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Lower Miocene alligatoroids (Crocodylia) from the Castillo Formation, northwest of Venezuela

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Abstract

Crocodyliform diversity was particularly high during the middle and late Miocene of South America, with up to 12 species recovered from a single geological unit. Nonetheless, the early Miocene fossil record of low-latitude vertebrates is scarce; hence, crocodylians remain poorly known in the region. The Castillo Formation, located in the northwest of Venezuela, preserves an interesting vertebrate fauna with a well-constrained late early Miocene age. Previous work dealing with crocodylians of this formation only recorded three taxa: the gavialoid *Siquisiquesuchus venezuelensis* and *Gryposuchus* sp. and indeterminate alligatoroid remains. New cranial and mandibular material recently recovered from the Castillo Formation allows us to document four previously unrecognised alligatoroid forms: *Purussaurus* sp., *Caiman* sp., an indeterminate caimanine and an indeterminate alligatoroid. With six taxa, the crocodylian ssemblage reveals a previously undocumented relatively high taxonomic diversity in the early Miocene. The Castillo crocodylians show a broad range of morphological disparity and body sizes ranging from small (2.5 m–62 kg) to large (7.5 m–1600 kg) taxa. Thus, crocodylian niche partition, as well as the abundance and variety of resources and environmental heterogeneity of aquatic ecosystems in South America, were already established by at least the early Miocene. The presence of *Caiman* in ~18 Ma strata represents the unequivocally earliest record of the taxon in South America and allows us to propose that the origin of the jacareans is more likely to have occurred during or before the early Miocene, challenging previous molecular hypotheses.

Keywords Caimaninae · Alligatoroids · South America · Castillo formation · Early Miocene

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Abbreviations

MCNC	Museo de Ciencias Naturales de Caracas,
	Caracas, Venezuela
IVIC	Colección de Paleontología del Instituto
	Venezolano de Investigaciones Científicas,
	Caracas, Venezuela

Introduction

Over the past two decades, ongoing exploration of the Castillo Formation (upper Oligocene to lower Miocene) in Venezuela allowed the recovery of a rich vertebrate assemblage from a period with a poor palaeontological record in northern South America (Brochu and Rincón 2004; Sánchez-Villagra and Clark 2004; Sánchez-Villagra et al. 2010; Rincón et al. 2014, 2016a; Solórzano and Rincón 2015; Ferreira et al. 2016; Núñez-Flores et al. 2017; Solórzano et al. 2017). Though crocodyilian diversity so far recognised from the Castillo Formation appears to be low, it includes the oldest named gavialoids in South America (SA), *Siquisiquesuchus venezuelensis* and *Gryposuchus* sp. and indeterminate alligatoroid remains (Brochu and Rincón 2004; Sánchez-Villagra et al. 2010; Solórzano et al. 2017).

This contrasts with the astonishingly diverse crocodyliform fauna of the Miocene of South America (Langston 1965; Brochu 1999; Cozzuol 2006; Riff et al. 2010; Scheyer et al. 2013; Bona et al. 2013a, b; Salas-Gismondi et al. 2015). Miocene crocodyliform assemblages in South America are dominated in terms of taxonomic diversity by gryposuchine gavialoids and caimanines (Langston 1965; Riff et al. 2010; Brochu 2011; Scheyer et al. 2013; Salas-Gismondi et al. 2015, 2016; Moreno-Bernal et al. 2016; Souza et al. 2016; Cidade et al. 2017), with crocodylids and sebecids also present (e.g. Langston 1965; Paolillo and Linares 2007; Riff et al. 2010). These crocodyliforms show a wide range of variation in body size, including giant taxa such as Gryposuchus and Purussaurus (10-m length, 5 tons) and small 'crusher' caimanines (1.5-2 m length, 10-820 kg height; Riff and Aguilera 2008; Scheyer et al. 2013; Salas-Gismondi et al. 2015; Aureliano et al. 2015). They also display a wide range of snout morphotypes (Brochu 1999, 2001; Salas-Gismondi et al. 2015), which indicates niche partitioning during the Neogene (Riff et al. 2010).

In South America, the Paleogene alligatoroid fossil record is sparse (e.g. Bona et al. 2007; Riff et al. 2010). Modern South American crocodylian diversity, which only includes four genera and eight currently recognised species (and never more than four sympatric species), is also lower than that observed during the middle and late Miocene when crocodylians reached the zenith of their diversity (Brochu 1999; Martin 2008; Bona et al. 2013a, b; Scheyer et al. 2013; Escobedo-Galván et al. 2015; Salas-Gismondi et al. 2015). The better-known Neogene crocodylian assemblages come from the middle Miocene of Colombia (Langston 1965) and Peru (Salas-Gismondi et al. 2015, 2016), as well as the late Miocene of Argentina (Bona et al. 2013a, b), Venezuela (Scheyer et al. 2013; Scheyer and Delfino 2016) and Brazil (Cozzuol 2006; Riff et al. 2010).

In contrast, the diversity of early Miocene crocodyliforms remains poorly known. It consists of indeterminate gavialoids from the Pirabas Formation (Brazil), material resembling *Ikanogavialis* and *Purussaurus* from the Barzalosa Formation (Colombia), gavialoids and caimanines from the early to middle Miocene of the Guajira Peninsula (Colombia), isolated remains of *Purussaurus* from the late Oligocene to early Miocene of Contamana (Peru), indeterminate crocodylians from the early-middle Miocene Gaiman Formation (Argentina) and gavialoids (*Siquisiquesuchus* and *Gryposuchus*) and indeterminate alligatoroid remains from the Castillo Formation of Venezuela (Simpson 1935; Brochu and Rincón 2004; Moreno-Bernal 2006; Sánchez-Villagra et al. 2010; Moraes-Santos et al. 2011; Moreno-Bernal et al. 2016; Antoine et al. 2016; Solórzano et al. 2017). However, these early Miocene crocodylians were recognised based mostly on fragmentary material, which in some cases has not been figured or properly described. The poor chronostratigraphic framework of some records also precludes a better understanding of early Miocene crocodylian diversity in SA.

Over the last few years, several field trips to the southern exposures of the Castillo Formation at the Sierra de la Baragua (Lara State, Venezuela) have resulted in the discovery of several specimens with alligatoroid affinities, as well as other vertebrate taxa (e.g. Rincón et al. 2014). In order to increase our knowledge of the taxonomic diversity and ecological adaptations of early Neogene crocodylians from previously scarcely sampled areas in the northernmost portion of South America, a new alligatoroid assemblage from the Castillo Formation is described here.

Material and methods

Most of the material here described comes from two localities, Cerro La Cruz and Cerro Zamuro, where sediments of the Castillo Formation are well-exposed. Both localities are close to the village of La Mesa, north of the town of Carora, Lara State, along the southern-most exposures of the Sierra de La Baragua in northwest Venezuela (Fig. 1a, b; Fig. S1). Additional remains were recovered from a rather small outcrop of the Castillo Formation at the Quebrada Agua Viva locality, which is located around 5 km west of Cerro La Cruz (Fig. 1a, b). See Fig. 2 and Table S1 (Electronic Supplementary Materials) for a detailed stratigraphic and geographical provenance of the materials.

All the specimens are housed in the paleontological collection of Instituto Venezolano de Investigaciones Científicas (IVIC) in Caracas, Venezuela. Measurements were taken with a digital calliper and are in millimetres. Systematics follows Brochu (2003). Following Hastings et al. (2016), teeth and alveoli of the dentary are referred to with 'd' followed by their position within the jaw, beginning from the anterior end.

Body size estimation: Estimations of body size on extinct taxa could provide an important line of evidence for understanding their role in ancient ecosystems (Aureliano et al. 2015). Consequently, we use the dorsal cranial length (DCL = skull length) to predict the total length (TTL in mm) and the body mass (BM in kg) of the caimanines from the Castillo Formation. Although several equations have been proposed in the literature, we use those of Hurlburt et al. (2003) and Aureliano et al. (2015); see details in the Electronic Supplementary materials (ESM 2).

Fig. 1 Geographical and geological settings of the Cerro La Cruz locality (Castillo Formation. Lara state. Venezuela): a continental and b regional geographic location with large-scale geological units (black star indicates the location of the study area); c local geological map showing the sampled localities (blue star = Quebrada Agua Viva; red star = Cerro La Cruz; black star = Cerro Zamuro). Abbreviations: Tpem, Matatere Formation (Eocene); Tolmc, Castillo Formation (early Miocene); Qal, Alluvial (Quaternary)



Geological setting

The Castillo Formation crops out cover a wide semicircular area that extends through the northwestern Venezuelan states of Falcón and Lara. During Oligo–Miocene times, the formation formed the northwest to southeast edge of the Falcón Basin (Wheeler 1960, 1963). This formation was deposited in environments ranging from shallow water to brackish facies, along with local continental facies (Wheeler 1960, 1963).

Based on the southern-most exposures of the Sierra de La Baragua (Lara State, Venezuela), Rincón et al. (2014) updated the geology, chronology, and palaeontology of Cerro La Cruz, the locality with the greatest diversity of vertebrates in the Castillo Formation. The locality of Cerro Zamuro is 500 m to the east of Cerro La Cruz and forms the core of an elongated dome on a hinge line oriented N65E. Cerro La Cruz represents the northeast flank of this dome (Fig. 1c; Solórzano et al. 2017). Geological and palaeontological surveys of Cerro Zamuro reveal minor differences with the lithology described for Cerro La Cruz. Both localities show alternating packages of siliciclastic and carbonate sediments (Fig. 2; Rincón et al. 2014; Solórzano et al. 2017). Although geographically close, stratigraphic correlation between both localities is not completely clear, because they are bisected by a nearly NSorientated dextral fault, and lateral variation of sediments of the Castillo Formation in Lara state is high (Solórzano et al. 2017).

The Cerro La Cruz sequence was deposited mainly in near-shore marine environments, probably with brackish facies and local episodes of continental environments in which nonmarine vertebrates are more commonly found (Rincón et al. 2014, 2016a; Solórzano and Rincón 2015). Four isotopic ages obtained from analyses of strontium (⁸⁷Sr/⁸⁶Sr) ratios suggest that the Cerro La Cruz sequences were deposited during the early Miocene (17.21–19.27 Ma; Burdigalian; Rincón et al. 2014).



Fig. 2 Generalised stratigraphic sections of Cerro La Cruz and Cerro Zamuro (modified from Rincón et al. 2014 and Solórzano et al. 2017), showing the stratigraphic provenance of the alligatoroid remains

Since the year 2000, ongoing fieldwork in the Castillo Formation in the vicinity of Cerro La Cruz resulted in the recognition of a diverse vertebrate assemblage. It includes freshwater and marine fishes, giant marine birds, turtles, gavialoid crocodylans, mylodontoid sloths, notoungulates, litopterns, and odontocetes (Sánchez-Villagra and Clark 2004; Brochu and Rincón 2004; Sánchez-Villagra et al. 2010; Rincón et al. 2014, 2016a; Solórzano and Rincón 2015; Ferreira et al. 2016; Nuñez-Flores et al. 2017; Solórzano et al. 2017). An updated list of the vertebrates of the Castillo Formation is in the Electronic Supplementary Material (Table S2).

