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Taxonomic review of two fossil crocodylians from the Cenozoic of South America and its implications for the crocodylian fauna of the continent

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Abstract

The crocodylomorph fauna of the Cenozoic of South America is one of the richest and most diverse in the world. The most diverse group within that fauna is Alligatoroidea, with nearly all of its species belonging to the Caimaninae clade. Many of the fossil alligatoroid species from the Cenozoic of South America were proposed based on very incomplete remains, and as a result their validity requires revision. Two such species are *Balanerodus logimus* Langston, 1965, from the middle Miocene of Colombia and Peru, and *Caiman venezuelensis* Fortier & Rincón, 2012, from the Pliocene-Pleistocene of Venezuela. This study has performed a thorough review of the taxonomic status of these two alligatoroid species, concluding that *B. logimus* is a *nomen dubium* and that *Ca. venezuelensis* is a junior synonym of the extant species *Ca. crocodilus*. This review offers a significantly more accurate scenario for alligatoroid diversity in the Cenozoic of South America in different epochs such as the Miocene and Pleistocene. Additionally, the record of *Ca. crocodilus* from the Pleistocene of Venezuela is the first fossil record that can be assigned to this species.

Key words: El Breal de Orocual-Honda Group-Miocene-Pliocene-Pleistocene-Caimaninae

Introduction

All extant crocodylomorphs belong to the crown-group Crocodylia, which is phylogenetically defined as the clade formed by the most recent common ancestor of *Alligator mississippiensis* (Daudin, 1802), *Crocodylus niloticus* Laurenti, 1768, and *Gavialis gangeticus* (Gmelin, 1789) and all of its descendants. Crocodylia is divided into three main groups: Alligatoroidea Gray, 1844 (sensu Brochu, 2003), which assembles all crocodylians closer to *A. mississippiensis* (Daudin, 1802) than to *Cr. niloticus* Laurenti, 1768 or *G. gangeticus* (Gmelin, 1789); Crocodyloidea Fitzinger, 1826 (sensu Brochu, 2003) which includes all crocodylians closer to *Cr. niloticus* than to *A. mississippiensis* or *G. gangeticus*; and Gavialoidea Hay, 1930 (sensu Brochu, 2003), which includes all crocodylians closer to *G. gangeticus* than to *A. mississippiensis* and *Cr. niloticus*.

Specifically, Alligatoroidea is a clade whose most ancient fossil records are from the Late Cretaceous of North America (Brochu, 1999, 2003, 2011). The group had a significant radiation in the Cenozoic, being very abundant in the Americas but also with significant records in Europe, represented by *Arambourgia*, *Diplocynodon* and *Hassiacosuchus*, and in Asia, through genera such as *Alligator*, *Krabisuchus* and *Protoalligator* (Stefano, 1905; Weitzel, 1935; Brochu, 1999; Martin, 2010; Martin & Lauprassert, 2010; Martin *et al.*, 2014; Skutschas *et al.*, 2014; Wang *et al.*, 2016). Phylogenetically, Alligatoroidea is divided into two main clades: all alligatoroids closer to *Caiman crocodilus* (Linnaeus, 1758) than to *Alligator mississippiensis* form the predominantly South American Caimaninae Brochu, 1999 (sensu Brochu, 2003), while those closer to *A. mississippiensis* than to *Ca. crocodilus* form the predominantly North American Alligatorinae Kälin, 1940 (sensu Brochu, 2003).

Caimanine alligatoroids comprise six out of the eight crocodylian species that inhabit South America today and also

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include the majority of the fossil species from the crocodylomorph fauna of the Cenozoic of South America (see Cidade *et al.*, 2019 for a review). The oldest unequivocal records of caimanines are from the Paleocene of South America (see Brochu, 2011; Bona *et al.*, 2018). The ancestor of the earliest South American caimanines has likely come from North America, dispersing between the Late Cretaceous and the Paleocene (Brochu, 1999, 2010, 2011; Cidade *et al*., 2017, 2019).

Most of the alligatoroid fossil species recorded from South America were assigned to Caimaninae (Brochu, 1999, 2010, 2011; Riff *et al*., 2010; Bona *et al*., 2013, 2018; Cidade *et al.*, 2019). The only fossil alligatoroid from South America not assigned to Caimaninae is *Balanerodus logimus*, a taxon described by Langston (1965) based an isolated globular tooth (UCMP-45787, holotype), along with 118 isolated globular teeth, all from the middle Miocene Honda Group of Colombia. Langston (1965) originally assigned this species to "Alligatoridae *incertae sedis*". In later publications, additional material was assigned to this species: a fragment of a right maxilla with two teeth from the Honda Group (Langston & Gasparini, 1997) and an isolated tooth from the middle Miocene Fitzcarrald Arch of Peru (Salas-Gismondi *et al*., 2007). However, neither of these studies offered a classification for a higher taxonomic level for *Balanerodus logimus*. The notably fragmented nature of all the fossil material attributed to this species has made its validity questionable (e.g. Salas-Gismondi *et al*., 2015), with it even being described as "enigmatic" (Langston & Gasparini, 1997). However, no formal taxonomic review of *Balanerodus logimus* has been performed, which will be presented in this paper.

