

BIZARRE NOTOSUCHIAN CROCODYLIFORM WITH ASSOCIATED EGGS FROM THE UPPER CRETACEOUS OF BOLIVIA

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The Mesozoic record of fossil vertebrates from Bolivia (Fig. 1) was restricted heretofore to Campanian–Maastrichtian dinosaur footprints (e.g., Leonardi, 1989; Suárez Riglos, 1995; Lockley et al., 2002; McCrea et al., 2001; Meyer et al., 2001) and isolated and poorly informative dinosaur teeth and bones (Aguilera et al., 1989; Gutierrez and Marshall, 1994). Discovery of several, almost complete skeletons of a new notosuchian taxon constitutes the most important body-fossil discovery for the Mesozoic of Bolivia, adding substantially to the meager record of this region of South America. At least two partially disarticulated skeletons and two complete eggs were found together in a small area, constituting one of the few available associations of skeletal remains and eggs for extinct crocodyliforms. In this paper we describe this material as a new genus and species. We consider only the skull morphology, because most of available postcranial remains are still under technical preparation.

Institutional Abbreviation—**MNK-PAL**, Museo 'Noel Kempff Mercado,' Santa Cruz de la Sierra, Bolivia.

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Clark, 1986

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

NOTOSUCHIA Gasparini, 1971 (sensu Sereno et al., 2001)

YACARERANI BOLIVIENSIS gen. et sp. nov.

(Figs. 2, 3)

Hypodigm—MNK-PAL5063 (holotype), a complete and exquisitely preserved skeleton; MNK-PAL5064, almost complete lower jaws articulated with partial right pterygoid, ectopterygoid, jugal, squamosal, partial quadrates, 12 vertebrae, left femur, proximal end of right femur, partial right tibia, and partial right fibula.

Locality and Horizon—A locality (17° 34' 7" S, 63° 51' 3" W) cropping out in Amboro National Park, Santa Cruz de la Sierra, Bolivia (Fig. 1). Cajones Formation, Upper Cretaceous. Although the Cajones Formation has been regarded as Maastrichtian (López, 1975; Aguilera et al., 1989), the age of the level producing MNK-PAL5063 and MNK-PAL5064 is interpreted here as Turonian–Santonian (see Discussion).

Diagnosis—Notosuchian characterized by the following autapomorphies: nasals rostrally expanded above the external nares, palatines bearing a median sagittal crest, retroarticular process rounded and rostro-caudally short, jugal laterally expanded forming an ornamented prong at level of postorbital bar, incisiviforms separated from molariforms through a diastema, and

molariform tooth rows rostrally convergent and almost in touch each other.

Etymology—Generic name derives from two words of the Guarani Indian language, *yacaré* (the South American crocodile), and *rani* (first). Specific epithet after the Republic of Bolivia.

DESCRIPTION

The skull of *Yacarerani* is 95 mm long (Fig. 2A–C). Tight fusion among frontals and parietals suggests adulthood. The snout is short and narrow. The external nares are terminal and confluent. The nasals are constricted anteriorly, a unique trait among notosuchians. The premaxilla bears a prominent rostral process, which is dorsally curved, and presumably anchored the cartilaginous internarial bar. This process is much more developed than in the other notosuchians.

The jugal exhibits a laterally projected prong (jp; Fig. 2A–C), which is dorsoventrally flat and heavily sculptured. When the mandible is occluded, the flat ventral surface of the jugal prong lies over an also flattened area in the dentary-surangular contact (dsa; Fig. 2D) of the mandible. The distal body of the quadrate is vertically oriented (Fig. 2A), as in most notosuchians, but its articulation with the articular bone is situated more ventrally than usual. The articular condyles of the quadrate are asymmetrical (i.e., the medial one is more acute and ventrally more projected than the lateral condyle). The glenoid cavity of the articular bone is rostrocaudally elongate (gl; Fig. 2D), indicative of jaw propalinal movement. The retroarticular process of the jaw is remarkably reduced anteroposteriorly and does not exceed the level of the paroccipital process, whereas in other notosuchians (e.g., *Notosuchus*, *Malawisuchus*) the retroarticular process extends farther caudally. The lower jaw has a distinctive symphyseal region, which is narrower and more elongate in dorsal view (ds; Fig. 1E) than that of the other notosuchians.