Systematic palaeontology

Crocodylia Gmelin, 1789 (sensu Benton and Clark, 1988) Alligatoroidea Gray, 1844

Alligatoroidea gen. et sp. indet.

Materials: IVIC–P–2667, IVIC–P–2916, two isolated teeth.

Occurrence: Both teeth come from the level Cast–40. Cerro La Cruz, lower Miocene, Castillo Formation, Lara State, Venezuela.

Description: Small, globular-shaped, anteroposteriorly compressed teeth with relatively low crowns and pseudoziphodont mesiodistal carinae and radiating coronal crenulations. Crenulations are absent on the crowns, but the presence of a small depression or fossa is noticeable (Fig. 3).

Measurements: IVIC–P–2916, anteroposterior length = 17.6 mm, height = 18.5 mm, mediolateral length = 20.1 mm; IVIC–P–2667, anteroposterior length = 18.1 mm, height = 20.4 mm, mediolateral length = 18.3 mm.



Fig. 3 Isolated teeth of Alligatoroidae gen. et sp. indet (**a–b** IVIC–P–2667; **c–d** IVIC–P–2916) from the lower Miocene Castillo Formation (Venezuela). Scale bar = 1 cm

Remarks: Until recently, crocodylians with posterior globular teeth were rather uncommon in the Neogene of South America. The first such record is in Langston (1965), who erected a taxon based on isolated teeth, Balanerodus longimus, from the late Oligocene/early Miocene of Colombia (Langston and Gasparini 1997). Langston (1965) described two types of teeth for Balanerodus: small posterior teeth, nearly spherical and acorn-shaped, with crenulations radiating from the coronae and pronounced lateral carinae; and larger, rather conical anterior teeth. These traits are indistinguishable from those observed in the materials recovered from Cerro La Cruz (Fig. 3). Later, Langston and Gasparini (1997) attributed to Balanerodus a maxillary fragment with bulbous teeth recovered from the middle Miocene of La Venta (Colombia). There have also been tentative reports of Balanerodus beyond Colombia. Bryan Patterson in a personal communication to Medina (1976) mentioned its presence in the upper Miocene Urumaco Formation (Venezuela), although the author did not provide any illustration or catalogue number of the specimens revised. Additionally, Salas-Gismondi et al. (2007) mentioned an isolated tooth similar to Balanerodus from the middle Miocene Pebas Formation in Peru.

Recently, four new caimanines with posterior globular teeth were described: Gnatusuchus, Kuttanacaiman, and Caiman wannlangstoni from the middle Miocene of Peru and Globidentosuchus from the late Miocene of Venezuela (Scheyer et al. 2013; Salas-Gismondi et al. 2015). These are based on relatively well-preserved skulls and mandibles, although their holotypes come from localities where Balanerodus had been previously reported (Medina 1976; Salas-Gismondi et al. 2007). The posterior teeth of Gnatusuchus are globular but without carinae, and Kuttanacaiman bears low, globular, and laterally compressed teeth (Salas-Gismondi et al. 2015), unlike the Cerro La Cruz specimens. The posterior teeth of Globidentosuchus are subspherical and tightly spaced, but they are indistinguishable from those referred to Balanerodus (Langston 1965; Scheyer et al. 2013) or the Cerro La Cruz specimens. Riff et al. (2010) stated that Balanerodus is poorly known and their attribution is open to further scrutiny. Furthermore, Salas-Gismondi et al. (2015) suggested that 'bulb-shaped crowns' indistinguishable from those of Balanerodus longimus pertain instead to specific areas of Purussaurus mandibles, undermining its recognition as a distinct taxon. Until the last hypothesis is tested (after specimens with teeth in situ are recovered), we prefer to assign the Cerro La Cruz materials no more precisely than Alligatoroidea. These globular teeth are different from those of the other Castillo caimanine with globular teeth, Caiman sp., as the former have radiating coronal crenulations and a small fossa in the posterior tooth crown.

Fig. 4 Cranial remains of Caimaninae gen. et sp. indet. (IVIC–P–2921) from the lower Miocene Castillo Formation (Venezuela) in dorsal (**a** with schematic drawing (**b**)), lateral (**c**), ventral (**d**) and occipital (**e**) views. f, frontal; p, parietal; po, postorbital; sq., squamosal; so, supraoccipital. Scale bar = 5 cm



Family Alligatoridae Cuvier, 1807 Subfamily Caimaninae Brochu, 1999

Caimaninae gen. et sp. indet.

Material: IVIC–P–2921, fragment of skull table preserving the squamosal, postorbital, supraoccipital, incomplete frontal, and some portions of the braincase.

Occurrence: Cerro Zamuro; lower Miocene, Castillo Formation, Lara State, Venezuela (Figs. 1 and 2 (right) as 'alligatoroid').

Description and comparison: Skull table similar in size to adult specimens of the extant *Caiman* (see discussion below), with a flat dorsal surface ornamented with nearly circular small pits. Their lateral borders converge anteriorly and show a slight constriction along the squamosal (Fig. 4a, b), resembling modern jacareans (Brochu 1999). In dorsal view, the posterior edge of the skull table is slightly concave resembling

the common condition in Caimaninae except for *Purussaurus* (Brochu 1999; Scheyer et al. 2013; Cidade et al. 2017).

The partially preserved frontal bears an indistinct ridge in the post-orbital region. The parietal is relatively large and excluded from the posterior border of the skull table by the supraoccipital (Fig. 4a, b), as in most caimanines except for Purussaurus, Paleosuchus and Tsoabichi (Cidade et al. 2017). The frontoparietal suture is concavoconvex. This suture is located entirely on the skull table and close to the orbital edge, unlike Caiman gasparinae, C. lutescens and C. wannlangstoni in which the frontoparietal suture is closer to the anterior edge of the supratemporal fenestrae (Bona and Carabajal 2013; Cidade et al. 2015; Salas-Gismondi et al. 2015). The frontal-parietal-postorbital triple joint is located at the level of the anterolateralmost edge of the skull table, as in Globidentosuchus, Kuttanacaiman, C. wannlangstoni and modern jacareans (Brochu 1999; Salas-Gismondi et al. 2015). The parietal and the squamosal meet along the posterior wall of the supratemporal fenestra.

In dorsal view (Fig. 4a, b), the supratemporal fenestrae are small, unlike those of *Purussaurus* (Cidade et al. 2017), oval, anteromedially elongate, and closer to the orbits than the posterior edge of the skull table. The dermal bones of the skull roof overhang the rims of the supratemporal fenestrae, a morphological feature present in adult individuals of crown *Caiman* but, unlike *Paleosuchus*, in which the fenestrae are obliterated late in ontogeny, and *Culebrasuchus*, in which a fossa surrounds the fenestra (Brochu 1999; Hastings et al. 2013; Bona and Carabajal 2013; Cidade et al. 2017).

The supraoccipital is small, nearly trapezoidal, and occupies the posteromedial part of the skull table (Fig. 4a, b). The supraoccipital contacts the squamosals laterally. The supraoccipital is rather narrow, and its maximum width along the posterior edge of the skull table is narrower than the space between the medial margins of the supratemporal fenestrae (Fig. 4a, b). In this, it resembles modern jacareans and *Centenariosuchus* (Brochu 1999; Hastings et al. 2013), but is distinct from *Globidentosuchus*, which shows a crescentshaped supraoccipital wider than the space between the two supratemporal fenestrae (Scheyer et al. 2013). Two deep pits can be noticed along the anterior portion of the dorsal exposure of the supraoccipital (Fig. 4a). The suture between the supraoccipital and the parietal is sinuous (Fig. 4b).

The squamosal forms the posterolateral portion of the skull table and contributes to the supratemporal fenestra. As the fenestrae are comparatively small, the contact between the squamosal and parietal appears to be unusually long, especially in comparison to the supraoccipital-squamosal suture length (Fig. 4a, b). The medial sutures of the squamosal with the parietal and supraoccipital are not parallel; the parietalsquamosal suture is anterolaterally inclined. Distinctly, in some caimanines (e.g. Tsoabichi greenriverensis; Caiman crocodilus, C. latirostris, C. yacare; Melanosuchus niger) the medial squamosal sutures are nearly anteroposteriorly directed or subparallel to the lateral sides of the skull table (Brochu 1999, 2010; Bona and Desojo 2011; Foth et al. 2013). There is a very small protuberance on the posterolateral border of the squamosal (Fig. 4c). Although eroded, the squamosal forms the roof of the external otic aperture and that it extends anteriorly to terminate near the postorbital bar (Fig. 4c).

The postorbital forms the anterolateral margin of the skull table and contacts the frontal anteromedially, the parietal medially, and the squamosal posteriorly (Fig. 4b). Its contact with the parietal is longer than that with the frontal. The posteromedial portion of the postorbital–squamosal suture is not linear and lies along the anterolateral margin of the supratemporal fenestra (Fig. 4b).

In lateral view, the posterior margin of the otic aperture is bowed, a trait present in most members of Brevirostres (Brochu 1999, 2010, 2011; Cidade et al. 2017). The external auditory meatus is ventrally broad. The quadrate is poorly preserved, with its sutural surface for the quadratojugal missing. The squamosal–quadrate suture is not clear, but it appears to end at the posteroventral corner of the external auditory meatus, as in *Gnatusuchus* (Fig. 4c; Brochu 1999, 2011; Salas-Gismondi et al. 2015). Intriguingly, the septum separating the otic recess is distinctively thick and massive, contrasting with modern jacareans, *Mourasuchus arendsi* and modern species of *Alligator* in which this structure is rather feeble (Fig. 4c; Brochu 1999; Bona et al. 2013c).

Though eroded and partially covered by gypsum and sediment (which are hard to remove without damage to the specimen), some braincase structures can be recognised in ventral view (Fig. 4d) that are, in general, similar to extant caimanines (Brochu 1999; Bona and Carabajal 2013). The ventral surface of the frontal has a medial groove, with a concave surface, for passage of the olfactory tract. The laterosphenoid forms the anterolateral wall of the braincase and extends dorsally forming the anteroventral area of the medial wall of the supratemporal fossa, similar to the condition described for *C. gasparinae* (Bona and Carabajal 2013).

In occipital view, the posterior margin of skull table overhangs the base of the occipital plate (Fig. 4a). The basioccipital and basisphenoid are badly preserved. The supraoccipital appears to be subtriangular in shape, and the preserved left posttemporal fenestra is narrow and shallow. The occipital surface of the supraoccipital is flat and not depressed relative to the squamosal or parietal (Fig. 4e). Although to varying degrees, Centenariosuchus, Gnatusuchus, Mourasuchus, Purussaurus, Melanosuchus fisheri, Caiman gasparinae, C. lutescens, C. wannlangstoni and adults of modern jacareans show a concave to flat supraoccipital, which is also rather depressed relative to the squamosals (Medem 1963; Medina 1976; Aguilera et al. 2006; Bona and Desojo 2011; Bona et al. 2013a, b, c; Salas-Gismondi et al. 2015). The rather concave posterior portion of the skull table in occipital view is typical of adult caimanines; in IVIC-P-2921, however, it is rather flat, indicating that the specimen is probably a juvenile.

