

THE ALLIGATOROIDEA OF ARGENTINA: AN UPDATE OF ITS FOSSIL RECORD

PAULA BONA¹ AND FRANCISCO BARRIOS²

¹CONICET. División Paleontología Vertebrados, Museo de La Plata. Paseo del Bosque s/n, B1900FWA La Plata, Argentina. paulabona26@gmail.com

²Museo Municipal Carmen Funes, Plaza Huinul. Av. Córdoba 55, Q8318EBA Neuquén, Argentina. fbarrios84@gmail.com

Abstract. The fossil record of Alligatoroidea in Argentina is mainly represented by Caimaninae alligatorids. This lineage recorded two important moments in its natural history, one at the beginning of the Paleogene (Late Paleocene–Middle Eocene) and the other in the Neogene (Late Miocene). The most ancient record of alligatoroids in South America comes from the Early Paleocene of Patagonia. It includes basal forms of caimanines such as *Necrosuchus ionensis*, *Eocaiman palaeocenicus*, *Eocaiman cavernensis*, and probably a new species of alligatoroid, which provide key morphological information on the evolutionary and biogeographic history of these crocodylians. Another important moment of the evolutionary history of caimanines is the diversification of the lineage observed during the Miocene. Although there is some isolated cranial material of caimanines from the Late Miocene of northwestern Argentina, the most abundant and diverse fossil Miocene material comes from the northeast, from a level informally called “Conglomerado Osífero”. Two genera of caimanines are known from this stratigraphic level (*Caiman* and *Mourasuchus*) with at least five valid species. Here we present an update of the knowledge of Cenozoic alligatoroids of Argentina, as a tribute to Zulma Gasparini for her invaluable contribution to the understanding of the crocodylian evolution in South America.

Key words. Crocodylia. Alligatoroids. Cenozoic. South America. Argentina.

Resumen. LOS ALLIGATOROIDEA DE ARGENTINA: UNA PUESTA AL DÍA DE SU REGISTRO FÓSIL. El registro fósil de Alligatoroidea en Argentina está representado mayormente por aligatósidos Caimaninae. Este linaje registra dos momentos importantes en su historia natural, uno en el comienzo del Paleógeno (Paleoceno tardío/Eoceno medio) y otro en el Neógeno (Mioceno tardío). El registro más antiguo de aligatósidos en América del Sur proviene del Paleoceno temprano de Patagonia. Este registro es muy relevante porque incluye formas de caimaninos basales como *Necrosuchus ionensis*, *Eocaiman palaeocenicus*, *Eocaiman cavernensis* y probablemente una nueva especie de aligatósido, quienes proporcionan información morfológica clave en la historia evolutiva y biogeográfica de este grupo de crocodylios. Otro momento importante de la historia evolutiva de los caimanines se observa durante el Mioceno, cuando este linaje se diversifica. Aunque hay algo de material craneano aislado del Mioceno tardío en el noroeste de Argentina, el material mioceno más abundante y diverso proviene del noreste, de un nivel informalmente llamado “Conglomerado Osífero”. De dicho nivel estratigráfico, se reconocen dos géneros de caimaninos (*Caiman* y *Mourasuchus*) con al menos cinco especies válidas. Aquí presentamos una actualización del conocimiento de los aligatósidos del Cenozoico de Argentina, en homenaje a Zulma Gasparini por su inestimable contribución a la comprensión de la evolución de los cocodrilos en América del Sur.

Palabras clave. Crocodylia. Aligatósidos. Cenozoico. América del Sur. Argentina.

ALLIGATOROIDEA is a clade of Crocodylia (*sensu* Benton and Clark, 1988) which comprises the alligatorids (Caimaninae and Alligatorinae) recorded two main moments of the evolutionary history of Alligatoridae (*sensu* Brochu, 2003), one in the early Paleogene and the other during the Neogene (when this lineage diversified). The most ancient alligatorids in this part of the continent were recorded in the Early Paleocene of Patagonia, Argentina (Kuhn, 1933; Simpson, 1933, 1937; D’Erasmus, 1934; Rusconi, 1937; Langston, 1965; Bonaparte *et al.*, 1993; Bona, 2004, 2007). This record is extremely relevant because it includes basal forms from

the Early Paleocene and Eocene, which provided key morphological information on the evolutionary history of these crocodylians (*i.e.*, *Eocaiman paleocenicus*, *E. cavernensis* and *Necrosuchus ionensis*). Argentinean fossil alligatorids are in general fragmentary and belong to the clade Caimaninae (Brochu, 1999, 2011; Bona, 2007) which together with Alligatorinae constitutes one of the two clades of Alligatoridae. After the Eocene, the alligatorid record is interrupted until the Late Miocene, being not recorded during the Oligocene in this territory (Gasparini and Báez, 1975; Gasparini, 1981).

During the Neogene, the exceptional crocodylian fossil

record of the Miocene Amazonian sedimentary basins of Colombia, Brazil, Peru and Venezuela has shown a high diversity of alligatorids including an intriguing frequency of giant forms and endemic communities dominated by small blunt-snouted taxa with crushing dentitions (Langston, 1965; Aguilera *et al.*, 2006; Scheyer *et al.*, 2013; Salas-Gismondi *et al.*, 2015). Although this Amazonian diversity is remarkable, an overview on the high-latitude record of South American caimanines is essential for a comprehensive view of the history of the group (Bona *et al.*, 2013a), especially considering that the richest record of Alligatoridae in Argentina belongs to the Late Miocene. Despite some isolated cranial material of caimanines from the Late Miocene in Northwestern Argentina (Starck and Anzótegui, 2001; Bona *et al.*, 2014), the most abundant and diverse Miocene material comes from a level informally called "Mesopotamiense" or "Conglomerado Osífero" that crops out in the area of the city of Paraná (Cione *et al.*, 2000; Bona *et al.*, 2013a,b). This record corresponds mainly to cranial and postcranial fragmentary elements of different taxa, which have been studied by numerous authors since the mid-nineteenth century (Bravard, 1858; Burmeister, 1883; Ambrosetti, 1887; Scalabrini, 1887; Rovereto, 1912; Rusconi, 1933, 1935; Patterson, 1936; Langston, 1965; Gasparini, 1968, 1973, 1981, 1985; Langston and Gasparini, 1997). Contrary to modern day ecosystems, in which overall alligatorid diversity is declining and no more than two species occur sympatrically (Scheyer *et al.*, 2013), the "Conglomerado Osífero" could have housed at least six species of caimanines (Gasparini, 1996; Bona *et al.*, 2012, 2013a, b; Bona and Paulina Carabajal, 2013). Finally, during the Pliocene–Pleistocene, Argentinean alligatorids were represented by a well-preserved specimen from Salta Province (Barrios, 2013) and some fragmentary materials from the Pleistocene of Salta and Entre Ríos (Patterson, 1936; Noriega *et al.*, 2004).

The study of these reptiles has provided valuable information to support numerous hypotheses related to the evolutionary and biogeographical history of the group and even of other vertebrates (*e.g.*, Simpson, 1933, 1937; Langston, 1965; Sill, 1968; Pascual and Odreman Rivas, 1971; Báez and Gasparini, 1977, 1979; Pascual, 1986; Taplin and Grigg, 1989; Gasparini, 1996; Brochu, 1999, 2004).

Besides the contribution of Langston (1965), who in his study on the Cenozoic crocodylians of Colombia gave special attention to the southern record of alligatorids, complete and detailed treatments of the fossil Alligatoridae of Argentina date back to the beginning of the 20th century (Rovereto, 1912; Rusconi, 1933) and then, near the seventies, when Zulma Gasparini began with her study on the fossil crocodiles of Argentina. In her thesis "Revisión de los Crocodilia (Reptilia) fósiles del territorio argentino: su evolución, sus relaciones filogenéticas, su clasificación y sus implicancias biogeográficas" (Gasparini, 1973), unfortunately unpublished, she dedicated a whole chapter to the analysis of the Alligatoridae, marking an inflection point in the knowledge of this group.

Here we present an update of the knowledge of the Cenozoic alligatorids of Argentina, and dedicate it to Zulma Gasparini in gratitude for her invaluable contribution to the understanding of the evolution of these reptiles in South America (Gasparini, 1981, 1985, 1996; Gasparini and Báez, 1975; Báez and Gasparini, 1977, 1979; Gasparini *et al.*, 1986) and for having influenced numerous paleoherpetologist all over the world (*e.g.*, A. Aguilera, A. Albino, A. Buscalioni, J. Bocquentin-Villanueva, P. Bona, C. Brochu, L. Codorníu, J. Desojo, M. de la Fuente, M. Fernández, D. Fortier, Y. Herrera, J. O'Gorman, F. Ortega, A. Otero, D. Riff, M. Sánchez-Villagra, L. Salgado, R. Salas-Gismondi, J. Souza-Filho, J. Sterli, A. Paulina Carabajal, D. Pol).

Institutional Abbreviations. **AMNH**, American Museum Natural History, New York, USA; **AMU-CURS**, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; **FMNH-P**, Field Museum of Natural History, Paleontology, Chicago, USA; **MACN-PV**, Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia", Paleontología Vertebrados, Buenos Aires, Argentina; **MAS-PALEO**, Museo Antropológico de Salta, Colección Paleontológica, Salta, Argentina; **MLP**, Museo de La Plata, Buenos Aires, Argentina; **MPEF-PV**, Museo Paleontológico Egidio Feruglio, Paleontología Vertebrados, Trelew, Chubut, Argentina; **PVL**, Colección Paleontología Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; **UCMP**, Museum of Paleontology, University of California, Berkeley, USA; **UFAC**, Universidade Federal do Acre, Rio Branco, Acre, Brazil.

