Taxonomic and phylogenetic review of *Necrosuchus ionensis* (Alligatoroidea: Caimaninae) and the early evolution and radiation of caimanines

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Alligatoroidea is the most species-rich crocodylomorph clade of the Cenozoic of South America, with nearly all species belonging to the Caimaninae clade. However, the earliest records of Caimaninae in South America, which are from the Palaeocene, are based mostly on incomplete specimens, which increases the importance of detailed taxonomic and phylogenetic studies on these taxa. This paper offers a taxonomic and phylogenetic review of *Necrosuchus ionensis*, a caimanine species from the Salamanca Formation of the Palaeocene of Argentina. *Necrosuchus ionensis* is considered a valid species, albeit with a different diagnosis from that proposed by previous authors. The phylogenetic analysis shows, for the first time, that *N. ionensis* belongs to the derived Caimaninae clade Jacarea. However, a better understanding of the Jacarea clade is needed, and alternative placements for *N. ionensis* might be considered. Nevertheless, the placement of *N. ionensis* as a derived caimanine raises interesting perspectives on the early evolution and radiation of caimanines, which are thoroughly discussed in this paper together with other results obtained in this study, such as the recovery of the North American caimanines *Bottosaurus* and *Tsoabichi* as a clade.

ADDITIONAL KEYWORDS: Crocodylia – *Necrosuchus* – Palaeocene – Palaeogene – Salamanca Formation – South America.

INTRODUCTION

Alligatoroidea Gray, 1844 (*sensu* Brochu, 2003) is a crocodylian clade formed by *Alligator mississippiensis* (Daudin, 1802) and all crocodylians closer to it than to *Crocodylus niloticus* Laurenti, 1768 or *Gavialis gangeticus* (Gmelin, 1789). The fossil record of Alligatoroidea traces back to the Late Cretaceous of North America (Brochu, 2003). All alligatoroids phylogenetically closer to *Caiman crocodilus* (Linnaeus, 1758) than to *Al. mississippiensis* form the clade Caimaninae Brochu, 1999, whose fossil record is predominantly from the Cenozoic of South America. Additionally, there are six recognized extant caimanine species [*C. crocodilus*, *Caiman latirostris* (Daudin, 1802), *Caiman yacare* (Daudin, 1802), *Melanosuchus niger* (Spix, 1825), *Paleosuchus palpebrosus* (Cuvier,

1807) and *Paleosuchus trigonatus* (Schneider, 1801)], all of which are exclusively South American except for *C. crocodilus*, which also occurs in Central America, the Caribbean and Mexico (Carvalho, 1951; Medem, 1981, 1983; Venegas-Anaya *et al.*, 2008; Cossette & Brochu, 2018; Cidade *et al.*, 2019). However, recent studies have shown a likelihood that more species might be recognized in the future, especially from *C. crocodilus*, which might be a complex of cryptic species (e.g. Venegas-Anaya *et al.*, 2008; Escobedo-Galván *et al.*, 2015).

The most ancient unequivocal records of Caimaninae are from the Palaeocene of South America (see Brochu, 2011; Bona *et al.*, 2018). Although fossils from the Late Cretaceous of the US state of Montana (see Bryant, 1989; Brochu, 1999) and from the Palaeocene of Texas (Brochu, 1996) have been referred to the group, their phylogenetic placement has never been tested (Brochu, 2010). South American caimanines are

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proposed to descend from North American ancestors that dispersed between the Late Cretaceous and the Palaeocene (Brochu, 1999, 2010, 2011; Cidade *et al.*, 2017, 2019; Bona *et al.*, 2018) owing to most basal alligatoroids and most members of the sister group of Caimaninae, Alligatorinae, being from North America (Brochu, 1999, 2010, 2011). Another factor to consider is the presence of alligatoroids in the Late Cretaceous of North America (see Brochu, 1997b, 1999) and their absence in the South American deposits of the same epoch. The alligatoroid fossil record of South America is almost exclusively represented by Caimaninae (Brochu, 1999, 2010, 2011; Riff *et al.*, 2010; Bona *et al.*, 2012, 2018; Cidade *et al.*, 2018). The only fossil alligatoroid not assigned to Caimaninae is *Balanerodus logimus* Langston, 1965, which has been described as an 'Alligatoridae *incertae sedis*' (see Langston, 1965: p. 114).

The Caimaninae record of the Palaeogene of South America is sparse, especially when compared with the mega-diverse record of the same group in the Miocene of the continent (see Gasparini, 1996; Riff *et al.*, 2010; Bona *et al.*, 2012; Cidade *et al.*, 2019). The Palaeogene record of South American caimanines is concentrated in the Palaeocene, with the species described being *Eocaiman palaeocenicus* Bona, 2007 and *Necrosuchus ionensis* Simpson, 1937 from the Salamanca Formation of Argentina, *Eocaiman itaboraiensis* Pinheiro et al., 2013 from the Itaboraí Basin of Brazil, *Notocaiman stromeri* Rusconi, 1937 from the Las Violetas Formation of Argentina and *Protocaiman peligrensis* Bona et al., 2018 from the Salamanca Formation of Argentina. The only species described from the Eocene is *Eocaiman cavernensis* Simpson, 1933 from the Sarmiento Formation of Argentina. In the Oligocene, there are no records of caimanines at a specific level; Chiappe (1988) proposed the species *Caiman tremembensis* Chiappe, 1988 from the Tremembé Formation of Brazil, but Fortier *et al.* (2014) considered the fossils assigned to the species to belong to an indeterminate caimanine, making *C. tremembensis* a *nomen dubium*.

Despite the sparsity of the Palaeogene record of South American caimanines, their study is fundamental to understand the early evolution and radiation of the group. It follows that it is important to have an accurate taxonomy and phylogenetic systematics of those species in order to ensure that the evolutionary inferences may be as soundly based as possible. Our knowledge on the early evolutionary history of Caimaninae is hindered by the fact that most of the South American Palaeogene occurrences of the group are made of incomplete fossils (see Simpson 1933, 1937; Rusconi, 1937; Chiappe, 1988; Bona, 2007; Brochu, 2011; Pinheiro *et al.*, 2013; Fortier *et al.*, 2014; Bona *et al.*, 2018; Cidade *et al.*, 2019). Nevertheless, this only increases the need for comprehensive taxonomic and phylogenetic assessments of these species for a better understanding of the early evolution of Caimaninae.