Yacarerani constitutes an extreme case of heterodonty among crocodylomorphs: the dentition consists of four insciviforms in both premaxilla and dentary and six molariforms in both maxilla and dentary. The first dentary tooth is conical and highly procumbent, and it is the largest of the dental series (1d; Fig. 2A, B, D). This tooth occludes between the similarly procumbent first and second premaxillary teeth (1, 2pm; Fig. 2A). A diastema separates the insciviforms (both upper and lower) from the molariform series (Fig. 3A, B). Furthermore, the lower incisiviform series is longitudinally arranged, in sharp contrast to the molariform series, which are obliquely oriented and form an angle of approximately 30° with the longitudinal axis of the skull. Moreover, the rostralmost teeth of each molariform tooth series are almost in contact on the axial plane

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FIGURE 1. Location of fossil site (star) in Amboro National Park, Bolivia. Scale bar equals 200 km.

(Fig. 3C, D). This separation of the main oral cavity from the rest of the dental series constitutes a feature not previously documented in Mesozoic tetrapods, and its functional significance is unknown.

The molariform teeth are multicusped. They are oval in occlusal view and their major axes are obliquely oriented with respect to the tooth row (Figs. 2B, D; 3), a feature that *Yacarerani* shares with *Notosuchus*, *Adamantinasuchus*, and *Sphagesaurus*. The occlusal surfaces of the upper molariforms are linguodistally oriented, whereas those of the lower molariforms are labiomesially facing (Fig. 3A, B).

The occlusal surface of each molariform tooth is formed by a central multicusped crest, aligned with the major axis of the tooth, and surrounded by both mesial and distal lower multicusped crests (Fig. 3E, F). Such crests are roughly parasagittally oriented with respect to the long axis of the skull. The cusps of each crest are connected by narrow laminae. The crests converge at the crown base as well as at the apex (Fig. 3F). Extensive wear facets are located on the apical portion of the median crest of opposing dentary and maxillary teeth. No wear is observed between the crests. Wear facets match in size, shape, and location, and are suggestive of a tooth-to-tooth occlusion and intraoral food processing.

MNK-PAL5063 and MNK-PAL5064 represent two almost complete and articulated individuals of *Yacarerani* found in close association. Eggs were found directly beneath these skeletons, below which no more fossils were detected. There is no evidence of scavenging or weathering, and we infer that this fossil assemblage forms an autochthonous association. Although sedimentological information is not available, the volume occupied by the bones and eggs is roughly tubular, a shape that is consistent with an underground gallery. These taphonomic conditions suggest that *Yacarerani* may have had burrowing habits, a behavior that has been inferred for other notosuchians on taphonomic evidence (e.g., Gomani, 1997; Vasconcellos and Carvalho, 2006) as well as anatomical features (Buckley et al., 2000).

Two complete, unhatched eggs and an isolated eggshell fragment were found closely associated with the skeletal remains (Fig. 4). The eggs are elliptical, as is characteristic of Crocodyliiformes (Hirsch and Koring, 1992), with a long diameter of 30 mm and a short diameter of 16 mm. The eggshell is 0.2 mm thick, and its external surface is smooth, in accordance with other extinct crocodyliiform eggs (Hirsch and Koring, 1992). Poor preservation of the isolated eggshell fragment precludes a histological description. The size and external morphology of the eggs are similar to those found in association with *Mariliasuchus amarali* (Ribeiro et al., 2006) from the Upper Cretaceous Araçatuba Formation of Brazil.

DISCUSSION

Phylogenetic analysis (Supplementary Data 1, <http://www.vert-paleo.org/publications/JVPCContent.cfm>) positions *Yacarerani* among a subclade of notosuchians (Fig. 5) that includes *Comahuesuchus* (Bonaparte, 1991; Martinelli, 2003), *Mariliasuchus* (Carvalho and Bertini, 1999; Zaher et al., 2006), and *Adamantinasuchus* (Nobre and Carvalho, 2006). This group of highly derived South American notosuchians radiated during the Turonian–Santonian and produced one of the most complex tooth morphologies reported for crocodyliiforms. This clade is distinguished from the remaining notosuchians by the following derived traits: dorsal part of postorbital with anterior and lateral edges only; bar between orbit and supratemporal fossa narrow, and sculpturing restricted to anterior surface; jugal does not extend rostral to the anterior margin of orbit; cross section of distal end of the quadrate mediolaterally wide and anteroposteriorly thin; ventral half of lacrimal tapering ventroposteriorly; large foramen present on the lateral surface of jugal, near its