Remarks: Based on the large exposure of the supraoccipital on the dorsal skull, we confidently assign the remains here described (IVIC-P-2921) to Caimaninae (Brochu 2010, 2011; Hastings et al. 2016). IVIC-P-2921 lacks the squamosal eminences in the posterior portion of the skull table present in Mourasuchus arendsi (Gasparini 1985; Bocquentin-Villanueva and Souza-Filho 1990; Bona et al. 2013c; Scheyer and Delfino 2016; Cidade et al. 2017). Unlike IVIC-P-2921, the supratemporal fenestrae of Culebrasuchus are open and wide; in Paleosuchus, they are small early in ontogeny and later become obliterated; in Gnatusuchus and Purussaurus they are larger and cylindrical; and in Centenariosuchus, they are severely constricted (Brochu 1999, 2010; Aguilera et al. 2006; Hastings et al. 2013; Salas-Gismondi et al. 2015). The configuration of bones around the supratemporal fenestrae in IVIC-P-2921 is similar to that of jacareans (Caiman and Melanosuchus), but also resembles those of Kuttanacaiman

and *Globidentosuchus* (Brochu 1999; Scheyer et al. 2013; Salas-Gismondi et al. 2015). Only minor traits could potentially separate IVIC–P–2921 from *Kuttanacaiman* and *Globidentosuchus*, because in both the frontoparietal suture is linear (concavoconvex in IVIC–P–2921; Scheyer et al. 2013; Salas-Gismondi et al. 2015). But this trait appears to be intraspecifically variable in modern forms.

The large exposure of the supraoccipital on the skull table blocking the parietal from the posterior edge of the skull table in IVIC-P-2921 is the typical jacarean configuration, but this is also present in other caimanines such as Centenariosuchus, Culebrasuchus, Globidentosuchus, Mourasuchus, Gnatusuchus, Kuttanacaiman and Caiman wannlangstoni (Brochu 1999, 2010; Brochu and Carbot-Chanona 2015; Cidade et al. 2017). In general, the shape of the supraoccipital in dorsal view varies within living jacarean species, but the anterior margin is usually linear and perpendicular to the sagittal plane (Brochu 1999; Brochu and Carbot-Chanona 2015). In some cases, the lateral margins of the supraoccipital are oriented anteromedially, giving the supraoccipital a trapezoidal shape, while in others, the parietal bears a pair of short triangular posterior processes that extend along the anterolateral margins of the supraoccipital (Brochu and Carbot-Chanona 2015). In IVIC-P-2921, the lateral margins of the supraoccipital are straight and anteriorly oriented, and the posterior border is also straight, whereas at the anterior border, the parietal bears three short processes extending posteriorly, with the medial of these processes deeply penetrated the supraoccipital (Fig. 4b). This configuration is present in some specimens of modern Melanosuchus niger (Medem 1963: Fig. 2A, pp. 21), but the trait is probably ontogenetically and intraspecifically variable.

Unlike extant Caiman, adults of the Castillo jacarean have a slightly concave supraoccipital (e.g. Bona and Desojo 2011). Studies of ontogenetic variation on the skull of two modern Caiman species, C. yacare and C. latirostris, show that in adults of both, concavity of the rear edge of the skull table increases (Blanco et al. 2014). The modest concavity of the posterior border of the skull table (in dorsal view), as well as the relatively flat dorsal surface of the supraoccipital (in occipital view) probably indicates that IVIC-P-2921 represents a juvenile. If IVIC-P-2921 represents a juvenile specimen, it could reach significantly larger sizes at maturity, as the size of the skull table resembles those of adult modern Caiman (Tables S3 and S5). It is impossible to refer IVIC-P-2921 to any particular caimanine lineage; it could represent a new species, but only the recovery of additional diagnostic material will clarify the taxonomy as well as the phylogenetic relationships of this specimen.

Because the alligatoroid assemblage here described also includes a form that exhibits similarities to *Caiman brevirostris* (see below), further comparison between IVIC–P–2921 and this species is necessary. Both share a concavoconvex frontoparietal suture (Brochu 1999; Fortier et al. 2014), but the posterolateral processes of the squamosals are better developed in *C. brevirostris* (Fortier et al. 2014). Recently, Scheyer and Delfino (2016) assigned a skull (MCNC–1829) recovered from the upper Miocene of the Urumaco Formation (Venezuela) to *C. brevirostris*. In MCNC–1829 the parietal reach the posterior border of the skull table, and the supratemporal fenestrae appear to be larger in a less expanded skull table; thus IVIC–P–2921 differs from the caimanine referred to *C. brevirostris* by Scheyer and Delfino (2016).

Genus *Purussaurus* Barbosa–Rodrigues, 1892 *Purussaurus* sp.

Material: IVIC–P–668, fragment of right mandible with associated left jugal; IVIC–P–2215, 2216, IVIC–P–3585 and IVIC–P–3586, four isolated teeth; IVIC–P–2089, isolated fragment of maxilla; IVIC–P–2112, isolated ilium; IVIC–P–3520, posterior fragment of mandible.

Occurrence: Levels Cast–38, Cast–40 and Cast–47 from the Cerro La Cruz locality, Lara state, northwestern Venezuela (Fig. 2a). The two isolated teeth are from the Quebrada Agua Viva (Fig. 1). Lower Miocene (17.21–18.85 Ma) of the Castillo Formation (Rincón et al. 2014).

Descriptions and comparison

IVIC-P-668: This is a well-preserved fragment of right mandible associated with a left jugal but lacking the splenial, coronoid, surangular, and angular bones (Fig. 5). The dentary preserves at least 15 alveoli, but only two fragmented teeth are in situ. As the posterior portion of the dentary is absent, it is not possible to quantify the total number of alveoli.

The dentary is gently curved between the fourth and tenth alveoli (Fig. 5a, b), as in most caimanines (Brochu 1999). In lateral view (Fig. 5c, d), the dentary at the level of d4 and d5 is higher than at the level of d11-d12, unlike Eocaiman in which d4-d5 are lower than d11-d12 (Bona 2007; Pinheiro et al. 2012). The first five alveoli are the largest (> 18-mm diameter), and d4 is the largest of these. Although partially eroded, d1 is similar in size to d4, and d3 and d4 are separated. Posteriorly to d5, the alveoli diminish in size and the largest dentary alveolus immediately caudal to d5 is d12. This condition is similar to some extant (Caiman, Melanosuchus, Paleosuchus) and extinct (Purussaurus, Centenariosuchus, Kuttanacaiman) caimanines (Brochu 1999; Salas-Gismondi et al. 2015, 2016; Cidade et al. 2017). The first nine alveoli are close to the lateral margin of the dentary in dorsal view, but caudally to d10 they are medially displaced, resembling the condition in Purussaurus (Langston 1965; Aguilera et al. 2006).

The dentary is uniformly robust, but its width in dorsal view is variable: towards its anterior section (first six alveoli), the dentary is wide (unlike *Purussaurus mirandai* or *P. brasiliensis*), while after d6, it becomes narrower (Fig. 5a, b),



Fig. 5 Associated remains of *Purussarusus* sp. (IVIC–P–668) from the lower Miocene Castillo Formation (Venezuela). Fragment of the anterior portion of a right mandible in dorsal (**a**, with a schematic drawing (**b**)), lateral (**c**) and medial views (**d**); isolated posterior mandibular fragment in lateral (**e**) and dorsal (**f**) views; and associated left jugal in dorsal view (**g**);

h detail of a *Rhinoptera* tooth attached in the anterior portion of the dentary (scale bar = 5 mm). ma, mandibular symphysis; sa, surangular; ar, articular; mg, meckelian groove; d, dentary; s, splenial. Scale bar = 5 cm

resembling *P. neivensis* (Langston 1965; Price 1967; Aguilera et al. 2006; Salas-Gismondi et al. 2015). The largest diastema occurs between d2 and d3 (10 mm), an area that is constricted in dorsal view (Fig. 5a). The space between d1 and d2 is slightly shorter (8 mm) but occupies a flat and posteriorly inclined area. The last condition resembles those mentioned for *P. neivensis*, in which relatively wide gaps occur only between the first three alveoli (Langston 1965). After d4, diastema is reduced (<4 mm). Medial to the dental alveoli, there are small and deep circular pits of up to 8 mm of diameter which are very visible along the anterior portion of the dentary. The anterolateral portion of the dentary (extending from the area between d1 and d4) is deeply ornamented. Caudally, the only well-marked pits along the lateral dentary surface are the elongated and uniformly spaced neurovascular foramina.

The dentary symphysis is short, distinctly oblong, and extends to the anterior portion of the d4 (Fig. 5a, b). This arrangement is reminiscent of those described for *Purussaurus*, in which the symphysis might reach d4 or d5 (Langston 1965; Bocquentin-Villanueva et al. 1989; Aguilera et al. 2006). Although the splenial is eroded, it is possible to infer, based on the articular surface, that it was excluded from the mandibular symphysis and that its anterior tip passed dorsal to the Meckelian groove (Fig. 5d), as in most caimanines (excluding the basal *Globidentosuchus* and *Gnatusuchus*; Hastings et al. 2016; Cidade et al. 2017). The splenial dorsorostral tip extends to the anterior portion of d5, and its dorsocaudal tip appears to reach the dorsal alveoli in the medial portion of d15. In contrast, in *P. mirandai*, the splenial extends from d8 and forms the internal border of alveoli 16–21 (Aguilera et al. 2006).

An associated eroded fragment of the posterior part of the right mandible is present, including the surangular and the articular with the retroarticular process, but with the foramen aëreum missing (Fig. 5e, f). The dorsal surface of the posterior part of the surangular is ornamented (Fig. 5e). The associated left jugal is robust and relatively well-preserved, but contacts with the quadratojugal, maxilla or lacrimal are not preserved (Fig. 5g). In dorsal view, the jugal is nearly triangular. The lower temporal bar is oval in cross section and elongate, without a strong curvature, along the dorsal margin. The infratemporal border is markedly less concave than the infraorbital one. The ascending process is short (56 mm high), oval (in cross section) and thin (29-mm width). The base of this process is separate from the lateral jugal surface by a shallow groove. In the infraorbital portion, the jugal surface is ornamented, while the lower temporal bar has a weak ornamentation. In the dorsolateral margin of the jugal, there are some anteroposteriorly aligned foramina, which are presumably neurovascular.