One such species is *N. ionensis*, which was described from a fragmentary holotype consisting of a right dentary, other cranial fragments and a partial postcranium (AMNH-3219). Upon describing the species, Simpson (1937) thought it to be close to *Leidyosuchus* Lambe, 1907 or *Borealosuchus* Brochu, 1997a (both of which were considered the same genus, *Leidyosuchus*, at the time), but further studies by Brochu (1997a, 2011) established it as a caimanine alligatoroid. However, the diagnoses already proposed for *N. ionensis* did not thoroughly differentiate it from other caimanines and, as such, a review on the taxonomic validity of the species is considered necessary. Given this issue, the main objective of the present study is to perform a taxonomic review of *N. ionensis* and a review of its phylogenetic placement. Additionally, an updated, comprehensive overview on the early evolution of the Caimaninae clade is also offered, which is based not only on the results of this study but also on those of recently published assessments of the South American caimanine record of the Palaeogene (e.g. Brochu, 2011; Pinheiro *et al.*, 2013; Bona *et al.*, 2018).

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York; CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro; DGM, Divisão de Geologia e Mineralogia, Rio de Janeiro (currently MCT, Museu de Ciências da Terra, Rio de Janeiro); 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; UCMP, University of California Museum of Paleontology, Berkeley; UFAC, Universidade Federal do Acre, Rio Branco; USNM, United States National Museum, Washington.

MATERIAL AND METHODS

Besides the holotype and only known specimen of *N. ionensis* revised in the present study, several specimens of extant caimanine species (*C. crocodilus*, *C. latirostris*, *C. yacare*, *M. niger*, *Pa. palpebrosus* and *Pa. trigonatus*) were analysed for comparisons of

characters of systematic and taxonomic relevance. A list of the specimens analysed is available in the List of osteological specimens of extant Caimaninae species used for anatomical comparisons from the Supporting Information.

The morphological data matrix used in the phylogenetic analysis was scored in the software Mesquite, v.2.75 (Maddison & Maddison, 2011). The matrix is the same as that used by Souza-Filho *et al.* (2019), in which most taxa, characters and scorings are based on Brochu (2011). The only changes from the matrix of Souza-Filho *et al.* (2019) were in the scoring of some characters of *N. ionensis* (for details, see 'Details on character scoring' in the Supporting Information), in the inclusion of *Bottosaurus harlani* (Meyer, 1832) from the scoring of Cossette & Brochu (2018) and in the exclusion of *Melanosuchus fisheri* Medina, 1976 from the analysis, because that taxon was considered as non-valid in recent taxonomic reviews (Bona *et al.*, 2017; Foth *et al.*, 2018). Given that the matrix of this analysis includes more characters than used by Cossette & Brochu (2018), many characters were originally scored for *Bo. harlani* in this study; the complete scoring of this taxon can be found in the 'Character Matrix' in the Supporting Information.

The analysis was performed with 94 operational taxonomic units, with 93 eusuchian taxa in the ingroup, the non-eusuchian crocodyliform *Bernissartia fagesii* Dollo, 1883 as the outgroup and a total of 187 characters. The complete list of taxa and characters used in the analyses, along with the complete matrix of scored characters by taxon and a Nexus file with the matrix used in this study are available in the Supporting Information.

The analysis was performed using Tree Analysis software in New Technology (TNT; Goloboff *et al.*, 2008). An initial analysis was performed with 7465 replications, a random seed value of '0' and 20 cladograms saved per replication. The branch-swapping algorithm selected was 'tree-bisection-reconnection'. The characters were unordered and non-additive. This analysis generated 3773 most parsimonious trees of 645 steps that were subjected to a second analysis, which resulted in 23 040 most parsimonious trees with the same number of steps. Posteriorly, a Pcr Prune (Goloboff & Szumik, 2015; see also Pol & Escapa, 2009) analysis was also performed in TNT to identify unstable taxa that were creating polytomies and to obtain an alternative topology by excluding the unstable taxa while acknowledging the possible placements of such taxa in the alternative topology. A TNT file with the matrix used in this study is available in the Supporting Information.

RESULTS

SYSTEMATIC PALAEONTOLOGY

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

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

CAIMANINAE BROCHU, 2003 (FOLLOWING NORELL, 1988)

NECROSUCHUS SIMPSON, 1937

Emended diagnosis: A caimanine with the following combination of characters: differs from all other caimanines (except *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 and some specimens of *Paleosuchus*) in having the 13th dentary alveolus as the largest immediately caudal to fourth; differs from *Purussaurus* in having a slender mandibular ramus and in not having the first four alveoli as the largest of the mandibular ramus; differs from *Paleosuchus* in having an atlantal rib without a thin lamina in the anterior end, and the posterior mandibular alveoli and teeth not lateromedially compressed.

Type specimen: Necrosuchus ionensis Simpson, 1937.

Diagnosis: Same as for the genus, because it is the only species.

Holotype and only known specimen: AMNH 3219, right dentary with associated cranial fragments and partial postcranial skeleton.

Occurrence: Salamanca Formation, Palaeocene of Argentina.

Description and comparisons

After being described originally (Simpson, 1937), the holotype and only known specimen of *N. ionensis* was subjected to a detailed redescription by Brochu (2011), making a detailed assessment on the anatomy of this species unnecessary. However, given our reanalysis of the holotype and of what has been published since about *N. ionensis*, it is considered that its status as a valid species requires revision.

Two characteristics indicate that *N. ionensis* is a caimanine alligatoroid: the presence of a slender process ventral to the basioccipital tubera (Brochu, 2011: Character 176, state 2; Fig. 1), which among Crocodylia is found only in caimanines, and is present in all Caimaninae taxa except *Culebrasuchus* (Hastings *et al.*, 2013); and the splenial being excluded from the mandibular symphysis, with the anterior
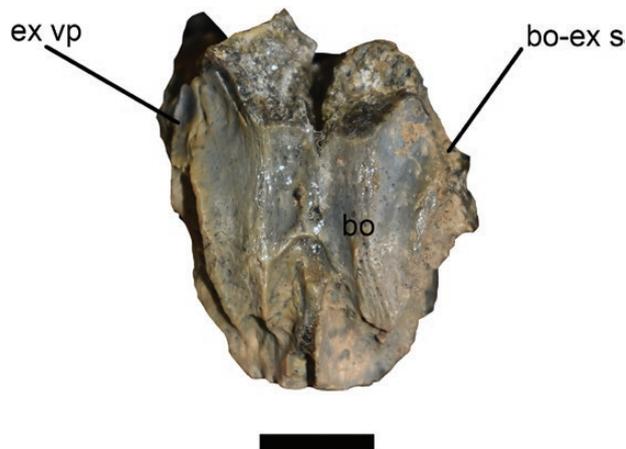
Figure 1. *Necrosuchus ionensis* (AMNH-3219, holotype), basioccipital (bo), left exoccipital ventral process (ex vp) and the suture between the basioccipital and the ventral process of the right exoccipital (bo-ex s). Scale bar: 1 cm.