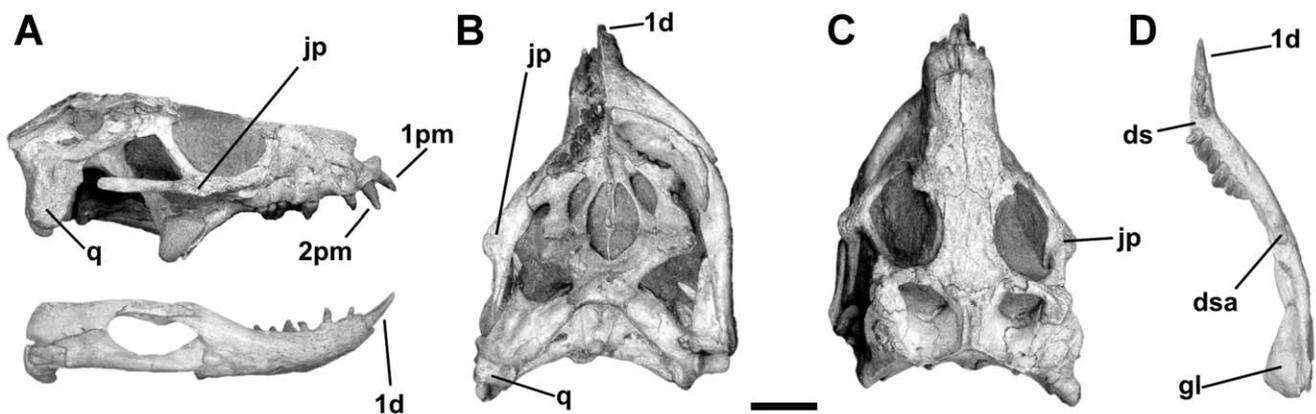


FIGURE 2. *Yacarerani boliviensis* gen. et sp. nov., MNK-PAL5063. Skull and lower jaw in **A**, right lateral, **B**, ventral, and **C**, dorsal views. **D**, right lower jaw in dorsal view. Scale bar equals 2 cm. **Abbreviations:** 1d, first dentary tooth; 1pm, 2pm, first and second premaxillary teeth; ds, symphyseal region of dentary; dsa, flattened area in the dentary-surangular contact; gl, glenoid cavity; jp, laterally projected prong of jugal; q, quadrate.