GEOLOGICAL SETTING AND LOCALITIES

Paleocene

Salamanca Formation (Lesta and Ferello, 1972). Fossil material corresponds to cranial and postcranial isolated fragments of alligatorids (Simpson, 1937; Bonaparte *et al.*, 1993; Bona, 2004, 2007; Fig. 2.1–2, 4) recovered from the upper levels of the Salamanca Formation (Upper Danian; Andreis, 1977; Bertels, 1977; Iglesias *et al.*, 2007; Woodburne *et al.*, 2014), informally called “Banco Negro Inferior” and “Banco Verde” (Feruglio, 1949; Miembro Hansen, Andreis *et al.*, 1975; see Bond *et al.*, 1995 and Woodburne *et al.*, 2014); Peligran? SALMA (South American Land Mammal Ages) *sensu* Gelfo *et al.* (2009). These levels crop out mainly in the coast of Chubut Province, Argentina, in several localities between Bahía Bustamante and Comodoro Rivadavia (e.g., Bajada de Hansen, Cerro Hansen, “El Gauchito”, Estancia La Teresa, Puerto Visser, Estancia Las Violetas –near to Malaspina– and Punta Peligro; Fig. 1).

Rio Chico Group (Legarreta and Uliana, 1994; *sensu* Raigemborn *et al.*, 2010) La Violetas Formation (Raigemborn *et al.*, 2010). The fossil material corresponds to a fragmentary mandible (Rusconi, 1937; Fig. 2.3), from a level called “Notostilopense inferior o basal” (Ameghino, 1899), recently considered as Las Violetas Formation (Middle Paleocene; Andreis, 1977) by Raigemborn *et al.* (2010), near Puerto Visser in the Chubut Province.

Eocene

Sarmiento Formation (Feruglio, 1938; *sensu* Raigemborn *et al.*, 2010). Material (fairly complete skull and mandible; Simpson, 1933; Fig. 2.5) comes from the level “*Notostylops* Beds” (Ameghino, 1906), Gran Barranca locality, near the Colhué-Huapi Lake in the Chubut Province, recently considered as Sarmiento Formation by Raigemborn *et al.* (2010); Barrancan SALMA, Late Eocene *sensu* Gelfo *et al.* (2009).

Miocene

“Conglomerado Osífero” (*sensu* Frenguelli, 1920; see Cione *et al.*, 2005). This level crops out discontinuously in the Paraná River banks, from the vicinity of Paraná further north. It overlies the marine Paraná Formation (Bravard, 1858), and is characterized by the presence of levels of quartz gravel, clay clasts and numerous isolated fragments of continental

and marine vertebrates (Brandoni and Scillato-Yané, 2007; Brandoni, 2011). Crocodylian remains correspond to cranial and postcranial fragments (Bravard, 1858; Burmeister, 1883; Ambrosetti, 1887; Scalabrini, 1887; Rovereto, 1912; Rusconi, 1933, 1935; Patterson, 1936; Langston, 1965; Gasparini, 1968, 1973, 1981, 1985; Langston and Gasparini, 1997; Bona and Paulina Carabajal, 2013; Bona *et al.*, 2013a,b; Fig. 3). Based on the evidence of stratigraphic relations and the fossil vertebrates recorded, Cione *et al.* (2000) suggested a correlation of this unit with the late Miocene Huayquerian (for South America) and the Tortonian of the international scale. This conglomerate is considered by several authors as a level of the Ituzaingó Formation (Pliocene; De Alba, 1953; Herbst, 1971; Cione *et al.*, 2000; Brandoni, 2011; Brunetto *et al.*, 2013), which crops out along the cliffs of the left margin of the Paraná River in the provinces of Corrientes and Entre Ríos.

Palo Pintado Formation (Díaz and Malizzia, 1983). A frag-



Figure 1. Location map of the geographic distribution of the Argentinean fossil and extant Alligatoridae.

mentary mandible was collected from the upper beds of this unit, exposed in the Quebrada de Salta in the southern Calchaquí Valley, in the southwest of Salta Province, Argentina (Bona *et al.*, 2014; Fig. 4.1). This unit comprises fluvial levels deposited during the Late Miocene, between 10 Ma (K/Ar) (Galli *et al.*, 2008) and 5.2 Ma (Coutand *et al.*, 2006; Bywater-Reyes *et al.*, 2010).

Pliocene/Pleistocene

Piquete Formation (Orán Group, Gebhard *et al.*, 1974). Remains fairly complete of one alligatorid were found in the Piquete Formation, at the right margin of Rosario-Horcones River, northwest of Rosario de la Frontera City, south of Salta Province, Argentina (Barrios, 2013; Fig. 4.3). Numerical ages of these units are scarce (Arias *et al.*, 1978), but magnetostratigraphic studies indicate that this formation was deposited between 5 and 1.3 Ma (Pliocene/Early Pleistocene) (Gebhard *et al.*, 1974; Reynolds *et al.*, 1994).

Pleistocene

"Upper Chaco Beds" (Patterson, 1936). Alligatorid materials come from the Quebrada Agua Blanca, eastern Salta Province, Argentina. They were found in a hard sandstone concretion in association with mammal remains that indicate a Pleistocene age for the assemblage (Patterson, 1936; Fig. 4.2).

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789, *sensu* Benton and Clark, 1988

ALLIGATORIDAE Cuvier, 1807, *sensu* Norell *et al.*, 1994

Genus and species indet.

Figure 2.4

Referred Material. MLP 80-X-10-1, skull table.

Occurrence. The specimen MLP 80-X-10-1 comes from the

Banco Negro Inferior of Punta Peligro area (Chubut Province, Argentina; Fig. 1); upper levels of the Salamanca Formation (Lesta and Ferello, 1972), Upper Danian (Andreis, 1977; Bertels, 1977; Iglesias *et al.*, 2007; Woodburne *et al.*, 2014).

Comments. The cranial material belongs to a middle sized specimen, preserving the skull table, left quadrate, both exoccipitals and supraoccipital, and lacking the basicranium. The general morphology of the skull table, together with the position of the foramen aërum in the dorsal surface of quadrate and the relative size of the quadrate condyles (lateral larger than the medial) allows us to refer this specimen to Alligatoridae. In addition, as in early alligatoroids, MLP 80-X-10-1 presents: the fronto-parietal suture reaching the medial margin of the supratemporal fenestra, in such a way that frontals form the anteromedial margin of the fenestra and prevent the broad contact between postorbital and parietal [character 150 (0); Brochu, 2011], and the supraoccipital slightly exposed on the skull table (Fig. 2.4), all features present in some North American alligatorines such as *Brachychampsa montana* Gilmore, 1911. Further detailed studies will certainly clarify the taxonomy and phylogenetic relationships of this specimen (Bona and Barrios, in study).

Notocaiman Rusconi, 1937

Figure 2.3

Type Species. *Notocaiman stromeri* Rusconi, 1937.

Holotype. PVL 752 (Gasparini, 1973) (N° 1205 of the old Paleontological Collection Rusconi). Left mandibular fragment with 14 alveoli (Rusconi, 1937, p. 3; Fig. 2.3).

Occurrence. About 15 km northwest of Puerto Visser, Chubut Province, Middle Paleocene, Las Violetas Formation (Raigemborn *et al.*, 2010). The locality Puerto Visser was erroneously considered as belonging to the Santa Cruz Province in the original description.

Comments. Rusconi (1937) described and characterized

Figure 2. Paleogene Argentinean Alligatoridae in dorsal view. 1, *Necrosuchus ionensis* (AMNH 3219), right dentary (modified from Brochu, 2011); 2, *Eocaiman palaeocenicus* (MPEF-PV 1933), mandibular fragments; 3, *Notocaiman stromeri* (PVL 752), left mandibular fragment (modified from Brochu, 2011); 4, Alligatoridae indet. (MLP 80-X-10-1), skull table; 5, *Eocaiman cavernensis* (AMNH 3158), mandible and rostrum (modified of Brochu, 1999). Scale bars= 5cm.

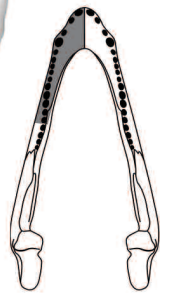
①



②



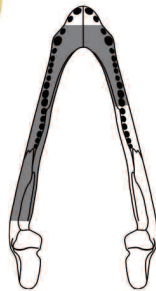
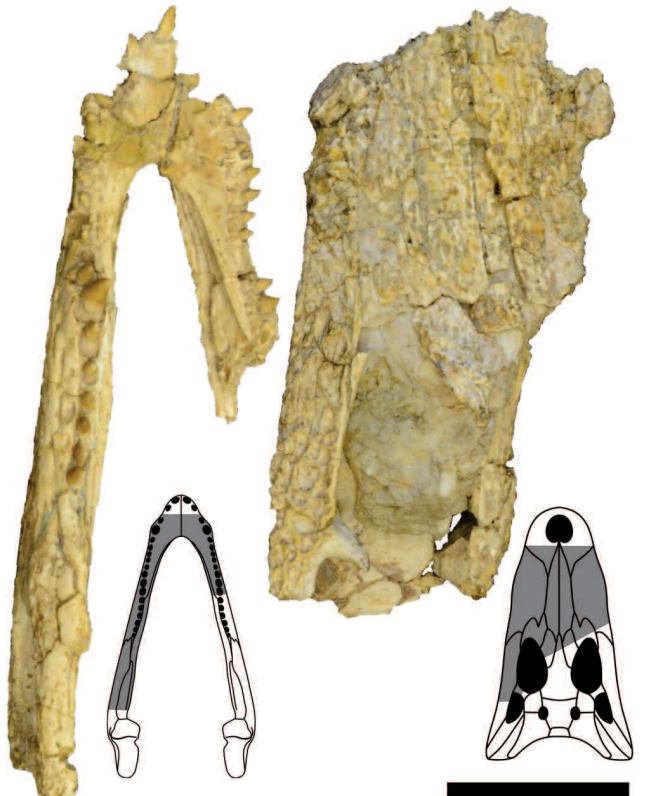
③



④



⑤



this species as a huge alligatorid with robust mandible and robust 13th and 14th teeth, among other characters. Langston (1965) provided a detailed discussion of this species (see Langston, 1965, p. 123–124) and pointed out that the most significant feature of this taxon was the relative size of the 12th and 13th teeth (not the 13th and 14th as stated by Rusconi, 1937), probably comparable to the condition seen in *Eocaiman* Simpson, 1933. Gasparini (1973) suggested that the characters enumerated by Rusconi (1937) and analyzed by other authors are insufficient to validate this species and considered PVL 752 as *Eusuchia* indet. As in *Eocaiman*, the symphysis extends beyond the 5th mandibular tooth (including 6th alveolous *sensu* Brochu, 2011: fig. 7C) and the dentary is anteriorly low and less festooned than in extant species. We agree with Langston (1965) and Brochu (2011) in considering *Notocaiman stromeri* as a valid species of alligatorid with a general morphology of the anterior part of the dentary similar to other Paleogene Caimaninae (Brochu, 2011). However, given the morphological similarities between *Notocaiman* and *Eocaiman* we do not rule out a synonymy between these two genera. Future revision of PVL 752 could test this hypothesis.

