



The crocodylomorph fauna of the Cenozoic of South America and its evolutionary history: a review

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ABSTRACT

The fossil crocodylomorph fauna of the Cenozoic of South America is very rich and diverse. Historically, few publications have been dedicated to providing an overall review of this fauna, with most reviews focusing on specific areas. However, the fact that many new species, taxonomic reviews and description of new specimens have been proposed in the last decade makes a comprehensive review of the fossil crocodylomorph fauna of the South American Cenozoic necessary. The only crocodylomorph lineages to have a fossil record comprising Late Cretaceous and Cenozoic deposits in South America is the Dyrosauridae. Sebecidae or its predecessors, however, are very likely to have inhabited the continent during the Cretaceous-Paleogene transition as well; both Dyrosauridae and Sebecidae are considered here to have survived the Cretaceous-Paleogene extinction while inhabiting South America. Caimaninae (Alligatoroidea) arrived either in the late Cretaceous or in the early Paleocene coming from North America. The fossil record of Caimaninae is present, however, only from the Paleocene. By the Eocene, there are no records of Dyrosauridae in South America; this group was globally extinct after the Eocene, possibly due to the global cooling that occurred by the end of the epoch. Sebecids and caimanines solely comprised the crocodylomorph fauna of the continent until the Miocene, where there are the first records of Gavialoidea (Gryposuchinae) and a possible first dispersion of Crocodyloidea, through the tentative tomistomines *Charactosuchus* and *Brasilosuchus*. Gryposuchinae likely arrived in the continent from Africa or from Asia during the Oligocene. *Charactosuchus* and *Brasilosuchus* may have come from North America where tomistomines lived from the Oligocene to the Pliocene. Sebecids were extinct after the middle Miocene; *Charactosuchus*, Gryposuchinae, *Purussaurus*, *Mourasuchus* and durophagous caimanines such as *Gnatusuchus* were extinct after the late Miocene. These extinctions are related to changes in the drainage basins caused by elevation of the Andes mountain range. Only the extant caimanine *Caiman*, *Melanosuchus* and *Paleosuchus* would survive the Miocene, being enriched by *Crocodylus* from the Pliocene onwards, which is likely that *Crocodylus* arrived in the American continents from Africa. The current fossil record indicates that these four genera comprise the extant crocodylian fauna of the continent since the Pliocene. Although our knowledge on crocodylomorph fossil fauna of the South American Cenozoic has increased continuously, especially in the last decade, much yet must be done, especially on the taxonomy and phylogeny of *Brasilosuchus* and *Charactosuchus*, fieldworks in Paleogene and Pliocene localities, and the evolution of the specialized Caimaninae morphotypes.

Abbreviations: American Museum of Natural History, New York, United States, AMNH; Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Urumaco, Venezuela, AMU CURS; Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela, CIAAP-UNEFM; Departamento de Geología, Centro de Tecnología e Geociências, Universidade Federal de Pernambuco, Recife, Brazil, DG-CTG-UFPE; Museo Geológico, Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Bogotá, Colombia, IGM; Museu de Ciências da Terra, Serviço Geológico Nacional, Rio de Janeiro, Brazil, MCT; Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina, MACN; Museo de Ciencias Naturales de Caracas, Caracas, Venezuela, MCNC; Museum of Comparative Zoology, Cambridge, United States, MCZ; Museo de La Plata, La Plata, Argentina, MLP; Museo Paleontológico Egidio Feruglio, Trelew, Argentina, MPEF; Museo de Historia Natural de San Marcos, Lima, Peru, MUSM; Instituto Miguel Lillo, Tucumán, Argentina, PVL; University of California Museum of Paleontology, Berkeley, California, UCMP; Florida Museum of Natural History, University of Florida, Gainesville, United States, UF; Universidade Federal do Acre, Rio Branco, Brazil, UFAC; Universidade Federal Uberlândia, campus Monte Carmelo, Brazil, UFU

