

# Late Miocene crocodylians from northeast Argentina: new approaches about the austral components of the Neogene South American crocodylian fauna

Paula Bona<sup>1</sup>, Douglas Riff<sup>2</sup> and Zulma Brandoni de Gasparini<sup>1</sup>

<sup>1</sup> CONICET, División Paleontología Vertebrados, Museo de La Plata. Paseo del Bosque s/n, 1900, La Plata, Argentina. Email: pbona@fcnym.unlp.edu.ar

<sup>2</sup> Instituto de Biologia, Universidade Federal de Uberlândia, Campus Umuarama, Bloco 2D – sala 28, Rua Ceará, s/n, 38400-902, Uberlândia, Minas Gerais, Brazil.

**ABSTRACT:** The richest and more explored regions concerning Miocene crocodylians in South America are the basins surrounding the areas of Urumaco (Venezuela), La Venta (Colombia), Acre (Northwest Brazil) and Paraná (Northeast Argentina). Fossils from the late Miocene in the Paraná area were recovered from the “Conglomerado Osífero” (Ituzaingó Formation) and assigned to several taxa of Caimaninae (Alligatoroidea) and to a taxon of Gavialoidea. The late Miocene “fauna” of crocodylians recorded in northeast Argentina differs from coeval ones of northern South America by the absence of crocodyloids, some alligatorid genera (such as *Purussaurus*, *Melanosuchus*, and *Paleosuchus*) and by the scarce gavialoid species. Giant forms, conspicuous in the northern South American deposits, are also absent in southern latitudes. Despite this, the austral South American crocodylian fauna exhibits strong affinities with the northern, contemporary forms, sharing taxa at generic (i.e. *Caiman* and *Gryposuchus*) and even specific levels (i.e. *Mourasuchus nativus*). The sharing of such freshwater taxa in the Miocene indicates partial connections of drainage basins through swamp areas on their boundaries, and is evidence against the assumption of an intracontinental coeval seaway link in this continent proposed by several authors.



**KEY WORDS:** Caimaninae, Crocodylia, Gavialidae.

Palaeontological research on Mio–Pliocene South American taxa has provided information supporting taxonomical and biogeographical hypotheses, many of them erected since the middle of the 20th century. The richest and most diverse record of Crocodyliformes in the South American Cenozoic corresponds to Neogene localities related to basins surrounding the areas of Urumaco (Venezuela), La Venta (Colombia), Acre (northwestern Brazil), Fitzcarrald (Peru) and Paraná (northeast Argentina). Two main groups are known from such basins: the Sebecidae, a non-eusuchian crocodyliform taxon which was an important component of the terrestrial Early–Middle Miocene northern South American faunas (Langston 1965; Gasparini 1996; Langston & Gasparini 1997; Salas-Gismondi *et al.* 2007; Riff *et al.* 2010); and the Eusuchia crocodylian eusuchians, which represents the most diverse reptilian group in such deposits. From the Upper Miocene onwards, only three eusuchian lineages remain worldwide, of which two are found in South America, the Gavialoidea and the Alligatoroidea, mainly in the Pan Amazonian region (*sensu* Hoorn *et al.*, 2010). In contrast to Sebecidae, it was not until after the Middle Miocene that these latter two groups greatly expanded their diversity (Riff *et al.* 2010). This change in the faunal composition is coincident with the demise of the palustrine environment that dominated northern South America, when the Western Amazonian wetland changed from a lacustrine (Pebas System) to a fluvial or fluviotidal system (Acre System). These changes were driven by the faster and more widespread Andean mountain building at the end of the Middle Miocene, around 12 Ma (Hoorn *et al.* 2010).

The origin of the South American Gavialoidea is a matter of debate. The most ancient continental records come from Upper Oligocene–Lower Miocene deposits in Venezuela (Castillo Formation; see Brochu & Rincón 2004) and Brazil (Pirabas Formation, see Morais-Santos *et al.*, 2011), as well from the Upper Oligocene San Sebastián Formation in Puerto Rico, which shows strong affinities with South American forms (Vélez-Juarbe *et al.* 2007). One or more transatlantic migrations from an African ancestor in the Oligocene or earlier is still a hypothesis often considered (Buffetaut 1982; Langston & Gasparini 1997; Vélez-Juarbe *et al.* 2007; Jouve *et al.* 2008), but see Riff *et al.* (2010) for an alternative point of view. Despite this, the diversity of South American gavialoids is astonishing, with South America serving as the main diversification focus. The Falcón Basin, in northern Venezuela, contains five gavialoid species represented by juvenile and adult specimens. Four of these species come from the late Miocene Urumaco Formation and one from the older Castillo Formation. Only one species has been described from the late Miocene Solimões Formation of Acre, but several new specimens from this unit, including new species, await description (Souza-Filho 1998; Riff & Oliveira 2008; Souza *et al.* 2011). The late Miocene appears to represent the pinnacle of South American gavialoid diversity, with the *Gryposuchus* Gürich, 1912 the most speciose taxon (Riff & Aguilera 2008). Before this time (late Oligocene–middle Miocene) and afterwards (Pliocene), only a single gavialoid species is known and after the Pliocene, the entire clade became extinct on the continent (Riff *et al.* 2010). However, the austral South American record, has just one gavialoid species, the medium-sized *Gryposuchus neogaeus* (Burmeister 1885),



**Figure 1** Geographic location map of the main outcrops of the level called “Conglomerado osífero”, Ituzaingó Formation. Modified from Brandoni & Scillato-Yané (2007).

based on two specimens from the Upper Miocene Ituzaingó Formation (Paraná region, Argentina). Despite previous seminal works focusing on the South American Gavialoidea (Langston 1965; Gasparini 1968; Buffetaut 1982; Langston & Gasparini 1997), a major revision of these occurrences, emphasising the northern diversity, is yet to be made. Nevertheless, this subject is beyond the scope of the present contribution.

Compared to gavialoids, the history of Alligatoroidea is better documented in South America, with the caimanines record beginning from the Lower Paleocene (Simpson 1937; Bona 2007). The Paleocene genus *Eocaiman*, originally described from Argentinian deposits, was also recorded by Langston (1965) in the Middle Miocene La Venta fauna of Colombia based on fragmented dentaries. Although additional material is required for confirmation of the presence of *Eocaiman* in Colombian deposits, the strong festooning in the alveolar row appears to distinguish the species from Argentinian taxa. Caimaninae is represented today only in South and Central America, with six species in three genera: *Caiman*, *Melanosuchus* and *Paleosuchus*. However, the zenith of caimanine diversity is recognised in the Miocene, with at least ten species in

five genera (*Caiman*, *Melanosuchus*, *Purussaurus*, *Mourasuchus*, *Balanearodus*). The Amazonian diversity is remarkable, including an intriguing frequency of giant forms (mainly the clade *Purussaurus-Mourasuchus*), but is important to consider that the high-latitude record of South American caimanines is fundamental to a comprehensive view of the history of the group. Langston (1965), in his study on the Tertiary Crocodylia of Colombia, gave special attention to the southern record of alligatorids, providing a seminal work on the South American crocodylian fauna. Since Langston (1965) and an unpublished thesis (Gasparini 1973), Neogene alligatorids of this region have not been studied in detail. This is the focus and the main goal of this present contribution.

Crocodylians of the Upper Miocene of Argentina come from a stratigraphic level informally known as “Mesopotamiense” or “conglomerado osífero” from the Ituzaingó Formation (Herbst 1971) exposed in the area of Paraná, Entre Ríos Province, Argentina (Fig. 1). Fossils are mainly cranial and post-cranial fragmentary material of different taxa of Crocodylia (*sensu* Benton & Clark 1988), which were the object of study 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 & Gasparini 1997). Most of this material, currently housed at Museo de La Plata and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, belonged to several private collections and remained without numbering for almost seventy years. This led to the misplacement and confusion of material over the years, resulting in misinterpretations and the creation of long lists of synonyms (see Rovereto 1912; Rusconi 1933).

The first study of “Mesopotamiense” vertebrates was made by Augusto Bravard, who collected and studied many fossil remains of mammals, reptiles, lizards, turtles and crocodylians. His work was preliminarily published in 1858 in the newspaper *El Nacional Argentino* and lithographed in a catalogue published in 1860, where he mentioned “*Crocodylus australis*”, the only species known for the “Mesopotamiense” for two decades. Burmeister (1883) reproduced and published the study of Bravard, providing a clear description of the type material of *C. australis* (unnumbered), assigning new material to this species and naming the longirostine *Ramphostoma neogaea* (Burmeister 1883). The taxonomic history of the different crocodylian species of the “Mesopotamiense” during the end of the 19th century can be traced in the works of Rovereto (1912) and Rusconi (1933).

Rovereto (1912) was the first author to perform a more detailed study of the “Mesopotamiense” vertebrate fauna. Although unnumbered, he presented clear illustrations of many material specimens, reassigning and describing several crocodylian species (i.e. *Alligator australis*, *A. lutescens*, *A. ameghinoi* and *Garialis neogaeus*). Later Rusconi (1933) numbered the material, and published an extensive and detailed systematic review of the fossil crocodiles of Paraná. He reported a diversity of taxa, erecting the genus *Xenosuchus* to include *X. lutescens* and *X. paranensis* (with two subspecies), proposing the name of *Ramphostomopsis* instead of *Ramphostoma* (Burmeister, 1883) and assigning the specimen described by Rovereto (1912) as *Garialis neogaeus* to *R. intermedius*. The subsequent studies of Argentine longirostine crocodylians were carried out by Rusconi (1935), Patterson (1936), Langston (1965), Gasparini (1968, 1973, 1985), Buffetaut (1982) and Langston & Gasparini (1997).

In his remarkable work on the Tertiary Crocodylia of Colombia, Langston (1965) dedicated a chapter to a review of the record of extinct alligatorids of South America, considering *Proalligator australis* (Burmeister 1885), *Caiman lutescens* (Rovereto 1912) and *C. praecursor* (Rusconi 1933) (Langston 1965, pp. 117, 118, 122, 127) valid for the Neogene of Argentina. In that work, he erected the new Family Nettosuchidae to include *Nettosuchus* (with *N. atopus*) which he later recognised as a junior synonym of *Mourasuchus* Price, 1964 (Langston 1966) and which recently has been considered a derived caimanine alligatorid lineage (Brochu 1999, 2003; Aguilera *et al.* 2006; Riff *et al.* 2010). This genus is represented in the Upper Miocene of Paraná with *Mourasuchus nativus* (Gasparini 1981), which is also known from the Neogene of Acre, Brazil (Bocquentin & Souza-Filho 1990).

Recent studies have enriched the systematic, evolutionary and biogeographic history of several crocodylian taxa of the Neogene of South America (Brochu 1999, 2003, 2011; Aguilera 2004; Aguilera *et al.* 2006; Sánchez-Villagra & Aguilera 2006; Paolillo & Linares 2007; Salas-Gismondi *et al.* 2007; Riff & Aguilera 2008; Riff *et al.* 2010), mostly focusing on the Neogene record of Amazonia and adjacent areas in northern South America. Despite such recent contributions, the progress of the knowledge of Neogene austral crocodylians recorded in the Southern Cone is comparatively poor (Cione *et al.* 2000). Thus, an exhaustive revision of the record is desirable.

As mentioned above, the taxonomic history of crocodylian fossils of Paraná is extensive and sometimes rather confusing. Given that context, we preferred to analyse this record from a conservative approach. The present contribution is a tribute to Prof. Emeritus Dr. Wann Langston Jr, with the aim to provide an update of the knowledge of the alligatorids of the late Miocene of northeastern Argentina, exploring its taxonomical diversity, and including a descriptive revision in a phylogenetic context.

The significant contribution of Langston (1965) directly and indirectly influenced several generations of eusuchian researchers worldwide (e.g. Z. Gasparini, R. Molnar, W. Sill, J. C. Bocquentin-Villanueva, E. Buffetaut, M. Norell; A. B. Busbey, C. Brochu, O. Aguilera, R. Salas-Gismondi, J. P. de Souza-Filho, O. Linares, P. Bona, D. Fortier and D. Riff).

**Institutional abbreviations.** MACN PV, Museo Argentino de Ciencias Naturales, “Bernardino Rivadavia”, Paleontología Vertebrados, Buenos Aires, Argentina; MLP, Museo de La Plata, Buenos Aires, Argentina; UCMP Museum of Paleontology, University of California, Berkeley, USA; UFAC, Universidade Federal do Acre, Rio Branco, Acre, Brazil; UNEFM-CIAAP Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela.

## 1. Material and methods

Fossil material from Paraná (Argentina) analysed in this study includes specimens from the “Conglomerado Osífero” level from the Ituzaingó Formation (Upper Miocene) housed at the MLP and MACN PV. Morphological comparisons were made using published illustrations (Price 1964; Langston 1965; Bocquentin-Villanueva 1984; Gasparini 1985; Bocquentin & Souza-Filho 1990; Brochu 1999; Aguilera *et al.* 2006; Sánchez Villagra & Aguilera 2006; Langston 2008) and direct evaluations with specimens housed in the UFAC. Cranial comparative material of extant alligatorid species used in this analysis belongs to herpetological collections at the MLP and MACN.