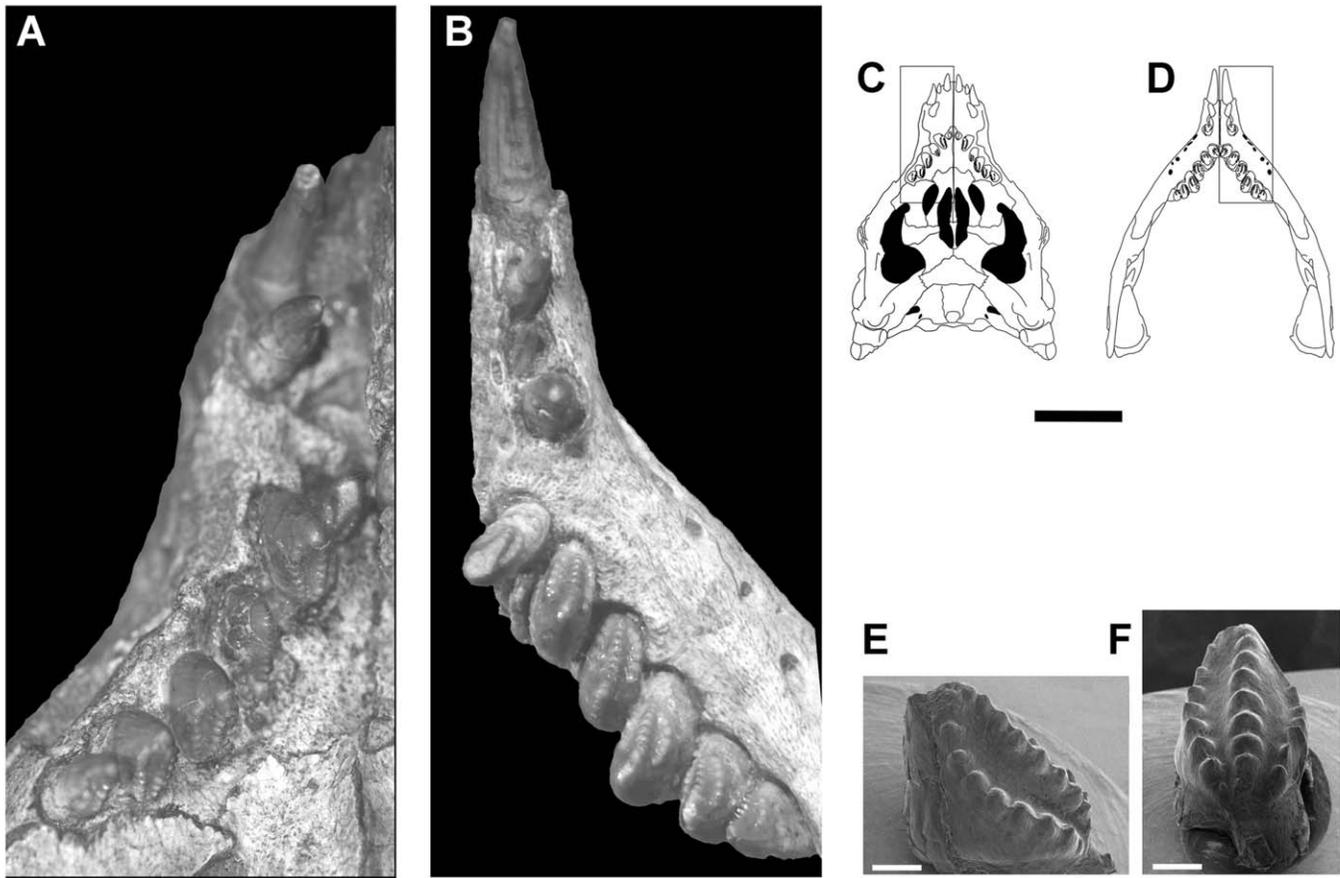


FIGURE 3. *Yacarerani boliviensis* gen. et sp. nov., MNK-PAL5063. **A**, upper and **B**, lower marginal teeth in occlusal view. **C**, composite reconstruction of skull in palatal view. **D**, composite reconstruction of mandible in dorsal view. **E**, **F**, isolated molariform tooth in **E**, mesial/distal and **D**, occlusal views. Scale bars equal 2 cm (**A–D**), and 1 mm (**E**, **F**).

anterior margin; procumbent premaxillary and anterior dentary alveoli; and ectopterygoid does not participate in palatine bar. Within this group, *Yacarerani* and *Adamantinasuchus* share similar teeth morphology, but they differ in several features, such as presence in the former taxon of a diastema separating insiciviform from molariform tooth rows; four premaxillary and six maxillary teeth in *Yacarerani* versus three and seven, respectively, in *Adamantinasuchus*; frontal median crest absent in *Yacarerani*; lateral temporal fenestra in *Yacarerani* dorsoventrally shallower than in *Adamantinasuchus*; skull roof straight in lateral view in *Yacarerani*, instead of being dorsally convex as in *Adamantinasuchus*; lacrimal with a ventral process in *Yacarerani*; tooth wear facets only present in *Yacarerani*.

The aptitude for anteroposterior movements of the jaws is a feeding-related trait that is exclusive to notosuchians among crocodylomorphs (e.g., Bonaparte, 1991; Clark et al., 1989). This trait has a wide distribution within notosuchians, but it is not unequivocally correlated with tooth complexity (i.e., *Notosuchus*, *Mariliasuchus*), suggesting that complex dental patterns evolved after propalinal motions of the jaw were acquired. In this regard, overall cranial morphology of *Yacarerani* (and *Adamantinasuchus*) closely resembles that of *Mariliasuchus*, although its teeth are completely different.

The Cajones Formation has been regarded as Maastrichtian but the age is far from settled. It was considered heretofore as Maastrichtian based on the possible presence of *Pucapristis*