An analogous situation (a fossil taxon with only very fragmented fossils being assigned to it) is seen in another alligatoroid taxon from the Cenozoic of South America: *Caiman venezuelensis*, from the Pliocene–Pleistocene "El Breal de Orocual" asphalt deposit from the Mesa Formation of Venezuela. *Ca. venezuelensis* was described by Fortier & Rincón (2012) based only on an incomplete left maxilla (OR-1677). Beyond the very fragmented nature of the holotype and only known specimen, *Ca. venezuelensis* exhibits some resemblances to the extant species *Ca. crocodilus*, as already pointed out by Fortier & Rincón (2012) and Escobedo-Galván *et al*. (2015). Considering these facts, a taxonomic review on the validity of this species is necessary and is being presented in this work.

The objective of this paper is to perform a detailed taxonomic review on the validity of the species *Balanarodus logimus* and *Caiman venezuelensis*. This study serves as a first step for future assessments that aim to address the evolution and paleoecology of the Crocodylomorph fauna of the Cenozoic of South America. In addition, this paper provides a broader and more precise view about the taxonomic content of the Crocodylomorph fauna during the Miocene and Pleistocene epochs.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; MACN, Museo Argentino de Ciéncias Naturales, Buenos Aires; MCT, Museu de Ciências da Terra, Rio de Janeiro; MN, Museu Nacional, Rio de Janeiro; MUSM, Natural History Museum of San Marcos University, Lima; IVIC, Instituto Venezolano de Investigaciones Científicas, San António de los Altos; OR, 'El Breal de Orocual' collection of the Instituto Venezolano de Investigaciones Científicas, San António de los Altos; UCMP, University of California Museum of Paleontology, Berkeley; USNM, United States National Museum, Washington; YPM PU, Yale Peabody Museum of Natural History, New Haven.

Materials and Methods

Aside from the holotypes of the two species reviewed by this paper, several specimens of other alligatoroid fossil species and of the extant caimanine species– *Caiman crocodilus*, *Ca. latirostris* (Daudin, 1802), *Ca. yacare* (Daudin, 1802), *Melanosuchus niger* (Spix, 1825), *Paleosuchus palpebrosus* (Cuvier, 1807) and *P. trigonatus* (Schneider, 1801) – were analysed as comparative material for characters of systematic and taxonomic relevance. The specimens analysed for each species are as follows:

Allognathosuchus wartheni Case, 1925: YPM-PU-16989.
Brachychampsa montana Gilmore, 1911: AMNH-5032, holotype.
Caiman crocodilus apaporiensis Medem, 1955: FMNH-69812, holotype; FMNH-69813, FMNH-69817, FMNH-69819, FMNH-69821, FMNH-69824, FMNH-69825, FMNH-69828, FMNH-69831, FMNH-69832 (all paratypes).
Caiman crocodilus (excluding *Ca. crocodilus apaporiensis*): AMNH-R-43291, AMNH-R-73048, AMNH-R-137179, FMNH-69842, FMNH-69854, FMNH-69855, FMNH-69865, FMNH-73700 MCT-148-RR, MCT-155-RR, MCT-300-RR, MN-67, MN-1030, MN-1031, MN-25188, MN-25461.
Caiman latirostris: AMNH-R-28367, AMNH-R-143183, MACN-30566, MACN-30567, MACN-30572, MACN-30610, MACN-30612, MCT-156-RR, MCT-157-RR, MN-69, MN-1041, MN-1254, MN-1255, MN-1257, MN-1455, MN-2078, MN-2333, MN-9756, MN-11254, MN-2395, MN-24588.
Caiman wannlangstoni Salas-Gismondi *et al*., 2015*:* MUSM-2377, holotype.

Caiman yacare: AMNH-R-97305, MACN-30540, MACN-30542, MACN-30558, MACN-30593, MACN-30595, MACN-30601, MACN-30602, MACN-30637, MACN-8267, MN-68, MN-1259, MN-9755, MN-12127.

Kuttanacaiman iquitosensis Salas-Gismondi *et al*., 2015: MUSM-1942.

Melanosuchus niger: AMNH-R-58130, MCT-286-RR, MN-61, MN-63, MN-64, MN-66, MN-81, MN-3174.

Paleosuchus palpebrosus: AMNH-R-137170, AMNH-R-137174, AMNH-R-145071, AMNH-R-93812, AMNH-R-97326, FMNH-69874, MCT-269-RR, MCT-291-RR, MN-317, MN-2356.

Paleosuchus trigonatus: AMNH-R-58136, AMNH-R-66391, AMNH-R-129259; AMNH-R-129260, MN-65, MN-2491, MN-9757, USNM-234047.

Procaimanoidea utahensis Gilmore, 1946: USNM-15996, holotype; USNM-15997, paratype.

SYSTEMATIC PALEONTOLOGY

CROCODYLIA GMELIN, 1789, *SENSU* BENTON & CLARK 1988

ALLIGATOROIDEA GRAY, 1844 (*SENSU* NORELL *ET AL*. 1994)

ALLIGATOROIDEA INDET.

Material: UCMP-45787 (holotype of *Balanerodus logimus*)

Occurrence: Honda Group, middle Miocene of Colombia

Description and Comparisons

The holotype of *Balanerodus logimus* is an isolated tooth crown with a globular shape and marked longitudinal crenulations (Langston, 1965; Fig. 1–A). Upon proposing *B. logimus* as a distinct species, Langston (1965) recognized that the holotype tooth and the 118 associated teeth resembled the alligatoroid *Allognathosuchus* Mook, 1921 and the then crocodylid *Bottosaurus* Agassiz, 1849 (currently recognized as an alligatoroid, see Cossette & Brochu, 2018). However, Langston (1965) argued that *Balanerodus logimus* was different from *Allognathosuchus* in having more "perfect rounded" crowns, in lacking apically flat teeth, and for exhibiting more developed mesial and distal carinae. Additionally, *Balanerodus logimus* is distinct from *Bottossaurus* according to Langston (1965) by presenting a pronounced division between crown and root.