To explore phylogenetic relationships of *Mourasuchus* species, a maximum parsimony analysis was carried out based on the data set characters published by Brochu (1999) and 32 eusuchians plus *Bernissartia fagesii* (species considered in the analysis are listed in Appendix 4). Following observations of Aguilera *et al.* (2006), character 93 (Brochu 1999) was reconsidered, modified and three new characters were incorporated (Appendix 1). The character matrix was revised after the re-study of: a sample of 20 specimens of *C. latirostris* (Bona & Desojo 2011); the holotype of *Mourasuchus arendsi* (skull and post-cranial remains, UNEFM-CIAAP-1297); the assessment of information in Price (1964) and Langston (1965) for *Mourasuchus atopus* and *M. amazonensis*; and the study of nine new specimens of *M. nativus* housed in the UFAC. *Caiman cf. lutescens* was recoded based on UCMP 39978 (Langston 1965, figs 78–79, pl. 2). The matrix was analysed with parsimony under equal weights using TNT 1.1 (Goloboff *et al.* 2008). A heuristic tree search of 1,000 replicates of Wagner trees with random addition sequences was performed followed by TBR (tree bisection-reconnection) branch-swapping methods, holding ten trees per replicate and collapsing zero-length branches (collapsing branches if supported ambiguously). This tree search strategy resulted in 30 most parsimonious trees of 265 steps [Consistency Index (CI) = 52, Retention Index (RI) = 78]. The strict consensus is shown in Figure 4.

Total cranial length of fossil material of *Caiman latirostris* was calculated based on allometric equations for cranial metric variables (Bona & Desojo 2011).

EPOCH	Formation	LITHOLOGY
	Tezanos Pinto	Loess
Pliocene to early Holocene	Hernandarias	Silty mudstone with gypsum
	Alvear	Fine sandstone and calcareous siltstone
late Miocene-Pliocene	Ituzaingó	Green mudstone
		Brown siltstone and sandstone
		Yellow sandstone
		"Conglomerado Osífero" Oyster shells
middle Miocene	Paraná	Green sandstone
		Green mudstone

**Figure 2** Integrated stratigraphic column of the Ituzaingó Formation in the area of Paraná, Entre Ríos province. Scale represents the maximum thickness of the "Conglomerado Osífero". Modified from Brandoni & Scillato-Yané (2007).

## 2. Geological setting

The Neogene fossil record in Argentina is principally from the Ituzaingó Formation (De Alba 1953; Herbst 1971), in a level informally called "Mesopotamiense" or "Conglomerado osífero" (*sensu* Frenguelli, 1920; see Cione *et al.* 2005). This unit emerges from Ituzaingó (Corrientes province) to Paraná (Entre Ríos province) (Fig. 1) and over the margins of Paraná River, from the vicinity of Paraná further north. The most explored localities include are La Celina [S 31° 37' 37", W 60° 20' 04"], Toma Vieja [S 31° 38' 42.5", W 60° 28' 06"] and Villa Urquiza [S 31° 38' 42.5", W 60° 22' 50.5"], Entre Ríos Province (Brandoni 2011; Brandoni & Scillato-Yané 2007) (Fig. 1). This level overlies the marine Paraná Formation (Bravard 1858) and is characterised by the presence of levels of quartz gravel, clay clasts and numerous isolated fragments of continental and marine vertebrates (Brandoni & Scillato-Yané 2007; Brandoni 2011) (Fig. 2).

Based on the evidence of stratigraphic relations and the fossil vertebrates recorded, Cione *et al.* (2000) proposed a correlation of this unit with the late Miocene Huayquerian (for South America) and the Tortonian of the international scale.

## 3. Systematic palaeontology

- Crocodylia Gmelin, 1789, *sensu* Benton & Clark, 1988
- Alligatoridae Cuvier, 1807, *sensu* Norell *et al.*, 1994
- Caimaninae Brochu, 2003 (following Norell 1988)
- Mourasuchus* Price, 1964

**Type species.** *M. amazonensis* Price, 1964.

**Emended diagnosis.** *Mourasuchus* is diagnosed by the following unambiguous synapomorphies: dentary linear between the fourth and tenth alveoli (Brochu 1999; character 68-2) and orbits smaller than the infratemporal fenestrae, reduced supratemporal fenestrae (character 165-2). This genus it is also characterised by the following combination of characters: an extremely wide, compressed and long rostrum related to the very small skull table; lateral border of rostrum straight without festooning; supratemporal surrounded anteriorly mainly by post-orbitals; prefrontals contacting in the midline, so that nasals do

not contact the frontal in dorsal view; wide external nares, larger than other cranial openings but entirely surrounded by premaxillae; laterotemporal arcades depressed, so lateral surfaces of jugal, quadrate and quadratojugal face dorsally; supraoccipital with large dorsal exposure and deep insertion into skull table; slender U-shaped mandibles that curve from first to fifth alveoli and then are linear posteriorly to sixth alveolus; very gracile mandibular symphysis extended only at level of first alveolus; small conical teeth with tiny lateral carinae; and upper and lower tooth rows with more than 40 teeth. Emended from Price (1964), Langston (1965) and Bocquentin & Souza-Filho (1990).

*Mourasuchus nativus* (Gasparini, 1985)

1985 *Carandaisuchus nativus* Gasparini, 51; Fig. 1.

1990 *Mourasuchus nativus* (Gasparini, 1985) Bocquentin & Souza Filho, p. 231, figs 2–4.

**Holotype.** MLP 73-IV-15-8. Skull table. (Fig. 3A, B).

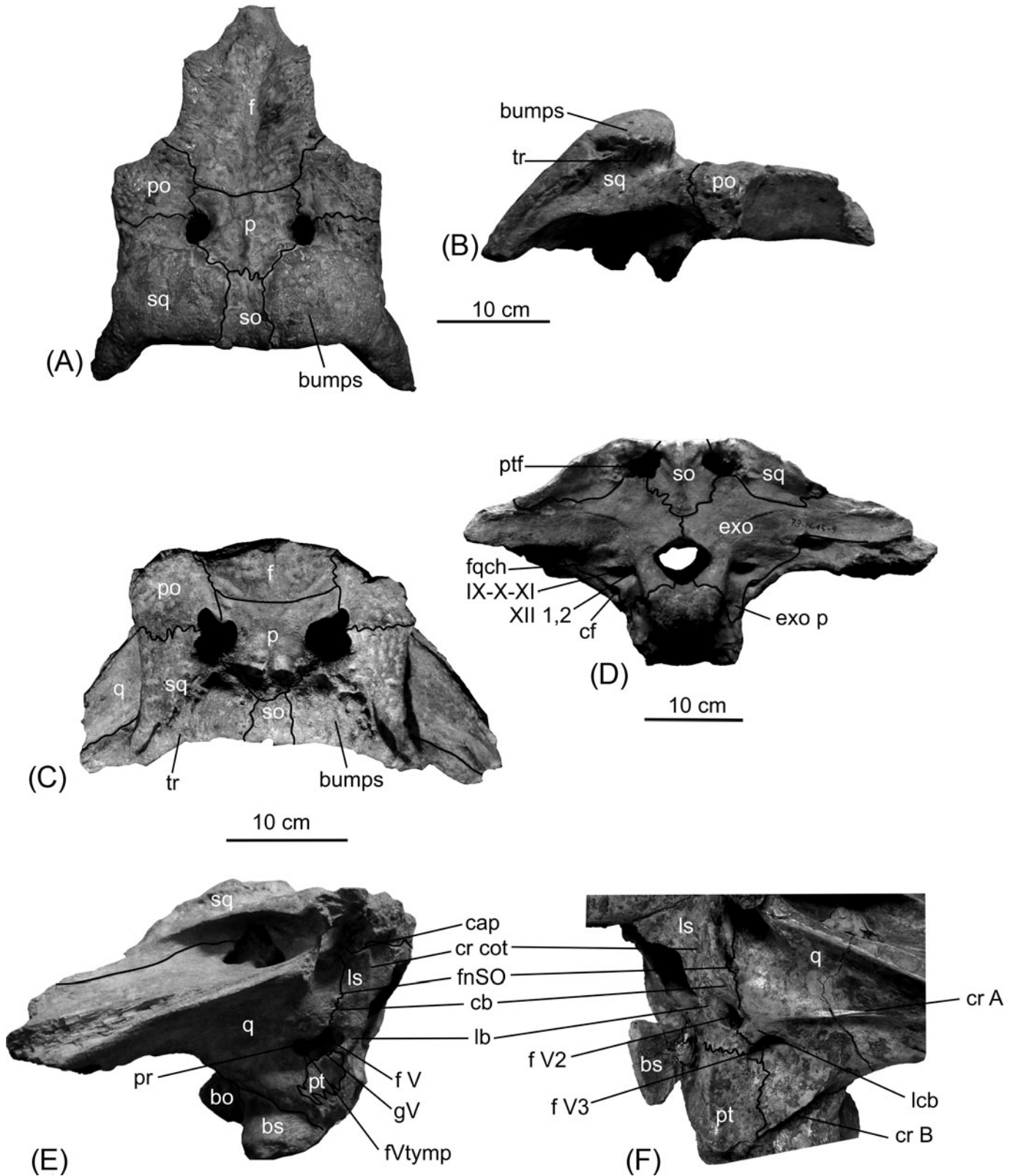
**Referred material.** MLP 73-IV-15-9, posterior sector of skull; UFAC-1397, left maxilla; UFAC-1424, posterior sector of skull and left mandibular ramus; UFAC-1431-1477-1666-2515-3530-3717-4259-4885-4925, posterior sector of skull; UFAC-1484, left mandibular ramus; UFAC-1485, right mandibular ramus; UFAC-1495, right maxilla.

**Emended diagnosis.** *Mourasuchus nativus* is diagnosed by the following features: transverse robust ridge at the posterior sector of skull table with developed squamosal eminences in adult stages; lateral bridge of quadrate dividing the trigeminal foramen into two separate openings for the passage of the maxillary (V2) and mandibular (V3) branches of the trigeminal nerve; large posttemporal fenestrae and large opening for the passage of tympanic ramus of trigeminal nerve, exposed on lateral view and aligned with trigeminal foramen. It differs from *Mourasuchus amazonensis*, *Mourasuchus arendsi* and *Mourasuchus atopus* by presence of middle crest on posterior dorsal surface of parietal and from *Mourasuchus atopus* by presence of a pronounced notch at lateral edge of jugals. *Mourasuchus nativus* also shows exoccipitals not projected ventrally at occipital tubera. Emended from Gasparini (1985) and Bocquentin & Souza Filho (1990).

**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); Ituzaingó Formation (Herbst 1971), Upper Miocene (Cione *et al.* 2000; Brandoni & Scillato-Yané 2007; Brandoni 2011) (Fig. 2).

Referred material housed in UFAC comes from the Niterói site, right bank of the Acre River, between the cities of Rio Branco and Senador Guimard [S 10° 08' 30.0", W 67° 48' 46.3"]; Solimões Formation, Upper Miocene.

**Description.** A complete description of the cranial osteology of this species is provided by Bona *et al.* (2012). In dorsal view (Fig. 3A, C), the skull table shows straight and parallel lateral margins that in the posterior sector are laterally oriented because of the squamosal projections at the paroccipital processes. The posterior margin of the skull table in *M. nativus* approximates a half-hexahedron, a feature shared with *Caiman*. Supratemporal fenestrae show different sizes and shapes that vary during ontogeny. In young specimens (MLP-73-IV-15-9, UFAC-2515-1666-4925), they are tri-lobed with a middle, anterolateral and posterolateral lobes. In adult specimens, these fenestrae are relatively small and their outlines vary from circular (MLP-73-IV-15-8) to tri-lobed (UFAC-1424-1431-4259-4885). Those curvatures of the margins of the supratemporal fenestra communicate with grooves over the skull roof, interpreted by Bona *et al.* (2012) as vascular marks. The medial and posterolateral ones are related to grooves that surround the squamosal eminences, more pronounced in larger specimens (see Bona *et al.* 2012 figs 2, 6). As in other young caimanines, in MLP-73-IV-15-9 the anterior opening of the



**Figure 3** *Mourasuchus nativus*: MLP 73-IV-15-8, Holotype in (A) dorsal and (B) lateral views; MLP 73-IV-15-9, fragment of posterior sector of skull in (C) dorsal, (D) occipital and (E) lateral views; UFAC-2515 in (F) lateral view. Abbreviations: bs = basisphenoid; bo = basioccipital; cap = capitae process; cb = caudal bridge of laterosphenoid; cf = carotid foramen; exo p = exoccipital; cr A = crest A; cr B = crest B; cr cot = cotylar crest of laterosphenoid; exo p = exoccipital process; f = frontal; fnsO = foramen for the trigeminal pra-orbital nerve; fqch = foramen for the cranioquadrate channel; fV = trigeminal foramen; fV<sub>2</sub>, fV<sub>3</sub> = foramina for the trigeminal tympanic branch; gV = lateral bridge of laterosphenoid; lcb = laterocaudal bridge of quadrate; ls = laterosphenoid; p = parietal; po = postorbital; pt = pterigoid; ptf = posttemporal fenestra; q = quadrate; so = supraoccipital; sq = squamosal; tr = transversal ridge; IX-X-XI = openings for glosopharyngeal (IX), vagus (X) and accessory (XI) nerves; XII 1,2 = openings for the respectively branches of hipoglossal nerve.

post-temporal canal is exposed in dorsal view in the supratemporal fossa and obliquely oriented. In MLP-73-IV-15-8 and in all UFAC specimens this opening is vertically oriented and covered by the dermal skull roof, a synapomorphy of the crown group caimans (Brochu 1999: 68). The infratemporal fenestra is not preserved in the Argentinian material of *M. nativus* but in UFAC-1424 (Bocquentin & Souza-Filho 1990, p. 231, fig. 3A), both infratemporal fenestrae are partially preserved. They are wider than long, probably triangular shaped and wider than the skull table width. As observed in that figure, the quadratojugal of *M. nativus* forms the posterior part of the lateral margin of the fenestra, and the lateral margin of jugal presents a marked notch. In contrast to the condition in most caimans, in both specimens of *M. nativus* the ornamentation is reduced, with bone surfaces particularly smooth, with crests and isolate cells and pits.

