems to be entire (Fig. 2), indicating that it was free and did not contact other bones. The teeth are robust but all are broken at different levels and none of them is completely preserved.

DISCUSSION

Scanferla and Agnolín (2015) referred this bone to Ceratophryidae based on: 1) pointed and non-pedicellate teeth, 2) exostosis, and 3) absence of *pars palatina*. The first two are some of the synapomorphies proposed for Ceratophryidae in phylogenetic analyses that included morphological data (*i.e.*, character 2 in Fabrezi, 2006; character 62 and 69 in Fabrezi and Quinzio, 2008), although it is worth noting that whereas 1) is an unusual condition among anurans, 2) has appeared several times within the group (see Nicoli, 2016 for discussion). Although in GHUNLPam 8633 all teeth are incomplete, they are broken at different levels, suggesting a non-pedicellate condition (Nicoli, 2016). Similarly, the ornamentation and degree of ossification of the preserved material suggest that it belonged to an exostosed skull.

With respect to the *pars palatina*, the unique condition of Ceratophryidae is that the maxillary *pars palatina* is dor-

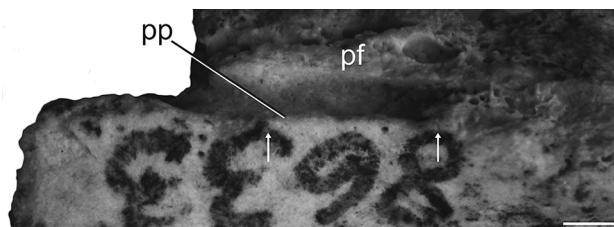


Figure 2. Detail of the maxilla from Quehué (GHUNLPam 8633) referred to *Lepidobatrachus* in dorso-lingual view; arrows over the fossil show the anterior and posterior limits of the entire margin of the *pars palatina*. Note the groove between the *pars palatina* and the robust section of the *pars facialis*. Abbreviations: **pf**, *pars facialis* (section); **pp**, *pars palatina*. Scale bar= 1 mm.

sally directed and fused anteriorly with other cranial elements (being absent as a discrete structure, at least in the anterior portion of the articulated maxilla). This feature was discussed in recent contributions (Nicoli, 2015; Nicoli *et al.*, 2017) and might represent a synapomorphy of Ceratophryidae. Despite the incomplete preservation of GHUNLPam 8633, it is evident that the *pars palatina* is strongly dorsally directed and that it was fused to other elements at its anterior and posterior ends. This latter condition seems to be homologous to the one observed in Ceratophryidae, where the distal margin of the *pars palatina* fuses with the ossifications of the nasal cartilages and the *planum antorbitale* (anteriorly) and with the pterygoid anterior ramus (posteriorly). Báez and Gómez (2017) recently analyzed the variation of the orientation of the maxillary *pars palatina* at the level of the *planum antorbitale* (character 52) in a series of phylogenetic analyses based on osteological data and including several ceratophryids. As these authors denoted, these analyses exclusively based on osteological characters resulted in heterodox hypotheses on the anuran relationships, and the included ceratophryids resulted always monophyletic but nested within an artificial clade of hyperossified taxa (Báez and Gómez, 2017). In this context, the optimization of the character about the orientation of the maxillary *pars palatina* did not result in a synapomorphy of Ceratophryidae. This is partly due to the position of several taxa (*e.g.*, *Uberabatrachus*, *Beelzebubo*) depicted along with Ceratophryidae in the artificial “hyperossified clade” and that were debatably scored with the same condition of ceratophryids. Additionally, other taxa included in this clade were ambiguously scored for this character (and contribute

to its ambiguous optimization; see Supplementary Online Information for a discussion).

The extant species of *Lepidobatrachus* are the only known ceratophryids in which the central portion of the *pars palatina* remains discrete, free from other elements, as in GHUNLPam 8633. In *Chacophrys*, *Ceratophrys*, and the Neogene *Lepidobatrachus australis*, the pterygoid anterior ramus articulates with a triangular pterygoid process of the maxillary *pars palatina* and reaches the level of the *planum antorbitale* (Nicoli, 2015). Thus the distal margin of the *pars palatina* contacts other cranial elements throughout all of its length, being absent as a discrete element (Nicoli, 2015: fig. 4C). In contrast, in the extant species of *Lepidobatrachus*, the pterygoid contacts the maxillary *pars palatina* only through the bar-like pterygoid process and the distal margin of the *pars palatina* remains free in its central portion (Fig. 1.4; Nicoli, 2015: fig. 4B).

