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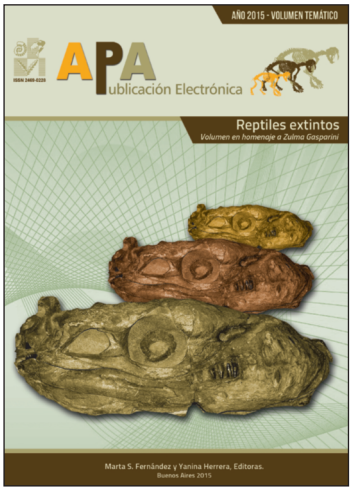

THE ALLIGATOROIDEA OF ARGENTINA: AN UPDATE OF ITS FOSSIL RECORD

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THE ALLIGATOROIDEA OF ARGENTINA: AN UPDATE OF ITS FOSSIL RECORD

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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 alligatorids of Argentina, as a tribute to Zulma Gasparini for her invaluable contribution to the understanding of the crocodilian 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 aligatóridos 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 aligatoroideos 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 aligatoroideo, quienes proporcionan información morfológica clave en la historia evolutiva y biogeográfica de este grupo de crocodilianos. 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 aligatóridos 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. Aligatoroideos. 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´Erasmo, 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 crocodilian 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 Northwesten 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 word (*e.g.*, A. Aguilera, A. Albino, A. Buscalioni, J. Bocquentin-Villanueva, P. Bona, C. Brochu, L. Codorniú, 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 Bahia 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). Crocodilian 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

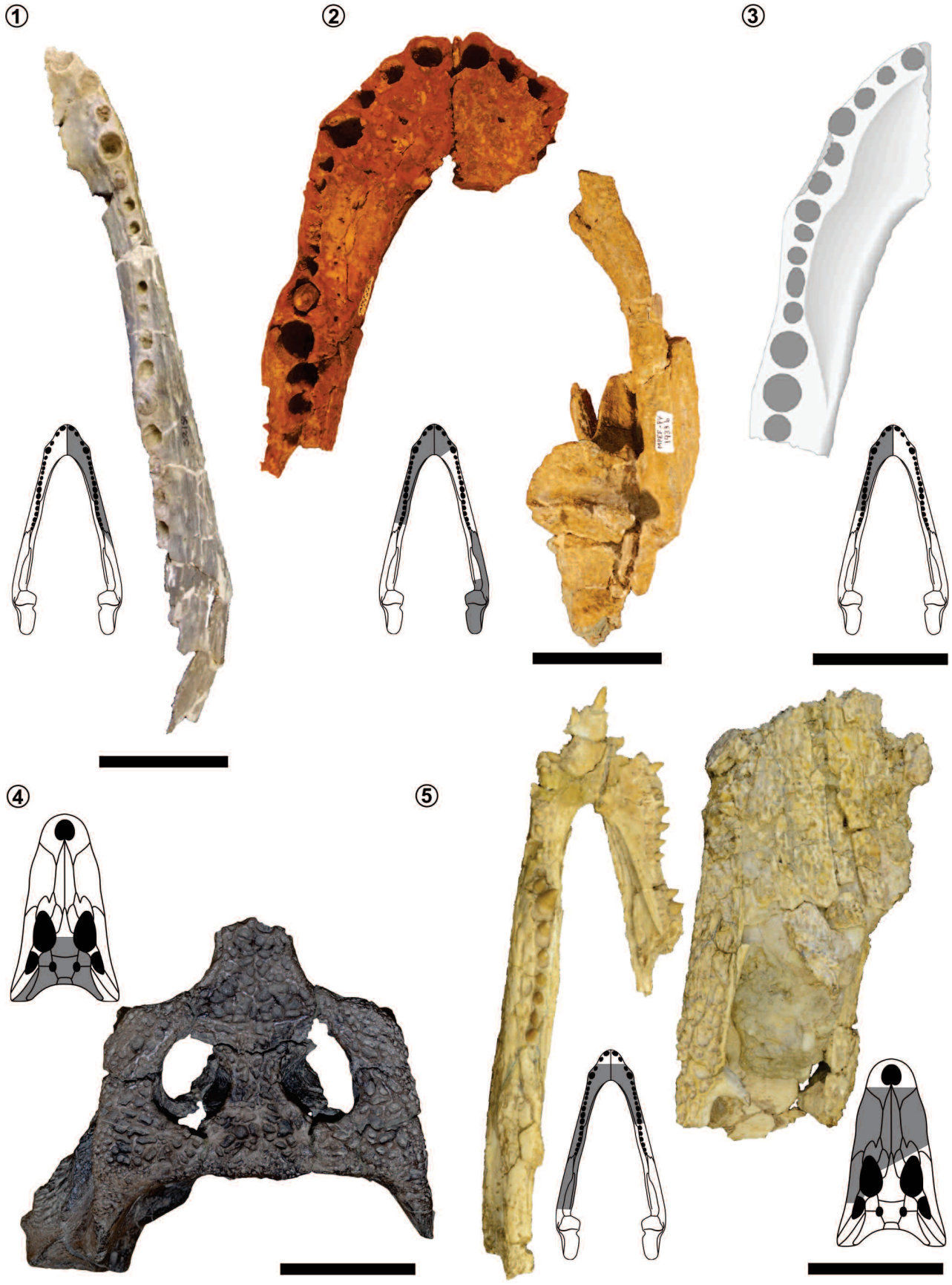
Type Species. *Notocaiman stromeri* Rusconi, 1937.