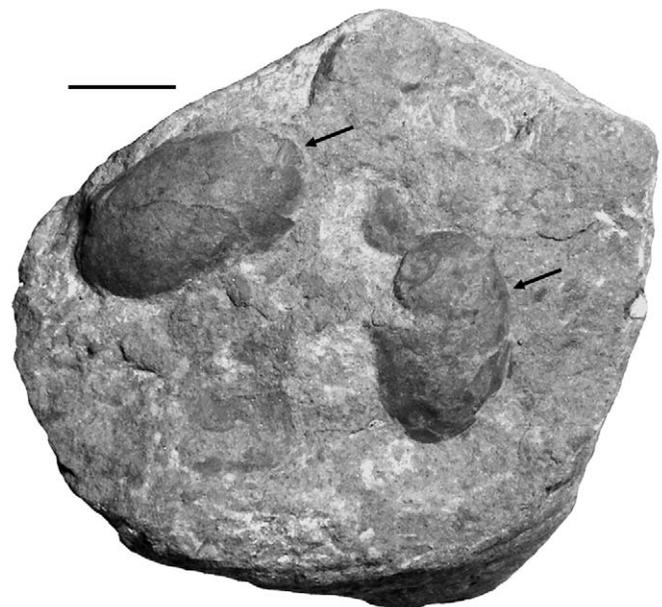


FIGURE 4. Unhatched eggs (arrows) found in association with *Yacarerani boliviensis*. Scale bars equal 2 cm.

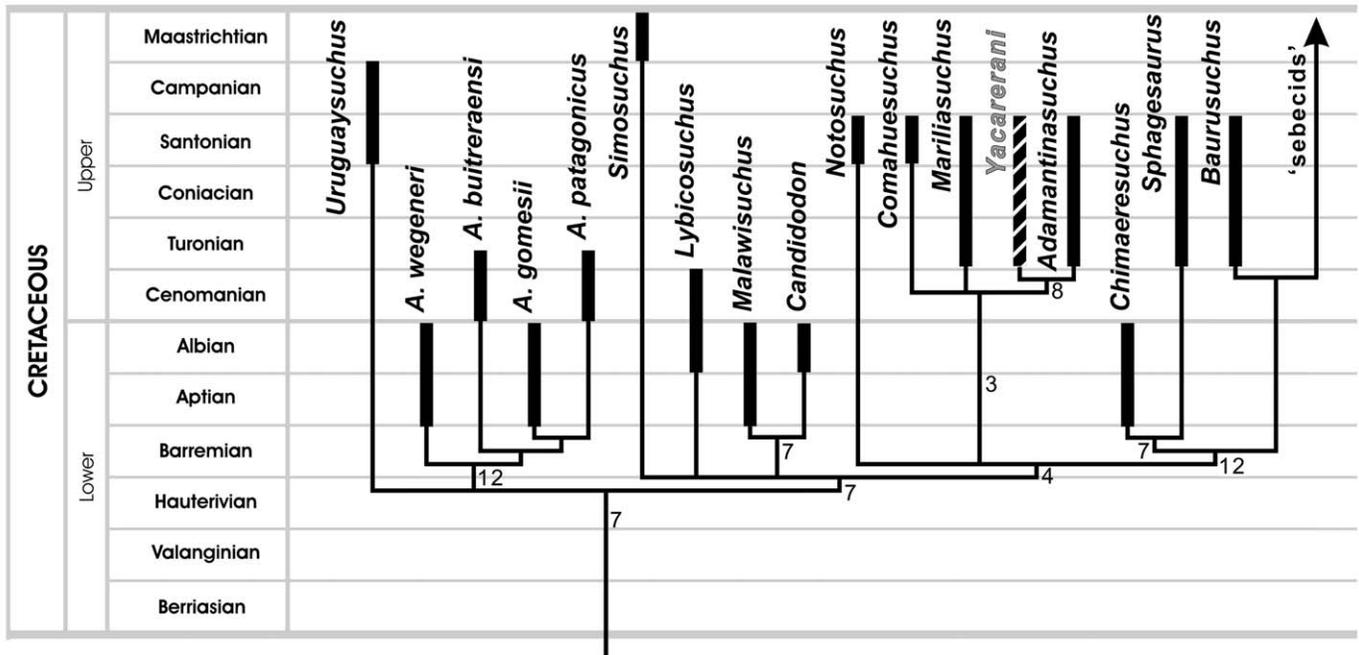


FIGURE 5. Strict consensus of 70 most parsimonious trees depicting phylogenetic relationships of *Yacarerani boliviensis* within Notosuchia. A dataset of 234 characters and 51 taxa, modified from Pol and Apesteguía (2005), was analyzed using TNT (Goloboff et al., 2003). Tree statistics: tree length = 749; consistency index = 0.37; retention index = 0.67. Values of Bremer support are shown beside the branches. See Supplementary Data 1 (<http://www.vertpaleo.org/publications/JVPCContent.cfm>) for details. Hatched line indicates uncertainty in the stratigraphic placement of *Yacarerani*.