CAIMANINAE Brochu, 2003 (following Norell, 1988)

Eocaiman Simpson, 1933

Type Species. *Eocaiman cavernensis* Simpson, 1933.

Eocaiman palaeocenicus Bona, 2007

Figure 2.2

Holotype. MPEF- PV-1933, partially complete mandible.

Referred Material. MPEF PV-1935, fragment of right dentary; MPEF- PV-1936, fragment of left dentary; MLP 90-II-12-117, tooth; MLP 90-II-12-124, tooth; MLP 93-XII-10-11, fragment of right dentary; MLP 93-XII-10-13, anterior fragment of left dentary; MLP 95-XII-10-20, anterior fragment of right dentary; MLP 95-XII-10-27, tooth; MACN-PV CH 1914, posterior fragment of right hemimandible; MACN-PV CH 1915, fragment of left dentary; MACN-PV CH 1916, anterior fragment of right dentary; MACN- PV CH 1627, posterior fragment of left hemimandible.

Occurrence. The holotype was found in El Gauchito locality

(45° 14' S, 67° 06' W; Fig.1), Chubut Province, Argentina; Salamanca Formation (Lesta and Ferello, 1972), from a level overlying the BNI (Feruglio, 1949; Bona *et al.*, 1998), Danian (Méndez, 1966; Bertels, 1975, 1977; Somoza *et al.*, 1995).

Comments. *Eocaiman* was erected by Simpson (1933) based on a skull with mandible of the Eocene of Patagonia, Argentina (AMNH 3158, see below). This author compared *Eocaiman* with *Allognathosuchus* Mook, 1921 (a North American alligatorine), comparisons that were used to support the hypothesis of a northern origin of caimans (Patterson, 1936), but regarded *Eocaiman* as a close relative of extant caimans. Later, Bona (2004, 2007) described *E. palaeocenicus* emending the generic diagnosis and extending the temporal distribution of the genus back to the Upper Paleocene. Recently, a new small species, *E. itaboraiensis* Pinheiro *et al.*, 2013, was described on the basis of an anterior fragment of a left mandibular rami and one isolated tooth from the middle–upper Paleocene Itaboraí Basin (Rio de Janeiro State, Brazil; Pinheiro *et al.*, 2013). *Eocaiman* is a basal Caimaninae (Brochu, 1999, 2011; Bona, 2007) with a low mandible at the symphyseal region and a long symphysis (extended back to the 5th alveolus). This genus is distributed from the Paleogene of Patagonia to the Middle Miocene of Colombia (Langston, 1965). The Paleocene *E. palaeocenicus* is a middle sized caiman with robust lower jaws. Together with *Necrosuchus ionensis* Simpson, 1937 (see below) and MLP 80-X-10-1 this species constitutes the earliest record of South American alligatorids.

Eocaiman cavernensis Simpson, 1933

Figure 2.5

Holotype. AMNH 3158, almost complete skull.

Occurrence. Sarmiento Formation (Feruglio, 1938; *sensu* Raigemborn *et al.*, 2010), Gran Barranca, south of Colhué-Huapi Lake, Chubut Province, Argentina.

Comments. This species was the first caiman described for Patagonia (Simpson, 1933). Compared to *E. palaeocenicus*, *E. cavernensis* is represented by more complete cranial remains (rostrum and lower jaw), with the mandible less robust but posteriorly higher. In his phylogenetic analysis of alligatorids, Brochu (1999) placed this taxon as a basal Caimaninae (see discussion below).

***Necrosuchus* Simpson, 1937**

Type Species. *Necrosuchus ionensis* Simpson, 1937.

***Necrosuchus ionensis* Simpson, 1937**

Figure 2.1

Holotype. AMNH 3219, right dentary with associated cranial fragments and partial postcranial skeleton referable to a single individual. This material was collected during the First Scarritt Expedition to Patagonia in 1931.

Occurrence. Salamanca Formation (Lesta and Ferello, 1972), locality Estancia Las Violetas, Chubut Province, Argentina. Paleocene, Peligran SALMA (Upper Danian; Andreis, 1977; Bertels, 1977; Iglesias *et al.*, 2007; Woodburne *et al.*, 2014; Fig. 1).

Comments. Simpson (1937) erected this species based on a fragmentary lower mandible and associated postcranial remains, but only the mandible was figured and described. He considered this species as a member of the family Crocodylidae and proposed a close relationship with the North American genus *Leidyosuchus* Lambe, 1907. Later, Brochu (1997, 1999) suggested a relationship between *N. ionensis* and caimanines (not with a crocodylid). The re-interpretation of *N. ionensis* as a basal caiman has biogeographical implications, establishing the presence of caimanines in southern South America early in the Cenozoic and extending back the early history of caimans (Brochu, 2011).

***Mourasuchus* Price, 1964**

Type Species. *Mourasuchus amazonensis* Price, 1964.

***Mourasuchus nativus* (Gasparini, 1985)**

Figure 3.5

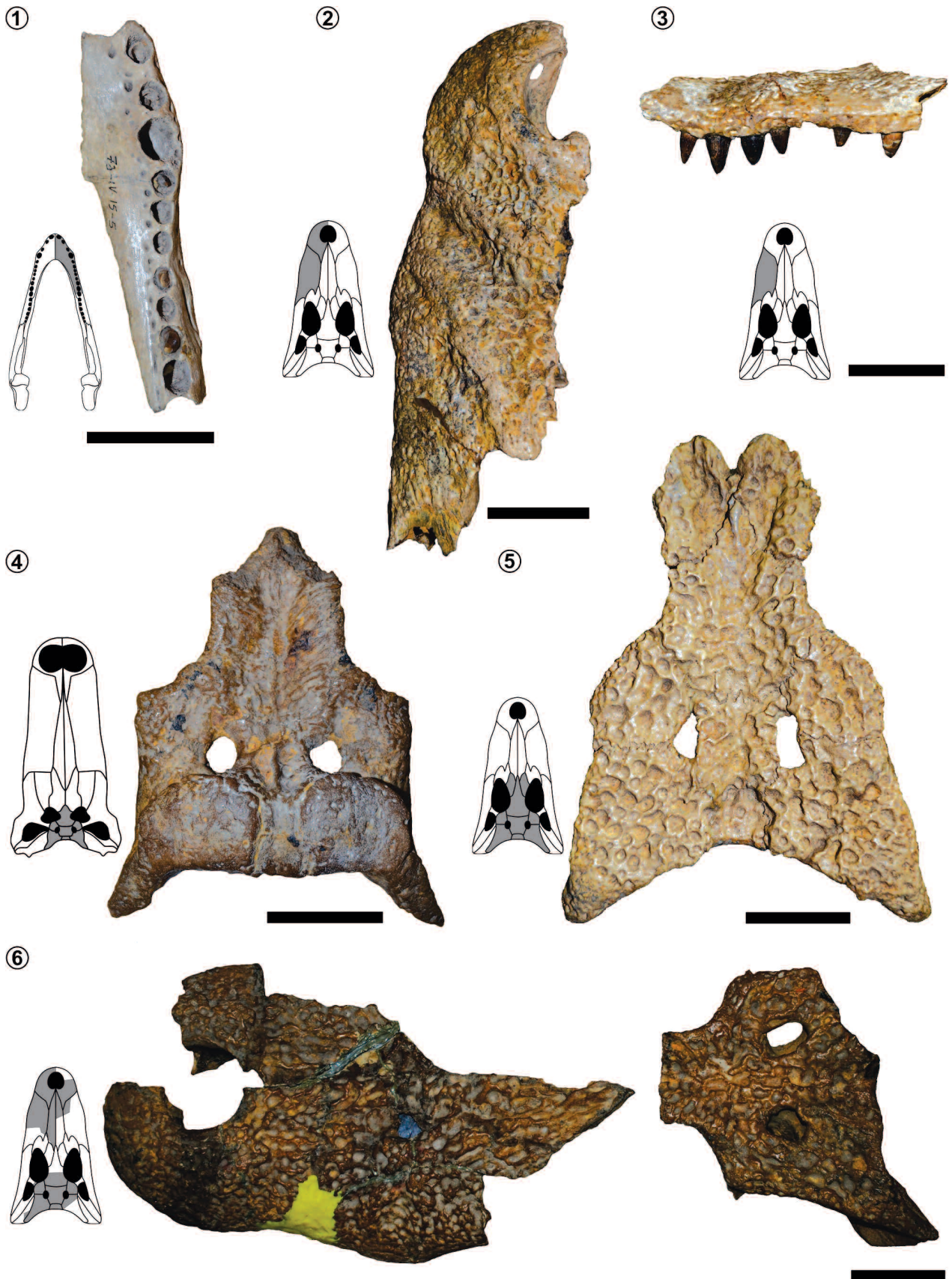
Holotype. MLP 73-IV-15-8, skull table.

Referred Material. AMU-CURS-212-218, skull fragments; MLP 73-IV-15-9, posterior part of the skull; UFAC-1397, left maxillae; UFAC-1424, posterior part of the skull and left hemimandible; UFAC-1431-1477-1666-2515-3530-3717-4259-4885-4925, posterior part of the skull; UFAC-

1484, left hemimandible; UFAC-1485, right hemimandible; UFAC-1495, right maxillae.