In occipital view (Fig. 3D), the skull table surface is particularly high because of the abrupt elevation of parietals, squamosals and supraoccipital. These bones all form a robust transversal crest situated over the posterior margin of the skull table. At this ridge, the squamosals form two bumps (or eminences). While their size varies with skull size, the posterior ridge is developed in all young and adult specimens (Fig. 3A–C). CT scan images show that these bumps are solid and not internally affected by the paratympanic sinus system (Bona *et al.* 2012, fig. 4). The occipital sector dorsal to the foramen magnum is high. As Gasparini (1985) pointed out, the dorsal margin of the squamosal descends abruptly at the paroccipital processes. The supraoccipital is also high and narrow, and delimits the huge post-temporal fenestrae medially. These fenestrae are large, similar in size to the supratemporal fenestrae, bounded ventrally by the exoccipitals, dorsally and laterally by the squamosals and medially by the supraoccipitals (Fig. 3D). The basioccipital plate (*sensu* Iordansky, 1973) is rectangular in shape. The ventral margin (basioccipital-basiphenoid suture) is horizontal and straight and, as in other crocodylians, it delimits the medial (odd and anterior) and lateral (pair and posterior) openings of the Eustachian tube (medial pharyngeal and pharyngotympanic recesses, respectively; Witmer *et al.* 2008). In contrast to other caimanines, the exoccipitals are not projected ventrally at the basioccipital tubera (Fig. 3D), extending ventrally only to the level of the ventral border of the occipital condyle. The basioccipital plate also bears the marked medial crest and, in association with the tuberosity, serves in all crocodylians as attachment for the tendons of the *M. basioccipitovertebralis* (= *M. rectus capitis anterior*) and the *M. occipitotransversalis profundus* (*M. longissimus capitis*; Iordansky 1973, p. 226).

In lateral view (Fig. 3B, E, F), the laterosphenoid forms the anterolateral wall of the cerebral cavity. As in other crocodylians, the laterosphenoid body forms the rostral border of the trigeminal foramen, which is posteriorly delimited by the prootic (Holliday & Witmer 2009). Dorsally, the postorbital process of the laterosphenoid is sutured caudally to the quadrate and dorsorostrally with the frontal. The laterosphenoid bears a marked longitudinal oblique crest (cranial crest of laterosphenoid, Fig. 3E, F), for the attachment of the *pseudotemporalis* muscle (Iordansky 1964; Holliday & Witmer 2007; Bona & Desojo 2011), that in *M. nativus* is more vertically oriented than in other caimanines. The crest extends from the dorsal surface of the postorbital process of laterosphenoid ventral and caudally over the cranial margin of the laterosphenoid lateral bridge. In MLP-73-IV-15-9 the lateral and caudal bridges of the laterosphenoid are preserved. As in other caimanines (e.g. *Caiman*, *Paleosuchus* and *Melanosuchus*), the caudal bridge is typically short, robust and encloses the supraorbital branch of the trigeminal nerve (Holliday & Witmer 2009; Bona & Desojo 2011). The supraorbital nerve runs

dorsally into a well-marked groove (Fig. 3F). The lateral bridge of this bone is complete and ventrally sutured with pterygoid. It forms the lateral bony limit of the *cavum epiptericum* which provides the passage of the ophthalmic ramus of trigeminal nerve (V1) and bears an accentuated groove for the maxillary nerve (V2). The trigeminal fossa is huge, caudo-rostrally oriented and bound by laterosphenoid (rostrally), quadrate (caudally) and pterygoid (ventrally). In *M. nativus*, the quadrate forms a laterocaudal bridge, caudal to the lateral bridge of the laterosphenoid and ventrally sutured to this bone (Fig. 3F). It is clear that this bridge divides the maxillary (V2) from mandibular (V3) trigeminal branches, and that V3 branch is caudoventrally oriented. Bona *et al.* (2012) pointed out that the presence of this bridge is correlated with the huge opening of the trigeminal fossa in this species. This bony structure lies just at the area of attachment of the *adductor mandibulae externus* muscle (see Holliday & Witmer 2007; Bona & Desojo 2011) and probably serves as a bony surface of attachment of this muscle. The quadrate in *M. nativus* is also more laterally facing and crests “A” and “B” (Iordansky 1964) are more laterally and caudally oriented than in other caimanines, respectively. The re-orientation of these crests and the trigeminal V3 branches are features probably related to a different orientation of adductor muscles, and osteologically correlates to the presence of a flat and elongated skull in this species (see Bona *et al.* 2012).

Although the prootic is not broadly exposed on the lateral braincase wall in most living crocodylians, in *M. nativus* it is more exposed than in other Caimaninae. At the posterior sector of the trigeminal foramen, it forms the caudal margin of the trigeminal foramen and the medial wall of the trigeminal fossa. The prootic also forms the rostral margin of the foramen for the passage of the tympanic trigeminal branch (Holliday & Witmer 2009), which in MLP-73-IV-15-9 is particularly large (almost equal to the trigeminal foramen), completely exposed in lateral view and horizontally aligned with the trigeminal foramen (Fig. 3E).

**Observations and phylogenetic relationships.** One of the earliest discussions about these bizarre crocodylians was made by Langston (1965), who described and named *Nettosuchus atopus* from the middle Miocene of Colombia, erecting the family Nettosuchidae to include it. At approximately the same time, Price (1964) described *Mourasuchus amazonensis* from the Upper Miocene of Brazil. Langston (1966) argued that *Nettosuchus* Langston, 1965 is a junior synonym of *Mourasuchus* Price, 1964, understanding its similarities with alligatorids. Recent cladistic analyses place this taxon among caimanines (Brochu 1999, 2003, 2010; Aguilera *et al.* 2006; Bona 2007; Brochu 2010; Fig. 4). Although *Mourasuchus* is endemic to South America (Langston & Gasparini 1997), the sister group relationships with North American Eocene *Orthogenysuchus olsenii* Mook, 1924 supported by those phylogenetic studies deserve consideration (Brochu 1999; Langston 2008; Brochu 2010; Riff *et al.* 2010; Fig. 4). Moreover, all phylogenetic analyses link *Purussaurus* with *Mourasuchus* and *Orthogenysuchus*. If so, the *Purussaurus* and *Mourasuchus* lineages would go back to the Eocene and multiple dispersal events between North and South America would be necessary to explain the biogeographic history of this clade (Brochu 1999, 2010). Future revisions of *Orthogenysuchus* will clarify this situation.

Beyond basic descriptive work (Price 1964; Langston 1965, 2008; Bocquentin-Villanueva 1984; Gasparini 1985), no detailed comparative anatomical or phylogenetic analyses of *Mourasuchus* species have been made. *Charandaisuchus nativus* was erected by Gasparini (1985) as a nettosuchid (following Langston 1965), based on two posterior fragments of skull table. Later, Bocquentin & Souza-Filho (1990) described more cranial



**Figure 4** Strict consensus cladogram of 30 most parsimonious trees of 265 steps showing *Mourasuchus* species relationships and the phylogenetic position of *Caiman gasparinae*. Derived character states for nodes 1–15 and non-caimanines species are listed in Appendix 4. White and black circles indicate homoplastic and non-homoplastic characters states, respectively.

material of this taxon and considered *Charandaisuchus* a junior synonym of *Mourasuchus*. Bona *et al.* (2012) provide a detailed study of the cranial anatomy of *M. nativus* and morphological features that clarify the phylogenetic relationships of the species.

To explore the phylogenetic relationships of *Mourasuchus nativus*, a maximum parsimony analysis was carried out (Fig. 4). *Mourasuchus* monophyly is supported by two unambiguous synapomorphies: the dentary is linear between the fourth and tenth alveoli (Brochu 1999, character 68-2) and the orbits are smaller than the infratemporal fenestrae, with reduced supratemporal fenestrae (character 165-2; Appendix 1). Character 68-2 is also present in some non-alligatoroids (e.g. *Tomistoma*, *Thoracosaurus*, *Eosuchus*, *Gavialis*, *Gryposuchus*, *Hesperogavialis*) but it is not homoplastic among alligatoroids (Fig. 4). Based on current morphological data, *Mourasuchus nativus* is the sister taxon of *M. amazonensis* + *M. arendsi* + *M. atopus*, a clade

unambiguously supported by the presence of a marked knob at the anterior-medial margin of the orbits (character 167-1, Appendix 1). This hypothesis assumes that all species of *Mourasuchus* were already differentiated at the Middle Miocene in South America. The *M. atopus* + *M. amazonensis* clade is unambiguously supported by the presence of a supratemporal fenestra surrounded anteriorly by the postorbital. (character 166-1; Fig. 4; Appendix 1). Exploring the phylogenetic position of *Mourasuchus nativus* within alligatoroids, it can be found that this species could be apomorphy based, defined by lateral edge of suborbital fenestra bowed medially (character 105-1; Brochu 1999), a character that is homoplastic within the group (Fig. 4, nodes 11 & 16; Appendix 5; Brochu 1999).

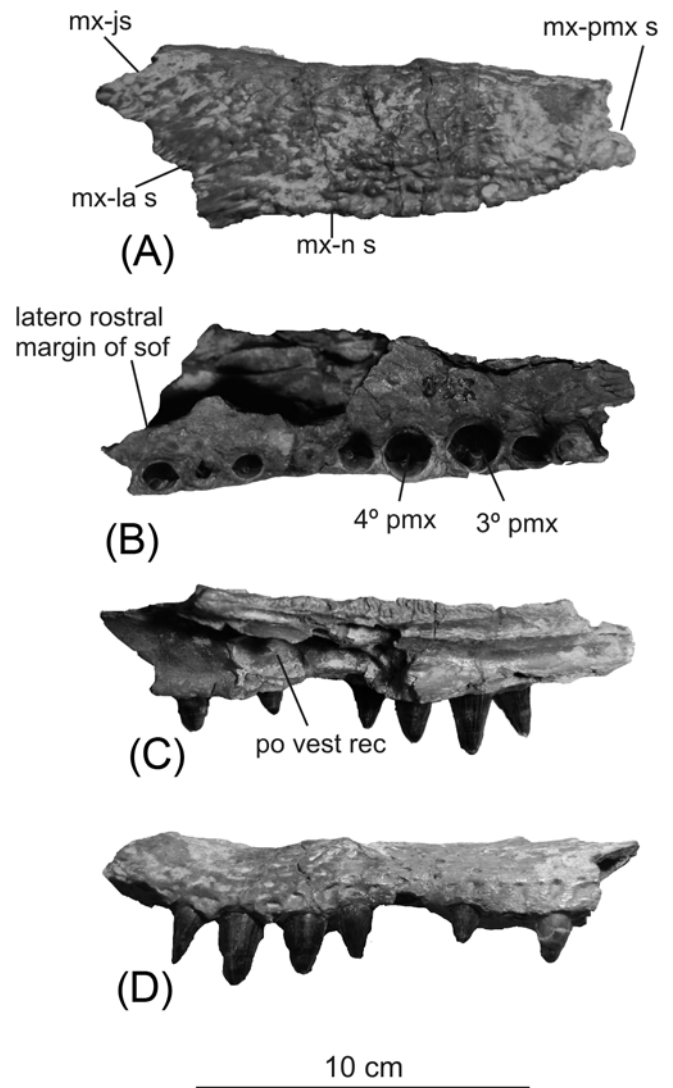
*Caiman* Spix, 1825

**Type species.** *Caiman fissipes* Spix, 1825.

**Diagnosis.** Snout not acute but blunted and anteriorly depressed; extensive inferior “molar” row, blunted and flattened; feet with divided fingers (*fissipalmati*) or frequently with semi palmated fingers, fourth tooth on each side of the lower jaw occluding in an real fossa in the maxilla (Translated from the original diagnosis). [Original diagnosis: “*Rostrum non acutum sed obtusum, supra depressum, largiusculum; arcus maxillaris inferior patens, obtusus, applanatus; pedes posteriores vel fissi vel frequenter semipalmati; dens inferior utrinque quartus in fossam maxillae superioris recondendus*” Spix (1825, p. 3)]

**Observations.** This *Caiman* type species is *Caiman fissipes* Spix, 1825 (= *Crocodylus latirostris* Daudin, 1802) by subsequent designation by Schmidt (1928). Osteological characters given by Spix (1825) are not exclusive to the genus and they are shared by almost all alligatorids and caimanines. Although phylogenetic proposals based on molecular data support the monophyly of *Caiman*, (e.g. DNA sequences of the mitochondrial cytochrome b gene, the nuclear Recombination Activating Gene 1 and the myelocytomatosis oncogene; Hrbek *et al.* 2008), cladistic analyses based on morphology propose the paraphyly of this genus (Norell 1988; Poe 1997; Brochu 1999, 2004, 2010, 2011; this paper; Fig. 4). Jacarea Gray, 1844 is defined by Brochu (1999: 74) as “a node based group comprising the last common ancestor of *Caiman crocodilus*, *C. yacare*, *C. latirostris* and *Melanosuchus niger* and all of its descendents”, based on four unambiguous synapomorphies i.e. anterior half of axis neural spine slopes anteriorly (character 11-1), iliac blade rounded with modest dorsal indentation (character 28-1), articular-surangular suture with anterior process ventral to lingual foramen (character 44-2) and lateral edge of suborbital fenestra bowed medially (character 105-1). As stated above, character 105-1 is homoplastic among alligatoroids (Brochu 1999; this paper).