Considering that the absence of a discrete *pars palatina* is a consequence of the articulation (and fusion) of this structure with other elements, this condition may be related with the degree of ossification and could vary during ontogeny. The development of the maxillary *pars palatina* of Ceratophryidae is largely unknown but some details on the maxillary development of *Ceratophrys cranwelli* were provided by Perí (1993) in her unpublished thesis. This author noted that the maxillary *pars palatina* appears as a discrete shelf, only slightly dorsally directed, in metamorphic larvae of *C. cranwelli*. Subsequently, this shelf extends dorsally to contact (and finally fuses with) the *pars facialis* and with other elements that gradually ossified (Perí, 1993). In the poorly ossified (and presumably young) individuals of *Chacophrys* (FML 1019) and *Ceratophrys* (*C. cranwelli* MACN 49410; *C. ornata* FML 1193) available for examination, it was possible to observe a discrete *pars palatina* in the central region of the maxilla when the anterior ramus of the pterygoid is incompletely developed and does not still reach the level of the *planum antorbitale*. However, in these specimens the maxilla is also comparatively small (no more than 21 mm in total length) and slender, without (or with few patches of) dermal ornamentation. All well-developed specimens of *Chacophrys* and *Ceratophrys* examined (see the Supplementary Online Information for a list of examined specimens) or described in the literature lack a discrete maxillary *pars palatina*.

In view of the recent phylogenetic relationships proposed for the three Ceratophryidae genera (Faivovich *et al.*, 2014), in which *Chacophrys* resulted the sister-taxon of *Lepidobatrachus*, the condition of the *pars palatina* observed in *Ceratophrys* and *Chacophrys* would be plesiomorphic for the group. The phylogenetic position of the fossil *Lepidobatrachus australis*, who shares with *Chacophrys* and *Ceratophrys* the absence of a discrete maxillary *pars palatina*, is crucial to establish the sequence of modification of this character in the *Lepidobatrachus* lineage. However, this position has not been still established. If *L. australis* is the sister-taxon of the extant *Lepidobatrachus*, this character would change once before the diversification of the extant species. Therefore, a discrete *pars palatina* in the central region of the maxilla could be a synapomorphy of the clade formed by the extant species of *Lepidobatrachus*. However, if *L. australis* is deeply nested within *Lepidobatrachus*, the optimization of this character would result as ambiguous. Even so, the co-occurrence of an exostosed skull with a large and robust maxilla strongly ornamented, non-pedicellate teeth, and a *pars palatina* only observable as a discrete element in the medial portion of the maxilla, observed in the fossil from Quehué, is a combination of characters exclusive of *Lepidobatrachus*, which supports the referral of GHUNLPam 8633 to this genus.

Scanferla and Agnolín (2015), however, assigned this fossil to *Ceratophrys*. This referral was based on the morphology of the ornamentation (interpreted as tuberculated in the fossil) and the shape of the *pars facialis*, which is not expanded over the subtemporal fenestra. None of these features are exclusive or invariant characters of *Ceratophrys*. The pattern of dermal ornamentation is a condition extremely variable among ceratophryids, even between different regions of the same specimen. Reticular patterns similar to the observed in GHUNLPam 8633 have been observed in different cranial regions of all ceratophryids (at least in some of the examined specimens of each species; see the supplementary online material for a list of examined specimens), including the maxillae of all analyzed *Lepidobatrachus* (Fig. 1.3). Similarly, although the maxillary *pars facialis* of *Lepidobatrachus llanensis* and *Lepidobatrachus asper* can extend over the subtemporal fenestra, this condition also varies intraspecifically and several specimens of these two species have *pars facialis* that are not extended (or only

slightly) over that fenestra (e.g., *L. llanensis* FML 5220, 5221, 1089; *L. asper* FML 5469). In addition, the *pars facialis* does not extend over the subtemporal fenestra in all the specimens examined of the two other *Lepidobatrachus* species (i.e., *L. australis* and *L. laevis*; Fig. 1.3) and of all other Ceratophryidae (see the Supplementary Online Information for a list of examined specimens).

Only one fossil species of *Lepidobatrachus* has been described previously, the Neogene *L. australis* from the middle levels of the Monte Hermoso Formation (Tomassini *et al.*, 2011; Tomassini *et al.*, 2013; Nicoli, 2015). No direct ages are available for these deposits and, although they are probably younger than those of the locality Quehué, their inferred ages are strongly influenced by assessments of “evolutionary stage” as bases for establishing chronostratigraphy (Faivovich *et al.*, 2014 and papers cited therein). In addition, the discovery of new presumable *Lepidobatrachus* remains from Huayquerías Fm. was recently reported in a scientific meeting (Turazzini, 2015). Intense studies are in progress in this formation by A. Forasieppi, F. Prevosti, and collaborators; preliminary results suggest that it might be synchronic with the El Jarillal Member of the Chiquimil Fm. and the lower part of Andalhuala Fm. (Bonini *et al.*, 2016). All these putative and confirmed records of *Lepidobatrachus* are outside the extant distribution of the genus, which is confined to the strongly seasonal Chacoan Region (Nicoli, 2015 and papers cited therein). This evidence suggests, on one hand, that *Lepidobatrachus* might have been broadly distributed in the central region of Argentina by the middle Neogene. On the other hand, this is in accordance with a marked seasonal environment developed in this region during these times, as previously suggested (e.g. Pascual *et al.*, 1996, Bonini *et al.*, 2016; although see Nicoli, 2015 for discussion).