Occurrence. The holotype and MLP 73-IV-15-9 come from the banks of the Paraná River, in the area of Paraná (Entre Ríos Province, Argentina; Fig. 1); "Conglomerado Osífero", Ituzaingó Formation (Herbst, 1971), Late Miocene (Cione *et al.*, 2000; Brandoni and Scillato-Yané, 2007; Brandoni, 2011; Deschamps *et al.*, 2013). Referred material housed in UFAC comes from the Niteroi site, right bank of the Acre River, between the cities of Rio Branco and Senador Guiomard; Solimões Formation, Upper Miocene (Bona *et al.*, 2013a).

Comments. This species is characterized by the extremely wide, compressed, and long rostrum with a straight lateral border without festooning, a skull with a relative small skull table but with prominent squamosal eminences (protuberances) in adult stages, and a slender U-shaped mandibles with numerous small conical teeth (Price, 1964; Langston, 1965; Gasparini, 1985; Bocquentin and Souza-Filho, 1990; Bona *et al.*, 2012; for the Synonymic List and a detailed history of this taxon see Bona *et al.*, 2013a). The genus *Mourasuchus* is endemic to South America (Langston and Gasparini, 1997). One of the earliest mentions about these bizarre crocodylians was made by Langston (1965), who described and named *Nettosuchus atopu*, Langston, 1965 from the middle Miocene of Colombia, erecting the family Nettosuchidae to include it. Recent cladistic analyses place this taxon among caimanines, linking *Purussaurus* Barbosa-Rodrigues, 1892 with *Mourasuchus* (Brochu, 1999, 2003, 2010; Aguilera *et al.*, 2006; Bona, 2007; Bona *et al.*, 2013a; Salas-Gismondi *et al.*, 2015). This species was originally named by Gasparini (1985) as *Charandaisuchus nativus* based on two posterior fragments of skull table. Later, Bocquentin and Souza-Filho (1990) described more cranial material of this taxon and considered *Charandaisuchus* a junior synonym of *Mourasuchus*, and recently, Bona *et al.* (2012, 2013a) provided a detailed study of the cranial anatomy of *M. nativus* and morphological features that clarify the phylogenetic relationships of the species. This species inhabited the Amazonian basin during the Late Miocene, from Venezuela (Urumaco Formation) to northeast Argentina ("Conglomerado Osífero") (Bona *et al.*, 2013a,b; Scheyer *et al.*, 2013).



Caiman Spix, 1825

Type Species. *Caiman latirostris* (Daudin, 1802).

Caiman australis (Burmeister, 1885)

Figure 3.6

Holotype. MACN PV 258, complete left maxilla.

Occurrence. Banks of the Paraná River, in the area of Paraná (Entre Ríos Province, Argentina; Fig. 1); “Conglomerado Osífero”, Ituzaingó Formation (Herbst, 1971), Late Miocene (Brandoni and Scillato-Yané, 2007; Brandoni, 2011).

Comments. *Caiman australis* is known from a left maxillary fragment. It is a narrow-snouted caiman with reduced interalveolar maxillary spaces, and ornamentation with predominance of prominent and elongated grooves and bumps (for a detailed comment about the taxonomic history of this species see Rusconi, 1933; Langston, 1965; Gasparini, 1973, 1981; Bona *et al.*, 2013a,b). Based on fragmentary and disassociated material, Bravard (1858) erected the name *Crocodylus australis* to include all the cranial and postcranial remains of non-longirostrine crocodylians from the “Conglomerado Osífero”. An expanded detailed description of *Crocodylus australis* was given later by Burmeister (1885), but the first formal diagnosis and discussion of diagnostic characters of *Crocodylus australis* was provided by Rovereto (1912), who figured the type material. Available morphological information used to reconstruct phylogenetic relationships is insufficient to propose the phylogenetic position of this species within alligatorids (Brochu, 1999, 2010, 2011; Bona *et al.*, 2013a,b). Nevertheless, *Caiman australis* is one of at least five valid *Caiman* species recorded in the Late Miocene of Argentina, supporting the hypothesis of the great diversification of *Caiman* in these latitudes during the Late Miocene (Bona *et al.*, 2013a,b).

Caiman gasparinae Bona and Paulina Carabajal, 2013

Figure 3.3

Holotype. MLP 73-IV-15-1, skull represented by a rostrum with articulated fragments of premaxillae, maxillae, nasals, left lacrimal and a partial braincase lacking the basicranium.

Referred Material. MACN PV 5555, fragment of right premaxilla.

Occurrence. Banks of the Paraná River, in the area of Paraná (Entre Ríos Province, Argentina; Fig. 1); “Conglomerado Osífero” Ituzaingó Formation (Herbst, 1971), Late Miocene (Brandoni and Scillato-Yané, 2007; Brandoni, 2011).

Comments. *Caiman gasparinae* was erected and described by Bona and Paulina Carabajal (2013) on the basis of an almost complete skull. It is a huge broad-snouted caiman with a low rostrum and narial opening broadly distanced from the anterior margin of premaxilla (for the synonymic list and a detailed history of this taxon see Bona and Paulina Carabajal, 2013; Bona *et al.*, 2013a,b). *Alligator? ameghinoi* Rovereto, 1912 was based on isolated large cranial and postcranial remains. Later, Rusconi (1933) erected the genus *Xenosuchus* to include all the large-sized alligatorids from the Neogene of Paraná, being a fragment of maxilla (MACN PV 5555) among the materials referred to this taxon. Later, Gasparini (1973) assigned MLP 73-IV-15-1 to *Caiman latirostris*, but gave no description of the specimen or any justification for that assignation. Both MLP 73-IV-15-1 and MACN PV 5555 belong to *Caiman gasparinae*, a species nested within the Jacarea clade (*sensu* Brochu, 1999; Bona *et al.*, 2013a). This species differs from other Miocene large forms, such as *Purussaurus*, and from other broad-snouted caiman species, such as *C. latirostris*, and represents one of the largest known *Caiman* species, to which numerous huge mandibular and postcranial remains found in the area of Paraná may pertain. The position of the narial opening at the premaxilla together with the general shape of the snout of *C. gasparinae* differs also from other caimans, such as *Melanosuchus* Gray, 1862.

Caiman latirostris (Daudin, 1802)

Figures 3.1, 4

Figure 3. Miocene Argentinean Alligatoridae. 1, *Caiman latirostris* (MACN-PV 5416), left fragment of a rostrum in dorsal view; 2, *Caiman* cf. *C. yacare* (MLP 73-IV-15-5), right dentary fragment in dorsal view; 3, *Caiman gasparinae* (MLP 73-IV-15-1), snout and skull table in dorsal view; 4, *Caiman lutescens* (MACN-PV 13551), skull table in dorsal view; 5, *Mourasuchus nativus* (MLP 73-IV-15-8), skull table in dorsal view; 6, *Caiman australis* (MACN-PV 258), left maxilla in lateral view. Scale bars= 5cm.

Referred material. MACN PV 5416, left premaxilla and maxilla; MACN PV 5576, left premaxilla; MLP 73-IV-15-16, fragment of left premaxilla; MLP 73-IV-15-12, fragment of braincase; MLP 89-XII-5-1, fragment of left dentary; MAS-PALEO- 001/2011; FMNH-P 15029.

Occurrence. Banks of the Paraná River, in the area of Paraná, Entre Ríos Province, Argentina, and Salta Province, Argentina (Fig. 1); “Conglomerado Osífero”, Ituzaingó Formation (Herbst, 1971), (Brandoni and Scillato-Yané, 2007; Brandoni, 2011), Palo Pintado Formation (Mauri, 1948; Díaz and Malizzia, 1983), Piquete Formation (Gebhard *et al.*, 1974), Upper Chaco Beds, Late Miocene to Recent (NE of Argentina, Paraguay, Bolivia, N of Uruguay and S–SE of Brazil).

Comments. Broad-snouted *Caiman*, with a rounded snout and presence of rostral crest (for a detail description of this species and a synonymic list see Cei, 1993; Bona and Desojo, 2011; Barrios, 2013; Bona *et al.*, 2013a,b). A comparative study of the cranial morphology in *Caiman latirostris* was made by Bona and Desojo (2011) suggesting that several skull fragments of crocodiles from the “Conglomerado Osífero” could be assigned to this species (Bona *et al.*, 2013a,b). Rovereto (1912, p. 346) erected *Alligator lutescens* on the basis of the large size of several isolated cranial and postcranial fragments. Among these, there is a left rostral fragment that can be identified as *Caiman latirostris* (Bona *et al.*, 2013a: fig. 7A–D) and a skull table (MACN-PV 13551) that constitutes the holotype of *A. lutescens* (see below). Although these materials were not associated, this author assumed that given their sizes they belong to a single species. Following Gasparini (1973, 1981), Bona *et al.* (2013a,b) regarded *A. lutescens* in part (Rovereto, 1912, p. 346, fig. 4a) and *Xenosuchus lutescens* in part (Rusconi, 1933, p. 80, fig. 11a) as junior synonyms of *C. latirostris*, remarking that this species was represented in the Late Miocene by specimens larger than the extant ones.

Caiman latirostris is also recorded in the Late Miocene (Bona *et al.*, 2014), and Plio–Pleistocene (Patterson, 1936; Barrios, 2013). This record suggests that the current distribution of *Caiman latirostris* in high latitudes (*e.g.*, north-central Argentina) was driven by environmental and climatic changes occurred during the late Neogene linked to tectonic events (see Starck and Anzótegui, 2001; Bona *et al.*, 2014).

Caiman lutescens (Rovereto, 1912)

Figure 3.4

Holotype. MACN-PV 13551, skull table.

Occurrence. Banks of the Paraná River, in the area of Paraná (Entre Ríos Province, Argentina; Fig. 1); “Conglomerado Osífero”, Ituzaingó Formation (Herbst, 1971), Late Miocene (Brandoni and Scillato-Yané, 2007; Brandoni, 2011).