The posterior upper and lower teeth of most alligatoroid species have blunt crowns, distinct from the acute crowns seen in the anterior and middle teeth. Posterior teeth with distinctive globular crowns similar to *Balanerodus logimus* can be seen not only in *Allognathosuchus* (see Case, 1925; Brochu, 2004; Fig. 1–B) but also in the posterior upper and lower teeth of *Melanosuchus niger* (Fig. 1–G), *Caiman latirostris* (Fig. 1–H) *Gnatushchus* Salas-Gismondi *et al*., 2015, *Kuttanacaiman* Salas-Gismondi *et al*., 2015, (Fig. 1–C), *Ca. wannlangstoni*, (Fig. 1–D) and *Purussaurus* Barbosa-Rodrigues, 1892 (see Salas-Gismondi *et al*., 2015). Posterior globular crowns are also known in several extinct basal alligatoroids such as *Brachychampsa* Gilmore, 1911 (see Brochu, 2004; Fig. 1–E), *Albertochampsa* Erickson, 1972, *Stangerochampsa* Wu *et al*., 1996, *Diplocynodon hantoniensis* (Wood, 1846) (see Rio *et al*., 2019) and the extinct alligatorids *Procaimanoidea utahensis* (Fig. 1–F) and *P. kayi* Mook, 1941. Additionally, two isolated teeth with a similar morphology assigned as "Alligatoroidea gen. et. sp. nov." have been reported from the early Miocene Castillo Formation of Venezuela (Solórzano *et al*., 2019). Except *Gnatusuchus*, which can be distinguished from the holotype of *Balanerodus logimus* for lacking carinae (see Salas-Gismondi *et al*., 2015), the globular teeth of these alligatoroids exhibit crowns that are largely similar to the holotype of *Balanerodus logimus*, without any systematically relevant differences. Generally, the crowns of the posteriormost teeth are even more globular than the first posterior teeth, but some of these posterior-most globular crowns (for example in *Allognathosuchus wartheni*, Fig. 1–B) are different from the holotype of *Balanerodus logimus*, in which they are anteroposteriorly expanded and dorsoventrally compressed. In *Bottosaurus harlani* (Meyer, 1832), the most posterior teeth are globular but more lateromedially compressed than the holotype of *Balanerodus logimus*, which bears more resemblance to the first set of posterior-most teeth of *Bottosaurus harlani*, which are less lateromedially compressed (see Cossette & Brochu, 2018). However, the enamel of *Bottosaurus harlani* teeth display apical wrinkling (Cossette & Brochu, 2018), which is absent in *Balanerodus logimus* and thus distinguishes this last species from the former.

Thereby, it is probable that UCMP-45787 was the crown of a posterior maxillary or mandibular tooth, but not of one of the posteriormost teeth, if the morphology of most extant and extinct alligatoroid species is considered.