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1. Introduction

Crocodylomorphs have a very taxonomically rich and morphologically diverse fossil record throughout the Cenozoic of South America. These include not only fossils assigned to the crocodylian genera that currently inhabit the continent (Patterson, 1936; Medina, 1976; Souza-Filho, 1987; Salas-Gismondi et al., 2007, 2015; Fortier et al., 2009, 2014; Bona and Carabajal, 2013; Bona et al., 2013a, 2014, 2017a; Scheyer et al., 2013; Foth et al., 2017), but also a myriad of exclusively fossil taxa (e.g. Rovereto, 1912; Rusconi, 1933, 1935, 1937; Patterson, 1943; Simpson, 1937a, 1937b; Langston, 1965; Langston and Gasparini, 1997; Aguilera, 2004; Paolillo and Linares, 2007; Riff et al., 2010, 2012; Scheyer and Moreno-Bernal, 2010; Bona et al., 2013a; Bona and Barrios, 2015; Salas-Gismondi et al., 2015; Scheyer and Delfino, 2016), including some that possess ecomorphotypes that are absent in the current continental crocodylian fauna.

These morphotypes include the terrestrial, top predators sebecids (Simpson, 1937a; Colbert, 1946; Langston, 1965; Gasparini, 1972; Buffetaut and Hoffstetter, 1977; Paolillo and Linares, 2007; Molnar, 2010, 2013; Kellner et al., 2014; Molnar and Vasconcellos, 2016), the longirostrine, marine, estuarine and freshwater inhabitants Dyrosauridae (Cope, 1886; Barbosa et al., 2008; Andrade and Sayão, 2014; Hastings et al., 2010, 2011, 2015), the giant, semi-aquatic top predator *Purussaurus* (Barbosa-Rodrigues, 1892; Nopcsa, 1924; Mook, 1941; Langston, 1965; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006; Aureliano et al., 2015), the giant, flat-headed “duck faced” putative “gulp-feeder” *Mourasuchus* (Price, 1964; Langston, 1965, 1966, 2008; Bocquentin-Villanueva, 1984; Gasparini, 1985; Bocquentin and Souza-Filho, 1990; Cidade et al., 2017), highly adapted durophagous caimanines like *Gnatusuchus*, *Kuttanacaiman* and *Globidentosuchus*, among others (Langston, 1965; Salas-Gismondi et al., 2015) and the longirostrine, predominantly piscivorous gavialoids (Gryposuchinae, which also included large-sized taxa such as *Gryposuchus*; Gürich, 1912; Langston, 1965; Gasparini, 1968; Sill, 1970; Bocquentin-Villanueva and Buffetaut, 1981; Buffetaut, 1982; Kraus, 1998; Brochu and Rincón, 2004; Riff and Aguilera, 2008; Salas-Gismondi et al., 2016) and crocodyloids (*Charactosuchus* and *Brasiliosuchus*; Langston, 1965; Souza-Filho and Bocquentin-Villanueva, 1989; Souza-Filho, 1991; Souza-Filho et al., 1993).

Taxonomic and morphological diversity aside, evolution, biogeography and history of faunistic successions of the South American Cenozoic crocodylomorphs exhibit close relation to several important geographical, geological and biological events in history of both the continent and the world. These include the K-Pg extinction, the possible terrestrial link between South and North America between the Cretaceous and the Paleogene, the global temperature drop of the end of the Eocene, the orogeny of the Andes Chain, the origin of the modern drainage basins of the Amazon and Paraná rivers and the closure of the Panama Isthmus, among others. All these issues make the crocodylomorph fossil fauna of the South American Cenozoic not only one of the most interesting of the world but they also highlight that their study and comprehension have vital importance on a better understanding on both biological and geomorphological history of the continent during the Cenozoic.