branisi and *Gasteroclupea branisai* (López, 1975; Aguilera et al., 1989), two taxa that were also documented in Maastrichtian marine beds in Perú (Vilquechico Formation; Jaillard et al., 1993), northwestern Argentina (Yacoraite Formation; Cione and Pereira, 1985), and elsewhere in Bolivia (El Molino Formation; Cione and Pereira, 1985). However, the locality that produced *Yacarerani* comprises red sandstones of fluvial origin. Because *Yacarerani* is related most closely to *Adamantinasuchus* (Nobre and Carvalho, 2006) from the Adamantina Formation of the Bauru Group, Brazil (Dias-Brito et al., 2001), we infer a Turonian–Santonian age for the level of the Cajones Formation that produced MNK-PAL5063 and MNK-PAL5064.

Fossil content of the Cajones Formation is congruent with that of the Turonian–Coniacian Adamantina Formation of Brazil (Candeiro and Martinelli, 2006) and the Santonian Bajo de la Carpa Formation of northwestern Patagonia (Bonaparte, 1991; Candeiro and Martinelli, 2006), in which notosuchian crocodyli-forms are among the most abundant tetrapod remains (Pol and Gasparini, 2007). Diversity in dental patterns may reflect different dietary habits, and depict notosuchians as a very versatile group that filled a vast range of ecological niches during the Cretaceous. The high taxonomic and morphological diversity of notosuchians in South America occurred during Aptian through Campanian times, and contrasts sharply with the Cretaceous crocodylian fauna from North America, Asia, and Europe, which is composed mainly by neosuchian taxa (e.g., basal Eusuchia) and basal crocodyli-forms (e.g., *Gobiosuchus*, *Zosuchus*, *Sichuanosuchus*). The latter fauna does not exhibit the variety in dental pattern and numerical abundance that characterizes southern notosuchians (Pol and Gasparini, 2007).

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LITERATURE CITED

- Aguilera, E., H. Salas, and E. Peña. 1989. La Formación Cajones: Cretácico terminal del subandino central de Bolivia. *Revista Técnica YPF* 10:131–148.
- Bonaparte, J. F. 1991. Los vertebrados fósiles de la formación Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico superior. *Revista Museo Argentino Ciencias Naturales* 4:116–123.
- Buckley, G. A., C. A. Brochu, D. W. Krause, and D. Pol. 2000. A pug-nosed crocodyli-form from the Late Cretaceous of Madagascar. *Nature* 405:941–944.
- Candeiro, C. R. A., and A. G. Martinelli. 2006. A review of paleogeographical and chronostratigraphical distribution of mesoeucrocodylian species from the Upper Cretaceous beds from the Bauru (Brazil) and Neuquén (Argentina) groups, southern South America. *Journal of South American Earth Sciences* 22:116–129.
- Carvalho, I. S., and R. J. Bertini. 1999. *Marillasuchus*: um novo Crocodyli-forma (Notosuchia) do Cretáceo da Bacia Bauru, Brasil. *Geología Colombiana* 24:83–105.
- Cione, A. L., and S. M. Pereira. 1985. Los peces de la Formación Yacoraite (Cretácico tardío-Terciario?, Noroeste argentino) como indicadores de salinidad. *Revista de la Asociación Geológica Argentina* 40:83–88.
- Clark, J. M. 1986. Phylogenetic relationships of the crocodyli-form archosaurs. Ph.D. dissertation, University of Chicago, Chicago, 556 pp.
- Clark, J. M., L. L. Jacobs, and W. R. Downs. 1989. Mammal-like dentition in a Mesozoic crocodyli-form. *Science* 244:1064–1066.
- Dias-Brito, D., E. A. Musacchio, J. C. Castro, M. S. Maranhão, J. M. Suárez, and R. Rodrigues. 2001. Grupo Bauru: uma unidade continental do Cretácico no Brasil – concepções baseadas em dados micropaleontológicos, isotópicos e estratigráficos. *Revista de Paleobiología Gêneve* 20:245–304.