The sister-group relationship between *Caiman latirostris* and *Melanosuchus* (not completely supported in the present cladistic analysis, Fig. 4) is actually supported by only one unambiguous synapomorphy (i.e. rostral ridges very prominent; Brochu 1999, 2011). Given the lack of support in combined cladistic analyses as well as the weak support obtained from morphological data set, re-naming the genus (with the older name *Jacaretinga*, e.g. Norell 1988) or synonymising *Melanosuchus* with *Caiman* (Poe 1997) is premature (Brochu 1999). On the other hand, the unnamed clade “*C. yacare* + *C. crocodilus*” (Brochu 1999, p. 75) is supported by two synapomorphies: surangular with spur bordering the dentary tooth row lingually for at least one alveolus length; and occlusion pit between the 7th and 8th maxillary teeth (Brochu 1999; Fig. 4; characters 61-0 and 78-1). Given the fragmentary nature of fossil species of *Caiman*, the phylogenetic relationships including all *Caiman* taxa and an emended diagnosis of the genus have to be made on the basis of future morphological information. Detailed and accurate anatomical descriptions of extant species considering the intra-specific variability are scarce (Bona & Desojo 2011). These kinds of studies should be done to obtain new morphological data in order to clarify this situation and to define *Caiman* and most of its species osteologically. The monophyly of *Caiman* could be a taxonomical decision, considering *Melanosuchus* and *Caiman* as the same genus. Within Caimaninae, extant *Caiman* species and those described in this contribution share morphological features, such as the relative size of the temporal fenestrae and orbits (a plesiomorphic character within among alligatorids; character 165-1) and the pattern of relative size of premaxilla–maxilla alveoli and diastemata (e.g. all *Caiman* species have five premaxillary alveoli, and the 3rd and 4th maxillary alveoli are the biggest of the maxillary tooth row). Although these characters are also shared with *Melanosuchus*, *Caiman* species do not have the vomer exposed



**Figure 5** *Caiman australis*: MACN PV 258, Holotype in (A) dorsal (B) palatal, (C) medial and (D) lateral views. Abbreviations: mx-j s = maxilla-jugal suture; mx-la s = maxilla-lacrymal suture; mx-n s = maxilla-nasal suture; mx-pmx s = maxilla-premaxilla suture; po vest rec = recessus postvestibularis; sof = suborbital fenestra; 3° pmx, 4° pmx = 3° and 4° premaxillary alveoli.

in palatal view and almost all lack conspicuous rostral crests (except the broad snouted *Caiman latirostris*).

*Caiman australis* (Burmeister 1885)

- 1858 *Crocodylus australis* Bravard.  
 1883 *Crocodylus australis* (Bravard 1858); Burmeister, 1883, pp. 148–150 (in part).  
 1887 *Crocodylus meridionalis* Scalabrini, p. 37.  
 1887 *Alligator paranensis* Scalabrini, p. 37.  
 1887 *Proalligator australis* (Bravard 1858); Ambrosetti, pp. 420–426 (in part).  
 1898 *Alligator australis* (Bravard 1858); Ameghino, p. 240.  
 1912 *Alligator australis* (Bravard 1858); Rovereto, p. 341–346 (in part); fig. 2; plate XVI, 1a, b.  
 1932 *Proalligator australis* (Bravard 1858); Rusconi, p. 197.  
 1933 *Proalligator australis* (Bravard 1858); Rusconi, p. 59, figs 1, 2.  
 1936 *Proalligator australis* (Burmeister 1885); Patterson, p. 47–48 (in part).  
 1965 *Proalligator australis* (Burmeister 1885); Langston, p. 177–118.

**Holotype.** MACN PV 258, complete left maxilla (Fig. 5A–D).



**Emended diagnosis.** *Caiman* with a narrow snout, maxilla longer and narrower than extant *Caiman* species. 3rd and 4th alveoli are the largest of the series and similar in size. Maxillary interalveolar spaces reduced. Lateral margin of maxilla less festooned than in other *Caiman* species, in dorsal and lateral view. Maxillary ornamentation with predominance of prominent and elongated grooves and bumps.

**Occurrence.** Banks of Paraná River, in the area of Paraná (Entre Ríos province, Argentina; Fig. 1); Ituzaingó Formation (Herbst 1971), Upper Miocene (Brandoni & Scillato-Yané 2007, Brandoni 2011).

**Description.** In dorsal view, the natural limits of the maxilla are preserved (Fig. 5A). While the rostral and medial contacts of the maxilla with the premaxilla and nasal are preserved, only the medial part of the suture (for contact with lacrimal) is present caudally. The dorsal surface is ornamented with isolated pits and grooves, mainly longitudinally oriented that delimit small bumps. This ornamentation differs from that present in most of the skull bones of extant caimans, which are characterised by conspicuous cells. In this view, the lateral margin of the maxilla is practically straight, tapering forward. Maxillary proportions differ from other *Caiman* species: it is narrow and elongated, suggesting a narrow-snouted specimen. In palatal view (Fig. 5B), the medial maxillary contact is not preserved. The first to the ninth alveoli are preserved. The first, second and fifth to ninth alveoli are similar in size, and the third and fourth alveoli are the largest of the maxillary tooth row, a characteristic shared with other *Caiman* species. The interalveolar spaces are reduced except between the sixth and seventh alveoli. In this specimen, the rostral margin of suborbital fenestra is preserved, showing that it is extended rostrally to the level of the 8th alveolus. In medial view (Fig. 5C), maxillary recesses for the nasal sinuses that pneumatise the rostrum in extant crocodylians are less complex than in other *Caiman* species, such as *C. latirostris* (e.g. *recessus caviconchalis*, Witmer 1995; Bona & Desojo 2011).

**Observations.** Based on fragmentary and disassociated material, Bravard (1858, 1860) erected the name *Crocodylus australis* to include all the cranial and postcranial fossil remains of non-longirostrine crocodylians from the “Mesopotamiense”. Unfortunately, Bravard (1858; reprinted by Burmeister 1883) did not provide any illustration or detailed description of those materials, and both papers had limited distribution. Although parts of the “Catalogue” provided by Bravard (1860) are in the British Museum of Natural History, the sections on fossil crocodylians appear to be missing (Langston 1965). An expanded detailed description of *Crocodylus australis* was given later by Burmeister (1885), based on maxillary, dental, and vertebral material. Although Burmeister neither numbered this material nor specified a type, the description of the maxilla matches precisely to MACN PV 258 (Fig. 5). Based on an isolated fragment of premaxilla, dentary, teeth and postcranial elements, Ambrosetti (1887) erected the genus *Proalligator* to include this species. He inferred that the fragment of premaxilla belonged to the same specimen of Bravard and noted that the depressions for occlusion of the dentary teeth, present in both cranial specimens, indicated that *Crocodylus australis* was not a “crocodylino” but an “alligator” (Ambrosetti 1887, p. 420). Unfortunately, he gave no argument to justify a new generic name.

The first formal diagnosis and discussion of characters of *Crocodylus australis* was proposed by Rovereto (1912) (as *Alligator australis*; for a detailed comment about the taxonomic history of this species, see Rusconi 1933; Langston 1965; Gasparini 1973). Rovereto (1912) indicated that certain features of the teeth that differentiate *C. australis* (i.e., the size and proportions of the maxilla) described by several authors as characteristic of this species, were erroneously attributed. Langston (1965,

p. 118) provided an emended diagnosis of this taxon: “Alligatorids of presumed *Caiman* habitus with rostrum relatively wider than *Caiman sclerops* but narrower than in *Caiman latirostris*; sculpture pronounced, consisting of ridges and deep furrows instead of tips; facial canthi not strongly developed, festooning of maxilla not pronounced. Teeth relatively large, widely spaced, and less differentiated in size than in living species...” In our opinion, the proportions of MACN PV 258, indicate that this specimen had a rostrum longer and narrower than extant *Caiman* species, including *Caiman crocodylus*. These general proportions fit with those present in extant species of *Paleosuchus*, but in *Caiman australis* the snout is low and not quadrangular in section as in *Paleosuchus*. Although any observation related to the tooth morphology of this species cannot be made at present, we agree with Langston (1965) and Gasparini (1973) that in *Caiman australis*, the maxillary alveoli are less differentiated in size but the interalveolar spaces in MACN PV 258 are reduced.

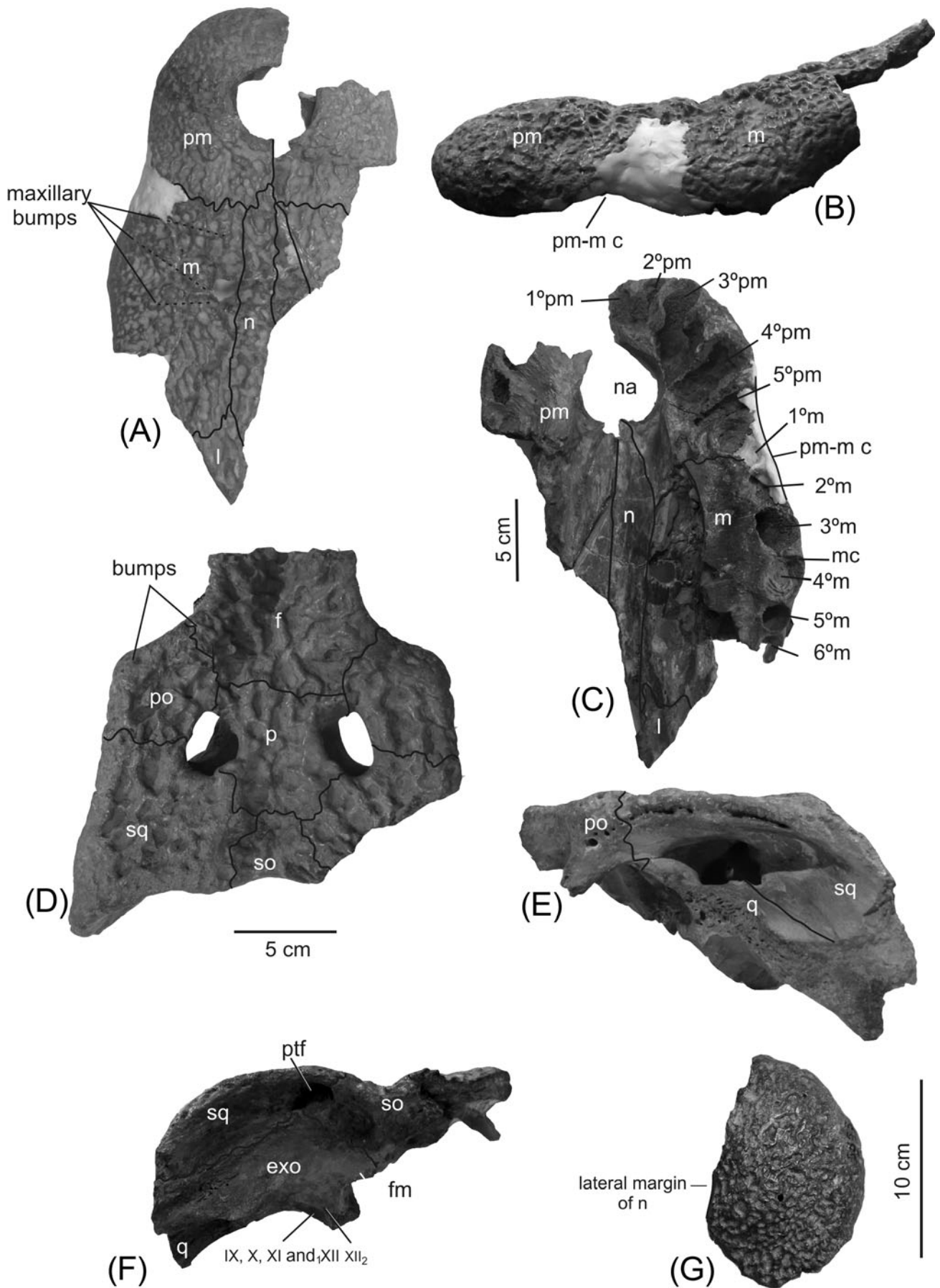
Taxonomic assignation referrals should be based preferably on apomorphies than on the presence of a unique combination of characters. Nevertheless, fossil specimens are often fragmentary, especially those of *Caiman*. This is the case of *C. australis*, which is known from a maxillary left fragment. Available morphological information used to reconstruct phylogenetic relationships among alligatorids caimanines (Brochu 1999, 2010, 2011; this paper) is insufficient to propose the phylogenetic position of this species within alligatorids. However, the occlusion pattern of the mandibular tooth and the presence of the larger 3rd and 4th maxillary alveoli are features that allow us to consider this species as an alligatorid *Caiman* (Gasparini 1973, 1981). Even though the relative size of the maxillary alveoli is similar to that of *Melanosuchus*, *Caiman australis* differs from it by the proportions of the snout and the absence of a conspicuous maxillary crest.

Several cranial and postcranial elements have been assigned to *Caiman australis* but never in association with maxillary material (e.g. Ambrosetti 1887; Rovereto 1912; Rusconi 1933; Sáez 1928; Gasparini 1973). This includes several partial dentaries with particular features, such as similar alveolar sizes, reduced interalveolar spaces, symphyseal mandibular section that is low and narrow with the symphysis extending to the fourth and fifth alveoli, which are seen in MACN PV 5533, 5535, 5537 and 5588. Furthermore, the hollow between the sixth and seventh maxillary alveoli for occlusion of the corresponding mandibular teeth in MACN PV 258 is coincident with hypertrophy of the twelfth dentary teeth preserved in the material MLP-73-IV-15-2 assigned by Gasparini (1973) to *Caiman australis*. This material has the alveolus more laterally situated than in other *Caiman* species. The left dentary fragment MACN PV 5588 has an implanted 4th tooth which is less curved than in extant *Caiman* extant species, with distinctively spaced and pronounced longitudinal striations.

*Caiman australis* is one of at least five species of this genus recorded in the late Miocene in Argentina, supporting the hypothesis of the great diversification of *Caiman* in these latitudes during the late Miocene (see below).

- Caiman gasparinae* Bona & Paulina Carabajal (in press).  
 1887 *Crocodylus paranensis* Scalabrini, p. 37.  
 1912 *Alligator? ameghinoi* Rovereto, pp. 360–367 (en parte), fig. 16.  
 1933 *Xenosuchus paranensis* Rusconi, pp. 67–80 (en parte), fig. 9.