IVIC-P-3520: This is an isolated posterior fragment of a mandible preserving the retroarticular processes, the glenoid fossa and the caudal portions of the angular, articular and surangular are preserved (Fig. 6a, b). The retroarticular process is very short and robust (nearly subtriangular in dorsal view), projects posterodorsally, and is not dorsally inclined but rather longitudinally concave, resembling the retroarticular processes reported from *Purussaurus* (Bocquentin-Villanueva et al. 1989; Aguilera et al. 2006). The surangular extends to the posterior end of the retroarticular process, as in *P. neivensis* and extant caimans (Brochu 1999).

Fig. 6 Additional *Purussarusus* sp. remains from the lower Miocene Castillo Formation (Venezuela). Isolated fragment of posterior mandible in medial (**a**) and dorsal (**b**) views. **c** Fragment of (left?) maxilla (IVIC–P–2089) in ventral view. **d** Left ilium (IVIC–P–2112) in medial view. **e** Isolated tooth (IVIC–P–2216). mxT, maxillary teeth. Scale bar = 5 cm, unless otherwise noted



IVIC-P-2089: This is an isolated and eroded fragment of a putative very large left maxilla. Two alveoli are preserved on the ventrolateral margin (Fig. 6c). These are large (~20-mm maximum diameter) and oval, similar to those of *Purussaurus* (Aguilera et al. 2006). The dorsal surface of the maxilla is highly eroded. Because no sutures were observed, it is difficult to assume the position of the maxillary fragment.

IVIC-P-2112: This is an isolated large, robust left ilium 220 mm in length and 115 mm in height from the ischiadic peduncle to the top of the iliac blade (Fig. 6d). It preserves most of the acetabulum. Its main shape somewhat resembles those of extant and extinct caimanines (Langston 1965, 2008; Brochu 1999, 2011), albeit larger. The dorsal iliac blade is rather smooth and curved, with a modest dorsal indentation towards its posterior tip (Brochu 1999, 2011). The posterior tip of the iliac blade is robust and somewhat pointed. The postacetabular process is short and comprises approximately 35% of the total ilium length, as in Melanosuchus but in contrast to Mourasuchus, Caiman and Paleosuchus, in which it comprises 45–50% of ilium length (Langston 1965, 2008; Brochu 1999). Dorsal expansion of the dorsal iliac blade edge is noticeable when compared with extant caimanines and is greater than in Mourasuchus atopus (see Langston 1965). The acetabulum is deep, wide and open anterodorsally (unlike extant Caiman; Brochu 1999). The ischiadic peduncle is robust and nearly triangular in cross section.

IVIC-P-2215, IVIC-P-2216, IVIC-P-3585 and IVIC-P-3586: These isolated teeth display varying degrees of erosion, but they are large, robust, blunt, sub-circular at the base and slightly mediolaterally compressed. The larger teeth have serrated mesiodistal carinae (Fig. 6e–g).

Remarks: The configuration of the splenial (excluded from mandibular symphysis and with its anterior tip passing dorsal to the Meckelian groove) allows referral to Caimaninae (Brochu 1999; Hastings et al. 2016). The large size of the material (dentary, jugal, teeth, ilium) and the configuration of the dentary symphysis (short and oval) indicate similarities with the extinct caimanine *Purussaurus* (Aguilera et al. 2006). Furthermore, the overall morphology of the teeth and retroarticular processes found in the Castillo Formation are indistinguishable of those described for *Purussaurus* (Langston 1965; Aguilera et al. 2006; Hastings et al. 2013; Aureliano et al. 2015), providing a second line of evidence for the presence of this taxon in the Castillo Formation.

At present, three *Purussaurus* species have been described from the Neogene of South America: middle Miocene *P. neivensis* (known from La Venta, Colombia and Iquitos, Peru), and upper Miocene *P. mirandai* (Urumaco Formation, Venezuela) and *P. brasiliensis* (Solimões Formarion; Brazil; Langston 1965; Price 1967; Aguilera et al. 2006; Bocquentin-Villanueva et al. 1989; Scheyer et al. 2013; Aureliano et al. 2015). Since these species are distinguished based on cranial criteria (e.g. naris size; Brochu 1999; Bocquentin-Villanueva et al. 1989; Aguilera et al. 2006), we decline to refer the Castillo material to a particular species until more diagnostic elements are recovered.

Based on dorsal cranial length (DCL), late Miocene Purussaurus are definitively larger than middle Miocene P. neivensis (Langston 1965; Aguilera et al. 2006; Aureliano et al. 2015). Even though no complete mandible has been reported for these taxa (e.g. Mook 1941; Langston 1965; Salas-Gismondi et al. 2015), the Cerro La Cruz materials resemble P. neivensis in size (see details below). Compared with the Peru specimens assigned to P. neivensis (Salas-Gismondi et al. 2015), the Cerro La Cruz mandible shows a more festooned tooth row. The retroarticular processes of P. mirandai and P. brasiliensis are more elongate and narrower than IVIC-P-3520 (Price 1967; Aguilera et al. 2006). Therefore, the Purussaurus remains here described may be closely related to P. neivensis. Nevertheless, the possibility that the Castillo Formation material might represent a new Purussaurus species cannot be excluded.

Purussaurus is one of the most bizarre alligatoroids (Brochu 1999), but it is also one of the most successful and persistent caimanines in the Neogene of South America. Purussaurus has a wide geographic distribution, including Venezuela, Peru, Bolivia, Colombia, Brazil and possibly Panama, as well as a long stratigraphic range (Aureliano et al. 2015; Salas-Gismondi et al. 2015; Antoine et al. 2016; Moreno-Bernal et al. 2016; Rincón et al. 2016b). Although the earliest Purussaurus species, P. neivensis, is of middle Miocene age, indeterminate Purussaurus records have been recently reported from late Oligocene to early Miocene of eastern Peru (Antoine et al. 2016), the lower Miocene Barzaloza Formation of Colombia (Moreno-Bernal 2006), the lower to middle Miocene Castilletes Formation of Colombia (16.7-14.2 Ma; Moreno et al. 2015; Moreno-Bernal et al. 2016), and possibly the lower Miocene Culebra Formation of Panama (19.83–19.12 Ma; Hastings et al. 2013). The fossil record of Purussaurus in Venezuela is also rather continuous during the early to late Miocene (Scheyer et al. 2013; Rincón et al. 2016b). With a constrained age of

Fig. 7 Associated remains of *Caiman* sp. (IVIC–P–2932) from the lower Miocene Castillo Formation (Venezuela). Fragment of mandible in dorsal (a), medial (b) and lateral (c) views; thoracic vertebrae in posterior (d), anterior (e) and left lateral (f) views. ma, mandibular symphysis; mg, meckelian groove. Scale bar = 5 cm



17.21–18.27 Ma (Burdigalian, early Miocene), *Purussaurus* from Cerro La Cruz constitute some of the earliest and well-dated records of this giant caimanine in northern South America.

Finally, one of the specimens referred to *Purussaurus*, the mandible IVIC–P–668, was recovered from a bioclastic limestone mainly composed of reworked foraminifera, gastropods and molluses. Towards the anterior portion of the mandible there is an attached ray tooth tentatively attributed to *Rhinoptera* sp. (Fig. 5h; see discussion below).

Genus *Caiman* Spix, 1825 *Caiman* sp.

Material: IVIC–P–2932, eroded fragment of left mandible preserving the dentary, splenial, articular and surangular bones, and one vertebra.

Occurrence: Cast–40, Cerro La Cruz, lower Miocene of the Castillo Formation, Lara State, Venezuela.

Description and comparison: The left mandibular fragment preserves 14 alveoli with some in situ teeth (Fig. 7a–c). The first four alveoli are large and arranged in an anteromedially oriented linear sequence (Fig. 7a). Beginning with d4, the alveoli are also lineally positioned but with an anterocaudally oriented axis. Therefore, in dorsal view, at the level of d4 an angle of ~130° is formed in the lateral area of the dentary between d1–d4 and d4–d14 (Fig. 7a). After d4, the alveoli are sequentially positioned more medially up until reaching the medial area of the dentary (in dorsal view; (Fig. 7a).

Among the first four teeth, d1 and d4 are the largest, while d2 is the smaller. The larger interalveolar space occurs between d2 and d3, resembling *C. brevirostris* (Souza-Filho 1987; Fortier et al. 2014). D4 is not confluent with d3. Almost all alveoli are nearly circular, and most teeth are not mediolaterally compressed, although d1 is anteroposteriorly compressed (Fig. 7a). D12 and d13 are closely packed, but with eroded crowns. The relatively well-preserved d14 tooth, found in situ, is low-crowned, notably blunt and subcircular in cross-section, resembling those described for *Caiman brevirostris* and *C. wannlangstoni* (Fortier et al. 2014; Salas-Gismondi et al. 2015). In addition, d14 is the largest of the mandibular sequence, as in *C. brevirostris* (Souza-Filho 1987; Fortier et al. 2014).

The dentary symphysis is short and extends to the posterior level of d4 (Fig. 7a), resembling some modern jacareans (Brochu 1999; Cidade et al. 2017). In lateral view, the anterior portion of the dentary is poor ornamented (Fig. 7c). The dentary is gently curved (in lateral view) between d4 and d12, similar to most alligatoroids (Brochu 1999; Scheyer et al. 2013; Hastings et al. 2016). Although the splenial is badly preserved, its anterior process ends dorsal to the Meckelian groove and appears to end close to the mandibular symphysis (at the level of d5), although

it is excluded from the mandibular symphysis itself (Fig. 7b). This trait is present in caimanines except *Globidentosuchus* and *Gnatusuchus* (Brochu 1999; Scheyer et al. 2013; Salas-Gismondi et al. 2015; Hastings et al. 2016).

The surangular fragment preserves the articular fossa and the posterodorsal section of the external mandibular fenestra. Sutures with the angular (ventrally) and articular (medially) are also preserved (Fig. 7b). The lateral surface of the articular is eroded and lacks visible ornamentation. The surangular displays no diagnostic features and resembles that of almost all caimanines. The associated vertebra is poorly preserved but is probably from the thoracic region (Fig. 7d–f). The vertebral centrum is nearly subtriangular in cross section, and its ventral surface shows an anterior ventral process. The preserved neural canal is nearly oval in anterior view. Based on the open neurocentral suture, it is not possible to determinate whether the specimen is a juvenile or an adult (Brochu 1996; Ikejiri 2012).