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.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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.

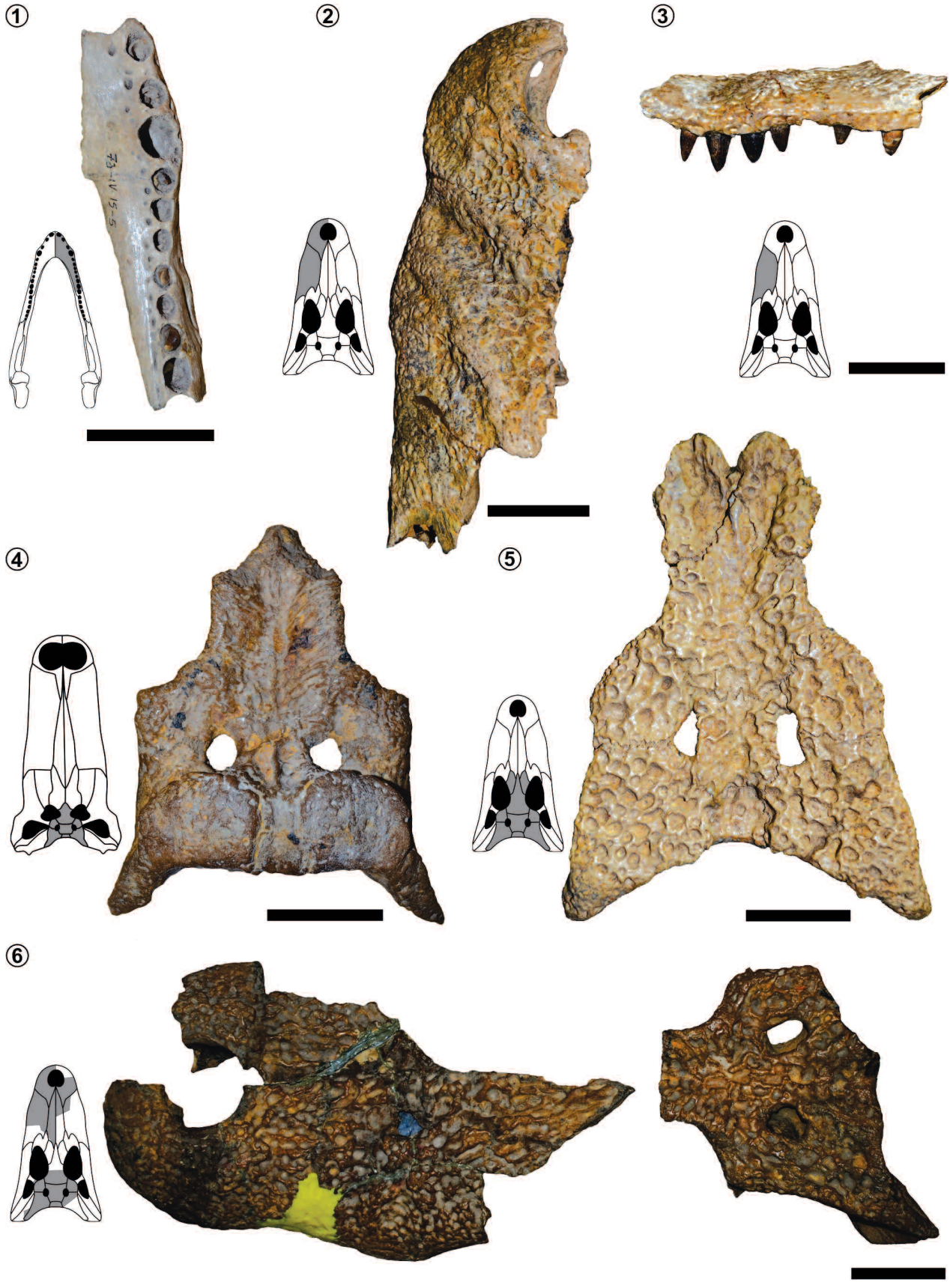
Mourasuchus nativus (Gasparini, 1985)
Figure 3.5