**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 (Fig. 6A–F).



**Figure 6** *Caiman gasparinae*: MLP-73-IV-15-1 (A–F) and MACN PV 5555 (G): snout in dorsal (A), left lateral (B) and ventral (C) views; braincase in dorsal (D), left lateral (E) and occipital (F) views; fragment of right premaxilla in dorsal (G) view. Abbreviations: exo = exoccipital-opistotic complex or otoccipital; f = frontal; fm = foramen magno; m = maxillar; 1°–6° m = 1°–6° maxillar; n = nasal; na = narina; p = parietal; pm = premaxilla; pm–m c = premaxillary–maxillary curvature; po = postorbital; ptf = posttemporal foramen; q = quadrate; so = supraoccipital; sq = squamosal; 1°–5° pm = 1°–5° premaxillar alveoli; IX, X, XI = openings for glosopharyngeal (IX), vagus (X) and accessory (XI) nerves; XII<sub>1</sub>, XII<sub>2</sub> = openings for the respectively branches of hipoglossal nerve. Modified from Bona & Paulina Carabajal (2013).

**Referred material.** MACN PV 5555; fragment of right premaxilla (Fig. 6G).

**Occurrence.** Banks of Paraná River, in the area of Paraná (Entre Ríos province, Argentina; Fig. 1); Ituzaingó Formation (Herbst 1971), upper Miocene (Brandoni & Scillato-Yané 2007; Brandoni 2011).

**Description.** A detailed description and a taxonomic treatment of this taxon is provided by Bona & Paulina Carabajal (2013). The following description, mainly based on specimen MLP-73-IV-15-1 (Fig. 6A–F), summarises the main cranial morphology of this species and its particular morphological features. The general morphology of the skull is similar to that present in other *Caiman* species (outline and relative dimension and contacts of skull bones). The cranial bones are characterised by crests and depressions forming an irregular surface of marked ridges delimiting interconnected pits. There are also some ornamental bumps (bony convexities) on the maxilla and the skull table. This kind of ornamentation is not the typical pattern observed in extant caimans. In both MLP-73-IV-15-1 and MACN PV 5555 (Fig. 6A, B, G) the irregular ornamentation extends further rostrally than in other *Caiman* species.

The rostral portion preserved in MLP-73-IV-15-1 belongs to a large-sized and broad-snouted caimanine, with a low and short rostrum. As in other caimans, a marked curvature at premaxilla-maxilla suture is present in dorsal and lateral views (Fig. 6A, B). The external naris is a single, sub-circular, dorsally-oriented opening that is broadly separated from the anterior margin of premaxilla, as seen in MACN PV 5555. In lateral view, both premaxillae have a lower dorsal surface behind the naris. In dorsal view, they are laterally expanded. In MLP 73-IV-15-1, the nasals do not reach the external naris because of the relatively large rostral contact of premaxilla at the midline (this feature varies intraspecifically in *Caiman*; Bona & Desojo 2011). The nasal is sub-rectangular, similar to that present in *C. yacare*, with straight and parallel lateral margins tapering rostral and caudally. In spite of its broad snouted condition, in this species the nasals are relatively narrow. Maxillary crests are also absent and only four isolated bumps are observed in the left maxilla, which are elongate and obliquely oriented (caudomedially–rostromedially; Fig. 6A). In palatal view (Fig. 6C), five premaxillary and six maxillary alveoli are preserved on the left side of the rostrum. In MLP-73-IV-15-1, the interalveolar spaces of the premaxilla are reduced in size, except for the 3rd, which is larger than the biggest premaxillary alveolus, the 4th. The premaxillary–maxillary alveoli follow the general *Caiman*–*Melanosuchus* pattern (Fig. 6C), with five premaxillary alveoli where the 4th is larger than the 3. Furthermore, the 3rd and 4th maxillary alveoli are larger than the others.

On the skull table, the supratemporal fenestrae are relatively small, with dermal bones of the skull roof overhanging their rims, a morphological feature present in adult specimens of the crown group caimans (Brochu 1999). As in *Caiman* and *Melanosuchus*, the orbits are larger than the infratemporal fenestrae and the supratemporal fenestrae are smaller, though not obliterated. The lateral margins of the skull table diverge caudally. Its dorsal surface is deeply concave at the midline, especially on the frontal and the supraoccipital. Ornamental protuberances are also present in this section of the skull along at the caudal and caudomedial margins of the orbits (Fig. 6D). The edges of the orbit and the lateral and caudal margins of the skull table are strongly thickened. In lateral view, the descending process of the postorbital, at the postorbital pillar, is subtriangular in cross-section. The pyramidal corpus of the laterosphenoid (Holliday & Witmer 2009) is Y-shaped, with the rostral margin slightly concave and the postorbital process narrow. In occipital view, exoccipital-ophisthotic complex and

squamosals form a high and dorsoventrally concave occipital table with a curved dorsal margin (Fig. 6F). Lateral to the foramen magnum, the three foramina for the opening of cranial nerves XII<sub>1</sub>, XII<sub>2</sub>, and X–XI are visible. They show a pattern similar to that present in caimans (Bona & Desojo 2011). In contrast to other caimans, in MLP-73-IV-15-1 the carotid foramen is visible only in lateral view (Fig. 6F). The carotid canal has a similar trajectory as in other caimans (Bona *et al.* 2012). Nevertheless, unlike another caimans, this foramen is bound by the *crista tuberalis* posteriorly and not anteriorly, an autapomorphic character of this species (Bona & Paulina Carabajal, in press).

**Observations.** *Alligator? ameghinoi* Rovereto, 1912 was based on isolated large cranial and postcranial remains. The syntype is formed by three vertebrae, a premaxilla and a mandibular fragment. Rovereto (1912) provided good illustrations of this material that allows us to identify the right premaxilla (p. 364, fig. 16a) as MCN 5555, described in this contribution. Later, Rusconi (1933) erected the genus *Xenosuchus* to include all the large-sized alligatorids from the Neogene of Paraná. In the diagnosis, this author mentioned a series of characters related to the huge proportions of the bones and teeth, and some general features shared by other alligatorids (e.g. “five teeth in premaxilla”; Rusconi 1933, p. 67). This author assigned two species to this genus: *Xenosuchus paranensis* (Scalabrini, 1887), with the subspecies *X. paranensis ameghinoi*, and *X. lutescens* (Rovereto, 1912). *Xenosuchus paranensis* was described, based on dentaries, vertebrae, humeri and a premaxilla. Although the premaxillary fragment was not described and only schematically drawn following Rusconi (1933, p. 81, fig. 9), we recognise that the premaxilla corresponds to MACN PV 5555, as well as part of the syntype of *A.? ameghinoi* figured by Rovereto (1912): a fragment of right premaxilla with four alveoli preserved (2nd–5th) and external naris separated from the rostral edge of the snout. Unfortunately, it cannot be established whether the premaxilla figured by these authors corresponds to that described by Scalabrini (1887) as *Crocodylus paranensis*, but we agree with Langston (1965, p. 121): “Rusconi who evidently did not examine the specimen states that by “hueso incisivo” Scalabrini meant premaxilla. But if it is so the statement that only part of a right bone contained eight teeth is curious indeed. He observes that if the bone in question had been a maxilla (a reasonable assumption) the great size of what Scalabrini supposed to be the third premaxillary alveolus would have no significance. If parts of premaxilla and maxilla were involved together, the description is equally meaningless. From the typological viewpoint therefore *Crocodylus paranensis* seems to be a *nomen vanum*. . . I follow Patterson in regarding all original *paranensis* specimens as *Caiman*.”

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 same large-sized taxon, with external naris separated from the rostral edge of the snout. Based on the skull morphology of MLP-73-IV-15-1, both specimens can be referred to as an alligatorid species, with parietals excluded from the posterior edge of the skull table (Brochu 1999, character 82-3; modified from Norell 1988, character 11). Although in the present cladistic analysis this character is an ambiguous synapomorphy for this clade, *Caiman gasparinae* is linked with caimanines by shared dorsal edges of orbits upturned (103-1, homoplastic) and medial parietal wall of supratemporal fenestra bearing foramina (104-1). Both features are preserved in MLP-73-IV-15-1. As is shown in Figure 4, *Caiman gasparinae* is included in the clade Jacarea (Brochu 1999), supported by four synapomorphies (44-2, 105-1, 143-1, 153-2). The incisive foramen (153-2) is not preserved in either MLP-73-IV-15-1 or

MACN PV 5555, but canthi rostralii are very prominent in *Caiman gasparinae* (143-1). Nevertheless, unlike the broad snouted *C. latirostris*, in *C. gasparinae* the canthi are short, with prominent bumps and no conspicuous crests on the maxillary surface (Fig. 6).

This species differs from other large forms, such as *Purussaurus*, by: the outline, size and morphology of the narial openings; the shallow premaxillary height in lateral view; the relative proportions of orbits and temporal fenestrae; and the skull table outline. The snout features (i.e. narial position, bone proportions and sculpturing) differentiate this taxon from other extant *Caiman* species. In particular, it differs from *C. latirostris* in not having conspicuous maxillary crests and the different proportion of the snout bones (i.e. in *Caiman latirostris*, the nasals are wider). Although this species is a broad-snouted caimanine, it presents relatively narrowed nasals, differing from the broad snouted *C. latirostris*, in which nasals are proportionally wider with lateral convex margins (and not parallel and straight as in *Caiman gasparinae*). The posterior section of the skull also shows peculiar morphological conditions in the position of the opening of lateral carotids, which are laterally situated and do not open on the occipital table, general feature in caimans. This taxon represents one of the largest known *Caiman* species, pertaining to the numerous huge mandibular and postcranial remains found in the area of Paraná.

*Caiman latirostris* (Daudin 1802)

1802 *Crocodylus latirostris* Daudin, p. 417.

1825 *Caiman fissipes* Spix, fig. 3.

1912 *Alligator australis* (Bravard 1858); Rovereto, p. 341 (in part), fig. 1a.

1936 *Caiman paranensis* (Scalabrini 1887); Patterson, p. 50 (in part).

1912 *Alligator lutescens* Rovereto, p. 346 (in part), fig. 4a.

1933 *Proalligator australis* (Bravard 1858); Rusconi, p. 59 (in part), fig. 10.

1933 *Xenosuchus lutescens* (Rovereto 1912); Rusconi, p. 80 (in part), fig. 11a

**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.

**Occurrence.** From the late Miocene, banks of Paraná River, in the area of Paraná Entre Ríos province, Argentina (Fig. 1); Ituzaingó Formation (Herbst 1971), (Brandoni 2011; Brandoni & Scillato-Yané 2007; Fig. 2) to the Recent (NE of Argentina, Paraguay, Bolivia, N of Uruguay and S – SE of Brazil).

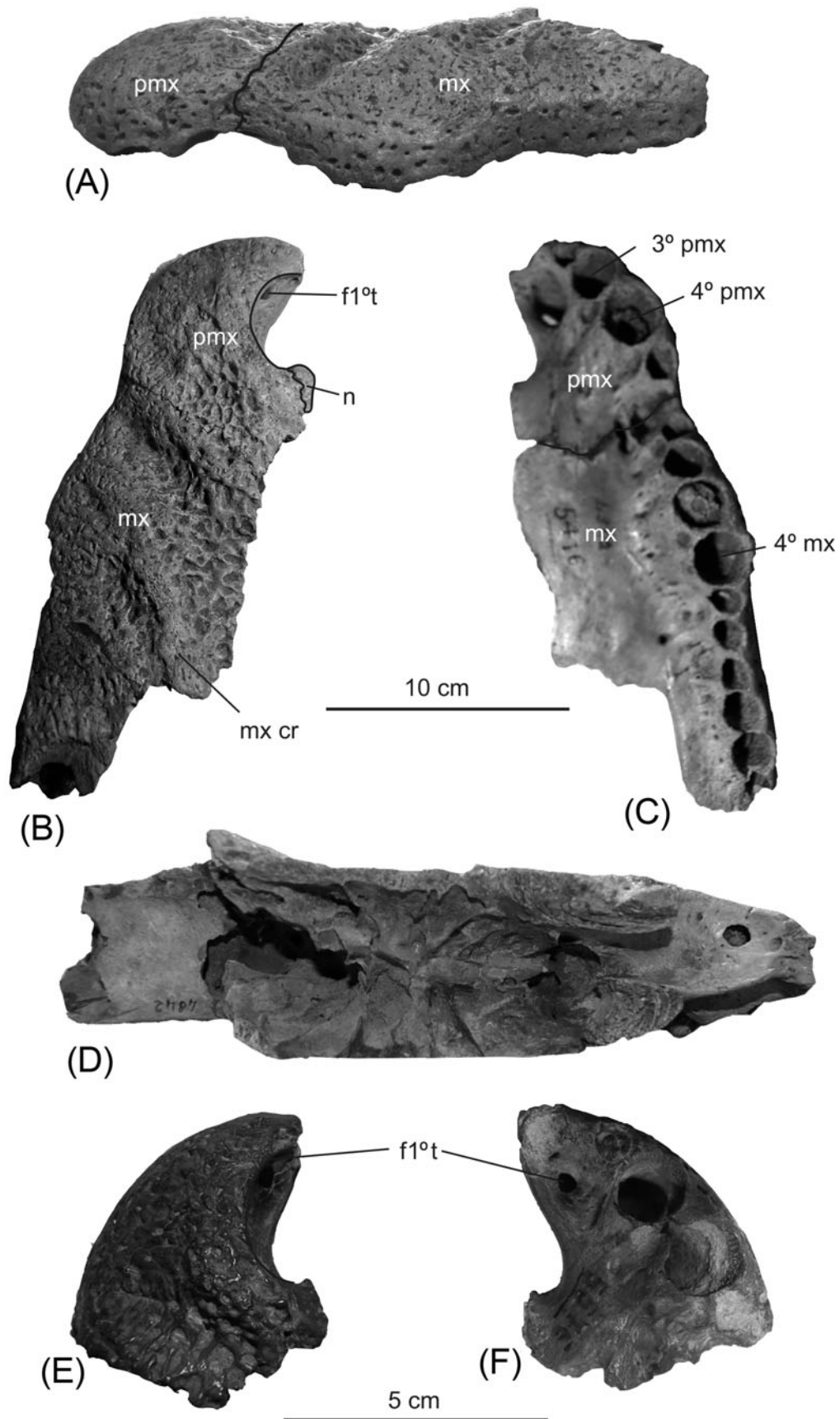
**Description.** A complete description of the osteology of skull and mandible of this species was published by Bona & Desojo (2011) based on extant specimens. The following description is based on those Miocene materials assigned to *C. latirostris* in this contribution. MACN PV 5416 is a fragment of a left rostrum from a large, broad-snouted specimen (Fig. 7A–D). As in extant specimens, the premaxillary–maxillary curvature is marked in lateral view (Fig. 7A). Nevertheless, this curvature is moderate in MACN PV 5416 in dorsal view (Fig. 7B). The skull of extant specimens of *C. latirostris* has a triangular outline with the lateral margins converging rostrally and, although the premaxillary–maxillary curvature is practically absent in dorsal view, the lateral margin of premaxilla becomes rounded, as in the huge MACN PV 5416 (Bona & Desojo 2011, fig. 2A, B). In this specimen, the dorsal surface of the snout shows two pronounced maxillary crests. In *C. latirostris* and *Melanosuchus*, the posterior one extends continuously and caudo-rostrally over the dorsal surface of prefrontal, lacrimal and maxilla, from the medial margin of the orbit to almost the lateral margin of the maxilla. In MACN PV 5416, this crest is continuous over the