Figure 2. Comparison between the proximity of the splenial anterior tip to the mandibular symphysis in *Necrosuchus ionensis* and extant *Caiman*. A, *N. ionensis* (AMNH-3219, holotype), right mandibular ramus in medial view. B, *Caiman crocodilus* (AMNH-R-43291), left mandibular ramus in medial view. C, *Caiman latirostris* (MN-2395), left mandibular ramus in medial view. D, *C. crocodilus* (MN-1031), right mandibular ramus in medial view. Abbreviations: d, dentary; sp at, splenial anterior tip. Scale bars: 1 cm.

tip of the splenial passing dorsal to the Meckelian groove (Brochu, 2011: Character 54, state 2; Fig. 2A). This last feature is present in all caimanines except *Globidentosuchus brachyrostris* Scheyer, Aguilera, Delfino, Fortier, Carlini, Sánchez, Carrillo-Briceño, Quiroz & Sánchez-Villagra, 2013, *Gnatusuchus* and *E. itaboraiensis*. The scapulocoracoid synchondrosis of the holotype seems to be closing (see Brochu, 2011; Fig. 3A, B), and given that the holotype was not an osteologically mature individual upon death (Brochu, 2011), this possible early closure of the synchondrosis would be another feature to indicate that *N. ionensis* belongs to Caimaninae (see Brochu, 1995, 1997b: Character 24; equivalent to Brochu, 2011: Character 25). In fact, the species has been recovered consistently in the Caimaninae clade by phylogenetic analyses that have included it (Brochu, 2011; Fortier *et al.*, 2014; Hastings *et al.*, 2016).

However, the differential diagnosis proposed by Brochu (2011) for *N. ionensis* requires revision. Two of the characters used (the presence of a slender process ventral to the basioccipital tubera, and the dentary symphysis extending back to a level immediately behind the fourth dentary alveolus) are respectively shared with caimanines and the taxa of the crown-group caimanines according to Brochu (2011). Two other characteristics are, according to Brochu (2011), shared with other taxa: the first four dentary alveoli being widely spaced from one another is a feature typically present in caimanine taxa, and the presence of ≥ 18 dentary alveoli is shared with taxa such as *E. cavernensis*, *Caiman* and *Melanosuchus* Gray, 1862 (see Brochu, 2011). Upon commenting on the last character, Brochu (2011) also notes that the dentary of *N. ionensis* is slender. A slender dentary can also
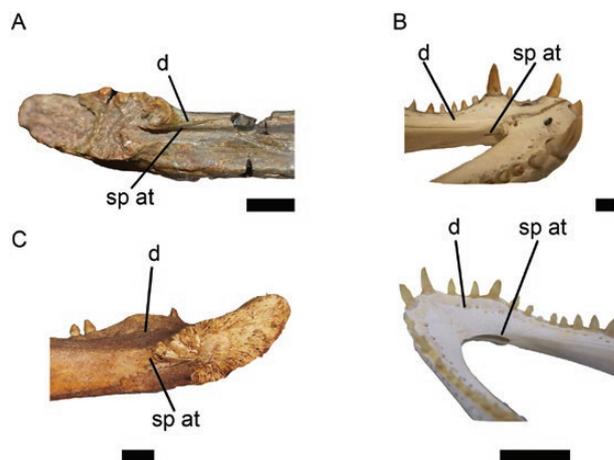
be seen in several caimanines, such as *Paleosuchus* (GM Cidade personal observation), *E. cavernensis*, *Centenariosuchus* and *Tsoabichi* (see Simpson, 1933; Brochu, 2010; Hastings *et al.*, 2013). Additionally, the possibility that the width of the dentary might be subject to ontogenetic or individual variations makes this character not useful for taxonomy.

The last character included in the diagnosis of Brochu (2011) is the splenial bearing a slender anterior process that extends almost to the dentary symphysis. As previously mentioned, the splenial of *N. ionensis* does not participate in the symphysis, and the anterior tip of the splenial passes dorsal to the Meckelian groove, which is a common character among caimanines (Brochu, 2011; Hastings *et al.*, 2013; Cidade *et al.*, 2017; Fig. 2A), but how close the splenial gets to the symphysis is variable in at least two extant caimanines: *C. crocodilus* and *C. latirostris*. Some specimens of *C. crocodilus* exhibit splenials whose anterior tip is close to the symphysis (AMNH R 43291, AMNH R 137179, FMNH 69817, FMNH 69821, FMNH 69824, FMNH 69825, FMNH 69831 and FMNH 69842; Fig. 2B), whereas in others the anterior tip is more distant (FMNH 69819, FMNH 69832, FMNH 69854, FMNH 69855, FMNH 69865, FMNH 73700 and MN 1031; Fig. 2D). The same difference is observed for *C. latirostris*, in which some specimens exhibit the anterior tip of the splenial close to the symphysis (MN
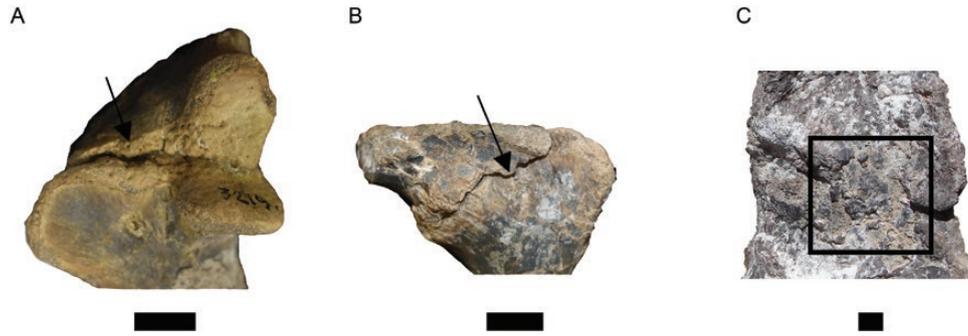
Figure 3. Comparison between the possible beginning of the closure (indicated by arrows) of the left scapuloracoid synchondrosis in *Necrosuchus ionensis* (A, lateral view; B, medial view) and the beginning of the closure of the same structure (black square) in the left scapuloracoid of the holotype of *Mourasuchus arendsi* (CIAAP-1297) in medial view (C; see also Cidade *et al.*, 2018). Scale bars: 1 cm.