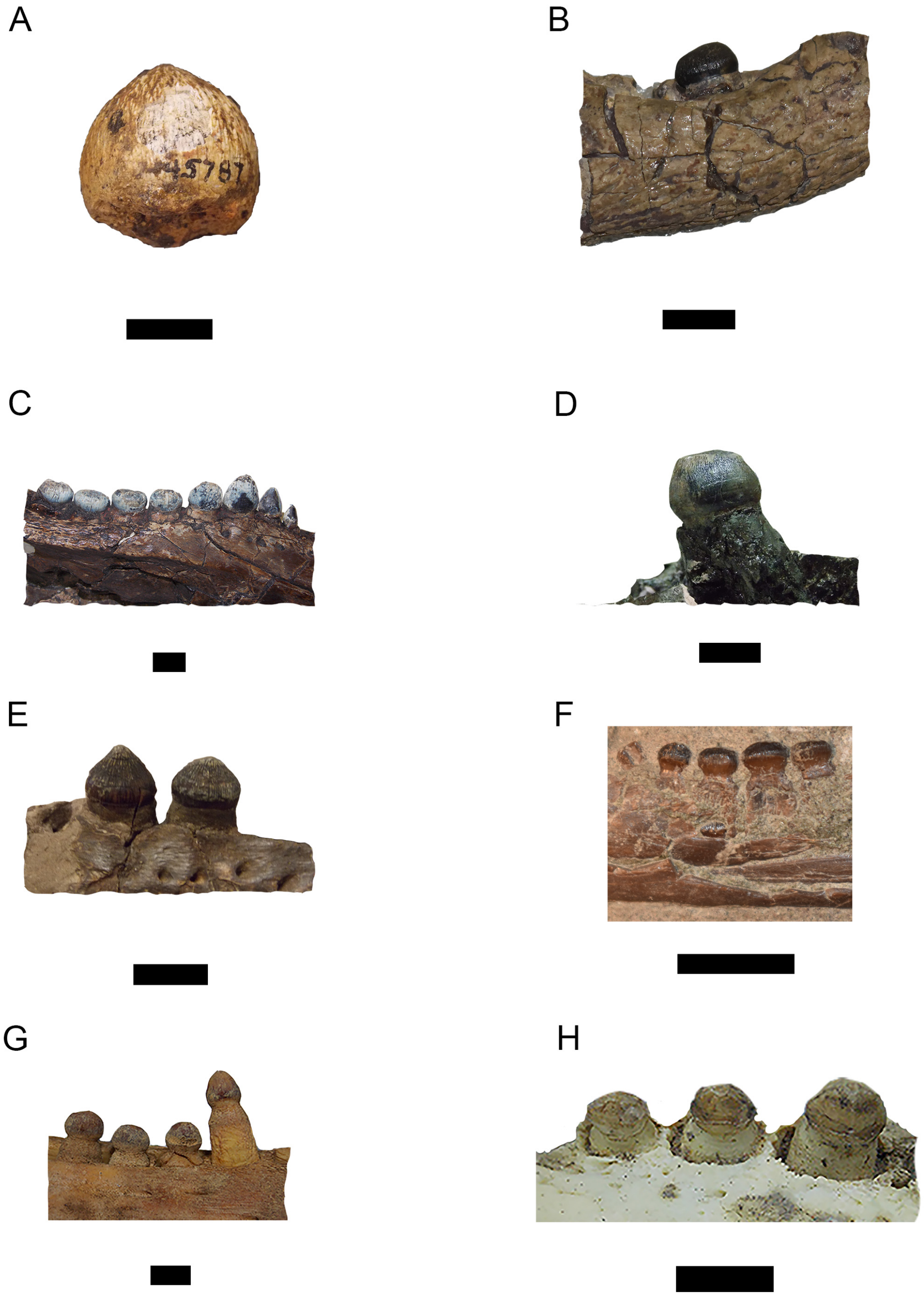

FIGURE 1. Comparison between similar globular teeth crowns found among alligatoroids. A, *Balanerodus logimus*, holotype, in labial view (UCMP-45787). B, *Allognathosuchus wartheni* (YPM PU-16989), right dentary tooth in lateral view. C, *Kuttanacaiman iquitosensis* (MUSM-1942), left dentary teeth in medial view. D, *Caiman wannlangstoni* (MUSM-2377, holotype), right maxillary tooth in lateral view. E, *Brachychampsa montana* (AMNH-5032, holotype), right maxillary teeth in medial view. F, *Procaimanoidea utahensis* (USNM-15997, paratype), posterior right dentary teeth in medial view. G, *Melanosuchus niger* (MN-64), posterior right dentary teeth in lateral view. H, *Caiman latirostris* (MACN-30612), posterior left maxillary teeth in medial view. Scale bars = 1 cm.

Taxonomic Review

The holotype of *Balanerodus logimus* does not present any autapomorphies when compared to other fossil and extant alligatoroids, including several taxa that were named before it (*Allognathosuchus*, *Purussaurus*, *Melanosuchus niger* and *Caiman latirostris*). As such, this species is considered to be a *nomen dubium*, and the holotype of *Balanerodus logimus* is designated as Alligatoroidea indet.

The other 118 isolated teeth referred to *B. logimus* by Langston (1965) were not directly analysed in this work, but the description indicates the presence of the same general structure as the holotype (Langston, 1965, p. 114–115). As such, these are also assigned to Alligatoroidea indet., along with a tooth (MUSM-1261) assigned to *B. logimus* by Salas-Gimsondi *et al*. (2007). The specimen assigned to *B. logimus* by Langston & Gasparini (1997) comprises a right maxilla with two teeth, from the Honda Group (middle Miocene, Colombia).This specimen was also not directly analysed in this work, and its new taxonomic assignment shall be assessed in a future study of the specimen. Nevertheless, these issues do not change the status of *B. logimus* as a *nomen dubium,* due to the absence of distinctive characters of the name-bearing specimen (the holotype) in comparison with previously described alligatoroids.

CAIMANINAE BROCHU, 1999 (SENSU BROCHU, 2003 FOLLOWING NORELL 1988)

CAIMAN CROCODILUS (LINNAEUS, 1758)

Material: OR-1677 (holotype of *Caiman venezuelensis* Fortier & Rincón, 2012)

Occurrence: El Breal de Orocual tar pit, Pliocene–Pleistocene of Venezuela (see Rincón et al., 2009; Onary et al., 2018, for the age of the locality).

Description and Comparisons

The holotype and only known specimen of *Caiman venezuelensis* (OR-1677; Figs. 2–A and 3–A) is an incomplete left premaxilla and a very small portion of the left maxilla. It preserves the third, fourth and fifth premaxillary alveoli, part of the second alveolus, and the occlusal pit for the fourth mandibular alveolus. Only the tooth of the fifth alveolus is preserved, and only the posterolateral portion of the incisive foramen is preserved. The suture with the right premaxilla is preserved and is large, extending anteriorly until the anterior margin of the fourth alveolus.