Remarks: The posterior low-crowned tooth of IVIC-P-2932 is a notable trait and resembles those described for some South American caimanines: Gnatusuchus, Kuttacaiman, Caiman wannlangstoni, and C. brevirostris (Scheyer et al. 2013; Fortier et al. 2014; Salas-Gismondi et al. 2015). However, several traits differentiate those taxa from the material described here. In Gnatusuchus, the dentary has an extensive diastema separating the first seven anterior alveoli from four closely spaced posterior alveoli, the mandible has a shovellike morphology with a long mandibular symphysis reaching d11, and the anterior dentary teeth are strongly procumbent (Salas-Gismondi et al. 2015). Kuttacaiman also has a long symphysis, reaching the level of d6 (Salas-Gismondi et al. 2015). In C. wannlangstoni, the posterior teeth are smooth to ribbed within the upper half of the crown and the mandibular symphysis extends to the anterior portion of d6 (Salas-Gismondi et al. 2015). In contrast, the dentary of IVIC-P-2932 resembles that of C. brevirostris. Both taxa share blunt posterior teeth, with d14 being the largest tooth of the sequence; an angle in the anterior portion of the dentary; small size of d2; and the wide diastema between d2 and d3 (Fortier et al. 2014). However, in IVIC-P-2932, the dentary symphysis is shorter, extending only to d4, unlike C. brevirostris in which it reaches d5; Souza-Filho 1987; Fortier et al. 2014). As C. brevirostris is only known from two or three specimens (Souza-Filho 1987; Fortier et al. 2014; Scheyer and Delfino 2016), and considering the high intraspecific and ontogenetic variations displayed in modern caimanines (e.g. Blanco et al. 2014), we prefer to use a conservative taxonomic approach and refer the Castillo material only to Caiman, despite its resemblances to C. brevirostris.

Body size estimation for Castillo Formation crocodylians

As the material recovered from the Castillo Formation is fragmentary, we estimated dorsal cranial length (DCL) of these crocodylians based on morphometric considerations relative to modern and fossil taxa, as well as direct measurements from specimens when possible (e.g. *Siquisiquesuchus venezuelensis* holotype; Brochu and Rincón 2004). From some taxa, DCL measurements were taken from the literature (see Table S5).

The mandible fragment referred to *Purussaurus* (IVIC–P– 668) is 400 mm in length and includes at least 15 alveoli. Bocquentin-Villanueva et al. (1989) and Aguilera et al. (2006) pointed out that the anteroposterior length of the lower tooth row in *Purussaurus* occupies nearly the anterior half of the dentary length. Thus, we infer that the mandible from Cerro La Cruz was nearly 900 mm in length. As the ratio between length of the mandible and DCL observed in late Miocene *Purussaurus* is ~ 0.87 (see Bocquentin-Villanueva et al. 1989; Aguilera et al. 2006), we infer a DCL of approximately 783 mm for *Purussaurus* from the Castillo Formation (IVIC–P–668).

The holotype of C. brevirostris (UFAC 196) is an incomplete rostrum with an associated right mandibular ramus (Souza-Filho 1987; Fortier et al. 2014). In a referred specimen (MCNC-1829; Scheyer and Delfino 2016), the length between the anterior tip of the dentary and the posterior portion of the external mandibular fenestra is approximately 250 mm, while the same distance in UFAC 196 is nearly 230 mm (Fortier et al. 2014). The DCL of MCNC-1829 is 255 mm, similar in size to the previously mentioned measurement for the same specimen. In addition, the length between the anterior tip of the dentary and the posterior border of d14 is 10.5 mm in IVIC-P-2932, while the same distance in MCNC-1829 is 14 mm. This suggests that IVIC-P-2932 could reach only approximately 75% of the DCL of the MCNC specimen. Thus, we obtained a rough minimum DCL for the holotype of C. brevirostris of approximately 235 and 190 mm for IVIC-P-2932.

In order to estimate DCL of IVIC-P-2921 (Caimaninae gen. et sp. indet.), we explored the relationships between width (at the mid-length of the supratemporal fenestrae) and anteroposterior length of the skull table (STw and STapl, respectively) in relation with DCL in modern caimanines. Twenty-three modern caimanine skulls were measured (see Electronic Supplementary Material; Fig. S2; Table S3). For estimating relationships among variables, a simple regression analysis (ordinary least squares regression) was performed using Past 3.06 (Hammer et al. 2001). The results are shown in EMS 2 (Fig. S2; Table S4). Both variables, ST_w and ST_{abl}, show a significant linear correlation with DCL (ESM 2; Table S4), allowing reliable DCL estimation in fossil specimens (alligatoroids) in which only a skull table is available. Therefore, values of DCL could be estimated with the coefficients shown in Table S4 for both STw and STapl. In the case of IVIC-P-2921, STw is 87.3 mm, and STapl is 67.7 mm; therefore, we are able to infer DCL of approximately 328 mm for the specimen (Table S4). Direct measurements were taken on a skull (MCNC-1829) referred to Caiman brevirostris

Discussion

When the fossil record of Cenozoic crocodylians of South America-and particularly that of caimanines-is evaluated in both chronological and biogeographical contexts, its inequality is quite remarkable. In the Paleogene, three genera and five species of caimanine are recognised (Bona 2007; Riff et al. 2010; Brochu 2011; Pinheiro et al. 2012; Bona and Barrios 2015), while modern Caimaninae diversity encompasses three genera (Paleosuchus, Caiman, Melanosuchus) with six currently recognised species (Martin 2008; Oaks 2011). It is in the Miocene that Caimaninae reaches its peak of diversity, with at least nine genera and more than 15 species recognised. Most are based on relatively complete cranial and mandibular remains (Langston 1965; Brochu 1999, 2010; Aguilera et al. 2006; Scheyer et al. 2013; Salas-Gismondi et al. 2015; Cidade et al. 2017). Caimaninae also reached a wide geographic distribution during the Miocene throughout South America (e.g. Riff et al. 2010) and north into Panama (Hastings et al. 2013) and Mexico (Brochu and Carbot-Chanona 2015).

(Schever and Delfino 2016) and in the holotype of

Siquisiquesuchus venezuelensis (Brochu and Rincón 2004).

The most diverse crocodylian assemblages in South America come from localities of middle and late Miocene age (Langston 1965; Cozzuol 2006; Riff et al. 2010; Bona et al. 2013a, b; Scheyer et al. 2013; Salas-Gismondi et al. 2015). In contrast, early Miocene localities remain poorly sampled. In South America, the few localities of early Miocene and late Oligocene age appear have low crocodylian diversity, with a maximum of three taxa in a same geological unit (e.g. Moreno-Bernal et al. 2016). Regarding alligatoroids, only Caiman tremenbensis (see below), Mourasuchus, and Purussaurus have been reported (Chiappe 1988; Moreno-Bernal et al. 2016; Antoine et al. 2016). These, together with gavialoids, appear to be the only widespread crocodylians during the late Oligocene to the early Miocene (Chiappe 1988; Brochu and Rincón 2004; Moreno-Bernal 2006; Moreno-Bernal et al. 2016; Hastings et al. 2013; Antoine et al. 2016; Solórzano et al. 2017). Consistent with this perspective, Purussaurus is also particularly common in the lower Miocene beds of the Castillo Formation (Table S1).

The putative oldest member of Jacarea (sensu Brochu 1999) is *C. tremembensis*, described from the upper Oligocene Tremembé Formation in southeastern Brazil (Chiappe 1988). It was based on a fragmentary left dentary and some postcranial elements (Chiappe 1988). However, the diagnosis provided by Chiappe (1988) can be applied to almost all known

caimanines, and many of the diagnostic features of the taxa are present in juvenile specimens of recent Caiman and Melanosuchus according to Fortier et al. (2014), who regard C. tremembensis as a nomen dubium, while also suggesting that it may not belong to Jacarea. Oaks (2011), in a molecular Bayesian relaxed-clock dating analysis, inferred that the age of the most recent common ancestor of Jacarea (Caiman + Melanosuchus) is likely middle Miocene. This is consistent with the palaeontological data known before this study, as Caiman was previously recognised only from the middle Miocene (Langston 1965; Schever et al. 2013; Fortier et al. 2014; Salas-Gismondi et al. 2015). Nevertheless, some of the materials described here belong unequivocally to the Jacarean clade. As the age of the beds from which this specimen was recovered is well-constrained between 17.2 and 18.9 Ma (early Miocene, Burdigalian; Rincón et al. 2014), the new finding documents the initial stages of the radiation of jacareans and represents the earliest appearance of Caiman in the fossil record. This challenges the time-calibrated phylogeny of Oaks (2011) as indicating that the most recent common ancestor of Jacarea is at least of early Miocene age.

The four alligatoroids here recognised from the Castillo Formation, plus the previous record of the gavialoids Siguisiquesuchus venezuelensis and Gryposuchus sp. (Brochu and Rincón 2004; Solórzano et al. 2017), illustrate the early Neogene stage in the evolution of the successful and diverse crocodylian assemblages in tropicalequatorial South America. With at least six taxa, the crocodylian diversity in the Castillo Formation does not reach that of tropical areas of younger periods along the Miocene (Cozzoul 2006; Riff et al. 2010; Scheyer et al. 2013). Nonetheless, its diversity is considered high as the highest number of extant species in a same area of this region is four (Marioni et al. 2013) and there are few modern ecosystems with more than two or three sympatric crocodylian species (Thorbjarnarson 1992; Brochu 2001). The new findings from the Castillo Formation also support the perspective that diverse crocodylian assemblages dominated by caimanines and gryposuchines were already established by the early Miocene (~18 Ma) in northern South America (Moreno-Bernal et al. 2016).

Due to the poor state of preservation of the specimens so far recovered from the Castillo Formation, a phylogenetic analysis is beyond the scope of the present contribution. However, future discoveries of better preserved material could add reliable data for polarisation of several traits on early Miocene caimanine assemblages and refine our understanding about the phylogenetic relationships of the group. With the data here presented, it is notable that at least two distinct caimanine lineages were preserved simultaneously in the Castillo Formation: the forms related to Jacarea and *Purussaurus*. These groups, together with *Mourasuchus* and gryposuchinae gavialoids, appear to have dominated the Orinoquian Amazonian ecosystems during the Miocene (e.g. Riff et al. 2010; Cidade et al. 2017).

Palaeoenvironmental and palaeoecological considerations

The Castillo Formation has been interpreted as representing an extensive marginal marine system including a diverse range of terrestrial, fluvial, tidal and brackish to open marine subtidal environments (Wheeler 1960, 1963; Johnson et al. 2009; Sánchez-Villagra et al. 2010; Rincón et al. 2014; Solórzano and Rincón 2015; Núñez-Flores et al. 2017). In the studied area (Cerro La Cruz and its surroundings at Sierra de La Baragua in Lara) the near-shore marine environment is dominant (Rincón et al. 2014; Solórzano and Rincón 2015; Núñez-Flores et al. 2017). Interestingly, from two levels along the middle part of the Cerro La Cruz sequence, some continental mammals and freshwater taxa were found, documenting the presence of local continental environments (Rincón et al. 2014, 2016a; Ferreira et al. 2016). Several of the specimens here described were also recovered from these continental or freshwater beds, which are here informally named Cast-40 and Cast-47 (Fig. 2; Table S1). The only exception is the Purussaurus mandible (IVIC-P-668), which was found in Cast-42 (Fig. 2) embedded in a bioclastic limestone with small molluscs and a ray tooth (*Rhinoptera*; Fig. 5h). Curiously, Rhinoptera is typical of shallow near-shore marine and brackish environments (Smith and Merriner 1985). Therefore, IVIC-P-668 could document euryhaline tolerance in Purussaurus, but post mortem transportation is also possible.