1255, MN 2078, MN 69, MN 1257 and MN 2395; Fig. 2C), whereas in others the anterior tip is more distant (MN 1041, MACN 30566 and MCT 156-RR). The specimens that exhibit the splenial anterior tip more distant from the symphysis are juveniles or subadults, which raises the possibility of an ontogenetic variation in this character. However, detailed studies about the relationship between the anterior tip of the splenial and the mandibular symphysis in extant caimanines are lacking. Nevertheless, the presence of the anterior tip of the splenial close to the symphysis in *C. crocodilus* and *C. latirostris* and the variation seen in those species make this character not recommendable to be used in taxonomy, at least for the time being, until detailed ontogenetic studies eventually reveal otherwise.

However, there is one character that differs in *N. ionensis* from most other caimanines: the 13th dentary alveolus as the largest immediately caudal to the fourth dentary alveolus (Fig. 4B), which had already been noted by Simpson (1937) and which fits *N. ionensis* into state 0 (the 13th or the 14th dentary alveolus as the largest immediately caudal to the fourth) of Character 51 of Brochu (2011). In most caimanines, the largest dentary alveolus immediately caudal to the fourth is either the 11th or the 12th (state 2 of the same character): *C. crocodilus*, *C. latirostris*, *C. yacare*, *Centenariosuchus*, *Melanosuchus* and *Paleosuchus* (even though there is individual variation in this last genus, as detailed below; see Fig. 4). Other caimanines have the 13th or the 14th alveolus as the largest, together with a series of large alveoli behind them (state 1): *C. brevirostris* and *G. brachyrostris*.

In other taxa of Caimaninae, a series of large posterior alveoli starts with a large 12th alveolus (*C. wannlangstoni* and *Kuttanacaiman*). In *N. ionensis*, the 14th alveolus is only slightly smaller than the 13th, but the alveoli posterior to it are progressively slightly smaller instead. In *No. stromeri*, the largest alveoli are the 15th and 16th. In *Mourasuchus*, the
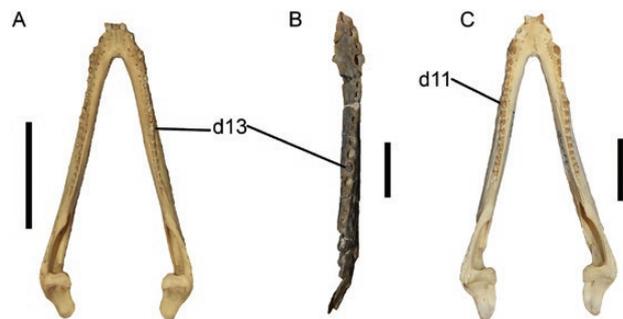

Figure 4. Comparison of the size of the 13th dentary alveolus relative with the other alveoli in *Necrosuchus ionensis* and *Paleosuchus*. A, *Paleosuchus palpebrosus* (AMNH-R-137170), mandibular rami in dorsal view. B, *Necrosuchus ionensis* (AMNH-3219, holotype), right mandibular ramus in dorsal view. C, *Pa. palpebrosus* (AMNH-R-97328), mandibular rami in dorsal view. Abbreviations: d11, 11th dentary alveolus; d13, 13th dentary alveolus. Scale bars: 5 cm.

first to the fifth alveoli are the largest of the tooth row, after which the alveoli become progressively smaller (see Langston, 1965). At least two *Purussaurus* specimens [*Pu. brasiliensis* specimens DGM 527-R (see Price, 1967) and UFAC-4559 (GM Cidade personal observation)] exhibit the 13th alveolus as the largest; most alveoli are not preserved in the holotype of *Purussaurus neivensis* (Mook, 1941), while in the holotype of *Purussaurus mirandai* Aguilera, Riff & Bocquentin-Villanueva, 2006 the alveoli posterior to the fourth become progressively smaller (Aguilera *et al.*, 2006). However, *N. ionensis* is markedly distinct from *Purussaurus* by overall mandibular morphology. In the latter, the mandibles are remarkably massive in accordance with the large size of *Purussaurus* (see Langston, 1965; Aguilera *et al.*, 2006; Aureliano *et al.*, 2015) and because the first four alveoli are the largest of the dentary in *Purussaurus* (see Barbosa-Rodrigues,

1892; Price, 1967; Aguilera *et al.*, 2006; Salas-Gismondi *et al.*, 2015), whereas in *Necrosuchus* (see Simpson, 1937: fig. 3) and most caimanines (the other exception being *Mourasuchus*, as noted above), one or more alveoli behind the tenth alveolous either approaches or overcomes the size of the first and fourth alveoli, which are usually the largest between the first four.

In some specimens of both species of *Paleosuchus*, the 13th alveolus is either larger or of the same size as the 12th and the 11th (*Pa. palpebrosus*: AMNH R 137170, AMNH R 137174, AMNH R 145071, AMNH R 93812, FMNH 69874, MCT 291-RR; *Pa. trigonatus*: MN 65, MN 2491, AMNH R 129259, AMNH R 129260, AMNH R 66391 and USNM 234047; Fig. 4A), thus varying from the standard in the genus (Fig. 4C), which is state 2 of Character 51 of Brochu (2011). This alone raises the possibility that *Necrosuchus* can be considered a *Paleosuchus* specimen, but *Necrosuchus* differs from the latter in other characters: the atlantal rib of *Necrosuchus* lacks the thin laminae in the anterior end that is present in *Paleosuchus* (see Brochu, 2011, in the scoring of Character 7); the dorsal margin of the iliac blade of *Necrosuchus* is rounded, with a modest dorsal indentation (Brochu, 2011: Character 34, state 1; Fig. 5A), similar to *Caiman* (e.g. *C. crocodilus*; Fig. 5B) but different from *Paleosuchus*, in which the dorsal margin of the iliac blade is narrow, with a dorsal indentation (Brochu, 2011: Character 34, state 3; Fig. 5C); and, most notably, the posterior alveoli and teeth of *Paleosuchus* are lateromedially compressed, whereas those of *Necrosuchus* are circular (Brochu, 2011: Character 79; Fig. 4).