maxillary surface and interrupted posteriorly only because both the lacrimal and prefrontal are not preserved in this specimen. In MACN PV 5416 and MACN PV 5576 (Fig. 7B, E), the premaxillae delimit the narial openings and are confluent, as in other caimanines.

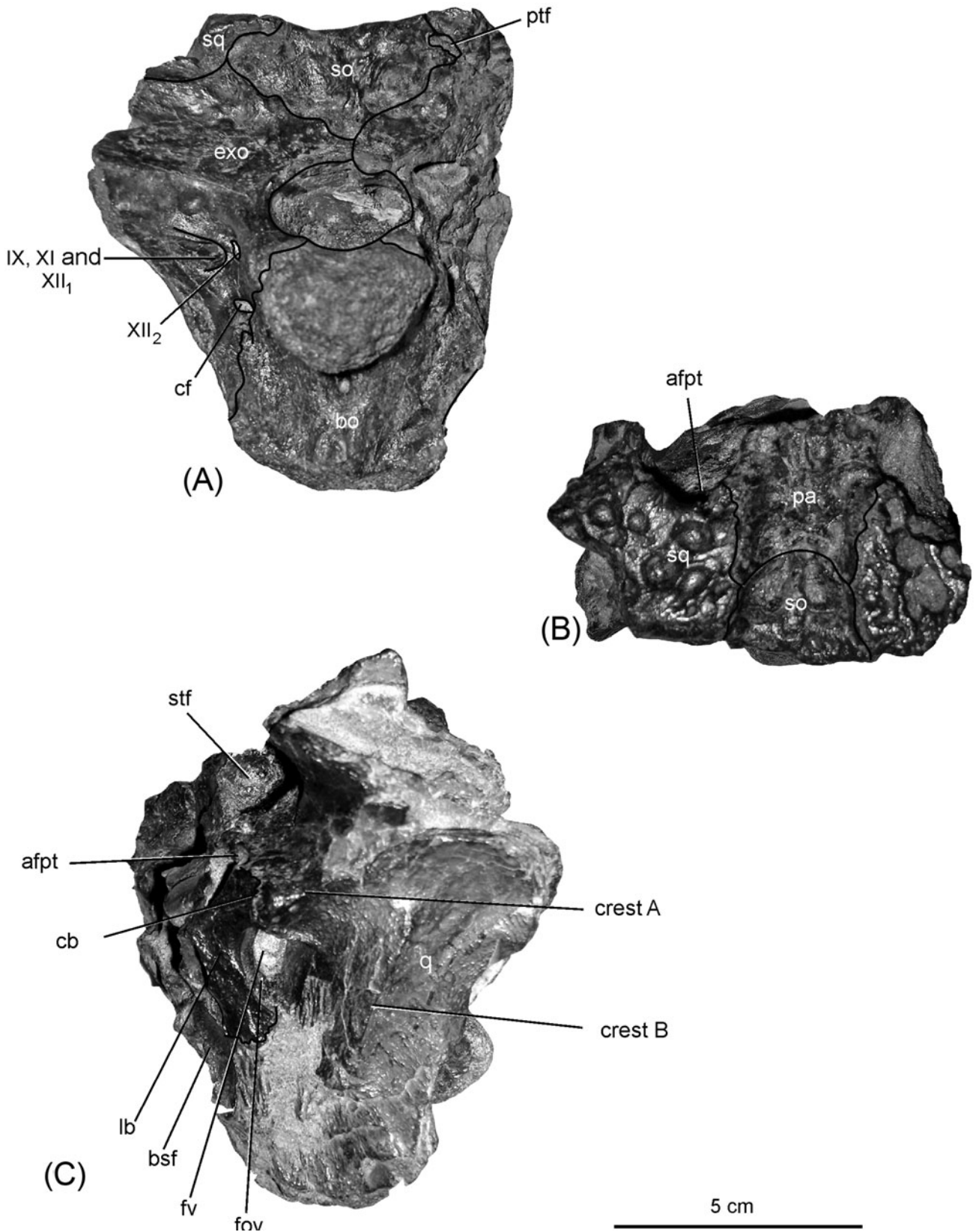
Similar to most specimens of *Caiman latirostris*, the nasals contact the posterior margin of the external naris in MACN PV 5416. Nevertheless, this condition varies intraspecifically but not ontogenetically and, in some extant specimens of *C. latirostris*, the premaxillae contact each other dorsomedially, excluding nasals from the posterior margin of the external naris (Bona & Desojo 2011). Contrary to the condition present in some *Caiman* species (e.g. *C. yacare*), in *C. latirostris* the caudolateral margin of the naris forms a narrow edge, which is also present in MACN PV 5416, MACN PV 5576 and MLP 73-IV-15-16. In lateral view (Fig. 7A), the ventral margin of maxilla is convex with a rostral and a caudal curvature, as in other caimanines. In palatal view (Fig. 7C), the first ten maxillary alveoli are preserved. As in other caimans, their size increases from first to fourth, decreases from fourth to fifth and then increases from seventh to ninth. As in *C. latirostris* and contrary to the condition observed in *Melanosuchus*, in palatal view the maxillae contact each other along the middle line, so the vomer is not exposed on the palatal table. In MACN PV 5416, MACN PV 5416, MACN PV 5576 and MLP 73-IV-15-16, the premaxilla delimits the incisive foramen, which in *C. latirostris* is heart- or teardrop-shaped (as in MACN PV 5576 and MACN PV 5416 respectively; Fig. 7C, F). In MACN PV 5416 and MACN PV 5576, the anterior ventral surface of the premaxilla has a pit that receives the first mandibular tooth. Similar to some extant specimens of *C. latirostris*, this tooth pierces the palatal surface of the premaxilla (but never its dorsal anterior surface, as in other caimanines such as *C. yacare*, *C. crocodilus*, *Melanosuchus* or *Mourasuchus*). In caimans, the presence of a perforation of 1st mandibular tooth in the premaxilla varies within species, but not ontogenetically. In medial view (Fig. 7 D), the maxillary recesses for the nasal sinuses (Witmer 1995) are complex with many diverticula as in *Caiman latirostris*.

MLP 73-IV-15-12 (Fig. 8) is a braincase fragment. In dorsal view, the medial section of the posterior margin of the skull table is straight and perpendicular to the sagittal plane (as in extant caimanines; i.e. *Caiman*, *Melanosuchus*, *Paleosuchus*; Fig. 8B). The rostral opening of the temporal canal is seen through the supratemporal fenestra and is obliquely oriented, showing that this fragment belongs to a juvenile specimen (Brochu 1999). The parietal delimits the supratemporal fenestra medially and, together with the supraoccipital, forms a shallow depression with two smooth lateral ridges that extend from the medial edge of the supratemporal fenestra to the posterior margin of the skull table (as in *C. latirostris*).

As in other caimanines, the supraoccipital extends over the skull table and the dorsal surface is slightly concave with a poorly pronounced median crest. This crest is more pronounced in adult specimens (Bona & Desojo 2011). In occipital view (Fig. 8A) the supraoccipital is wider than high, pentagonal shaped and forms the ventromedial margin of the reduced post-temporal fenestra. Exoccipitals are sutured at the midline, delimiting the foramen magnum dorsally and dorsolaterally and, as in caimanines, they are projected ventrally to the basioccipital tubera (Brochu 1999). Laterally to the foramen magnum, the three horizontally aligned foramina for the passage of cranial nerves IX, X, XI, and XII are preserved at the left side (Fig. 8A). As in *C. latirostris* from medial to lateral they correspond to the separated opening for XII2 and XIII1 branches and the single opening for nerves IX, X, and XI. Characteristic of this species, this last foramen is the largest and is horizontally



**Figure 7** *Caiman latirostris*: MACN 5416, left fragment of a rostrum in (A) lateral, (B) dorsal, (C) palatal and (D) medial views; MACN 5576, left premaxilla in (E) dorsal and (F) palatal views. Abbreviations: f1°t = foramen for the 1° mandibular tooth; mx = maxilla; mx cr = maxillary crest; n = nasal; pmx = premaxilla; 3°pmx–4°pmx = 3° and 4° premaxillary alveoli; 4° mx = 4° maxillary alveolus.



**Figure 8** *Caiman latirostris*: MLP 73-IV-15-12 braincase fragment in (A) occipital, (B) dorsal and (C) lateral views. Abbreviations: afpt = anterior foramen of the posttemporal canal; bo = basioccipital; bsf = basisphenoid; cb = caudal bridge of laterosphenoid; cf = carotid foramen; exo = exoccipital; ~~afpt = foramen~~; ~~finso = foramen for the trigeminal supraorbital nerve~~; fov = trigeminal fossa; fv = trigeminal foramen; lb = lateral bridge of laterosphenoid; pa = parietal; ptf = posttemporal fenestra; q = quadrate; so = supraoccipital; sq = squamosal; stf = supratemporal fossa; IX-X-XI = openings for glosopharyngeal (IX), vagus (X) and accesory (XI) nerves; XII<sub>1</sub>, XII<sub>2</sub> = openings for the respectively branches of hipoglosal nerve.

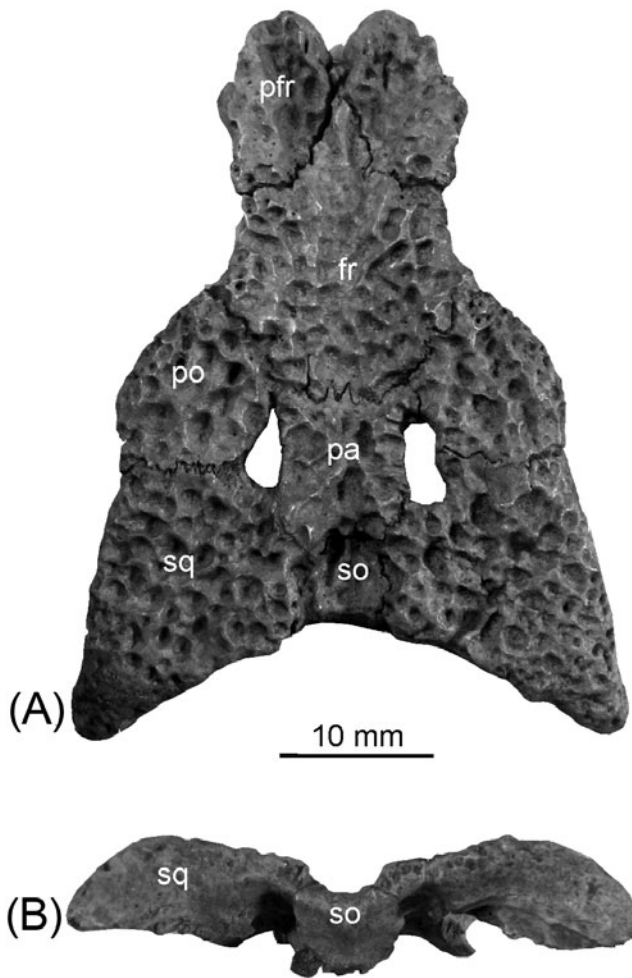
oriented. Ventrally to all these foramina, the carotid foramen (for the passage of the internal carotid arteries) is also preserved. As in other caimans, the basioccipital is hexagonal and forms the occipital condyle and the medioventral margin of the foramen magnum. In lateral view (Fig. 8C), the laterosphenoid forms the rostro-lateral wall of the preserved braincase and extends dorsally, forming the anteroventral area of the medial wall of the supratemporal fossa. Together with the prootic, it delimits the trigeminal opening in equal proportions, forming the anterior margin. The lateral and caudal laterosphenoid bridges are preserved (Holliday & Witmer 2009). As in *C. latirostris*, the lateral bridge contacts the pterygoid ventrally by a relatively long suture (Bona & Desojo 2011). The broad laterosphenoid caudal bridge for the passage of the supra-orbital nerve (the first branch of the trigeminal maxillary nerve; Holliday & Witmer 2009) articulates with the quadrate. The quadrate surface preserved in this specimen has the rostral part of the “crest A” (Iordansky 1964) for the attachment of adductor muscles. As in extant specimens of *C. latirostris* and contrary to other caimanids such as *C. yacare*, *C. crocodilus* and *Melanosuchus*, this part of the crest reaches the laterosphenoid-quadrate suture and is situated ventrally to the opening for the supraorbital nerve (Bona & Desojo 2011).