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

Referred Marterial. 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, Boquentin 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).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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 *Crocodilus australis* to include all the cranial and postcranial remains of non-longirostrine crocodylians from the "Conglomerado Osífero". An expanded detailed description of *Crocodilus australis* was given later by Burmeister (1885), but the first formal diagnosis and discussion of diagnostic characters of *Crocodilus 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

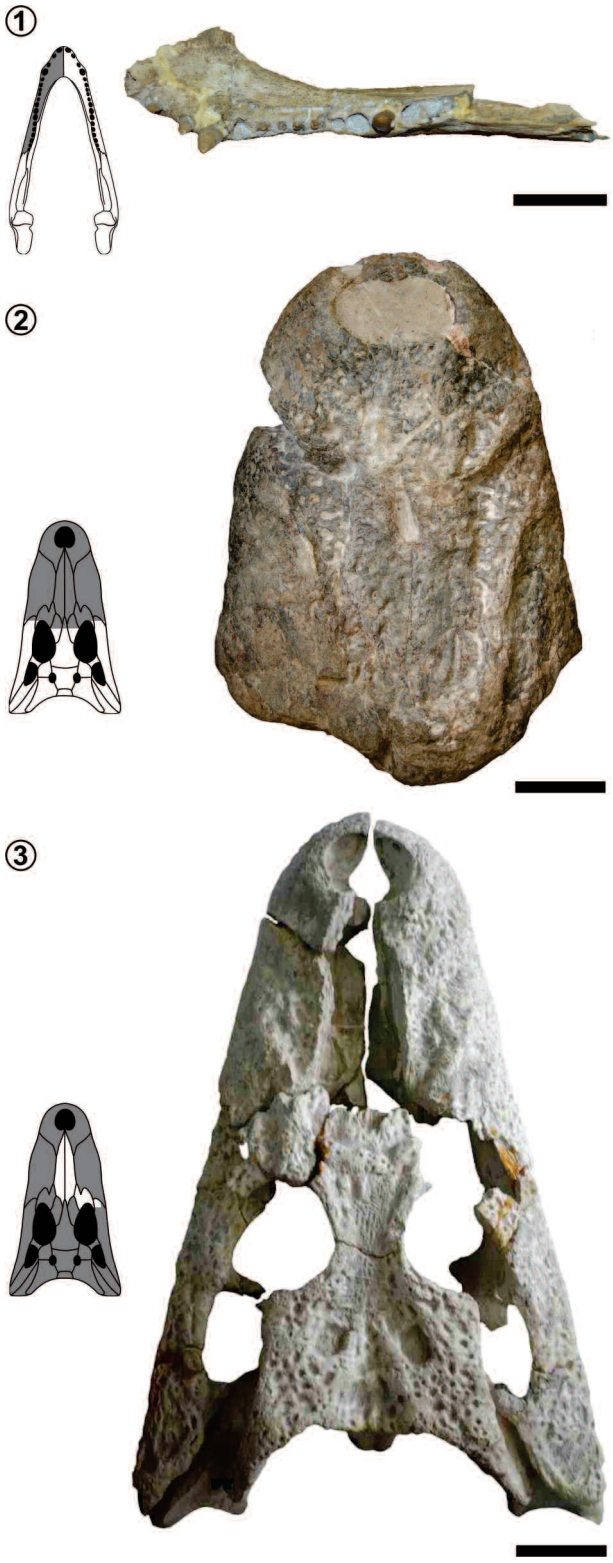

Figure 4. Mio/Pleistocene Alligatoridae from northwestern Argentina, ***Caiman latirostris*** in dorsal view; **1, MLP 89-XII-5-1**, left dentary; **2, FMNH-P 15029**, rostrum; **3, MAS-PALEO 001/2011**, cranium. Scale bars= 5cm.

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 Alligatoroidae 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 where 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 crocodilian history as this contribution are still influenced by the legacy of a pioneer paleontologist as Zulma Gasparini.

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