Comments. *Caiman lutescens* is a huge caimanine represented only by a skull table (Bona *et al.*, 2013a: fig. 9). Rovereto (1912, p. 346–349) provided a brief description of some of the diagnostic characters of this species, such as a longitudinal depression of the skull table at the middle line, and short frontal with its cranial end poorly extended between pre-frontals (for a detailed comment of the taxonomic history of this taxon see Gasparini, 1973 and Bona *et al.*, 2013a,b). Recently, an emended diagnosis of this taxon has been provided, along with a discussion on its systematic position and nomenclature (Mendez Cidade *et al.*, 2015; Bona *et al.*, in study). *Caiman lutescens* is diagnosed as a Caimaninae nested within the crown-group caimans with a unique combination of skull characters, some of them autapomorphies (*i.e.*, supraoccipital ventrally positioned between the dorsally elevated squamosals; frontal extremely short, with a reduced rostral process meeting prefrontals). Given the lack of phylogenetic resolution and that the emended diagnosis of the species does not match with any of the currently known Caimaninae genera (Mendez Cidade *et al.*, 2015), further research is still needed in order to better establish its generic status and its relationships within Caimaninae.

Caiman cf. lutescens Langston (1965) from the Middle Miocene of Colombia (La Venta) is represented by an incomplete skull with no skull table (UCMP 39978, Langston, 1965, p. 75, figs. 32–34, pl. 2). Langston (1965) used the holotype of *C. lutescens* to reconstruct the skull table of *Caiman cf. lutescens*, but there is not enough evidence to justify that assumption (see Brochu, 1999; Bona *et al.*, 2013a,b). This specimen of La Venta shows a *Caiman*-like general morphology, with some similarities with *C. latirostris*, but has no comparable features with *C. lutescens* of Argentina. The presence of *C. lutescens* was mentioned for the Upper Miocene of Venezuela by the record of a left rostral

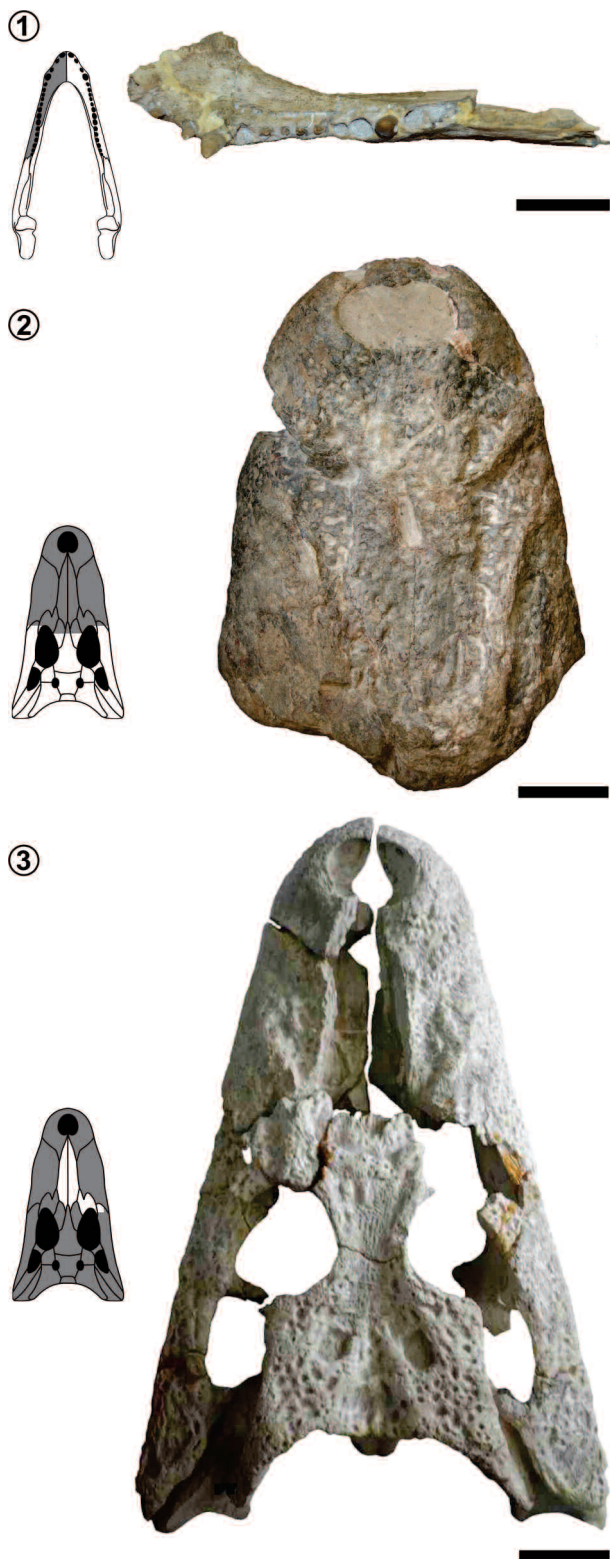


Figure 4. Mio/Pleistocene Alligatoridae from northwestern Argentina, *Caiman latirostris* in dorsal view; 1, MLP 89-XII-5-1, left dentary; 2, FMNH-P 15029, rostrum; 3, MAS-PALEO 001/2011, cranium. Scale bars= 5cm.

fragment, similar to *Caiman* cf. *lutescens* (Sánchez-Villagra and Aguilera, 2006: fig. 3P, Q; Scheyer and Moreno-Bernal, 2010). Although its general morphology is similar to *Caiman* cf. *lutescens* and to *C. latirostris*, the skull table configuration of this specimen is also unknown so it cannot be assigned to *C. lutescens*, at the moment only known by a skull table from the Miocene of Paraná, Argentina.

Caiman cf. *C. yacare* (Bona *et al.*, 2013a)

Figure 3.2

Referred Material. MLP 73-IV-15-5, MLP 73-IV-15-6, right dentary fragments; MLP 73-IV-5-17, MACN PV 5417 fragments of right maxilla (Fig. 3.2).

Occurrence. Banks of Paraná River, in the area of Paraná (Entre Ríos province, Argentina; Fig. 1); "Conglomerado Osífero", Ituzaingó Formation (Herbst, 1971), Late Miocene (Brandoni and Scillato-Yané, 2007; Brandoni, 2011).

Comments. The first mention of *Caiman* cf. *C. yacare* in the "Mesopotamiense" was made by Gasparini (1973), based on several mandibular remains, and was later accepted in other works (Gasparini, 1981, 1996; Cione *et al.*, 2000; Piña and Argañaraz, 2000; Bona *et al.*, 2013a,b). Later, Fortier *et al.* (2009) reported the occurrence of *C. yacare* in the Niterói outcrops of the Solimões Formation in northwestern Brazil. The fossil record of *C. yacare* in Brazil and *Caiman* cf. *yacare* in the area of Paraná shows that during the Late Miocene this species had already reached its modern distribution. Additionally, it also shows that the Miocene specimens would have reached larger sizes than the extant forms (Bona *et al.*, 2013a,b).

DISCUSSION AND FINAL REMARKS

The Paleogene record of alligatoroids in Argentina is concentrated in the Chubut Province being the most ancient record for South America (*e.g.*, *Necrosuchus*, *Eocaiman*). The knowledge of this Patagonian fossil record is essential for the understanding of the biogeographical history of this lineage. Before this study, the fossil record of Alligatoroidea in Argentina was exclusively represented by Caimaninae but the skull table recovered in Paleocene rocks at the coast of Chubut Province might change this scenario. This cranial fragment reveals that basal alligatoroids were already

present in South America at that time (Bona and Barrios, in study). For many years a single dispersal event from North to South America was sufficient to explain the presence of alligatorids (caimans) in this part of the continent (Simpson, 1933, 1937; Sill, 1968; Gasparini, 1973; Brochu, 1999, 2010; Hastings *et al.*, 2013). The recent finding of a Caimaninae (*Tsoabichi greenriverensis*) in the Eocene of North America and the controversial placement of the North American Eocene *Orthogenysuchus* nested within a derived clade of caimaninae (Brochu, 1999) make this scenario more complex (see Bona *et al.*, 2013a and cites herein for a detailed discussion of the systematic position of *Orthogenysuchus*). However, the earliest presence of this group in high latitudes in South America together with the absence of South American alligatorines, suggest a vicariant biogeographic model, in which both clades of Alligatoridae (Alligatorinae and Caimaninae) were separated by continental rifting during the Cretaceous (Brochu, 1999; Bona, 2004). These biogeographic scenarios must be clarified in the future by prospection and study of new early alligatoroids from Patagonia, Argentina, together with new interpretations on the Caimaninae phylogenetic relationships, especially the basal forms (Brochu, 2010).

As stated above, another important moment of the evolutionary history of caimanines occurred during the Miocene, when this lineage diversifies. The South American Miocene record of crocodylians in the Pan-Amazonian region (*sensu* Hoorn *et al.*, 2010) is characterized by the great taxonomic diversification of the caimanines clade (Langston, 1965; Gasparini, 1996; Brochu, 2003; Riff *et al.*, 2010; Bona *et al.*, 2013a,b) with a wide geographic distribution of several genera (*e.g.*, *Mourasuchus*, *Purussaurus*, *Caiman*) and local endemism at the species level (Bona *et al.*, 2013a,b; Scheyer *et al.*, 2013; Salas-Gismondi *et al.*, 2015). It is known that during the Miocene continental vertebrates in South America reached huge body sizes (*e.g.*, Cione *et al.*, 2005; Vizcaíno *et al.*, 2012; Vucetich *et al.*, 2015). Fossil Miocene crocodylians recorded in southernmost Pan-Amazonia (Paraná) are comparative smaller than the coeval records in the north (*e.g.*, *Purussaurus brasiliensis* reaches around 12 m of total length; Riff and Aguilera, 2008), probably related to Neotropic paleotemperatures (see Head *et al.*, 2009). Although *Caiman* species were larger than today, large predators

such as *Purussaurus* are absent in this assemblage. Adult specimens of *Mourasuchus nativus* are similar in size to other species of the genus (all about 1 m in dorsal skull length; Bona *et al.*, 2012).