The presence of a pit for the occlusion of the fourth mandibular tooth between the premaxilla and the maxilla allows an assignment of OR-1677 to Alligatoroidea (see Brochu, 1997, 1999). Non-caimanine alligatoroid fossils are not known from either the Pliocene or Pleistocene of South America (see Fortier & Rincón, 2012), thus it is likely that OR-1677 can be assigned to Caimaninae. Among caimanine taxa, the specimen can be clearly distinguished from the peculiar *Purussaurus* (see Aguilera *et al*., 2006; Aureliano *et al*., 2015) and *Mourasuchus* (see Langston, 1965; Cidade *et al*., 2017), which have very derived morphologies in the premaxillae; from *Paleosuchus*, which has only four premaxillary teeth (Brochu, 1997, 1999); and from *Melanosuchus* for not presenting the vomer ventrally in the posterior portion of the premaxilla (see Brochu, 1999). OR-1677 may be distinguished from *Caiman latirostris* by the presence of an occlusal fossa for the fourth mandibular tooth posteriorly to the fifth premaxillary alveolus, which does not occur in that species (Bona *et al*., 2013). Among the extant species of *Caiman* and the fossil caimanine species that preserve premaxillae, the holotype of *Ca. venezuelensis* differs in having significantly narrower premaxillae, which are longer than wide, with a long contact between both premaxillae posterior to the incisive foramen. The only extant caimanine with similarly long and narrow premaxillae is the subspecies *Ca. crocodilus apaporiensis*. Additionally, some specimens of *Ca. crocodilus apaporiensis* (the holotype FMNH-69812, FMNH-69813, FMNH-69821, FMNH-69824; Figs. 2–B and 3–B) exhibit a long contact between both premaxillae posterior to the incisive foramen. In another specimen (FMNH-69828), the left premaxilla is as long as in the aforementioned specimens, whereas the right premaxilla is shorter. The fact that this second character is exhibited by some of the largest specimens of *Ca. crocodilus apaporiensis* suggests that this trait appears late in ontogeny in this subspecies, although individual variation is also possible. The difference in size between the premaxillae of FMNH-69828 supports the hypothesis of individual variation. This issue, however, must be assessed by thorough ontogenetic studies on the subspecies.

These two characters shared by *Ca. crocodilus apaporiensis* and OR-1677 represent two of the diagnostic characters originally proposed by Fortier & Rincón (2012) for *Ca. venezuelensis*. Premaxillae that are narrow and significantly longer than wide, such as those of the holotype of *Ca. venezuelensis*, can be seen only in the specimens of *Ca. crocodilus apaporiensis*. However, narrow premaxillae that are nearly twice as long as they are wide (although not to the extent of *Ca. crocodilus apaporiensis* and *Ca. venezuelensis*) are also known in *Ca. crocodilus* specimens not assigned to *Ca. crocodilus apaporiensis* (MCT-148-RR, MCT-155-RR, MCT-300-RR, MN-25461), *Ca. yacare* (MACN-30595; Fig. 3–D), *Melanosuchus niger* (MCT-286-RR, MN-63, MN-81, MN-3174), and *Paleosuchus palpebrosus* (MCT-291-RR). Additionally, premaxillae contacting medially in ventral view for half of their length can also be observed in at least one specimen of *Ca. crocodilus* that is not assigned to *Ca. crocodilus apaporiensis* (MCT-148-RR; Fig. 3–C) and in *Paleosuchus* sp. (MCT-270-RR).