The specimens found in the study area consist of disarticulated fragmentary skeletal elements (Figs. 3, 4, 5, 6 and 7). Preservation of articulated crocodyliforms is frequently attributed to rapid burial, with decreasing degrees of articulation ascribed to increasing subaerial and subaqueous decay via taphonomic processes such as endogenous decay and scavenging, erosion, and transport in high-energy aqueous environments (Syme and Salisbury 2014). The fragmentary nature of the remains reported here might suggest post mortem transportation related with medium to high-energy environments, which may have carried these remains from certain distances to the deposition site. As modern crocodylians inhabit tropical and subtropical wetlands and coasts, their presence in the Castillo Formation argues for the existence of ancient freshwater aquatic environments in its surroundings (Medem 1983; Herron 1994; Latrubesse et al. 2010; Scheyer and Moreno-Bernal 2010; Riff et al. 2010; Salas-Gismondi et al. 2016; Souza et al. 2016). Nevertheless, the limited clastic terrigenous influx and the immature sandstone observed in the analysed section have been interpreted as suggesting fluvial environments of low water volume and short transport path (Rincón et al. 2014).

Unlike extant crocodylids, modern alligatorids lack salt glands, which mean they cannot survive indefinitely in salt water (Taplin et al. 1982; Grigg and Kirshner 2015). But, despite their apparent physiological limitations, some modern alligatoroid species are found in estuarine environments (Taplin 1988; Grigg et al. 1998; Grigg and Kirshner 2015) and are capable of long-distance, storm-driven dispersal along coastal regions (Elsey and Aldrich 2009; Brochu and Carbot–Chanona 2015). The disparate fossil record, as well as the phylogenetic relationships of Caimaninae, imply multiple crossings of the seaway separating North and South America (Brochu 2010; Hastings et al. 2013; Brochu and Carbot–Chanona 2015). These facts suggest that physiological limits do not preclude the possibility of *Purussaurus* living in euryhaline environments at the Castillo Formation.

The presence of seven individuals in the same stratigraphic level (Cast-40; Table S1) reveals the sympatric occurrence of at least three crocodylians in the Castillo Formation (Purussaurus, Caiman and Siguisiquesuchus). These could inhabit the same palaeoenvironment but probably occupied distinct ecological niches (see details below). This degree of co-occurrence is lower than that of the Pebas Formation (Peru), where up to seven species appear to have been sympatric (Salas-Gismondi et al. 2015, 2016). Recent work proposed that four different crocodylian morphotypes may have co-occurred at a single location in the Solimões Formation (Brazil; Souza et al. 2016). Moreover, in the late Miocene Urumaco (Venezuela) and Solimões (Brazil) Formations, 12 and 8 species were, respectively, identified, but as these frequently come from different stratigraphic levels and locations, their sympatric occurrence in most cases cannot be verified (Cozzuol 2006; Scheyer et al. 2013).

In most organisms, including crocodylomorphs, body size is a key feature because it affects metabolism, life history, size and population density, as well as energy and food availability in the food chain (White et al. 2007; Naisbit et al. 2011). Therefore, estimation of body size in extinct taxa can provide an important line of evidence for understanding their role in ancient ecosystems (Aureliano et al. 2015). During the late and middle Miocene, South American Neogene crocodylian assemblages exhibit pronounced disparity in terms of body size and snout shape (e.g. Riff et al. 2010; Scheyer et al. 2013; Salas-Gismondi et al. 2015). These differences are especially prominent among caimanines and have been considered the result of adaptation to particular ecological niches (Brochu 1999; Riff et al. 2010; Scheyer et al. 2013; Salas-Gismondi et al. 2015; Aureliano et al. 2015; Cidade et al. 2017). The observed body size ranges of Castillo Formation crocodylians (Table S5) encompasses relatively large predators such as Purussaurus (~5.8-m length, ~730 kg), mediumsized taxa (indeterminate caimanine, 2.5 m length, 62 kg) and rather small taxa (Caiman, 1.5 m length, 13 kg). In addition, the other crocodylians so far described from the Castillo Formation, the gavialoids *S. venezuelensis* and *Gryposuchus* sp. (Brochu and Rincón 2004; Solórzano et al. 2017), could also reach large body sizes over approximately 7.5-m length and 1600 kg (Table S5). Therefore, the body sizes of the Castillo Formation crocodylian assemblage resemble the broad range previously reported from middle and upper Miocene localities (e.g. Scheyer et al. 2013; Aureliano et al. 2015). The new findings confirm previous observations about the presence of large caimanines and the coexistence of large and small crocodylians in South American ecosystems since the early Miocene (Moreno-Bernal et al. 2016).

Heterogeneity of snout shapes found in the crocodylian assemblage of the Castillo Formation is also remarkable; blunt-snouted (*Caiman* sp. similar to *C. brevirostris*), large-snouted (*Purussaurus*) and slender-snouted (*Siquisiquesuchus* and *Gryposuchus*) taxa (sensu Brochu 2001) are all present. Although it does not reach the disparity of middle and upper Miocene localities (e.g. Cozzuol 2006; Bona et al. 2013a, b; Scheyer et al. 2013; Salas-Gismondi et al. 2015), snout shape variation also indicates different ecological adaptations in Castillo Formation crocodylians.

In the sampled area of the Castillo Formation, the most abundant crocodylian remains are referred to the putatively marine gavialoid *Siquisiquesuchus*, while caimanine remains are much less common (Solórzano et al. 2017; Fig. 2; ESM_1; Fig. S1). This is in agreement with the proposed coastal and shallow marine environments for deposition of this unit (Rincón et al. 2014; Solórzano and Rincón 2015; Núñez-Flores et al. 2017), while freshwater environments were less common and only locally distributed (Rincón et al. 2014). Conversely, co-occurrence of both *Siquisiquesuchus* and caimanines indicates the possibility that the latter could also inhabit estuaries (Solórzano et al. 2017).

While Miocene crocodylians of South America (with some exceptions, such as Mourasuchus) may have occupied similar ecological niches to their modern relatives (Langston 1965; Cidade et al. 2017), there is little direct evidence to suggest predation activity; nevertheless, a large number of vertebrates and invertebrates were available as prey to these forms (Riff et al. 2010; Salas-Gismondi et al. 2015; Aureliano et al. 2015). Into the Castillo Formation, we can identify many types of potential prey for crocodylians according to their body size, snout shape, tooth morphology and inferred habitat (ESM 1; Table S2). Medium- to large-sized animals that interacted with fresh water frequently, such as mega-herbivorous mammals (Xenarthra, Litopterna and Notoungulata); turtles (Chelus); and even smaller crocodylians, were likely taken by the top predator Purussaurus (Sánchez-Villagra et al. 2010; Rincón et al. 2014, 2016a; Aureliano et al. 2015). Castillo Formation Caiman has posterior bulbous crushing teeth that resemble those of some reptiles adapted to durophagous diet (e.g. Langston 1965; Ösi and Barrett 2011; Fortier et al. 2014; Salas-Gismondi et al. 2015) and, like C. brevirostris, it might be an ecological analogue of some populations of the extant C. latirostris that show adaptations to consume hard-shelled prey (Ősi and Barrett 2011; Fortier et al. 2014). Though freshwater molluscs have not been reported from the Castillo Formation, marine macroinvertebrates are abundant throughout its outcrops (Feldmann and Schweitzer 2004; Rincón et al. 2014). The dominant environment preserved in the study area is a near-shore marine complex, but some local facies such as subtidal shallow marine, lagoon and intertidal zone near mangroves might be inferred (Rincón et al. 2014; Solórzano et al. 2017). Thus, it is likely that, as with some modern populations of C. latirostris, early Miocene populations of the Castillo Formation Caiman (especially juveniles and sub-adults) could have survived in brackish wetlands, mangrove-lined and coastal salt waterways where marine molluscs and crabs were abundant (see Grigg et al. 1998; Ösi and Barrett 2011; Rincón et al. 2014; Grigg and Kirshner 2015). The indeterminate caimanine described here is probably a juvenile individual, but shows a body mass similar to modern male adult Caiman (Grigg and Kirshner 2015). In the Castillo assemblage, this caimanine could have acted as a mesopredator, catching any small or medium-sized vertebrate that could be caught, including fishes (e.g. Colossoma).

Conclusions

The new cranial and mandibular remains recently recovered from the Castillo Formation at the Lara State, Venezuela, allows us to describe a new alligatoroid assemblage of early Miocene age (Burdigalian). The assemblage includes four forms: Purussaurus sp., Caiman sp., Caimaninae gen. et sp. indet. and Alligatoroidea indeterminate. Along with previously known Siquisiquesuchus venezuelensis (Brochu and Rincón 2004) and Gryposuchus sp. (Solórzano et al. 2017), the Castillo Formation fauna (with six forms) illustrates high crocodylian species richness during the early Miocene in South America, with up to three sympatric forms. It also further documents the persistence of the caimanine-gavialoid assemblages throughout the Miocene in South America. The presence of Caiman in the wellconstrained chronological framework at the Castillo Formation (17.21–18.27 Ma; Rincón et al. 2014) allows us to propose that the origin of the jacareans appears to have likely occurred during the late Oligocene.

The disjunct sedimentary provenance of the major clades recognised in the study area, Gavialoidea and Alligatoroidea, reveals that the former were mainly distributed in coastal and estuarine environments. The alligatoroids, generally found in association with continental vertebrates, could inhabit the shallow water and short-distance fluvial environments proposed for the study area (Rincón et al. 2014). Occasional incursions into brackish environments were also likely, especially in young individuals.

The crocodylian assemblage from the Castillo Formation shows a broad range of morphological disparity represented by the presence of distinct different snout shape morphotypes that cover a significant part of the morphospatial range known for Crocodylia (Salas-Gismondi et al. 2015). It also displays a broad range of body sizes ranging from small (Caiman sp.) to large taxa (Siquisiquesuchus, Gryposuchus and Purussaurus). This reflects different ecological adaptations to particular ecological niches. Purussaurus was probably the top aquatic predator being able to feed on large prey (e.g. sloths, astrapotheres, toxodonts and even smaller crocodylians). By its size, the indeterminate caimanine could have been a mesopredator catching small to medium size vertebrates. Caiman sp., with durophagous adaptations, might have fed on mollusks. Siquisiquesuchus and Gryposuchus could have preyed on marine and/or estuarine fishes (Solórzano et al. 2017).

Durophagous adaptations have been noted in some of the most recently described South America Neogene caimanine taxa (Scheyer et al. 2013; Salas-Gismondi et al. 2015). From Venezuela, in the upper Miocene Urumaco Formation, there are at least three distinct taxa—*Globidentosuchus brachyrostris*, *C. wannlangstoni* and *C. brevirostris*—with globular posterior teeth (Sánchez-Villagra and Aguilera 2006; Scheyer et al. 2013; Salas-Gismondi et al. 2015; Scheyer and Delfino 2016). In the Castillo Formation, two forms show particular adaptations to a durophagous diet: *Caiman* sp. and the indeterminate alligatoroid. This particular adaptation reflects an abundance of hard-shelled prey in the northernmost portion of South America since the early Miocene and could have driven the ecological specialisation in several non-related lineages in Caimaninae (Salas-Gismondi et al. 2015; Cidade et al. 2017).