The alveolar pattern of the dentary of the fossil caimanine *T. greenriverensis* has some similarities with that of *Necrosuchus*. The alveolar counting of *T. greenriverensis* is not known, because the only significantly complete dentaries (those of the holotype, TMM 42509-1; see Brochu, 2010) have some anterior alveoli missing or fragmented. However, the posterior alveoli of the dentary exhibit two large alveoli followed by progressively slightly smaller ones, a morphology

also observed in *Necrosuchus*. Nevertheless, comparisons between the two taxa based on the specimens currently known are problematic, because *Necrosuchus* preserves only four alveoli posterior to the two largest posterior alveoli (Fig. 4B), whereas the holotype of *Tsoabichi* preserves from six to seven (see Brochu, 2010: fig. 1). Additionally, the placement of *Necrosuchus* in or close to the Jacarea clade, together with the placement of *Tsoabichi* as a member of the sister clade of *Paleosuchus* in the phylogenetic analysis of this paper, argues against a proximity between these two taxa.

Additionally, *N. ionensis* differs from *Eocaiman* in having the dentary at the level of the first and fourth teeth at the same level as at the 11th and 12th teeth, whereas in *Eocaiman* the dentary at the first level is lower than at the second (Pinheiro *et al.*, 2013: Character 124). It also differs from *E. itaboraiensis*, because in that species the splenial participates in the mandibular symphysis (Pinheiro *et al.*, 2013). *Necrosuchus* also differs from *Gnatusuchus* owing to the presence of an extensive mandibular symphysis and a 'shovel-like' process in the anterior portion of the mandible in *Gnatusuchus*, aside from the participation of the splenial in the mandibular symphysis in *Gnatusuchus* (see Salas-Gismondi *et al.*, 2015). From *Culebrasuchus*, *Necrosuchus* differs in having the dentary slightly curved between the fourth and tenth alveoli, whereas the same portion of the dentary in *Culebrasuchus* is linear (see Brochu, 2011: Character 50; Hastings *et al.*, 2013); additionally, the external mandibular fenestra in *Necrosuchus* is small, whereas in *Culebrasuchus* it is large (see Brochu, 2011: Character 63; Hastings *et al.*, 2013). Furthermore, the exoccipital sends slender process ventrally to the basioccipital tubera in *Necrosuchus*. In *Culebrasuchus*, the processes are absent and the exoccipitals are located exclusively dorsal to the basioccipital tubera (see Brochu, 2011: Character 176; Hastings *et al.*, 2013). Comparisons between *Necrosuchus* and *Pr. peligrensis* are limited
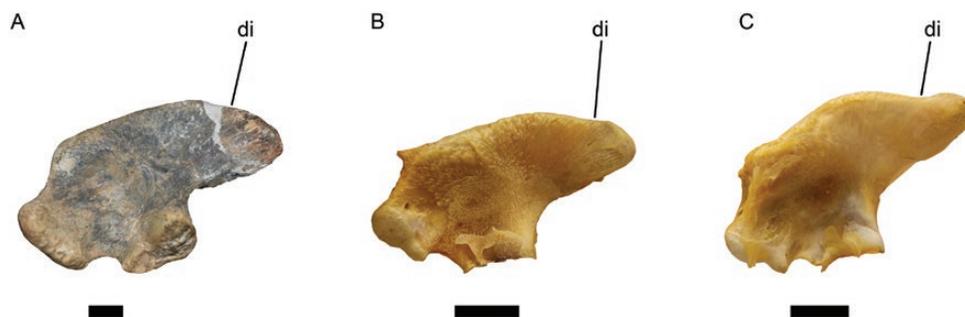

Figure 5. Comparison between the left ilia in lateral view of *Necrosuchus ionensis* (AMNH-3219; A), *Caiman crocodilus* (AMNH-R-137179; B) and *Paleosuchus palpebrosus* (AMNH-R-97326; C), showing the rounded dorsal margin of the iliac blade with modest dorsal indentation (di; A and B) and the narrow dorsal margin with di in C. Scale bars: 1 cm.

because the only bone present in both species is the quadrate, which exhibits no systematically relevant differences between them.

Taxonomic review

Necrosuchus ionensis is here considered a valid species. A taxonomic proximity between *Necrosuchus* and *Tsoabichi* may be cogitated given the tentative similarities between the two taxa. However, given the impossibility of performing a proper comparison between the two taxa from the specimens currently known and the different phylogenetic placements between the two species recovered in the present study, *Necrosuchus* and *Tsoabichi* must be maintained as distinct taxa until more complete specimens or further assessments clarify this issue. *Necrosuchus* is diagnosed as a caimanine with a unique combination of characters, provided in the emended diagnosis presented above, which is based on comparisons with extant and extinct caimanines.

PHYLOGENETIC ANALYSIS

The phylogenetic analysis resulted in a strict consensus of 23 040 most parsimonious trees with 645 steps. The topology of the Eusuchia clade as a whole did not change from the analysis of Souza-Filho *et al.* (2019). The only changes were observed in the Caimaninae clade (Fig. 6), which shows *Culebrasuchus mesoamericanus* Hastings et al., 2013 as the basal-most caimanine. More derived than *Culebrasuchus*, the genera *Gnatusuchus* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh & Antoine, 2015, *Globidentosuchus* Scheyer et al., 2013, *Eocaiman* Simpson, 1933 (with

its three species: *E. cavernensis*, *E. itaboraiensis* and *E. palaeocenicus*) and *Kuttanacaiman* Salas-Gismondi et al., 2015 appear as successive sister taxa to the crown-group Caimaninae. This last clade exhibits, as its most basal lineage, a clade formed by *Tsoabichi* Brochu, 2010 and *Bottosaurus* as the sister taxon to *Paleosuchus* Gray, 1862, followed by a lineage composed of *Caiman gasparinae* Bona & Carabajal, 2013 as the sister taxon to the four species of *Mourasuchus* Price, 1964 and then by the clade Jacarea Gray, 1844 (*sensu* Brochu, 1999).