**Observations.** As stated above, Rovereto (1912, p. 342) defined *Proalligator australis*, mainly based on the morphology of the left maxilla (MACN PV 258). Based on the size of the materials, he assigned to this species two mandibular fragments and a left premaxilla (the latter figured in Rovereto 1912, fig. 1a). His detailed description and illustration of the premaxilla suggests that the premaxilla of MACN PV 5576 (Fig. 7E, F) may be assigned to *C. latirostris* (by the presence of a narrow ridge at the posterior margin of nares; 1st mandibular tooth piercing only the palatal surface of premaxilla). In the same paper, Rovereto (1912, p. 346) erected *A. lutescens* on the basis of the large size of several isolated cranial and postcranial fragments. Among these, there are two skull fragments that can be identified as MACN PV 5416 and 13551 (Figs 7A–D, 9). Although these materials were not associated, this author assumed that, given their size, they belong to the same species. Even more, he points out that while the rostral fragment (MACN PV 5416) was similar in morphology to *Caiman latirostris* (see below), the skull table (MACN PV 13551) had some peculiar features. Rovereto (1912, pp. 346–349) referred to this material as follows: “The most noticeable remain of this species . . . is a skull table . . . Comparing this material with the largest skulls of *Caiman latirostris* that I could access, there are remarkable distinctions in the dimensions and some differences in the general aspect” [From the original: “El trozo mas vistoso de esta especie . . . es una parte superior de cráneo . . . Comparando este conjunto con el que corresponde al más grande de los cráneos que he podido proporcionarme del *Caiman latirostris*, se observan notables diferencias en las dimensiones y algunas en la configuración general.”] He provided a brief description of some of the diagnostic characters of this species: a longitudinal depression of the skull table at the middle line; frontal short with its cranial end poorly extended between pre-frontals; and the probable presence of long nasals (missing in the material). We accept the skull table description given by Rovereto as the original diagnosis of *A. lutescens* and the material MACN PV 13551 as the holotype (see Langston 1965, p. 121). Regarding the large size of specimens, Rusconi (1933) erected *de genus Xenosuchus*, with *X. paranensis* and *X. lutescens* (considered synonyms by Patterson 1937). Unfortunately, Rusconi could not see the skull table figured and described by Rovereto (1912), and chose the rostral fragment (MACN PV 5416) as the lectotype of *X. lutescens*, misreporting the number of the material as “4516” (Gasparini 1973).

A comparative study of the cranial morphology in *Caiman latirostris* (Bona & Desojo 2011) showed that in some specimens, the tip of the first mandibular tooth pierces the palatal surface of the premaxilla, but never at its dorsal anterior surface, as in other caimanines such as *C. yacare*, *Melanosuchus* and *Mourasuchus* (the condition seen in MACN PV 5416, 5576, MLP-73-IV-15-16). Similar to *Caiman crocodilus* and *Melanosuchus*, but contrary to other caimanines such as *C. yacare*, the rostral part of the quadrate crest “A” (Iordansky 1964) in *C. latirostris* is situated ventral to the opening for the supraorbital nerve (MLP 73-IV-15-12, Fig. 8C). The presence of a conspicuous and continuous second rostral crest at the maxilla and the kind of tooth pierce in the premaxilla allows the assignment of MACN PV 5416 to *C. latirostris*. Following Gasparini (1973, 1981), we regard *Alligator lutescens* in part (Rovereto 1912, p. 346, fig. 4a) and *Xenosuchus lutescens* in part (Rusconi 1933, 80, fig. 11a) as its junior synonyms. This species was represented in the late Miocene by specimens larger than the extant ones forms (e.g. MACN 5416 belongs to a specimen with an anterior snout width of 19 cm and a total cranial length of approximately 45 cm).

*Caiman cf. lutescens* Langston (1965) from the Middle Miocene of Colombia is represented by an incomplete skull lacking most of the occipital region, braincase, cranial table and right temporal arcade (UCMP 39978, Langston 1965, p. 75, figs 32–34; pl 2). Following the detailed description and illustrations of this material provided by Langston (1965), this specimen shows a *Caiman*-like general morphology, sharing some similarities with *C. latirostris*, such as the presence of rostral canthi, palatines widened rostrally and a triangular dorsal outline of the skull (the latter condition is present in young specimens of this species; Bona & Desojo 2011). Nevertheless, the relatively short snout of this specimen (e.g. short and wide nasals and maxillae), the presence of broad narial external openings and the absence of information of the skull table and brain case morphology lead us to assign UCMP 39978 to *C. latirostris* and, thus, to synonymise *Caiman cf. lutescens* is inappropriate. As stated above, the type material of *Alligator lutescens* Rovereto (1912) corresponds to a skull table with distinctive diagnostic characters (see below). Langston (1965) used this material to reconstruct this part of the skull of *Caiman cf. lutescens* but there is not enough evidence to justify that assumption (see Brochu 1999). MACN PV 13551 (Fig. 9) corresponds to a big sized adult caimanine, with supraoccipital extended on the skull table. As in *Purussaurus*, the skull table has a U- or V- like posterior margin with a table surface deeply convex along its sagittal line, relatively broad interorbital space, orbits probably not extended rostro-caudally, frontal extremely short with a reduced rostral process and squamosals laterally elevated with moderated caudo-lateral bumps. Nevertheless, contrary to *Purussaurus* and as in *Caiman* and *Melanosuchus*, supratemporal fenestrae are relatively small.

The presence of *C. lutescens* was mentioned for the Upper Miocene of Venezuela by the record of a left rostral fragment (Sánchez-Villagra & Aguilera 2006, fig. 3P, Q; Scheyer & Moreno-Bernal 2010). Although its general morphology is similar to *C. latirostris*, the skull table configuration of this specimen is unknown so it cannot be assigned to *C. lutescens*. Future analysis of this material will clarify the geographic distribution of *C. latirostris* in the Upper Miocene. From the available fossil evidence, we conclude that *C. lutescens* (only known from a skull table) and *C. latirostris* were found in the Upper Miocene in the area of Paraná. *Caiman latirostris* is one of the extant crocodylian species with the largest temporal distribution and represented in the Miocene of South America by large-sized specimens.



**Figure 9** *Caiman lutescens*: MACN 13552, skull table in (A) dorsal and (B) occipital views. Abbreviations: fr = frontal; pa = parietal; pfr = prefrontal; po = postorbital; so = supraoccipital; sq = squamosal.

#### *Caiman cf. yacare*

**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.

**Occurrence.** From the late Miocene; banks of Paraná River, in the area of Paraná Entre Ríos province, Argentina (Fig. 1); Ituzaingó Formation (Herbst 1971), (Brandoni & Scillato-Yané 2007; Brandoni 2011; Fig. 2) to the Recent (centre and NE of Argentina, Paraguay, Bolivia, and part of western Brazil).

**Description.** The following description is based on fragmentary material that exhibits morphological similarities with the extant species *C. yacare*. MLP 73-IV-15-5 and MLP 73-IV-15-6, correspond to rostral (symphyseal) fragments of dentary that belong to three different individuals. Similar to *C. yacare*, in these specimens the symphysis extends back to the anterior margin of the 5th alveolus, and is oriented such that it forms a 20° (MLP 73-IV-15-5) or 21° (MLP 73-IV-15-6) angles with the medial mandibular margin (Fig. 10B). In dorsal view, the preserved alveoli show a similar pattern of that of *C. yacare*. In MLP 73-IV-15-5 (Fig. 10B), the posterior part of the first to the 11th and the anterior part of 12th alveoli are preserved. The first and fourth alveoli are the largest, the fifth to seventh alveoli decrease in length, then the eighth to the tenth alveoli increase again and the 11th alveolus is large. As in *C. yacare*, the fragments of the premaxilla here assigned to *Caiman cf. yacare* shows the lateral and laterocaudal margin of the nostril with a broad edge and a lateral margin sub-parallel to the lateral margin of premaxilla. It is remarkable that MLP 73-IV-15-15

belongs to a large specimen with a lateral width equal to 10.4 cm (see comments below).

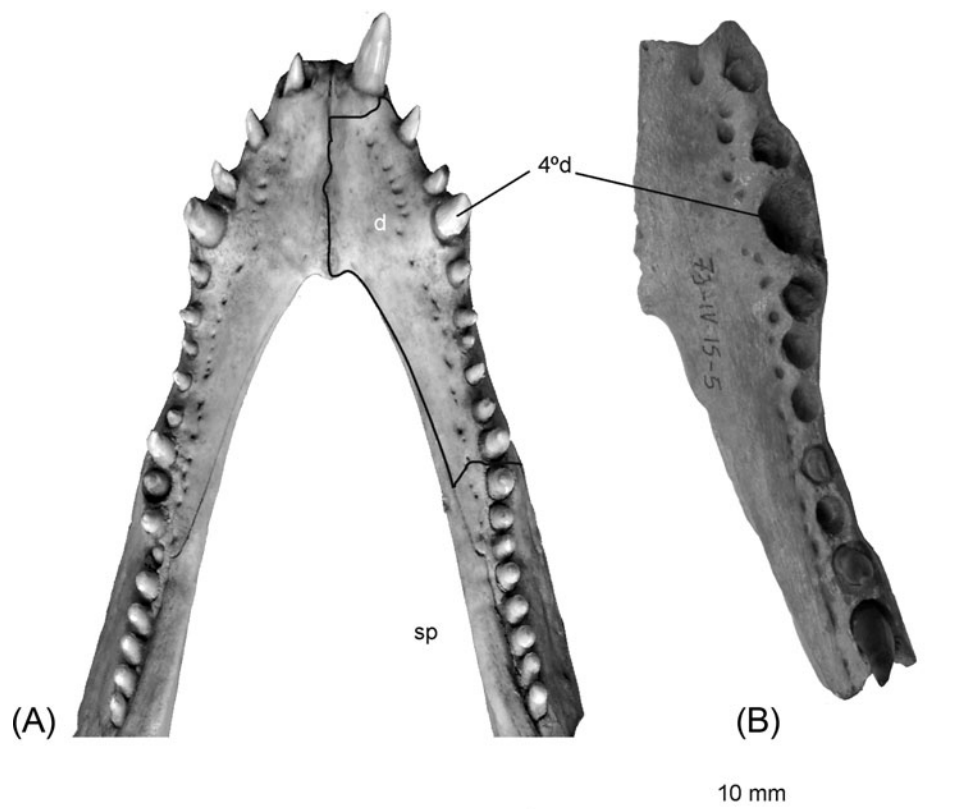
**Observations.** The first mention of *Caiman cf. yacare* in the “Mesopotamiense” was made by Gasparini (1973), based on several mandibular remains, and was later accepted in other works (Gasparini 1981, 1996; Cione *et al.* 2000; Piña & Argañaraz 2000). All the dentary fragments here assigned to *Caiman cf. yacare* shared morphological features with *Caiman yacare* (symphysis extended at posterior part of 5th alveolus and forming a 20°–30° angle with the medial margin of the mandible). The isolated fragments of the premaxilla have a broad ridge at the lateral and laterocaudal margin of nostrils (a feature present in extant specimens of this species). The first mention to a late Miocene occurrence of the extant *C. yacare* was made by Fortier *et al.* (2009), based on a skull from the Niterói outcrops of the Solimões Formation in northern Brazil. The record of dentary remains, together with these premaxillary fragments from the Parana area, reinforce the conclusion that *C. yacare* was already differentiated, but also show that it had a widespread distribution in the late Miocene. Moreover, also it shows that the Miocene specimens would have reached larger sizes than the extant ones.

#### 4. Discussion

The South American Miocene record of crocodylians in the Pan-Amazonia region (*sensu* Hoorn *et al.*, 2010) represents a moment in the evolutionary history of Eusuchia, characterised by the great taxonomic diversification of lineages such as Alligatoridae, Caimaninae and Gavialidae (Fig. 4) (Gasparini 1996; Langston 1965; Brochu 2003; Riff *et al.* 2010). Also, there was a wide geographic distribution of genera (*Mourasuchus*, *Purussaurus*, *Caiman*, *Gryposuchus*) and local endemism at the species level. As a result of the review of the crocodylian fossils of Paraná, the idea of a great taxonomic diversity of Caimaninae compared with other crocodylian taxa (e.g. gavialoids, represented only by *Gryposuchus neogaeus*, and crocodyloids) becomes clear. Although this diversity does not reach that of coeval areas of South America, such as late Miocene of Urumaco, Venezuela and Acre, Brazil, Paraná is distinguished by the wide diversification of *Caiman*. This variability exceeds the genus diversity that is present today, with three species: *C. latirostris*, *C. yacare* and *C. crocodilus*. When compared, it appears that the crocodylian fossil record of Paraná is also distinguished from other South American Upper Miocene crocodylian assemblages by the absence of Crocodylidae (recorded by three species of *Charactosuchus* in the Solimões Formation, Acre State, Brazil and by *Charactosuchus mendesi* in the Urumaco Formation, Falcon State, Venezuela) and caimanine genera such as *Melanosuchus* (i.e. *M. fisheri* from the Urumaco Formation, Venezuela; Scheyer & Moreno-Bernal 2010) or large-sized predators such as *Purussaurus* (see Latrubesse *et al.* 2007, table 1 and Riff *et al.* 2010, table 16-1 for comparisons between crocodyliforms occurrences in South American Miocene localities). Nevertheless, at the specific level, Paraná shares the presence of *Mourasuchus nativus* only with Acre.