Although previously published works have offered comprehensive revisions of such record (e.g. Gasparini, 1996; Figueiredo and Pinheiro, 2011), many have focused either on specific areas or countries, such as the Amazon region (Riff et al., 2010; Scheyer and Moreno-Bernal, 2010), Argentina (Gasparini, 1981; Bona et al., 2013a; Bona and Barrios, 2015) and Brazil (Riff et al., 2012), and, as a result, comprehensive revisions of the crocodylomorph fossil fauna of the Cenozoic of South America are scarce. Additionally, many new fossil species and revisions of previously proposed species have been recently published (Bona et al., 2013a, 2013b; 2017a, 2017b; 2018; Pinheiro et al., 2013; Scheyer et al., 2013; Fortier et al., 2014; Kellner et al., 2014; Hastings et al., 2015; Salas-Gismondi et al., 2015, 2016; 2018; Scheyer and Delfino, 2016; Cidade et al., 2017, 2018a; Foth et al., 2017), justifying, thus, the need for this comprehensive revision. Furthermore, an overview of the biogeography, faunal successions and paleoecology of the different groups that comprise the crocodylomorph fossil fauna of the Cenozoic of South America is also be provided.

2. Results

2.1. Crocodylomorpha of the Paleogene

When K-Pg extinction occurred, around 66 Ma ago (Renne et al., 2013), only one out of seven crocodylomorph lineages to survive already inhabited South America: Dyrosauridae (Fig. 1), which already has a record in the Late Cretaceous of the continent (Langston, 1965; Hastings et al., 2015). The clade Sebecidae (Fig. 2) has a large likelihood of being inhabiting South America during the K-Pg transition as well. Although Sebecidae itself is traditionally proposed as an exclusively Cenozoic group (see Pol and Powell, 2011), it has been proposed to be closely related either to Baurusuchidae, forming the clade Sebecosuchia (e.g. Turner and Calvo, 2005; Pol and Powell, 2011) or Peirosauridae, forming the clade Sebecia (e.g. Larsson and Sues, 2007). However, as both of these clades are predominantly from South America's Late Cretaceous (see Montefeltro et al., 2011; Martinelli et al., 2012) and Sebecidae itself is a predominantly South American group (see Gasparini, 1996; Paolillo and Linares, 2007; Kellner et al., 2014), with only a few occurrences assigned to the Eocene of Europe and North Africa (Berg, 1966; Kuhn, 1968; Antunes, 1975; Buffetaut, 1989; Ortega et al., 1996; Rossmann et al., 2000), Sebecidae has a large possibility to be already present in (or derived from taxa that already inhabited) South America when the extinction happened.

It is possible that alligatoroids already inhabited South America before K-Pg Extinction, but no fossils of the group are known in the continent before the Cenozoic. The only Alligatoroidea clade to inhabit the continent, Caimaninae (Figs. 3–6) *sensu* Brochu (1999), has a South American fossil record only from the Paleocene onwards. Remains from the Late Cretaceous of Montana, United States, have been assigned to Caimaninae (Bryant, 1989; Brochu, 1999), but a detailed analysis of these remains has not been carried out to date (Brochu, 2010; Cidade et al., 2017). Nevertheless, as the oldest records of Alligatoroidea are from the Late Cretaceous, with most of them from North America (Brochu, 1999, 2004, 2010, 2011) and as most basal alligatoroids and taxa of Alligatorinae, the sister-group of Caimaninae, are also from



Fig. 1. Examples of the Dyrosaurid diversity of the South American Paleocene. Skull of the holotype of *Cerrejinosuchus improcerus* (UF/IGM 29) in dorsal view (A); mandible of the holotype of *Acherontisuchus guajiraensis* (UF/IGM 34) in ventral view (B); skull of the holotype of *Anthracosuchus balrogus* (UF/IGM 67) in dorsal view (C). Scales = 10 cm.