Jacarea appears as a large polytomy, in which the only lineage containing more than one taxon is the one formed by *Acresuchus pachytemporalis* Souza-Filho et al., 2019 as the sister taxon of the three species of *Purussaurus* Barbosa-Rodrigues, 1892. The other nine taxa (*Caiman brevirostris* Souza-Filho, 1987, *C. crocodilus*, *C. latirostris*, *Caiman wannlangstoni* Salas-Gismondi et al., 2015, *C. yacare*, *Centenariosuchus gilmorei* Hastings et al., 2013, *M. niger*, *N. ionensis* and the specimen UCMP 39978) appear as independent lineages.

Given the polytomy in the Jacarea clade and the inclusion of *N. ionensis* within it, a Pcr Prune analysis was performed to find out which taxa were causing instability in this clade (Fig. 7). The analysis identified *Ce. gilmorei* and *N. ionensis* as the unstable taxa within the strict consensus of Jacarea. The pruning of these two species resulted in a more resolved topology, in which the clade formed by *Acresuchus* and *Purussaurus* appears as more basal to Jacarea, which included all remaining taxa (*C. brevirostris*, *C. crocodilus*, *C. latirostris*, *C. wannlangstoni*, *C. yacare*, *M. niger* and the specimen UCMP 39978) as a polytomy.
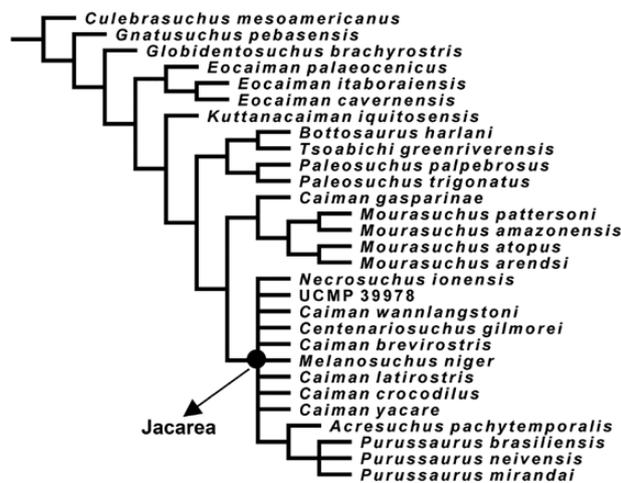

Figure 6. Strict consensus of the Caimaninae clade (23 040 trees) obtained in the phylogenetic analysis of the present study.
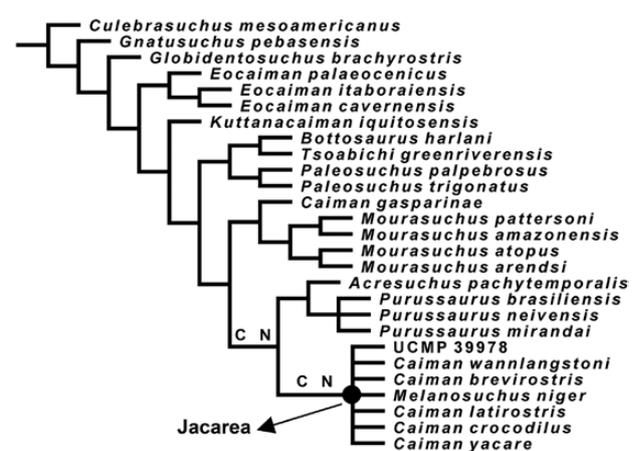

Figure 7. Topology of the Caimaninae clade (23 040 trees) obtained in the Pcr Prune analysis. Abbreviations: C, possible placements of *Centenariosuchus gilmorei*; N, possible placements of *Necrosuchus ionensis*.

Both *Centenariosuchus* Hastings, Bloch, Jaramillo, Rincon & MacFadden, 2013 and *Necrosuchus* had the same two alternative placements in the Pcr Prune analysis: either as more basal to the clade formed by *Acresuchus* + *Purussaurus* and Jacarea or as more basal that the clade Jacarea itself (Fig. 7).

The placement of *N. ionensis* either within Jacarea (in the strict consensus), as a stem Jacarea (one of the possibilities of the Pcr Prune analysis) or as basal to the *Acresuchus* + *Purussaurus* clade and Jacarea (another possibility of the Pcr Prune analysis) considered in the present study were not recovered by any previously published topology of the Caimaninae clade. All previous analyses recover the species in the crown-group caimanines either as part of a polytomy (Brochu, 2011, 2013; Fortier *et al.*, 2014; Hastings *et al.*, 2016) or forming a clade with *Tsoabichi* and *Paleosuchus* (Salas-Gismondi *et al.*, 2015; Bona *et al.*, 2018). As such, our result is significant because it shows the presence of derived caimanines already in the Palaeocene of South America, as will be discussed in more detail in the 'Discussion' below. However, owing to the incompleteness of the holotype and only known specimen of *N. ionensis*, further analyses are required to test the phylogenetic placement of this species. Furthermore, the placement of the *Acresuchus* + *Purussaurus* clade in both analyses differs from the topology of Souza-Filho *et al.* (2019), which recovered the clade as the sister taxon of another clade formed by *Centenariosuchus* as the sister taxon of Jacarea. The majority of the Caimaninae phylogenies before the inclusion of *Acresuchus* recovered *Purussaurus* either as the sister taxon of a clade composed of the North American Eocene taxon *Orthogenysuchus olseni* Mook, 1924 and *Mourasuchus* (Brochu, 1999; Aguilera *et al.*, 2006; Bona, 2007; Bona *et al.*, 2012; Scheyer *et al.*, 2013; Fortier *et al.*, 2014) or, after excluding *O. olseni* owing to non-published data from repreparation of the holotype (see Salas-Gismondi *et al.*, 2015), recovered *Purussaurus* as the sister taxon of *Mourasuchus* only (Salas-Gismondi *et al.*, 2015; Cidade *et al.*, 2017). This instability indicates that the phylogenetic placement of *Acresuchus* and *Purussaurus* also requires more in-depth study, which is also likely to reflect on the phylogeny of Jacarea and *N. ionensis*.