- Gasparini, Z. 1971. Los Notosuchia del Cretácico de América del Sur como un nuevo infraorden de los Mesosuchia (Crocodylia). *Ameghiniana* 8:83–103.
- Goloboff, P., J. Farris, and K. Nixon. 2003. T.N.T.: Tree Analysis Using New Technology. Version 1.8. Available at www.zmuc.dk/public/phylogeny. Accessed October 22, 2008.
- Gomani, E. 1997. A crocodyliform from the Early Cretaceous dinosaur beds, Northern Malawi. *Journal of Vertebrate Paleontology* 17:280–294.
- Gutierrez, F., and L. G. Marshall. 1994. Los primeros huesos de dinosaurios de Bolivia. Formación Cajones (Maastrichtiano) cerca de Santa Cruz de la Sierra. *Revista Técnica YPFB* 15:131–139.
- Hirsch, K. F., and R. Kohring. 1992. Crocodylian eggs from the Middle Eocene Bridger Formation, Wyoming. *Journal of Vertebrate Paleontology* 12:59–65.
- Jaillard, E., H. Cappetta, P. Ellenberger, M. Feist, N. Grambast-Fessard, J. P. Lefranc, and B. Sigé. 1993. Sedimentology, palaeontology, biostratigraphy and correlation of the Late Cretaceous Vilquechico Group of southern Peru. *Cretaceous Research* 14:623–661.
- Leonardi, G. 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation; pp. 165–178 in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge.
- Lockley, M. G., A. S. Schulp, C. A. Meyer, G. Leonardi, and D. K. Mamani. 2002. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* 23:383–400.
- López, R. M. 1975. Informe estratigráfico de los ríos Alto Moile, Alto Isarsama, Ichoa, Alto Beni y Tequeje. Informe YPFB GXG-2600.
- Martinelli, A. G. 2003. New cranial remains of the bizarre notosuchid *Comahuesuchus brachybuccalis* (Archosauria, Crocodyliformes) from the Late Cretaceous of Río Negro Province (Argentina). *Ameghiniana* 40:559–572.
- McCrea, R., M. G. Lockley, and C. A. Meyer. 2001. Global distribution of purported ankylosaur track occurrences; pp. 413–454 in K. Carpenter (ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington.
- Meyer, C. A., D. Hippler, and M. G. Lockley. 2001. The Late Cretaceous vertebrate ichnofacies of Bolivia - facts and implications. VII International Symposium on Mesozoic Terrestrial Ecosystems. Asociación Paleontológica Argentina, *Publicación Especial* 7:133–138.
- Nobre, P. H., and I. S. Carvalho. 2006. *Adamantinasuchus navae*: a new Gondwanan Crocodylomorpha (Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Gondwana Research* 10:370–378.
- Pol, D., and S. Apesteguía. 2005. New *Araripesuchus* remains from the Early Late Cretaceous (Cenomanian-Turonian) of Patagonia. *American Museum Novitates* 3490:1–38.
- Pol, D., and Z. Gasparini. 2007. Crocodyliformes; pp. 116–142 in Z. Gasparini, L. Salgado, and R. A. Coria (eds.), *Patagonian Mesozoic reptiles*. Indiana University Press, Bloomington.
- Sereno, P. C., H. C. E. Larsson, C. A. Sidor, and B. Gado. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science* 294:1516–1519.
- Ribeiro, C. M. M., I. S. Carvalho, and W. R. Nava. 2006. Ovos de crocodilomorfos da Formação Araçatuba (Bacia Bauru, Cretácico Superior), Brasil; pp. 285–292 in V. Gallo, P. M. Brito, H. M. A. Silva, and F. J. Figueiredo (eds.), *Paleontologia de Vertebrados Grandes Temas e Contribuições Científicas*. Editora Interciência, Rio de Janeiro.
- Suárez Riglos, M. 1995. Huellas de dinosaurios en Sucre. *Asociación Sucreña de Ecología. Anuario* 95:44–48.
- Vasconcellos, F. M., and I. S. Carvalho. 2006. Condicionante etológico na tafonomia de *Uberabasuchus terrificus* (Crocodyliformes, Peirosauridae) da Bacia Bauru (Cretáceo Superior). *Geociências* 25:225–230.
- Whetstone, K., and P. Whybrow. 1983. A “cursorial” crocodylian from the Triassic of Lesotho (Basutoland), southern Africa. *Occasional Papers of the University of Kansas Museum of Natural History* 106:1–37.
- Zaher, H., D. Pol, A. B. Carvalho, C. Riccomini, D. Campos, and W. Nava. 2006. Redescription of cranial morphology of *Mariliasuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). *American Museum Novitates* 3512:1–40.

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