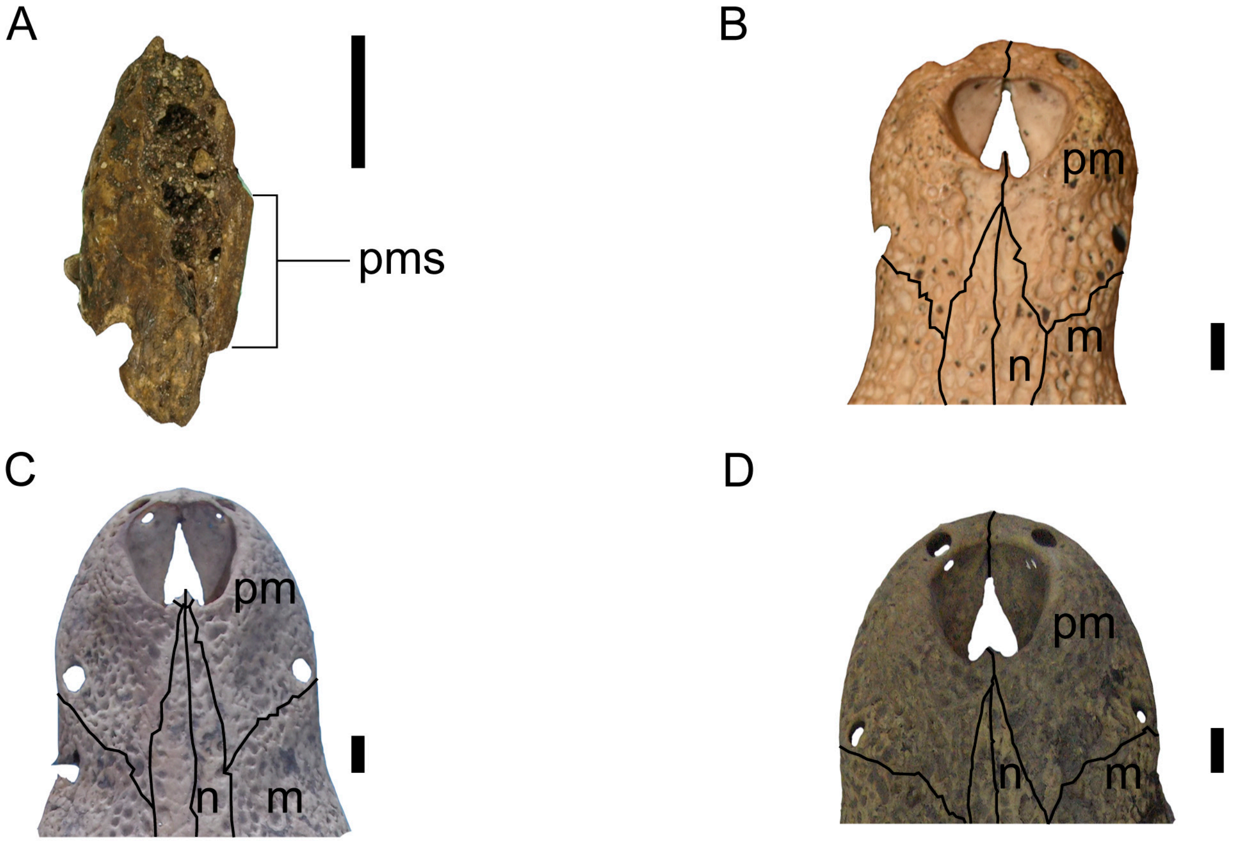

FIGURE 2. Comparison between the holotype of *Caiman venezuelensis* in dorsal view and extant *Caiman*. A, *C. venezuelensis* (OR-1677, holotype), in dorsal view. B, *C. crocodilus apaporiensis* (FMNH-69812, holotype), premaxillae in dorsal view. C, *C. crocodilus* (MCT-148-RR), premaxillae in dorsal view. D, *C. yacare* (MACN-30595), premaxillae in dorsal view. Abbreviations: m = maxilla, n = nasal, pm = premaxilla, pms = suture between both premaxillae. Scale bars = 1 cm.

Fortier & Rincón (2012) proposed three additional diagnostic characters for *Ca. venezuelensis*. The first, a "linear premaxillae suture posterior to the incisive foramen", occurs in several specimens of *Ca. crocodilus apaporiensis* (FMNH-69812, FMNH-69813, FMNH-69819, FMNH-69824, FMNH-69828, FMNH-69831, FMNH-69832), *Ca. crocodilus* not belonging to *Ca. crocodilus apaporiensis* (AMNH-43291, MCT-148-RR, MCT-155-RR, MCT-300-RR, MN-1031, Fig. 3–C), *Ca. yacare* (AMNH-R-97305, MACN-30542, MACN-30593, MACN-30602, MACN-30637, MN-68, MN-1259, MN-9755), and at least one specimen of *Ca. latirostris* (MCT-156-RR), *M. niger* (AMNH-R-58130) and *Paleosuchus* sp. (MCT-268-RR). The second diagnostic character, "tooth row relative to the last four premaxillary alveoli form a straight line rather than curved, in ventral view" is very evident in all specimens of *Ca. crocodilus apaporiensis* analysed in this study (except for FMNH-69819, which is a hatchling and thus exhibits an early stage of development), and is also seen in several specimens of the *Ca. crocodilus* not belonging to *Ca. crocodilus apaporiensis* (AMNH-43291, MCT-148-RR, MCT-155-RR, MN-25461; Fig. 3–C), *Ca. yacare* (AMNH-R-97305, MACN-30542, MACN-30558, MACN-30593, MACN-30595, MACN-30601, MACN-30602, MN-1259, MN-9755,; Fig. 3–D), and also in some specimens of *M. niger* (MN-64 and MN-3174). In some specimens of *P. palpebrosus* (AMNH-R-93812, MCT-269-RR, MCT-291-RR, MN-317), *P. trigonatus* (AMNH-R-66391, MN-65, MN-2491, MN-9757) and *Paleosuchus* sp. (MCT-268-RR and MCT-270-RR), the three last premaxillary teeth (which are homologous to the last three premaxillary teeth of other caimanines, see Brochu, 1997) also form a straight line in ventral view.

The third proposed diagnostic character of OR-1677, "incisive foramen long, reaching the fourth premaxillary alveolus", is actually rather common in all species of living Caimaninae, observed in many extant caimanine specimens analysed in this study, including: all specimens of *Ca. crocodilus apaporiensis*; *Ca. crocodilus* excluding *Ca. crocodilus apaporiensis* (AMNH-43291, AMNH-R-137179, MCT-148-RR, MCT-155-RR, MCT-300-RR, MN-1030, MN-1031, MN-25461); *Ca. latirostris* (AMNH-R-143183, MACN-30566, MACN-30567, MACN-30572, MACN-30610, MCT-156-RR, MN-1041, MN-1254, MN-1255, MN-1455, MN-2078, MN-2333, MN-9756, MN-11254, MN-24588); *Ca. yacare* (AMNH-R-97305, MACN-30542, MACN-30558, MACN-30593, MACN-30595, MACN-30601, MACN-30602, MACN-8267, MN-68, MN-1259, MN-9755, MN-12127); *M. niger* (AMNH-R-58130, MCT-286-RR, MN-61, MN-63, MN-64, MN-81, MN-3174,); *P. palpebrosus* (AMNH-R-93812, MCT-269-RR, MCT-291-RR, MN-317) and *P. trigonatus* (, AMNH-R-66391, MN-65, MN-2491, MN-9757).