In Paraná, two genera of caimanines are known (*Caiman* and *Mourasuchus*) with at least five valid species, *M. nativus*, *Caiman gasparinae*, *C. latirostris*, *C. australis* and *C. lutescens* and the possible presence of *Caiman yacare* (Bona *et al.*, 2013a,b). With these results, the idea of a great taxonomic diversity of Caimaninae in these latitudes becomes clear. Although this taxic diversity does not reach that of coeval areas of northern South America, Paraná is distinguished by the wide diversification of *Caiman* which exceeds the diversity present today, with only three species: *C. latirostris*, *C. yacare* and *C. crocodilus*. Current distribution of *Caiman* in South America probably represents a relict of a wider Miocene–Pliocene geographical distribution; ancestral range that matches with the south of the present zoogeographical “Dominio Subtropical” (Ringuelet, 1961; Gasparini, 1981). Today, except *C. crocodilus*, which is mainly distributed in northern South America, *C. latirostris* and *C. yacare* occupy an area, which in Argentina matches with the Paraná River system (Medem, 1983). The interpretation of the Miocene–Pleistocene record of *C. latirostris* in Argentina (Patterson, 1936; Barrios, 2013; Bona *et al.*, 2014) suggests that the paleoenvironmental dynamics in northwestern Argentina during the late Neogene was strongly influenced by the advance of the Andean orogeny. Hence, the current geographic distribution of the *Caiman* species in these latitudes might be explained in terms of a retraction of tropical faunas, a process linked to climatic changes related to orogenic causes (Bona *et al.*, 2014).

Finally, despite the new fossil discoveries and the advances on anatomy, embryology, taxonomy, phylogeny and biogeography, new approaches on crocodylian history as this contribution are still influenced by the legacy of a pioneer paleontologist as Zulma Gasparini.

ACKNOWLEDGMENTS

We are grateful to M. Fernández and Y. Herrera for the invitation to participate in this special volume in honor of Zulma Gasparini. We thank the curators of the Paleontological Collections A. Kramarz and S. Alvarez (MACN), M. Reguero (MLP), E. Ruigómez (MEF), and W. Simpson (FMNH) for the access to the material under their care. We also thank D. Fortier, R. Salas-Gismondi and C. Deschamps for

valuable comments that helped improving the quality of this paper. This work was partially funded by the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT PICT-2012-0748 to M. Fernández and PICT 2008-0261), Universidad Nacional de La Plata (UNLP 11/N 749 to M. Fernández) and the Municipalidad de Plaza Huinul. Finally, we want to thank Zulma for all her support in our professional and personal lives.

REFERENCES

- Aguilera, O.A., Riff, D., and Boquentin-Villanueva, J. 2006. A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the Upper Miocene Urumaco Formation, Venezuela. *Journal of Systematic Palaeontology* 4: 221–232.
- Ambrosetti, J.B. 1887. Observaciones sobre los reptiles fósiles Oligocenos de los terrenos Terciarios del Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba* 4: 409–426.
- Ameghino, F. 1899. Sinopsis geológico-paleontológica. In: J.A. Torcelli (Ed.), *Segundo Censo de la República Argentina*. Taller de Impresiones Oficiales, Buenos Aires, 1, p. 111–255.
- Ameghino, F. 1906. Les formations sédimentaires du Crétacé et du Tertiaire de Patagonie entre les faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* 15: 1–568.
- Andreis, R.R., Mazzoni, M.M., and Spalletti, L.A. 1975. Estudio estratigráfico y paleoambiental de las sedimentitas terciarias entre Pico Salamanca y Bahía Bustamante, Provincia de Chubut, República Argentina. *Revista de la Asociación Geológica Argentina* 30: 85–103.
- Andreis, R.R. 1977. Geología del área de Cañadón Hondo. Departamento de Escalante, Provincia del Chubut, República Argentina. *Obra del Centenario del Museo de La Plata* 4: 77–102.
- Arias, J.E., Alonso, R. y Malanca, S. 1978. Un gliptodontoideo de la Formación Piquete (Grupo Orán), provincia de Jujuy, República Argentina. *Revista del Instituto de Ciencias Geológicas* 3: 175–188.
- Barrios, F. 2013. Presencia de *Caiman latirostris* (Daudin, 1802) (Crocodylia, Alligatoridae) en la Formación Piquete (Plioceno–Pleistoceno temprano) de la provincia de Salta, Argentina: implicancias paleoambientales y sistemáticas. *Ameghiniana* 50: 522–534.
- Báez, A.M., and Gasparini, Z. 1977. Orígenes y evolución de los Anfibios y Reptiles del Cenozoico de América del Sur. *Acta Geológica Lilloana* 14: 149–232.
- Báez, A.M., and Gasparini, Z. 1979. The South American Herpetofauna: an evaluation of the fossil record. In: W.E. Duellman (Ed.), *The South American Herpetofauna: its Origin, Evolution, and Dispersal*. Museum of Natural History, University of Kansas, p. 29–54.
- Barbosa-Rodríguez, B. 1892. Les Reptiles fossiles de la vallée de l'Amazonie. *Vellosia* 2: 41–46.
- Benton, M.J., and Clark, J.M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In: M. Benton (Ed.), *The Phylogeny and Classification of Tetrapods*. Clarendon Press, Oxford, p. 295–338.
- Bertels, A. 1975. Bioestratigrafía del Paleoceno marino en la provincia del Chubut, República Argentina. *1° Congreso Argentino de Paleontología y Bioestratigrafía* (Tucumán), *Actas* 2: 271–316.
- Bertels, A. 1977. Paleogene foraminifera - South Atlantic. In: F.M. Swain (Ed.), *Stratigraphic micropaleontology of Atlantic Basins and borderlands*. Elsevier Scientific Publishing Company, Amsterdam, p. 411–439.
- Bocquentin, J.C., and Souza Filho, J. 1990. O crocodiliano *Carandaisuchus* como sinonimia de *Mourasuchus* (Nettosuchidae). *Revista Brasileira de Geociências* 20: 230–233.
- Bona, P., Cladera, G., and de la Fuente, M.S. 1998. Las tortugas pleurodiras de la Formación Salamanca (Paleoceno Inferior) en el área de Cerro Hansen, Provincia de Chubut, Argentina. *10° Congreso Latinoamericano de Geología y 6° Congreso Nacional de Geología Económica* (Buenos Aires), *Actas* 1: 269–274.
- Bona, P. 2004. [Sistemática y biogeografía de las tortugas y los cocodrilos paleocenos de la Formación Salamanca, provincia de Chubut, Argentina]. Tesis Doctoral, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata, 185 p. Unpublished.]
- Bona, P. 2007. Una nueva especie de *Eocaiman* Simpson (Crocodylia, Alligatoridae) del Paleoceno Inferior de Patagonia. *Ameghiniana* 44: 435–445.
- Bona, P., Degrange, F.J., and Fernández, M.S. 2012. Skull anatomy of the bizarre crocodylian *Mourasuchus nativus* (Alligatoridae, Caimaninae). *The Anatomical Record* 296: 227–239.
- Bona, P., and Desojo, J.B. 2011. Osteology and cranial musculature of *Caiman latirostris* (Crocodylia: Alligatoridae). *Journal of Morphology* 272: 780–795.
- Bona, P., and Paulina Carabajal, A. 2013. *Caiman gasparinae* sp. nov., a huge alligatorid (Caimaninae) from the late Miocene of Paraná, Argentina. *Alcheringa: An Australian Journal of Palaeontology* 37: 1–12.
- Bona, P., Riff, D., and Gasparini, Z.B. 2013a. Late Miocene crocodylians from northeast Argentina: new approaches about the austral components of the Neogene South American crocodylian fauna. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103, p. 551–570. Doi: 10.1017/S175569101300042X
- Bona, P., Riff, D., and Gasparini, Z.B. 2013b. Los Alligatoridae del Mioceno tardío de Argentina: el registro más austral de cocodrilos neógenos en América del Sur. In: D. Brandoni, and J.I. Noriega (Eds.), *El Neógeno de la Mesopotamia argentina*. Publicación Especial de la Asociación Paleontológica Argentina, Buenos Aires, p. 84–96.
- Bona, P., Starck, D., Galli, C., Gasparini, Z., and Reguero, M. 2014. *Caiman* cf. *latirostris* (Alligatoridae, Caimaninae) in the Late Miocene Palo Pintado Formation, Salta province, Argentina: paleogeographic and paleoenvironmental considerations. *Ameghiniana* 51: 26–36.
- Bonaparte, J., Van Valen, L., and Kramarz, A. 1993. La fauna local de Punta Peligro, Paleoceno inferior, de la provincia del Chubut, Patagonia, Argentina. *Evolutionary Monographs* 14: 1–61.
- Bond, M., Carlini, A., Goin, F., Legarreta, L., Ortiz Jaureguizar, E., Pascual, R., and Uliana, M. 1995. Episodes in South Land Mammal evolution and sedimentation: testing their apparent concurrence in a Palaeocene succession from Central Patagonia. *6° Congreso Argentino de Paleontología y Bioestratigrafía* (Trelew), *Actas*: 47–58.
- Brandoni, D. 2011. The Megalonychidae (Xenarthra, Tardigrada) from the late Miocene of Entre Ríos Province, Argentina, with remarks on their systematics and biogeography. *Geobios* 44: 33–44.
- Brandoni, D., and Scillato-Yané, G.J. 2007. Los Megatheriinae (Xenarthra, Tardigrada) del Terciario de Entre Ríos, Argentina: aspectos taxonómicos y sistemáticos. *Ameghiniana* 44: 427–434.
- Bravard, A. 1858. *Monografía de los terrenos marinos terciarios del Paraná*. Imprenta del Registro Oficial, Paraná, 107 p.
- Brochu, C.A. 1997. A review of "*Leidyosuchus*" (Crocodyliformes, Eusuchia) from the late Cretaceous through Eocene of North