The placement of *Bo. harlani* forming a clade with *Tsoabichi greenriverensis* Brochu, 2010 differs from the results of the analysis of Cossette & Brochu (2018). This recovered *Bo. harlani* forming a clade with the extant South American genus *Paleosuchus*, which in the analysis of this study is the sister group of the *Bottosaurus* + *Tsoabichi* clade. The phylogenetic relationships of these last two taxa, which are from

North America, are important for the understanding of the biogeography of the earliest caimanines, an issue that is addressed more comprehensively in the Discussion of this paper.

Another interesting issue of this analysis is the placement of *C. gasparinae*, from the Late Miocene of Argentina, as sister taxon to *Mourasuchus*. This differs from the topology of Bona *et al.* (2012), which places the species in the Jacarea clade. However, the overall morphology of *C. gasparinae* is more similar to that of jacarean or of other medium-sized caimanines than to that of *Mourasuchus*, which exhibits a distinct platyrostral, broad skull (Cidade *et al.*, 2017). Furthermore, the placement of the present analysis is supported by only one character: the nasals being excluded, at least externally, from the naris, while nasals and premaxillae are still in contact (Brochu, 2011: Character 82, state 2). In this way, it is possible that this topology was recovered owing to the fragmentary nature of the holotype and of the other specimen referred to *C. gasparinae* (see Bona & Carabajal, 2013; Bona *et al.*, 2012). However, the possibility that *C. gasparinae*, although not belonging to *Mourasuchus*, might be phylogenetically closer to it than to other caimanines can also be considered. Owing to these perspectives, we refrain from making a taxonomic review concerning the placement of *C. gasparinae* in the genus *Caiman* Spix, 1825. Further analyses are required to settle this issue.

DISCUSSION

EVOLUTION AND RADIATION OF EARLY SOUTH AMERICAN CAIMANINES

Although the caimanines of the Palaeocene of South America represent only the first unequivocal records of the clade and they are not as species-rich and diverse as the Miocene record of the group in the continent (Cidade *et al.*, 2019), they indicate that caimanines already had a significant diversity in the Palaeocene and in the Palaeogene of South America as a whole. One of the aspects of this significant diversity is the fact that caimanines already inhabited the area of current Argentina and the Rio de Janeiro state of Brazil in the Palaeocene (Pinheiro *et al.*, 2013; Bona *et al.*, 2018; Cidade *et al.*, 2019), which is important because they are thought to have dispersed to the continent from North America and thus achieved a wide distribution in South America already in the first epoch of the Cenozoic.

The other aspect is the ghost lineages that may be inferred from recent phylogenetic analyses of the Caimaninae clade, including the one performed in this

study. One of these directly involves South American Palaeocene caimanines: although *Eocaiman* has been recovered consistently as a basal caimanine (see Brochu, 1999, 2010, 2011; Bona, 2007; Pinheiro *et al.*, 2013), *Necrosuchus* has been recovered previously as a member of the crown-group Caimaninae (Brochu, 2011; Bona *et al.*, 2018; present analysis), and in the present study as close to the Jacaea clade in both the strict consensus and in the Pcr Prune analysis. The derived placement of *N. ionensis* indicates the existence of a 'ghost lineage' of caimanines that were already established in the Palaeocene. However, more complete specimens of *N. ionensis* are needed for a stronger phylogenetic assessment of the species that may or may not confirm this evolutionary scenario. The other 'ghost lineage' is the one indicated by the placement of the Miocene caimanines *Culebrasuchus*, *Gnatusuchus* and *Globidentosuchus* as the basal-most members of the clade (see Hastings *et al.*, 2013; Scheyer *et al.*, 2013; Salas-Gismondi *et al.*, 2015; present analysis). This 'ghost lineage' stretches from the Palaeocene to the Miocene and is distinct from that involving *Eocaiman* and *Necrosuchus*, because the former taxon appears as more derived than *Culebrasuchus*, *Gnatusuchus* and *Globidentosuchus* in the aforementioned analyses. The eventual finding of fossils that belong to this 'ghost lineage' (aside from the possible basal caimanine *Pr. peligrensis*; see below) would be important to understand not only the early evolution of the group as a whole, but also the evolution of the durophagous feeding habit present in *Globidentosuchus* and in the highly adapted *Gnatusuchus* (see Salas-Gismondi *et al.*, 2015; Cidade *et al.*, 2019) in particular.

The inclusion of the other two caimanine species of the Palaeogene of South America, *No. stromeri* and *Pr. peligrensis*, or only of *No. stromeri*, causes the topology of the Eusuchia clade to collapse, whereas the inclusion of only *Pr. peligrensis* collapses the Brevirostres clade. As such, they were not included in the final version of the analysis. In the only study that included both taxa (Bona *et al.*, 2018), *Pr. peligrensis* was recovered as the basal-most Caimaninae (more basal than *Globidentosuchus* and *Gnatusuchus*, whereas *Culebrasuchus* was recovered as an alligatorine, within the genus *Alligator* Cuvier, 1807). The placement of *Pr. peligrensis* in that analysis makes it the first of the possible components of the 'ghost lineage' of basal caimanines. This species is based only on an isolated skull table and left quadrate, which is important because it is the only Palaeocene caimanine of South America to preserve the skull table, and exhibits an interesting morphology: it has large supratemporal fenestrae more reminiscent of basal alligatoroids, alligatorines and *Culebrasuchus* (see Bona *et al.*, 2018), but has the medial borders of

the orbits slightly elevated, which is more reminiscent of the morphology seen in many caimanines (see Brochu, 1997, 1999). As such, *Pr. peligrensis* might be a 'transitional form' between the morphology of basal alligatoroids and those of more derived caimanines and is the first glimpse we have about the morphology of the skull table of the first caimanines. However, more complete specimens of this taxon are needed for its phylogenetic placement to be assessed thoroughly and for inferences about the cranial morphology of basal caimanines to be made on more complete data.