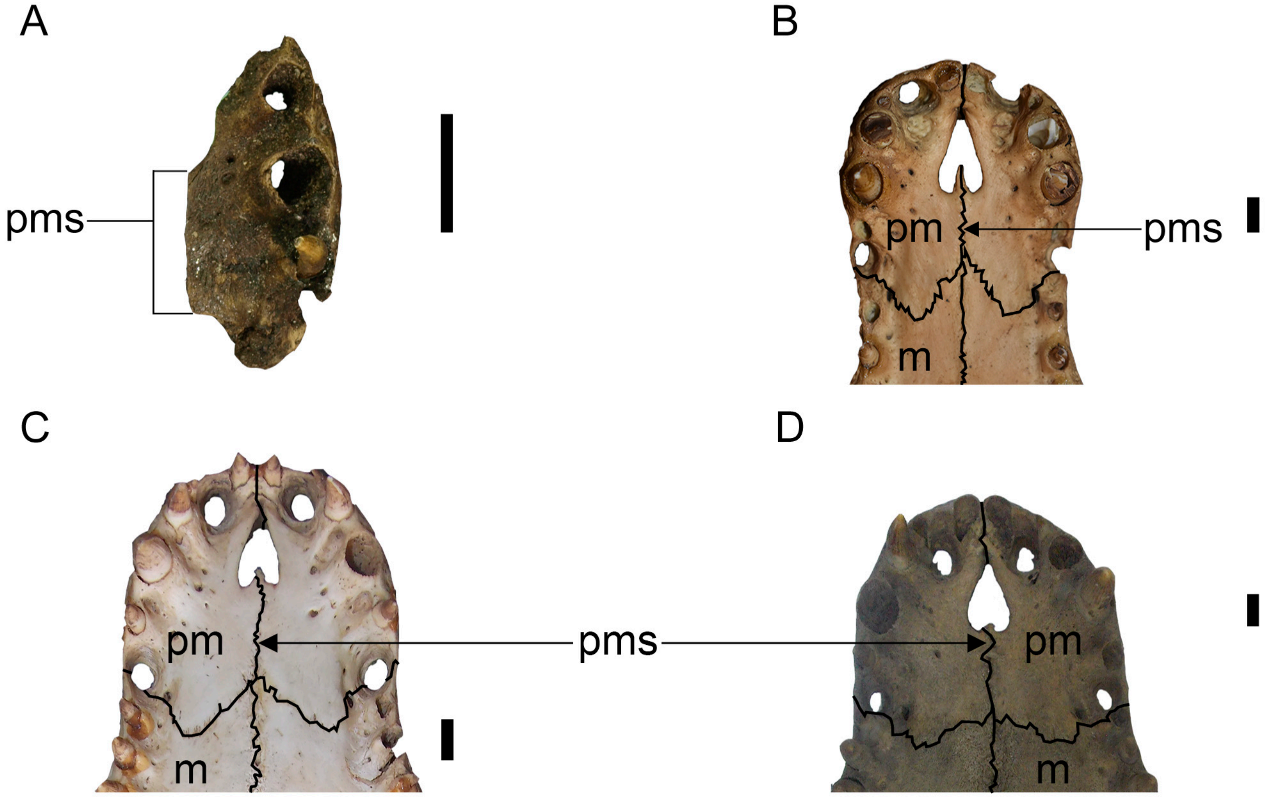

FIGURE 3. Comparison between the holotype of *Caiman venezuelensis* in ventral view and extant *Caiman*. A, *C. venezuelensis* (OR-1677, holotype), in ventral view. B, *C. crocodilus apaporiensis* (FMNH-69812, holotype), premaxillae in ventral view. C, *C. crocodilus* (MCT-148-RR), premaxillae in ventral view. D, *C. yacare* (MACN-30595), premaxillae in ventral view. Abbreviations: m = maxilla, pm = premaxilla, pms = suture between both premaxillae. Scale bars = 1 cm.

Taxonomic Review

From the five diagnostic characters proposed by Fortier & Rincón (2012) for *Caiman venezuelensis*, only the first two are found to be systematically relevant in this study. The character 'tooth row relative to the last four premaxillary form a straight line rather than curved, in ventral view', is here considered to be correlated with the lateromedial compression of the premaxillae already treated in one of the diagnostic characters. The shape of the suture between the premaxillae posterior to the incisive foramen, was found to be intraspecifically variable in the living caimanine specimens analysed in this work; thus the 'linear' shape of this structure in *Ca. venezuelensis* is not considered systematically relevant here. As for the character 'incisive foramen long, reaching the fourth premaxillary alveolus', the fact that this feature is present in most living caimanine specimens analysed in this study, indicates that it is not systematically relevant.

Therefore, based on the systematically relevant characters, the holotype and only known specimen of *Caiman venezuelensis* can be distinguished from all other fossil or extinct Caimaninae, except for some individuals of the extant species *Ca. crocodilus* (mostly *Ca. crocodilus apaporiensis*). Like OR-1677, *Ca. crocodilus apaporiensis* exhibits premaxillae that are significantly longer than wide, with some specimens exhibiting a large contact between both premaxillae posterior to the incisive foramen. As such, the characters that diagnose *Ca. venezuelensis* fall within the range of morphological variation seen in *Ca. crocodilus,* and as a result this study considers *Ca. venezuelensis* Fortier & Rincón, 2012 to be a junior synonym of *Ca. crocodilus* (Linnaeus, 1758). An affinity of the specimen OR-1677 to *Ca. crocodilus apaporiensis* is here suggested, but further studies and the finding of more complete fossils are needed for further assessments on the relationship between the specimen and the extant subspecies.

Discussion

The non-validity of the species *Balanerodus logimus* and *Caiman venezuelensis* found here, do not mean a significant decrease in the diversity of the respective crocodylomorph faunas to which they belong (see Cidade *et al.*, 2019 for a review). The middle Miocene fauna of the Amazon region of South America has seen an increase of taxa in the last few years from the Pebas Formation of Peru, which includes several eminent durophagous taxa such as *Gnatusuchus*, *Kuttanacaiman* and *Ca. wannlangstoni* (Salas-Gismondi *et al*., 2015).

Additionally, a durophagous habit has also been proposed for late Miocene taxa such as *Globidentosuchus* Scheyer *et al*., 2013 from the Urumaco Formation (Scheyer *et al*., 2013; Salas-Gismondi *et al*., 2015), *Caiman brevirostris* Souza-Filho, 1987 from the Solimões Formation (Fortier *et al*., 2014; Cidade *et al*., 2019), and *Eocaiman* Simpson, 1933 from the Paleocene–middle Miocene (Cidade & Hsiou, 2018). In this way, a number of durophagous caimanine taxa (of which *Balanerodus logimus* was thought to be one example) have been well-established in the recent years, especially in the middle Miocene, so the non-validity of this species does not reduce our understanding about the durophagous caimanine taxa of the Cenozoic of South America.