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Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

References

- Aguilera, O. A., Riff, D., & Bocquentin-Villanueva, J. (2006). A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the upper Miocene Urumaco Formation, Venezuela. *Journal of Systematic Palaeontology*, 4, 221–232.
- Antoine, P.–. O., Abello, M. A., Adnet, S., Altamirano-Sierra, A. J., Baby, P., Billet, G., et al. (2016). A 60-million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Research*, 31, 30–59.
- Aureliano, T., Ghilardi, A. M., Guilherme, E., Souza-Filho, J. P., Cavalcanti, M., & Riff, D. (2015). Morphometry, bite-force, and Paleobiology of the late Miocene caiman *Purussaurus brasiliensis*. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0117944.
- Blanco, M. V., Cassini, G. H., & Bona, P. (2014). Cranial morphological variation in *Caiman* (Alligatoridae, Caimaninae): a geometric morphometrics study of the ontogeny in the species *Caiman latirostris* and *Caiman yacare*. *Ciencias Morfológicas*, 16, 16–30.
- Bocquentin-Villanueva, J., & Souza-Filho, J. P. (1990). O crocodiliano sul–americano Carandaisuchus como sinonímia de Mourasuchus (Nettosuchidae). Revista Brasileira de Geociencias, 20, 230–233.
- Bocquentin-Villanueva, J., Buffetaut, E., & Negri, F. R. (1989). Nova interpretacao do genero *Purussaurus* (Crocodylia, Alligatoridae). In *Anais do* (Vol. XI, pp. 427–438). Curitiba Brasil: Congresso Brasileiro de Paleontologia.
- Bona, P. (2007). Una nueva especie de *Eocaiman* Simpson (Crocodylia, Alligatoridae) del Paleoceno Inferior de Patagonia. *Ameghiniana*, 44, 435–445.
- Bona, P., & Barrios, F. (2015). The Alligatoroidea of Argentina: an update of its fossil record. In M., Fernández, Y., Herrera (Eds.), *Reptiles Extintos Volumen en Homenaje a Zulma Gasparini* (pp. 143–158). Publicación Electrónica de la Asociación Paleontológica Argentina 15: Argentina.
- Bona, P., & Carabajal, A. (2013). *Caiman gasparinae* sp. nov., a huge alligatorid (Caimaninae) from the late Miocene of Paraná, Argentina. *Alcheringa*, 37, 1–12.
- Bona, P., & Desojo, J. B. (2011). Osteology and cranial musculature of *Caiman latirostris* (Crocodylia: Alligatoridae). *Journal of Morphology*, 272, 780–795.
- Bona, P., Riff, D., & Gasparini, Z. (2013a). Late Miocene crocodylians from northeast Argentina: new approaches about the austral components of the Neogene South American crocodylian fauna. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 103*, 551–570.
- Bona, P., Riff, D., & Gasparini, Z. (2013b). Los Alligatoridae del Mioceno tardío de Argentina: el registro más austral de cocodrilos neógenos en América del Sur. In D., Brandoni, J.I., Noriega, J.I. (Eds.), *El Neógeno de la Mesopotamia Argentina* (pp. 84–96). Asociación Paleontológica Argentina Publicación Especial 14: Argentina.
- Bona, P., Degrange, F. J., & Fernandez, M. S. (2013c). Skull anatomy of the bizarre crocodylian *Mourasuchus nativus* (Alligatoridae, Caimaninae). *The Anatomical Record*, 296, 227–239.
- Brochu, C. A. (1996). Closure of neurocentral sutures during crocodilian ontogeny: Implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology*, 16, 49–62.
- Brochu, C. A. (1999). Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Society of Vertebrate Paleontology Memoir*, *6*, 9–100.
- Brochu, C. A. (2001). Crocodylian snouts in space and time: phylogenetic approaches toward adaptive radiation. *American Zoologist*, 41, 564–585.
- Brochu, C. A. (2003). Phylogenetic approaches toward crocodylian history. Annual Review of Earth and Planetary Sciences, 31, 357–397.

- Brochu, C. A. (2010). A new alligatorid from the lower Eocene Green River Formation of Wyoming and the origin of caimans. *Journal of Vertebrate Paleontology*, 30, 1109–1126.
- Brochu, C. A. (2011). Phylogenetic relationships of *Necrosuchus ionensis* Simpson 1937 and the early history of caimanines. *Zoological Journal of the Linnean Society*, 163, 228–256.
- Brochu, C. A., & Carbot–Chanona, G. (2015). Biogeographic and systematic implications of a caimanine from the late Miocene of southern Mexico. *Journal of Herpetology*, 49, 138–142.
- Brochu, C. A., & Rincón, A. D. (2004). A gavialoid crocodylian from the Lower Miocene of Venezuela. *Special Paper on Palaeontology*, 71, 61–78.
- Chiappe, L. (1988). Un nuevo *Caiman* (Crocodylia, Alligatoridae) de la Formación Tremembe (Oligoceno), Estado de Sao Paulo, Brasil, y su significado paleoclimático. *Paula–Coutiana*, *3*, 49–66.
- Cidade, G.M., Barrios, F., Souza, R., & Bona, P. (2015). A new diagnosis, phylogenetic relationships and taxonomy of *Caiman lutescens* (Rovereto, 1912), Late Miocene, Argentina. 5° Congreso Latinoamericano de Paleontología Vertebrados (Montevideo), 80.
- Cidade, G. M., Solórzano, A., Rincón, A. D., Hsiou, A. S., & Riff, D. (2017). A new *Mourasuchus* (Alligatoroidea, Caimaninae) from the late Miocene of Venezuela, the feeding habits of *Mourasuchus* and the phylogeny of Caimaninae. *PeerJ*, 5, e3056. https://doi.org/10. 7717/peerj.3056.
- Cozzuol, M. A. (2006). The Acre vertebrate fauna: age, diversity, and geography. *Journal of South American Earth Sciences*, 21, 185– 203.
- Elsey, R. L., & Aldrich, C. (2009). Long-distance displacement of a juvenile alligator by Hurricane Ike. *Southeastern Naturalist*, 7, 746–749.
- Escobedo-Galván, A. H., Velasco, J. A., González-Maya, J. F., & Resetar, A. (2015). Morphometric analysis of the Rio Apaporis Caiman (Reptilia, Crocodylia, Alligatoridae). *Zootaxa*, 4059, 541–554.
- Feldmann, R.M., & Schweitzer, C.E. (2004). Decapod crustaceans from the Lower Miocene of north-western Venezuela (Cerro La Cruz, Castillo Formation). In M.R., Sánchez–Villagra & J.A Clarck (Eds.), Fossils of the Miocene Castillo Formation, Venezuela: contributions on Neotropical Palaeontology (pp. 71–86). London: Special Papers in Palaeontology 71.
- Ferreira, G. S., Rincón, A. D., Solórzano, A., & Langer, M. C. (2016). Review of the fossil matamata turtles: earliest well-dated record and hypotheses on the origin of their present geographical distribution. *Science of Nature*, 103, 28. https://doi.org/10.1007/s00114-016-1355-2.
- Fortier, D. C., Souza-Filho, J. P., Guilherme, E., Maciente, A. A. R., & Schultz, C. L. (2014). A new specimen of *Caiman brevirostris* (Crocodylia, Alligatoridae) from the late Miocene of Brazil. *Journal of Vertebrate Paleontology*, 34, 820–834.
- Foth, C., Bona, P., & Desojo, J. B. (2013). Intraspecific variation in the skull morphology of the black caiman *Melanosuchus niger* (Alligatoridae, Caimaninae). *Acta Zoologica*, 96, 1–13.
- Gasparini, Z. (1985). Un nuevo cocodrilo (Eusuchia) Cenozoico de América del Sur. Coletânea de Trabalhos Paleontológicos MME– DNPM (série Geologia), 27, 51–53.
- Grigg, G., & Kirshner, D. (2015). Biology and evolution of crocodylians. Clayton: CSIRO Publishing.
- Grigg, G., Beard, L. A., Moulton, T., Queiro-Melo, M. T., & Taplin, L. E. (1998). Osmoregulation by the broad-snouted caiman, *Caiman latirostris*, in estuarine habitat in southern Brazil. *Journal of Comparison Physiologic B*, 168, 445–452.
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST-Palaeontological statistics. https://www.uv.es/~pardomv/pe/2001_ l/past/pastprog/past.pdf
- Hastings, A. K., Bloch, J., Jaramillo, C. A., Rincon, A. F., & MacFadden, B. J. (2013). Systematics and biogeography of crocodylians from

the Miocene of Panama. *Journal of Vertebrate Paleontology, 33*, 239–263.