Notocaiman stromeri is based on only an incomplete anterior portion of a left mandibular ramus. The only phylogenetic analysis to include this taxon (Bona *et al.*, 2018) recovered it in the clade formed by the three species of *Eocaiman*. The robust shape of the bone and the large size of the posterior alveoli (see Rusconi, 1937) suggest that *N. stromei* might have been an early durophagous form in the Caimaninae, because large, globular posterior teeth is a trait commonly assigned to a durophagous feeding habit in alligatoroid crocodylians (see Brochu, 2004; Salas-Gismondi *et al.*, 2015), and a robust mandible could also aid in the ingestion of hard-bodied prey. Additionally, *Eocaiman* has also been suggested to be a durophagous taxon (see Cidade & Hsiou, 2018) because it has the anterior portion of the dentary at a lower level than the posterior portion and, in most of the specimens, the first dentary teeth are procumbent (Cidade & Hsiou, 2018). Both these characters could aid in movements to capture animals such as bivalves and gastropods. As such, *Eocaiman* and *No. stromeri* might be the earliest examples of durophagous feeding behaviour in the Caimaninae clade, which later in the Cenozoic would also be performed by more specialized durophagous taxa of the Miocene such as *Gnatusuchus*, *Globidentosuchus*, *Kuttanacaiman*, *C. wannlangstoni* and *C. brevirostris* (see Fortier *et al.*, 2014; Salas-Gismondi *et al.*, 2015; Cidade *et al.*, 2019). This durophagous habit might not have been a novelty of the Caimaninae clade: the Late Cretaceous basal alligatoroid *Brachychampsa* Gilmore, 1911 has also been proposed to be a durophagous taxon (see Brochu, 2004), and the same habit may be proposed for the other traditionally basal alligatoroids from the Late Cretaceous *Albertochampsa* Erickson, 1972 and *Stangerochampsa* Wu, Brinkman & Russell, 1996, which also exhibit posterior globular teeth (see Erickson, 1972; Wu *et al.*, 1996). In fact, some analyses have recovered a clade formed by these three genera as a sister group to the South American caimanines (Salas-Gismondi *et al.*, 2015; Bona *et al.*, 2018). This suggests that the alligatoroids that dispersed to South America to form the Caimaninae clade might already have been durophagous, with this habit continuing

not only in Caimaninae but also in the predominantly North American Alligatorinae clade, through taxa such as *Allognathosuchus* and *Ceratosuchus* (see Bartels, 1984; Brochu, 2004). Nevertheless, more complete material of *Eocaiman* and, especially, *No. stromeri* are needed to evaluate these hypotheses thoroughly.

Regarding North American early caimanines, the topology of our analysis places *Bo. harlani*, from the Late Cretaceous and Palaeocene of the USA, in a clade with *T. greenriverensis*, from the Eocene of the USA. Such placement indicates the presence of North American lineages of caimanines from the Late Cretaceous to the beginning of the Cenozoic, which creates a complex scenario for the early biogeography of Caimaninae (Bona *et al.*, 2018).

Given the derived placement of the clade formed by *Bottosaurus* and *Tsoabichi* in this analysis, the more phylogenetically straightforward scenario is a dispersion towards North America from a South American ancestor of the clade no later than the Late Cretaceous. Given that the two continents were separated for most of the time between the Jurassic and the Pliocene (Iturralde-Vinent, 2006; O'Dea *et al.*, 2016), the dispersal could be achieved either through a Late Cretaceous land connection that existed between the two continents (see Brochu, 1999, 2010, 2011; Cossette & Brochu, 2018; Cidade *et al.*, 2019) or between a dispersal across the sea. A direct dispersal through oceanic waters is not likely given the reduced tolerance of extant alligatoroids to salt water (Taplin & Grigg, 1989; Brochu, 1999; Cossette & Brochu, 2018); therefore, a gradual dispersal through islands and archipelagos that existed between the two continents at the time (see Iturralde-Vinent, 2006) is a more likely scenario if dispersal without a direct connection between the continents is considered. Another possibility is that *Bottosaurus* and *Tsoabichi* are remnants of an early population of caimanines that inhabited North America at least from the Late Cretaceous, thus not being derived from South American dispersants. However, given the topology found in this work, this would be a complex scenario that would implicate several dispersal events from North America towards South America involving the several caimanine taxa that are basal to the clade formed by *Bottosaurus* and *Tsoabichi*.

CONCLUSIONS

Necrosuchus ionensis, one of the most important components of the Palaeogene caimanine fauna, is considered a valid species in this study, albeit with a different diagnosis from those proposed in previous assessments (Simpson, 1937; Brochu, 2011). The emended diagnosis points out that *N. ionensis* differs from most caimanines in having the 13th dentary alveolus as the largest immediately caudal to fourth. This feature is also found in *Pu. brasiliensis* and in some specimens of the extant genus *Paleosuchus*, but *N. ionensis* differs from these two taxa in other features. The strict consensus of the phylogenetic analysis of the Caimaninae clade performed in the present study shows this species as a member of the clade Jacarea. However, given the polytomy recovered for the same clade in the strict consensus, Pcr Prune analyses showed two alternative placements for *N. ionensis*: as basal to Jacarea or basal to the clade formed by *Acresuchus* + *Purussaurus*. Nevertheless, any of these placements show the species as more derived than in previous analyses, and the presence of a derived caimanine in the Palaeocene of South America hints that the clade already had a significant diversity in the early stages of its radiation into the continent.

Such a scenario differs from that seen for other South American Palaeogene caimanines, such as *Eocaiman*, *Pr. peligrensis* and *No. stromeri*, which have been recovered in basal positions in the clade (see Brochu, 1999, 2011; Bona, 2007; Bona *et al.*, 2018; present study). The inclusion of *Pr. peligrensis* and *No. stromeri* in the dataset used in the present study resulted in large collapses in the topology, with both taxa being excluded from the final analysis as a result. Future studies and, hopefully, the finding of more complete material of both taxa might shed light on their phylogenetic placement and evolution.

Other interesting points raised by our phylogenetic analysis are a possible taxonomic reassessment of *C. gasparinae* and the recovery, for the first time, of a clade formed by *Bo. harlani* and *T. greenriverensis*, which are both early caimanines from North America. This raises interesting biogeographical questions, in addition to early evolutionary scenarios for the Caimaninae clade, which have to be assessed more thoroughly in later studies. Additionally, we suggest that early South American caimanines and their immediate ancestors might have been durophagous taxa, based on morphological characters present in these forms in addition to their possible phylogenetic proximity to the North American Late Cretaceous durophagous taxa *Brachychampsa*, *Albertochampsa* and *Stangerochampsa*. This scenario offers an interesting perspective that future studies might address to achieve better understanding of the origin, early radiation and morphological and ecological evolution of the Caimaninae clade.

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