A similar scenario may be pointed out for the Pliocene and Pleistocene of South America regarding the status of *Caiman venezuelensis* as a junior synonym of *Ca. crocodilus*. Although the crocodylomorph fauna of the Pliocene of South America is indeed low, with only the occurrences of *Crocodylus falconensis* Scheyer *et al*., 2013 from the San Gregorio Formation of Venezuela, and of *Crocodylus* sp. from the Ware Formation of Colombia (Moreno-Bernal *et al*., 2016), future fieldwork in these units, and the 'El Breal de Orocual' asphalt deposit will likely yield new crocodylomorph records. As pointed out by Fortier & Rincón (2012), although the fossil record of Caimaninae in the Pleistocene of South America is very rich in specimens, it is not yet rich in species. This is supported by the taxonomic review presented here, which shows it comprises only records of extant species (see also Cidade *et al.*, 2019). Nevertheless, a thorough analysis of this record may reveal a richer diversity of species in the Pleistocene of the continent, including not only fossils of extant species that were not yet recorded, but completely new species as well. Additionally, to our knowledge the assignment of OR-1677 to *Ca. crocodilus* represents the first fossil record of the species (see Fortier & Rincón 2012 and Cidade *et al*., 2019, for reviews of the crocodylian fossil fauna of the Cenozoic of South America).

The possible affinity between OR-1677 and *Caiman crocodilus apaporiensis* raises interesting evolutionary questions. The extant subspecies has a small geographic distribution, concentrated on the Upper Apaporis River in Colombia (Medem, 1955; Velasco & Ayarzagüena, 2010; Escobedo-Galván *et al*., 2011), although most recent studies have recorded the subspecies in other rivers and lakes in Colombia (Escobedo-Galván *et al*., 2015). As such, the occurrence of OR-1677 (assuming its assignment to *Ca. crocodilus apaporiensis*) in the Pliocene–Pleistocene of Venezuela would not only record the presence of *Ca. crocodilus apaporiensis,* but would significantly expand the present, known geographical distribution of the subspecies. However, some authors have suggested a cline of narrow-snouted caimans in Colombian and Venezuelan swamps (Ayarzagüena, 1984; Gorzula, 1994; Okamoto *et al.*, 2015). This perspective reinforces the caution of assigning *Ca. venezuelensis* as a junior synonym of *Ca. crocodilus* rather than of *Ca. crocodilus apaporiensis*. Additionally, cranial morphometric analysis of *Ca. croco-*

dilus apaporiensis performed by Escobedo-Galván *et al.* (2015) found a higher degree of difference between that subspecies and the other subspecies of *Ca. crocodilus* than between *Ca. yacare* (considered a full distinct species) and the other subspecies of *Ca. crocodilus* excluding *Ca. crocodilus apaporiensis*. This indicates that this subspecies may be considered a different species, but molecular analyses are needed to settle this issue (Escobedo-Galván *et al*., 2015). Nevertheless, the morphometric analysis of Escobedo-Galván *et al*. (2015) also found an overlap between *Ca. crocodilus apaporiensis* and *Ca. crocodilus* (Linnaeus, 1758), which also reinforces the perspective that *Ca. venezuelensis* is better seen as a junior synonym of *Ca. crocodilus* than *Ca. crocodilus apaporiensis*. This issue, however, can be reassessed upon an eventual taxonomic review of *Ca. crocodilus*, which may be a complex of cryptic species (Venegas-Anaya *et al*., 2008; Escobedo-Galván *et al*., 2011).

Molecular analyses have estimated the time of divergence between *Caiman crocodilus* and *Ca. yacare* between 2 to 5 million years ago (Oaks, 2011), a date that places it between the Pliocene and the Pleistocene. Nevertheless, there has been only tentative referrals of fossils to *Ca. yacare* for the late Miocene of South America (see Fortier *et al*., 2009; Bona *et al*., 2013), and no record of any kind of *Ca*. *crocodilus* until the one made in this study. Our referral of OR-1677 to *Ca*. *crocodilus* not only effectively records the presence of the species for the Pliocene–Pleistocene of South America and in the north of the continent (an area currently inhabited by the species), but also shows a perspective that more fossils of *Ca*. *crocodilus* may be found in the Pliocene or in the Pleistocene, or in older epochs of the continent, providing more information on the origin and evolution of this species.

Conclusions

This study concludes that the species *Balanerodus logimus* is a *nomen dubium*, with its holotype (UCMP-45787) being assigned as "Alligatoroidea indet.", and that *Caiman venezuelensis* Fortier & Rincón, 2012 is a junior synonym of *Ca. crocodilus* (Linnaeus, 1758). The record of a *Ca. crocodilus* fossil from the Pliocene–Pleistocene of Venezuela is the first published fossil record that can be assigned to this extant species. These taxonomic reviews provide a more accurate picture of the diversity of fossil alligatoroids in the Cenozoic of South America, which remains considerably high despite the non-validity of *B. logimus* and *Ca. venezuelensis* as distinct species. Additionally, this study demonstrates the importance of taxonomic reviews for a proper understanding of fossil diversity, which has been frequently overlooked even in comprehensive systematic studies of fossil taxa.

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