- America. *Journal of Vertebrate Paleontology* 17: 679–697.
- Brochu, C.A. 1999. Phylogenetics, taxonomy and historical biogeography of Alligatoroidea. In: T. Rowe, C.A. Brochu, and K. Kishi (Eds.), *Cranial morphology of Alligator mississippiensis and phylogeny of Alligatoroidea*. Society of Vertebrate Paleontology, Memoir 6, New York, 6, p. 9–100.
- Brochu, C.A. 2003. Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Sciences* 31: 357–396.
- Brochu, C.A. 2004. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. *Journal of Vertebrate Paleontology* 24: 857–873.
- Brochu, C.A. 2010. A new alligatorid from the Lower Eocene Green River Formation of Wyoming and the origin of caimans. *Journal of Vertebrate Paleontology* 30: 1109–1126.
- Brochu, C.A. 2011. Phylogenetic relationships of *Necrosuchus ionensis* Simpson, 1937 and the early history of caimanines. *Zoological Journal of the Linnean Society* 163: 228–256.
- Brunetto, E., Noriega, J.I., and Brandoni, D. 2013. Sedimentología, estratigrafía y edad de la Formación Ituzaingó en la provincia de Entre Ríos, Argentina. In: D. Brandoni, and J.I. Noriega (Eds.). *El Neógeno de la Mesopotamia argentina*. Publicación Especial de la Asociación Paleontológica Argentina, 14, p. 13–27.
- Burmeister, G. 1883. Reprint of Bravard, 1858: Monografía de los terrenos marinos terciarios del Paraná. *Anales del Museo Público de Buenos Aires* 3: 45–94.
- Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por Don Augusto Bravard y mencionados en su obra precedente. *Anales del Museo Nacional de Buenos Aires* 3: 95–173.
- Bywater-Reyes, S., Carrapa, B., Clementz, M., and Schoenbohm, L. 2010. Effect of late Cenozoic aridification on sedimentation in the Eastern Cordillera of northwest Argentina (Angastaco basin). *Geology* 38: 235–238.
- Cei, J.M. 1993. Reptiles del noroeste, nordeste y este de la Argentina. *Museo Regionale di Historia Naturali di Torino, Monografía* 14: 1–949.
- Cione, A.L., Azpelicueta, M.M., Bond, M., Carlini, A., Casciotta, J., Cozzuol, M.A., de la Fuente, M., Gasparini, Z., Goin, F., Noriega, J., Scillato-Yané, G., Soibelzon, L., Tonni, E., Verzi, D., and Vucetich, M.G. 2000. Miocene vertebrates from Entre Ríos Province, Argentina. In: F.G. Aceñolaza, and R. Herbst (Eds.), *El Neógeno de Argentina*. Serie de Correlación geológica del Instituto Superior de Correlación Geológica, Tucumán, Argentina, 14, p. 191–238.
- Cione, A.L., Casciotta, J.R., Azpelicueta, M.M., Barla, M.J., and Cozzuol, M.A. 2005. Peces marinos y continentales del Mioceno del área Mesopotámica Argentina, procedencia estratigráfica y relaciones biogeográficas. *Miscelánea INSUGEO* 12: 49–64.
- Coutand, I., Carrapa, B., Deeken, A., Schmitt, A.K., Sobel, E., and Strecker, M.R. 2006. Orogenic plateau formation and lateral growth of compressional basins and ranges: Insights from sandstone petrography and detrital apatite fission-track thermochronology in the Angastaco Basin, NW Argentina. *Basin Research* 18: 1–26.
- Cuvier, G.L.C.F.D. Baron. 1807. Sur les différentes espèces de crocodiles vivants et sur leur caractères distinctifs. *Annales du Muséum National d'Histoire Naturelle* 10: 8–66.
- Daudin, F.M. 1802. *Histoire naturelle, générale et particulière des Reptiles*. De L'Imprimerie de F. Dufart, Paris, 452 p.
- De Alba, E. 1953. Geología del Alto Paraná, en relación con los trabajos de derrocamiento entre Ituzaingó y Posadas. *Revista de la Asociación Geológica Argentina* 8: 129–161.
- D'Erasmo, G. 1934. Sopra alcuni avanzi di vertebrati fossili della Patagonia raccolti da Dott. E. Feruglio. *Accademia della Scienze Físiche e Matematiche Napoli, Atti* (2) 20 (8): 1–26.
- Deschamps, C.M., Vucetich, M.G., Montalvo, C.I., and Zárate, M.A. 2013. Capybaras (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the late Miocene-Pliocene sequences of South America. *Journal of South American Earth Sciences* 48: 145–158.
- Díaz, J.I., and Malizzia, D. 1983. Estudio geológico y sedimentológico del Terciario Superior del Valle Calchaquí (Dpto. San Carlos, Pcia. de Salta). *Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, Boletín Sedimentológico* 2: 8–28.
- Feruglio, E. 1938. Relaciones estratigráficas entre el Patagoniano y el Santacruciano en la Patagonia Austral. *Revista del Museo de La Plata (nueva serie) I, Geología* 4: 129–159.
- Feruglio, E. 1949. Descripción geológica de la Patagonia. *Yacimientos Petrolíferos Fiscales* 2: 1–349.
- Freguelli, J. 1920. Contribución al conocimiento de la geología de Entre Ríos. *Boletín de la Academia Nacional de Ciencias de Córdoba* 24: 55–256.
- Fortier, D., Brochu, C.A., and Souza Filho, J.P. 2009. The oldest record of *Caiman yacare*. *Journal of Vertebrate Paleontology (Supplement)* 29: 97.
- Gasparini, Z. 1968. Nuevos restos de *Rhamphostomopsis neogaeus* (Burm) Rusconi, 1933, (Reptilia, Crocodylia) del "Mesopotamiense" (Plioceno medio-superior) de Argentina. *Ameghiniana* 5: 299–311.
- Gasparini, Z. 1973. [Revisión de los Crocodylia (Reptilia) fósiles del Territorio Argentino: su evolución, sus relaciones filogenéticas, su clasificación y sus implicancias estratigráficas. Tesis Doctoral Facultad de Ciencias Naturales, Universidad Nacional de La Plata, La Plata, 158 p. Unpublished.].
- Gasparini, Z. 1981. Los Crocodylia fósiles de la Argentina. *Ameghiniana* 18: 177–205.
- Gasparini, Z. 1985. Un Nuevo cocodrilo (Eusuchia) Cenozoico de América del Sur. *MME-DNPM Série Geología Paleontología, Estratigrafía* 2: 51–53.
- Gasparini, Z. 1996. Biogeographic evolution of the South American crocodylians. *Münchner Geowissenschaftliche Abhandlungen* 30: 159–184.
- Gasparini, Z., and Báez, A.M. 1975. Aportes al conocimiento de la herpetofauna terciaria de la Argentina. *1º Congreso Argentino de Paleontología y Bioestratigrafía* (Tucumán), *Actas* 2: 377–415.
- Gasparini, Z., de la Fuente, M., and Donadío, O. 1986. Los reptiles cenozoicos de la Argentina: implicancia paleoambientales y evolución biogeográfica. *2º Congreso Argentino de Paleontología y Bioestratigrafía* (Buenos Aires), *Actas* 2: 119–130.
- Galli, C.I., Ramírez, A., Barrientos, C., Reynolds, J., Viramonte, J.G., and Idleman, B. 2008. Estudio de proveniencia de los depósitos del Grupo Payogastilla (Mioceno Medio-Superior) aflorantes en el río Calchaquí, provincia de Salta, Argentina. *17º Congreso Geológico Argentino* (San Salvador de Jujuy), *Actas* 1: 353–354.
- Gebhard, J.A., Giudici, A.R., and Gascon, J.O. 1974. Geología de la comarca entre el Río Juramento y Arroyo Las Tortugas, provincia de Salta y Jujuy, República Argentina. *Revista de la Asociación Geológica Argentina* 24: 359–375.
- Gelfo, J.N., Goin, F.J., Woodburne, M.O., and De Muizon, C. 2009. Biochronological relationships of the Earliest South American Paleogene Mammalian Faunas. *Palaeontology* 52: 251–269.
- Gilmore, C.W. 1911. A new fossil alligator from the Hell Creek beds of Montana. *Proceedings of the United States National Museum* 9: 297–302.