In Paraná, two genera of caimanines are known (*Caiman* and *Mourasuchus*) and only one gavialoid, *Gryposuchus neogaeus*. *Caiman* species recognised as valid in this contribution are *Caiman gasparinae*, *C. latirostris*, *C. australis* and *C. lutescens*. Currently, with the exception of *C. crocodilus* (which is mainly distributed in northern South America through the Amazonas, Orinoco and Magdalena river systems), *C. latirostris* and *C. yacare* occupy the more southern territory, which corresponds to the Paraná River system in Argentina (Medem 1983). The current distribution of *Caiman* probably represents





**Figure 10** (A) *Caiman yacare* MLP R 5045, anterior sector of mandible in dorsal view. (B) *Caiman* cf. *yacare* MLP 73 IV 15 5, right dentary fragment in dorsal view. Abbreviations: d = dentary; sp = splenial; 4°d = 4° dentary alveolus.

a relic of a much wider Neogene ancestral range that correlates to the southern zoogeographical “Dominio Subtropical” region (Ringuelet 1961).

It is known that during the Miocene, continental vertebrates in South America increased in size (e.g. Cione *et al.* 2005; Vizcaíno *et al.* 2012). In northern Amazonia (e.g. the Acre and Urumaco areas), large crocodylians were recorded, such as *Gryposuchus croizati*, and *Purussaurus brasiliensis*, reaching approximately 10 m, and 12 m total length, respectively (Riff & Aguilera 2008). In the Middle Miocene, *M. atopus* is represented by a skull 1.5 m long, and the sebecid *Barinasuchus* would have occupied the role of large terrestrial predator, with a rostrum 70 cm long (Paollilo & Linares 2007) and total skull length estimated between 90 and 100 cm. Fossil Miocene crocodylians recorded in Paraná (southernmost Pan-Amazonia) are smaller than the coeval records in the north, which could be related to Neotropical paleotemperature (see e.g. Head *et al.* 2009). Although *Caiman* species were larger than today, large predators such as *Purussaurus* are absent in this assemblage, and *Gryposuchus neogaeus* did not reach the body length shown by northern *Gryposuchus* species (specimens with skull 1 m long would reach similar sizes to modern gharials, up to 6 m in length; Whitaker & Basu 1983). Only adult specimens of *Mourasuchus nativus*, known mainly by basicranial fragments, are similar in proportion to other species of the genus, with dorsal skull lengths of 1 m (Bona *et al.* 2012).

During the early Miocene, marine transgressions covered extensive areas of South America. The most widespread of these (‘Paranense,’ ‘Amazonian’ and ‘Caribbean’; Räsänen *et al.* 1995) covered a large portion of Argentina, Uruguay, part of Paraguay, southern Bolivia, part of Brazil, Colombia, Venezuela, and Ecuador (Hernández *et al.* 2005, figs 1–3). The Miocene Paranense transgression extended over most of the Chaco-Paraná Basin depression (Uliana & Biddle 1988,

Hernández *et al.* 2005; Fig. 1). Marine deposits from the “Paranense” sea constitute the Paraná Formation (Aceñolaza 1976; Chebli *et al.* 1989; Cione *et al.* 2000), which emerges in Entre Ríos Province (Fig. 1) and underlies the continental levels of the Ituzaingó Formation (Fig. 2). This last stratigraphic unit was deposited during a regressive period by a river system and is composed of a basal conglomerate (“Conglomerado Osífero”) with abundant vertebrate remains, covered by yellow sandstones and green clay stones with scarce fossils (Cione *et al.* 2000). Following Cione *et al.* (2000), the Ituzaingó Formation, particularly the “Conglomerado Osífero” should be referred to as Tortonian (Late Miocene), an opinion followed by other authors (Cione *et al.* 2005; Cozzuol 2006; Latrubesse *et al.* 2007). Except for some fresh water fishes well-preserved inside nodules, vertebrate fossils from the fluvial deposits of the “Conglomerado Osífero” are typically disarticulated and most of them are remarkably eroded (Cozzuol 1996; Cione *et al.* 2000, 2005). This is the case of for the crocodylian remains. The taxonomical diversity found in the conglomerate (i.e. *Caiman* species) does not necessarily suggest that all species would have cohabited. On the contrary, taphonomical interpretations show that the crocodile remains could have been transported from different sectors of the same extensive region. The “Conglomerado Osífero” was deposited by a channel that collected the remains of crocodylians, probably from other adjacent areas such as creeks, wetlands and the “Proto-Paraná”. Crocodylians recorded in the Ituzaingó Formation probably represent sympatric species that did not necessarily share the same habitat. We regard the “Conglomerado Osífero” as a fluvial deposit that concentrated remains of crocodylians from a geographic area broad enough to hold six alligatorid species (*Mourasuchus nativus*, *Caiman gasparinae*, *Caiman australis*, *Caiman* cf. *yacare*, *Caiman lutescens* and *Caiman latirostris*) and one gharial species (*Gryposuchus neogaeus*), with different

ecological requirements. Moreover, given the completeness of the preserved specimens, only *G. neogaeus* appears to be an autochthonous inhabitant of the ancient “Paraná River”. Nevertheless, as Langston (1965) noted, current crocodylian species tend to overlap their areas of distribution, especially in South America (Carvalho 1951; Medem 1983) and in many cases co-habit in the same waters (e.g. *Paleosuchus* species; *Caiman yacare* and *Caiman latirostris*; *Melanosuchus niger* and *Caiman crocodilus*).

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## 6. Appendices

### 6.1. Appendix 1. List of characters modified from or added to the character matrix published by Brochu (1999)

93. Lacrimal makes broad contact with nasal; no posterior process of maxilla (0), or maxilla sends posterior process within lacrimal (1), or maxilla sends posterior process between lacrimal and prefrontal, lacrimal and nasal not in contact (2), or maxilla sends posterior process between lacrimal and nasal (3). Modified from Brochu (1999, Character 93).
165. Orbits equal or sub equal than infratemporal fenestrae (0); orbits larger than infratemporal fenestrae, supratemporal fenestrae smaller or obliterated (1); orbits smaller than infratemporal fenestrae, supratemporal fenestrae reduced (2) or orbits larger than infratemporal fenestrae, supratemporal fenestrae larger than orbits (3).
166. Supratemporal fenestra surrounded anteriorly by postorbital and parietal (0) or only by postorbital bones (1).
167. Prefrontal-frontal not thickened or thickened forming a flange (0) or thickened forming a marked knob (1) at the anterior-medial margin of the orbits.

### 6.2. Appendix 2. Original characters of the matrix published by Brochu (1999), which have been recorded in this work

The original coding is given in brackets.

*Purussaurus neivensis* (following Aguilera *et al.* 2006): Character 4: 1(0); Character 11: 1(0); Character 15: 1(?); Character 20: 0(1); Character 50: 1(0); Character 51: 1(0), Character 53: 1(?); Character 80: 0(1); Character 82: 2(?); Character 87: 0(1); Character 91: 0(1); Character 93 (with new coding): 3(1); Character 108: 0(1); Character 144: 1(0); Character 150: 1(0); Character 153: 0(1).

*Caiman latirostris*: Character 86: 0(1)

### 6.3. Appendix 3. Character scores of *Caiman gasparinae* and *Mourasuchus* species

*Mourasuchus nativus* ???? ???? ???? ???? ???? ???? ????  
11200 ?0111 011?? ???? 11?00 ?121? 1?010 2???0 23000 11141  
?1?0? ??001 ??111 01?0? ?1010 ???? 101?? ?0001 20?? ????  
1??? ?0?10 0?0? ???? ?01?2 00

*Mourasuchus arendsi* ???? 1?00? ?1? ???? ?1001 1?1?? ????  
???? ???? ???? ?11?? ???? ???? ?21? ???? ???? ?0?? ????  
???? ?0??1 ?10?0 ?000 ???? ?20?? ?1?0 0??? 1?1?0 ???? ?011  
10?10 ?10?? ???? 00??2 01

*Mourasuchus amazonensis* ???? ???? ???? ???? ???? ????  
???? ???? ???? ???? ???? ???? ???? ???? ?11 ???? 2??10 2??0?  
11?? ?12?2 ???? 0?1?? ???? ???? ?1?? ?1?? ???? ???? ????  
11011 1?0?? ???? ???? ????2 11

*Mourasuchus atopus* ???? ???? ???? ???? ?0?0 1?31? ?001?  
???? 11200 ?0111 011?? ???? ?1?00 ?1211 110?? ???? 23000  
11141 ?1?0? ?0?1 011?0 010?0 ???? ?0?? ?1?? ???? ???? ????  
?101? 1??1? ?10?? ???? 00??2 11

*Caiman gasparinae* ???? ???? ???? ???? ???? ???? ???? ????  
???? ???? ???? ???? ???? ???? ???? 2??11 23?0? 01?2? ?11?2  
?0?? 011?? ???? ???? ???? ?1?? ???? 21?? ???? 101?0 ????  
???? ???? 0?1?1 0?

### 6.4. Appendix 4. Scores of characters 93 and 165–167 of alligatorids taxa considered in the cladistics analysis

*Bernissartia\_fagesii* ? ?0; *Hylaeochampsa\_vectiana* 1 ?0;  
*Borealosuchus\_formidabilis* 0 ?0; *Leidyosuchus\_canadensis* 0  
?0; *Pristichampsus\_vorax* 0 ?0; *Diplocynodon\_darwini* 0 000;  
*Baryphracta\_deponiae* 0 ?00; *Stangerochampsa\_mccabei* 2 ?00;  
*Brachychampsa\_montana* 2 000; *Alligator\_sinensis*\_1 ?00;  
*Alligator\_mississippiensis* 1 100; *Alligator\_mefferdi*\_1 10?;  
*Alligator\_prenasalis* 1 ??; *Ceratosuchus\_burdoshi* ? ?00;  
*Navajosuchus\_mooki* 1 ?0; *Wannaganosuchus\_brachymanus* 1  
100; *Procaimanoidea\_kayi* 1 100; *Purussaurus\_mirandai* 3 000;  
*Purussaurus\_neivensis*\_3 000; *Orthogenysuchus\_olseni* ? 000;  
*Caiman\_yacare* 1 100; *Caiman\_crocodilus*\_1 100; *Caiman\_*  
*latirostris*\_1 100; *Caiman\_cf.\_lutescens*\_2 ?0?; *Melanosuchus\_*  
*fisheri* 1 100; *Melanosuchus\_niger*\_1 100; *Paleosuchus\_*  
*trigonatus* 0 1?0; *Paleosuchus\_palpebrosus*\_0 1?0;  
*Mourasuchus\_nativus* ? 200; *Mourasuchusarendsi* ? 201;  
*Mourasuchus\_amazonensis* 2 211; *Mourasuchus\_atopus* ? 211;  
*Caiman\_gasparinae* 1 10?.

### 6.5. Appendix 5. Apomorphy list

Derived states for Caimaninae groups and species are shown in Figure 4. The tree used to derive these apomorphies is shown in Figure 4 (unambiguous changes only) (\* = homoplastic characters).

*Hylaeochampsa vectiana*: 103 (2), 106 (1)\*, 117 (1)\*. Node 1: 70 (1), 140 (1), 141 (1), 146 (1). *Borealosuchus formidabilis*: 11 (1)\*, 33(1), 35 (0)\*, 39 (2)\*, 51 (0)\*, 58 (1)\*, 60 (0)\*, 78 (2), 97 (2)\*, 117 (82) \*, 118 (1), 135 (1). Node 2: 27 (1), 40 (1), 86 (1), 132 (1). *Pristichampsus vorax*: 28 (1)\*, 45 (1)\*, 52 (1)\*, 81 (2)\*, 103 (1)\*, 128 (1), 162 (1). Node 3: 26 (1), 34 (1), 88 (1), 91 (1)\*, 102 (1), 121 (1). *Leidyosuchus canadensis*: 94 (1)\*, 105 (1)\*. Node 4: 69 (1), 77 (1), 90 (1), 131 (1)\*. Node 5: 6 (0), 28 (4), 39 (2)\*, 86 (1)\*. *Diplocynodon darwini*: 43 (1)\*. *Baryphracta deponiae*: 87 (1)\*. Node 6: 5 (1), 10 (1), 52 (1)\*, 72 (1), 76 (2), 81 (1), 85 (0), 89 (2), 93 (2)\*, 152 (1). *Stangerochampsa mcca-bei*: 19 (1)\*, 35 (0)\*, 65 (1)\*. *Brachychampsa montana*: 37 (3), 41 (1)\*, 43 (1)\*, 82 (2)\*, 89 (1), 108 (1)\*. Node 7: 17 (1), 21 (1), 25 (1)\*, 81 (2)\*, 131 (2), 163 (1), 165 (1). Node 8: 68 (1). Node 9:

79 (0)\*, 124 (1)\*. *Ceratosuchus burdoshi*: 90 (0)\*. Node 10: 37 (2), 117 (1)\*. *Procaimanoidea kayi*: 65 (1)\*, 82 (1)\*, 88 (0)\*. Node 11: 105 (1)\*. Node 12: 95 (0), 142 (1)\*. *Alligator prenasalis*: 70 (0)\*. Node 14: 99 (1), 105 (0)\*, 106 (1)\*. *Alligator mississippiensis*: 41 (1)\*, 86 (1)\*. Node 15: 16 (1), 28 (1)\*, 29 (2)\*, 41 (1)\*, 43 (1)\*, 46 (1), 47 (1), 51 (0)\*, 58 (1)\*, 67 (1), 87 (1)\*, 103 (1)\*, 104 (1), 107 (1), 116 (1), 151 (2).

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