- Hastings, A. K., Reisser, M., & Scheyer, T. M. (2016). Character evolution and the origin of Caimaninae (Crocodylia) in the New World Tropics: new evidence from the Miocene of Panama and Venezuela. *Journal of Paleontology*, 90, 317–332.
- Herron, J. C. (1994). Body size, spatial distribution, and microhabitat use in the caimans, *Melanosuchus niger* and *Caiman crocodilus*, in a Peruvian lake. *Journal of Herpetology*, 28, 508–513.
- Hurlburt, G. R., Heckert, G. A., & Farlow, J. (2003). Body mass estimates of phytosaurs (Archosauria: Parasuchidae) from the petrified Forest Formation (Chinle Group: Revueltian) based on skull and limb bone measurements. *Paleontology and Geology of the Snyder Quarry, New Mexico Museum of Natural History and Science Bulletin, 24*, 105–114.
- Ikejiri, T. (2012). Histology-based morphology of the neurocentral synchondrosis in *Alligator mississippiensis* (Archosauria, Crocodylia). *The Anatomical Record*, 295, 18–31.
- Johnson, K. G., Sánchez-Villagra, M. R., & Aguilera, O. A. (2009). The Oligocene–Miocene transition on coral reefs in the Falcón basin (NW Venezuela). *Palaios*, 24, 59–69.
- Langston, W. (1965). Fossil crocodylians from Colombia and the Cenozoic history of the Crocodilia in South America. University of California Publications in Geological Sciences, 52, 1–152.
- Langston, W. (2008). Notes on a partial skeleton of *Mourasuchus* (Crocodylia, Nettosuchidae) from the Upper Miocene of Venezuela. *Arquivos do Museu Nacional, Rio de Janeiro, 66*, 125–143.
- Langston, W., & Gasparini, Z. B. (1997). Crocodylians, *Gryposuchus*, and the South Americans gavials. In R. F. Kay, R. L. Madden, R. L. Ciffelli, & J. J. Flynn (Eds.), *Vertebrate paleontology in the neotropics: the Miocene fauna of La Venta, Colombia* (pp. 113–154). Washington: Smithsonian Institution.
- Latrubesse, E. M., Cozzuol, M., Silva-Caminha, S. A. F., Rigsby, C. A., Absy, M. L., & Jaramillo, C. (2010). The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth–Science Reviews*, 99, 99–124.
- Marioni, B., Dutra-Araujo, D., Villamarín, F., & Da Silveira, R. (2013). Amazonian encounters with four crocodylian species in one single night. *Crocodile Specialist Group Newsletter*, 32, 10–13.
- Martin, S. (2008). Global diversity of crocodiles (Crocodilia, Reptilia) in freshwater. *Hydrobiologia*, 595, 587–591.
- Medem, F. (1963). Osteología craneal, distribución geográfica y ecología de *Melanosuchus niger* (Spix), (Crocodylia, Alligatoridae). *Revista de la Academia Colombiana de Ciencias*, 12, 5–19.
- Medem, F. (1983). Los Crocodylia de Sur America, Volumen 2. Bogotá, Colombia: Colciencias, Ministerio de Educacion Nacional, Bogotá.
- Medina, C. J. (1976). Crocodylians from the Late Tertiary of northwestern Venezuela: *Melanosuchus fisheri* sp. nov. *Breviora*, 438, 1–14.
- Mook, C. C. (1941). A new fossil from Colombia. *Proceedings of the* United States National Museum, 91, 55–61.
- Moraes-Santos, H., Bocquentin-Villanueva, J., & Mann-Toledo, P. (2011). New remains of a gavialoid crocodylian from the late Oligocene–early Miocene of the Pirabas Formation, Brazil. Zoological Journal of the Linnean Society, 163, 132–139.
- Moreno-Bernal, J.W. (2006). Reporte preliminar sobre los Crocodylia de la formación Barzalosa (Mioceno Inferior?), Valle Medio del Magdalena. II Congreso Colombiano de Zoología, Santa Marta, Colombia (libro de resúmenes), p. 487.
- Moreno-Bernal, J. W., Head, J., & Jaramillo, C. (2016). Fossil crocodylians from the High Guajira Peninsula of Colombia: Neogene faunal change in northernmost South America. *Journal* of Vertebrate Paleontology, 36, e1110586. https://doi.org/10.1080/ 02724634.2016.1110586.
- Naisbit, R. E., Kehrli, P., Rohr, R. P., & Bersier, L. F. (2011). Phylogenetic signal in predator-prey body-size relationships. *Ecology*, 92, 2183– 2189.

- Núñez-Flores, M., Rincón, A. D., Solórzano, A., Sánchez, L., & Cáceres, C. (2017). Fish–otoliths from the early Miocene of Castillo Formation, Venezuela: a view into the proto–Caribbean teleostean assemblages. *Historical Biology*. https://doi.org/10.1080/08912963. 2017.1282474.
- Oaks, J. R. (2011). A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *Evolution*, 65, 3285–3297.
- Ösi, A., & Barrett, P. M. (2011). Dental wear and oral food processing in *Caiman latirostris*: analogue for fossil crocodylians with crushing teeth. *Neues Jahrbuch für Geologie und Paläontologie– Abhandhungen, 261*, 201–207.
- Paolillo, A., & Linares, O. J. (2007). Nuevos cocodrilos Sebecosuchia del Cenozoico sudamericano (Mesosuchia: Crocodylia). *Paleobiologia Neotropical*, 3, 1–25.
- Pinheiro, A. E. P., Fortier, D. C., Pol, D., Campos, D. A., & Bergqvist, L. P. (2012). A new *Eocaiman* (Alligatoridae, Crocodylia) from the Itaboraí Basin, Paleogene of Rio de Janeiro, Brazil. *Historical Biology*, 25, 327–337.
- Price, L. I. (1967). Sobre a mandibula de um gigantesco crocodilideo extinto do alto rio Jurua, Estado do Acre. *Atas do Simposio sobre a Biota Amazonica, Geociencias, 1*, 359–371.
- Riff, D., & Aguilera, O. A. (2008). The world's largest gharials Gryposuchus: description of G. croizati n. sp. (Crocodylia, Gavialidae) from the Upper Miocene Urumaco Formation, Venezuela. Paläontologische Zeitschrift, 82, 178–195.
- Riff, D., Romano, P. S. R., Oliveira, G. R., & Aguilera, O. A. (2010). Neogene crocodile and turtle fauna in northern South America. In C. Hoorn & F. P. Wesselingh (Eds.), *Amazonia, landscape and species evolution* (pp. 259–280). London: Blackwell Publishing.
- Rincón, A. D., Solórzano, A., Benammi, M., Vignaud, P., & McDonald, H. G. (2014). Chronology and geology of an Early Miocene mammalian assemblage in North of South America, from Cerro La Cruz (Castillo Formation), Lara State, Venezuela: implications in the "changing course of Orinoco River" hypothesis. *Andean Geology*, 41, 507–528.
- Rincón, A. D., Solórzano, A., McDonald, H. G., & Núñez–Flores, M. (2016a). Baraguatherium takumara, gen. et sp. nov., the earliest mylodontoid sloth (Early Miocene) from Northern South America. Journal of Mammalian Evolution. https://doi.org/10.1007/s10914-016-9328-y.
- Rincón, A. D., Solórzano, A., Macsotay, O., McDonald, H. G., & Núñez-Flores, M. (2016b). A new Miocene vertebrate assemblage from the Rio Yuca Formation (Venezuela) and the northernmost record of typical Miocene mammals of high latitude (Patagonian) affinities in South America. *Geobios*, 49, 395–405. https://doi.org/10.1016/ j.geobios.2016.06.005.
- Salas-Gismondi, R., Antoine, P.-O., Baby, P., Brusset, S., Benammi, M., Espurt, N., et al. (2007). Middle miocene crocodiles from the Fitzcarrald Arch, Amazonian Peru. In 4th European meeting on the palaeontology and stratigraphy of Latin America Cuadernos del Museo Geominero n° 8 (pp. 355–360). Madrid: Instituto Geológico y Minero de España.
- Salas-Gismondi, R., Flynn, J. J., Baby, P., Tejada-Lara, J. V., Wesselingh, F. P., & Antoine, P.-O. (2015). A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proceedings of the Royal Society B*, 282, 20142490.
- Salas-Gismondi, R., Flynn, J. J., Baby, P., Tejada-Lara, J. V., Claude, J., & Antoine, P.-O. (2016). A new 13 million year old gavialoid crocodylian from proto-Amazonian mega-wetlands reveals parallel evolutionary trends in skull shape linked to longirostry. *PLoS One*, *11*, e0152453.
- Sánchez-Villagra, M.R., & Clark, J.A. (2004). Fossils of the Miocene Castillo Formation, Venezuela: contributions on neotropical palaeontology. *Special Papers in Palaeontology* (The paleontological Association, London) no. 71.

- Sánchez-Villagra, M. R., Aguilera, O. A., Sánchez, R., & Carlini, A. A. (2010). The fossil vertebrate record of Venezuela of the last 65 million years. In M. R. Sánchez-Villagra, O. A. Aguilera, & A. A. Carlini (Eds.), Urumaco and Venezuelan palaeontology—the fossil record of the northern Neotropics (pp. 19–51). Bloomington: Indiana University Press.
- Scheyer, T. M., & Delfino, M. (2016). The late Miocene Caimanine fauna (Crocodylia: Alligatoroidea) of the Urumaco formation, Venezuela. *Palaeontologia Electronica*, 19.3.48A, 1–57.
- Scheyer, T. M., & Moreno-Bernal, J. W. (2010). Fossil crocodylians from Venezuela in the context of south American faunas. In M. R. Sánchez–Villagra, O. A. Aguilera, & A. A. Carlini (Eds.), Urumaco and Venezuelan palaeontology—the fossil record of the northern Neotropics (pp. 192–213). Bloomington: Indiana University Press.
- Scheyer, T. M., Aguilera, O. A., Delfino, M., Fortier, D. C., Carlini, A. A., Sánchez, R., Carrillo-Briceño, J. D., Quiroz, L., & Sánchez-Villagra, M. R. (2013). Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nature Communications*, 4, 1907. https://doi.org/10.1038/ncomms2940.
- Simpson, G. G. (1935). Early and middle tertiary geology of the Gaiman region, Chubut, Argentina. American Museum Novitates, 775, 1–29.
- Smith, J. W., & Merriner, J. V. (1985). Food habits and feeding behavior of the cownose ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. *Estuaries*, 8, 305–310.
- Solórzano, A., & Rincón, A. D. (2015). The earliest record (early Miocene) of a bony-toothed bird from South America and a reexamination of Venezuelan pelagornithids. *Journal of Vertebrate Paleontolology*, 35, e995188.
- Solórzano, A., Núñez-Flores, M., & Rincón, A. D. (2017). Gryposuchus (Crocodylia, Gavialoidea) from the early Miocene of Venezuela. *Paläontologische Zeitschrift*. https://doi.org/10.1007/s12542-017-0383-3.

- Souza, R. G., Cidade, G. M., Campos, D. A., & Riff, D. (2016). New crocodylian remains from the Solimões Formation (lower Eocene– Pliocene), state of Acre, Southwestern Brazilian Amazonia. *Revista Brasileira de Paleontologia*, 19, 217–232.
- Souza-Filho, J.P. (1987). Caiman brevirostris sp. nov., um novo Alligatoridae da formação Solimões (Pleistoceno) do Estado do Acre, Brasil. In Anais X Congresso Brasileiro de Paleontologia (pp. 173-80). Rio de Janeiro: Sociedade Brasileira de Paleontologia.
- Syme, C. E., & Salisbury, S. W. (2014). Patterns of aquatic decay and disarticulation in juvenile Indo-Pacific crocodiles (*Crocodylus porosus*), and implications for the taphonomic interpretation of fossil crocodyliform material. *Palaeogeography, Palaeoclimatology, Palaeoecology, 412*, 108–123.
- Taplin, L. E. (1988). Osmoregulation in crocodylians. *Biological Reviews*, 63, 333–377.
- Taplin, L. E., Grigg, G. C., Harlow, P., Ellis, T. M., & Dunson, W. A. (1982). Lingual salt glands in *Crocodylus acutus* and *C. johnstoni*, and their absence from *Alligator mississippiensis* and *Caiman crocodilus. Journal of Comparative Physiology B: Biochemical*, *Systemic, and Environmental Physiology*, 149, 43–47.
- Thorbjarnarson, J. B. (1992). Crocodiles: an action plan for their conservation. Gland: IUCN.
- Wheeler, C. B. (1960). Estratigrafía del Oligoceno y Mioceno inferior de Falcón occidental y nororiental. *Memorias III Congreso Geológico Venezolano, Tomo, 1*, 407–465.
- Wheeler, C. B. (1963). Oligocene and lower Miocene stratigraphy of western and northeastern Falcón Basin, Venezuela. American Association of Petroleum Geologists Bulletin, 47, 35–68.
- White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, 22, 223–330.