- Gmelin, J. 1789. *Linnei Systema Naturae*. Beer, G. E. Leipzig, 1057 p.
- Gray, J.E. 1862. A synopsis of the species of alligators. *Annals and Magazine of Natural History* 3: 327–331.
- Hastings, A.K., Bloch, J.I., Jaramillo, C.A., Rincón, A.F., and Macfadden, B.J. 2013. Systematics and biogeography of crocodylians from the Miocene of Panama. *Journal of Vertebrate Paleontology* 33: 239–263.
- Head, J.J., Bloch, J.I., Hastings, A.K., Bourke, J.R., Cadena, E.A., Herrera, F.A., Polly, P.D., and Jaramillo, C.A. 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* 457: 715–717.
- Herbst, R. 1971. Esquema estratigráfico de la Provincia de Corrientes, República Argentina. *Revista de la Asociación Geológica Argentina* 26: 221–243.
- Hoorn, C., Wesselingh, F.P., Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F. R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., and Antonelli, A. 2010. Amazonia through time: andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330: 927–931.
- Iglesias, A., Wilf, P., Johnson, K.R., Zamuner, A., Cúneo, N.R., Matheos, S., and Singer, B.S. 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* 35: 947–950.
- Kuhn, O. 1933. Über Reste procoeler Crocodilier aus der obersten Kreide von Patagonien. *Palaeontologische Zeitschrift* 15: 81–93.
- Lambe, L.M. 1907. On a new crocodylian genus and species from the Judith River Formation of Alberta. *Transactions of the Royal Society of Canada* 4: 219–244.
- Langston, W. Jr. 1965. Fossil crocodylians from Colombia and the Cenozoic history of the Crocodylia in South America. *University of California Publications in Geological Sciences* 52: 1–15.
- Langston, W. Jr., and Gasparini, Z. 1997. Crocodylians, *Gryposuchus*, and the South Americans gavials. In: R.F. Kay, N.H. Madden, R.L. Cifelli, and J.J. Flinn (Eds.), *Vertebrate paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia*. Smithsonian Institution, Washington D.C., p. 113–154.
- Legarreta, L., and Uliana, M.A. 1994. Asociación de fósiles y hiatus en el Supracretácico-Neógeno de Patagonia: una perspectiva estratigráfica-secuencial. *Ameghiniana* 31: 119–120.
- Lesta, P., and Ferello, R. 1972. Región extraandina de Chubut y Norte de Santa Cruz. En: A. Leanza (Ed.), *Geología Regional Argentina*. Academia Nacional de Ciencias, Córdoba, p. 601–654.
- Mauri, E. 1948. [Observaciones geológicas en el sudoeste de la Provincia de Salta, departamentos Cafayate, San Carlos, Molinos, Guachipas y LaViña. Y.P.F. internal report. Buenos Aires, 87 p. Unpublished.]
- Medem, F. 1983. *Los Crocodylia de Sur América*. Universidad Nacional de Colombia, Bogotá, 270 p.
- Méndez, I. 1966. Foraminíferos, edad y correlación estratigráfica del Salamanquense de Punta Peligro (45° 30 S; 67° 11 W) Provincia del Chubut. *Revista de la Asociación Geológica Argentina* 21: 127–157.
- Mendez Cidade, G., Barrios, F., Souza, R., and Bona, P. 2015. A new diagnosis, phylogenetic relationships and taxonomy of *Caiman lutescens* (Rovereto, 1912), Late Miocene, Argentina. *5° Congreso Latinoamericano de Paleontología Vertebrados* (Montevideo), *Actas*: 80.
- Mook, C.C. 1921. *Allognathosuchus*, a new genus of Eocene crocodylians. *Bulletin of the American Museum of Natural History* 44: 105–110.
- Norell, M.A. 1988. [Cladistic approaches to paleobiology as applied to the phylogeny of alligatorids. Ph.D. dissertation, Yale University, New Haven, Connecticut, 279 p. Unpublished.]
- Norell, M.A., Clark, J.M., and Hutchison, J.H. 1994. The Late Cretaceous alligatoroid *Brachychampsia montana* (Crocodylia): new material and putative relationships. *American Museum Novitates* 3116: 1–26.
- Noriega, J.L., Carlini, A.A., and Tonni, E.P. 2004. Vertebrados del Pleistoceno tardío de la cuenca del Arroyo Ensenada (Departamento Diamante, provincia de Entre Ríos, Argentina). *Serie de Correlación Geológica (INSUGEO)* 12: 71–76.
- Pascual, R., and Odreman Rivas, O. 1971. Evolución de las comunidades de los vertebrados del Terciario argentino. Los aspectos paleozoogeográficos y paleoclimáticos relacionados. *Ameghiniana* 8: 372–412.
- Pascual, R. 1986. Evolución de los vertebrados cenozoicos: sumario de los principales hitos. *4° Congreso Argentino de Paleontología y Bioestratigrafía* (Mendoza), *Actas* 2: 209–218.
- Patterson, B. 1936. *Caiman latirostris* from the Pleistocene of Argentina, and a summary of South American Cenozoic Crocodylia. *Herpetologica* 1: 43–54.
- Pinheiro, A.E.P., Fortier, D.C., Pol, D., Campos, D.A., and Bergqvist, L.P. 2013. A new *Eocaiman* (Alligatoridae, Crocodylia) from the Itaboraí Basin, Paleogene of Rio de Janeiro, Brazil. *Historical Biology: An International Journal of Paleobiology* 25: 327–337.
- Piña, C.I., and Argañaraz, B. 2000. Presencia del género *Caiman* (Crocodylia: Alligatoridae) en la Formación Ituzaingó (Mioceno Sup.–Plioceno), Entre Ríos, Argentina. In: F.G. Aceñolaza, and R. Herbst (Eds.), *El Neógeno de Argentina*. Serie de Correlación geológica del Instituto Superior de Correlación Geológica, Tucumán, 14, p. 255–262.
- Price, L.I. 1964. Sobre o crânio de um grande crocodilídeo extinto do Alto Rio Juruá, Estado do Acre. *Anais da Academia Brasileira de Ciências* 36: 59–66.
- Raigemborn, M.S., Krause, J.M., Bellosi, E., and Matheos, S.D. 2010. Redefinición estratigráfica del Grupo Río Chico (Paleógeno Inferior), en el Norte de la Cuenca del Golfo San Jorge, Chubut. *Revista de la Asociación Geológica Argentina* 67: 239–256.
- Reynolds, J.H., Idleman, B.D., Hernández, R.M., and Naeser, C.W. 1994. Preliminary chronostratigraphic constraints on Neogene tectonic activity in the Eastern Cordillera and Santa Bárbara System, Salta Province, NW Argentina. *Annual Meeting Geological Society of America* (Seattle), *Abstracts* 26: A503.
- Riff, D., and Aguilera, O. 2008. The world's largest gharials *Gryposuchus*: Description of *G. croizati* n. sp. (Crocodylia, Gavialidae) from the Upper Miocene Urumaco Formation, Venezuela. *Palaeontologische Zeitschrift* 82: 178–195.
- Riff, D., Romano, P.S.R., Oliveira, G.R., and Aguilera, O.A. 2010. Neogene crocodile and turtle fauna in Northern South America. In: C. Hoorn, and F.P. Wesselingh (Eds.), *Amazonia, Landscape and Species Evolution*. Wiley-Blackwell, Oxford, p. 259–280.
- Ringuelet, R.A. 1961. Rasgos fundamentales de la zoogeografía de la Argentina. *Physis* 22: 151–170.
- Rovereto, C. 1912. Los cocodrilos fósiles en las capas del Paraná. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 22: 339–368.
- Rusconi, C. 1933. Observaciones críticas sobre reptiles Terciarios de Paraná (Familia Alligatoridae). *Revista de la Universidad Nacional de Córdoba* 20: 1–52.
- Rusconi, C. 1935. Observaciones sobre los gaviales fósiles Argentinos. *Anales de la Sociedad de Ciencias Argentina* 119: 203–214.
- Rusconi, C. 1937. Nuevo aligatorio del Paleoceno de Patagonia. *Boletín Paleontológico de Buenos Aires* 8: 1–5.

- Salas-Gismondini, R., Flynn, J.J., Baby, P., Tejada-Lara, J.V., Wesselingh, F.P., and Antonie, P.-O. 2015. A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proceedings Royal Society B* 282: 20142490. Doi: 10.1098/rspb.2014.2490.
- Sánchez-Villagra, M., and Aguilera, O. 2006. Neogene Vertebrates from Urumaco, Falcon State, Venezuela: diversity and significance. *Journal of Systematic Palaeontology* 4: 213–220.
- Scalabrini, P. 1887. *Cartas científicas al General Eduardo Racedo*. Museo de la Provincia de Entre Ríos, Tipografía y Encuadernación La Velocidad, Paraná, 209 p.
- Scheyer, T.M., and Moreno-Bernal, J.W. 2010. Fossil crocodylians from Venezuela in the context of South American faunas. In: M.R. Sánchez-Villagra, O.A. Aguilera, and A.A. Carlini (Eds.), *Urumaco & Venezuelan Paleontology: The fossil record of the Northern Neotropics*. Indiana University Press, Bloomington & Indianapolis, p. 192–213.
- Scheyer, T.M., Aguilera, O.A., Delfino, M., Fortier, D.C., Carlini, A.A., Sánchez, R., Carrillo-Briceño, J.D., Quiroz, L., and Sánchez-Villagra, M.R. 2013. Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nature Communications* 4: 1907. Doi: 10.1038/ncomms2940.
- Sill, W.D. 1968. The Zoogeography of the Crocodylia. *Copeia* 1: 76–88.
- Simpson, G.G. 1933. A new crocodylian from the *Notostylops* Beds of Patagonia. *American Museum Novitates* 623: 1–9.
- Simpson, G.G. 1937. An ancient eusuchian crocodile from Patagonia. *American Museum Novitates* 965: 1–20.
- Somoza, R., Cladera, G., and Archangelsky, S. 1995. Una nueva tafloflora paleocena de Chubut, Patagonia. Su edad y ambiente de depositación. 6° Congreso Argentino de Paleontología y Bioestratigrafía (Trelew), *Actas*: 265–269.
- Spix, J.B. 1825. *Animalia nova sive Species novae lacertarum quas in itinere per Brasiliam annis. MDCCCXVII–MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae Regis suscepto collegit et descripsit Dr. J.B. de Spix. T.O. Weigel Lipsiae*, 26 p.
- Starck, D., and Anzótegui, L.M. 2001. The late Miocene climatic change- Persistence of a climatic signal through the orogenic stratigraphic record in northwestern Argentina. *Journal of South American Earth Sciences* 14: 763–774.
- Taplin, L.E., and Grigg, G.C. 1989. Historical zoogeography of the eusuchian crocodylians: a physiological perspective. *American Zoologist* 29: 885–901.
- Vizcaíno, S.F., Cassini, G.H., Toledo, N., and Bargo, M.S. 2012. On the evolution of large size in mammalian herbivores of Cenozoic faunas of South America. In: B.D. Patterson, and L. Costa (Eds.), *Bones, Clones and Biomes. The History and Geography of Recent Neotropical Mammals*. University of Chicago Press, Chicago, p. 76–101.
- Vucetich, M.G., Arnal, M., Deschamps, C.M., Pérez, M.E., and Vieytes, E.C. 2015. A brief history of caviomorph rodents as told by the fossil record. In: A. Vassallo and D. Antonucci (Eds.), *Biology of caviomorph rodents; diversity and evolution*. Sociedad Argentina para el estudio de los Mamíferos, p. 11–62.
- Woodburne, M.O., Goin, F.J., Bond, M., Carlini, A.A., Gelfo, J.N., López, G.M., Iglesias, A., and Zimicz, A.N. 2014. Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. *Journal of mammalian Evolution* 21: 1–73.

Recibido: 15 de junio 2015

Aceptado: 23 de octubre 2015