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REFERENCES

- Albino, A.M., Montalvo, C.I., and Brizuela, S. 2013. New Records of Squamates from the Upper Miocene of South America. *Journal of Herpetology* 47: 590–598.
- Báez, A.M., and Gómez, R.O. 2017. Dealing with homoplasy: osteology and phylogenetic relationships of the bizarre neobatrachian frog *Baurubatrachus pricei* from the Upper Cretaceous of Brazil. *Journal of Systematic Palaeontology*. doi:10.1080/14772019.2017.1287130
- Bonini, R., Forasieppi, A.M., Prevosti, F.J., Garrido, A.C., Barbeau, D.L., Turazzini, G.F., Echarri, S., Pujos, F., Macphee, R., Verzi, D.H., Vera, B., Cerdeño, E., Perez, M.E., Rasia, L.L., Esteban, G., and de la Fuente, M. 2016. Avances en Paleontología, Estratigrafía y Edad de la Formación Huayquerías (Mioceno Tardío, Mendoza). *XXX Jornadas Argentinas de Paleontología de Vertebrados* (Buenos Aires), *Actas*: 59.
- Budgett, J.S. 1899. Notes on the batrachians of Paraguayan Chaco, with observations upon their breeding habits and development, especially with regard to *Phyllomedusa hypochondrialis* Cope. Also a description of a new genus. *Quarterly Journal of Microscopical Science* 42: 305–333.
- Cabrera, A.L. 1939. Sobre vertebrados fósiles del Plioceno de Adolfo Alsina. *Revista del Museo de La Plata, Sección Paleontología* 2: 3–35.
- Cenizo, M.M., Tambussi, C.P., and Montalvo, C.I. 2012. Late Miocene continental birds from the Cerro Azul Formation in the Pampean region (central-southern Argentina). *Alcheringa* 36: 47–68.
- Fabrezi, M. 2006. Morphological evolution of the Ceratophryinae (Anura, Neobatrachia). *Journal of Zoological Systematics and Evolutionary Research* 44: 153–166.
- Fabrezi, M., and Quinzio, S.I. 2008. Morphological evolution in Ceratophryinae frogs (Anura, Neobatrachia): the effects of heterochronic changes during larval development and metamorphosis. *Zoological Journal of the Linnean Society* 154: 752–780.
- Faivovich, J., Nicoli, L., Blotto, B.L., Pereyra, M.O., Baldo, D., Barrionuevo, J.S., Fabrezi, M., Wild, E.R., and Haddad, C.F.B. 2014. Big, bad, and beautiful: phylogenetic relationships of the horned frogs (Anura: Ceratophryidae). *South American Journal of Herpetology* 9: 207–227.
- Fischer von Waldheim, G. 1813. *Zoognosia tabulis synopticis illustrata, in usum praelectionum Academiae imperialis medico-chirurgicae mosquensis edita*. Third edition. Nicolai Sergeidis Vsevolozsky, Moscow, 465 p.
- Folguera, A., and Zárate, M. 2009. La sedimentación neógena continental en el sector extra-andino, Argentina central. *Revista de la Asociación Geológica Argentina* 64: 692–712.
- Forasieppi, A.M., MacPhee, R., Hernández del Pino, S., Schmidt, G.I., Amson, W., and Grohé, C. 2016. Exceptional skull of *Huayqueriana* (Mammalia, Litopterna, Macraucheniiidae) from the late Miocene of Argentina: anatomy, systematics, and paleobiological implications. *Bulletin of the American Museum of Natural History* 404: 1–76.
- Goin, F., Montalvo, C.I., and Visconti, G. 2000. Los Marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (Provincia de La Pampa, Argentina). *Estudios Geológicos* 56:

- 101–126.
- Kraglievich, L. 1934. *La Antigüedad Pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que la precedieron y sucedieron*. Imprenta El Siglo Ilustrado, Montevideo, 136 p.
- Montalvo, C.I., and Casadío, S. 1988. Presencia del género *Paleotodon* (Rodentia, Octodontidae) en el Huayqueriense (Mioceno tardío) de la provincia de La Pampa. *Ameghiniana* 25: 111–114.
- Nicoli, L. 2015. New fossil species of the extant genus *Lepidobatrachus* (Anura, Ceratophryidae) from the Late Miocene-Early Pliocene of central Argentina. *Journal of Vertebrate Paleontology* 35: e981636.
- Nicoli, L. 2016. A fossil ceratophryid anuran from the Late Miocene of West-Central Argentina. *Salamandra* 52: 153–160.
- Nicoli, L., Tomassini, R., and Montalvo, C.I. 2017. The oldest record of *Ceratophrys* (Anura, Ceratophryidae) from the Late Miocene of central Argentina. *Journal of Vertebrate Paleontology*. doi: 10.1080/02724634.2017.1261360
- Ortega Hinojosa, E.J. 1967. Descripción de los restos de un Scelidotheriinae (Edentata, Mylodontidae) de Edad Huayqueriense. *Ameghiniana* 5: 109–120.
- Pascual, R., and Bocchino, A. 1963. Un nuevo Borhyaeninae (Marsupialia) del Plioceno medio de Hidalgo (La Pampa). *Ameghiniana* 3: 97–107.
- Pascual, R., Ortega Hinojosa, E.J., Gondar, D., and Tonni, E.P. 1965. Las edades del Cenozoico mamífero de la Argentina, con especial atención a aquellas del territorio bonaerense. *Anales de la Comisión de Investigación Científica de la Provincia de Buenos Aires* 3: 165–193.
- Pascual, R., Ortiz-Jaureguizar, E., and Prado, J.L. 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. *Münchener Geowissenschaftlichen Abhandlungen* 30: 265–318.
- Perí, S.I. 1993. [Relaciones evolutivas de las especies de la subfamilia *Ceratophryinae* (Anura: *Leptodactylidae*). Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 223 p. Unpublished.].
- Prevosti, F.J., and Pardiñas, U.F.J. 2009. 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]. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280: 543–547.
- Reig, O.A. 1958. Propositiones para una nueva macrosistemática de los anuros. *Physis* 21: 109–118.
- Rovereto, C. 1914. Los estratos araucanos y sus fósiles. *Anales del Museo de Historia Natural de Buenos Aires* 25: 1–247.
- Rusconi, C. 1939. Lista de los mamíferos miocénicos de las Huayquerías de Mendoza. *Physis* 14: 461–471.
- Sabaj Pérez, M.H. 2014. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 5.0 (June 2017). Washington, DC: American Society of Ichthyologists and Herpetologists. World Wide Web: <http://www.asih.org/>
- Scanferla, A., and Agnolin, F. 2015. Nuevos aportes al conocimiento de la herpetofauna de la Formación Cerro Azul (Mioceno superior), provincia de La Pampa, Argentina. *Papéis Avulsos de Zoolo-gía* 55: 323–333.
- Simpson, G.G. 1940. Review of the mammal-bearing Tertiary of South America. *Proceedings of the American Philosophical Society* 83: 649–709.
- Sostillo, R., Montalvo, C.I., and Verzi, D.H. 2014. A new species of *Reigechimys* (Rodentia, Echimyidae) from the Late Miocene of central Argentina and the evolutionary pattern of the lineage. *Ameghiniana* 51: 284–294.
- Tomassini, R.L., Agnolin, F., and Oliva, C. 2011. First fossil record of the genus *Lepidobatrachus* Budgett, 1899 (Anura, Ceratophryidae), from the early Pliocene of Argentina. *Journal of Vertebrate Paleontology* 31: 1005–1009.
- Tomassini, R.L., Montalvo, C.I., Deschamps, C.M., and Manera, T. 2013. Biostratigraphy and biochronology of the Monte Hermoso Formation (early Pliocene) at its type locality, Buenos Aires Province, Argentina. *Journal of South American Earth Sciences* 48: 31–42.
- Tschudi, J.J. 1838. *Classification der Batrachier, mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien*. Petitpierre, Neuchâtel, 99 p.
- Turazzini, G.F. 2015. Registro de un nuevo taxón fósil afín a *Lepidobatrachus* (Anura: Ceratophryidae) en la Formación Huayquerías (Mioceno Superior), provincia de Mendoza, Argentina. *Ameghiniana* 53 (4R): 39.
- Verzi, D.H., Montalvo, C.I., and Deschamps, C.M. 2008. Biochronology and Biostratigraphy of the Upper Miocene of central Argentina, evidence from rodents and taphonomy. *Geobios* 41: 145–155.
- Visconti, G., Melchor, R.N., Montalvo, C.I., Umazano, A.M., and Eloorriaga, E.E. de. 2010. Análisis litoestratigráfico de la Formación Cerro Azul (Mioceno Superior) en la provincia de La Pampa. *Revista de la Asociación Geología Argentina* 67: 257–265.

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