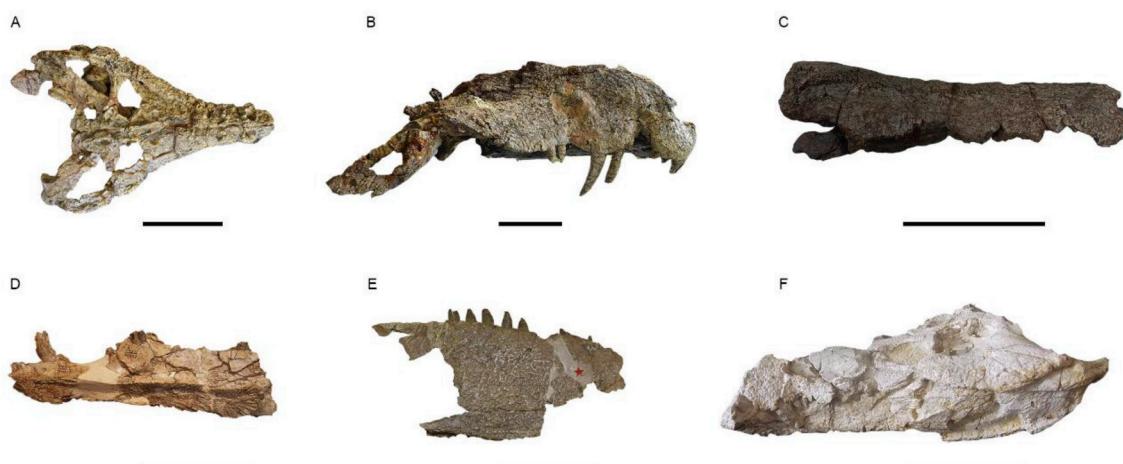


Fig. 2. Examples of the Sebecidae diversity of the South American Cenozoic. Skull of the holotype of *Lorosuchus nodosus* (PVL 6219) in dorsal view (A); skull of the holotype of *Bretesuchus bonapartei* (PVL 4735) in right lateral view (B); rostrum of the holotype of *Ayllusuchus fernandezii* (MLP 72-IV-4-2) in right lateral view (C); holotype of *Langstonia huilensis* (UCMP 37877) in medial view (D); left maxilla of the holotype of *Sebecus icaeorhinus* (AMNH 3160) in lateral view (E); skull of the holotype of *Sahitisuchus fluminensis* (MCT 1730-R) in left lateral view (F). Scales = 10 cm.

North America, a dispersion from this continent has been considered as the most plausible scenario for the occurrence of Caimaninae in South America from the Paleocene on (Brochu, 1999, 2010, 2011). Recent phylogenetic hypotheses (Salas-Gismondi et al., 2015; Cidade and Hsiou, 2017) have recovered the Late Cretaceous alligatoroids *Brachytrachyspsa*, *Stangerotrachyspsa* and *Albertotrachyspsa* as the basalmost caimanines; this topology, however, also agrees with the perspective that the remaining caimanines are original from a North American ancestor. In any scenario, the dispersion itself has been proposed to have occurred either in the Late Cretaceous or in the Paleocene (Brochu, 1999, 2010, 2011).

As North and South America were separated by the sea for most of the time between the Jurassic and the rise of the Isthmus of Panama in the Pliocene (see Iturrealde-Vinent, 2006; O'Dea et al., 2016), the dispersion has been proposed to have taken place either through a

relatively short-lasting land bridge existent between the two continents during this period (Rage, 1978, 1986; Lucas and Hunt, 1989; Brochu, 1999, 2010; 2011; Newbrey et al., 2009), or by the “hopping” through islands or archipelagos that existed between the two landmasses in the period (Brochu, 1999, 2010; 2011; for a detailed account of the islands and archipelagos of the time, see Iturrealde-Vinent, 2006). This second perspective would require at least some level of salt-water tolerance by early alligatoroids, which is shown by extant taxa of the group (Thorbjarnarson, 1992; Brochu, 1999) although not to the level of the high tolerance of salt-water exhibited by most crocodyloids (Taplin and Grigg, 1989).

The other two crocodylomorph lineages to inhabit South America (Gavialoidea and Crocodyloidea; Fig. 7) would arrive only later, either in the end of the Paleogene (Oligocene) or beginning of the Neogene (Miocene, see below), while the other two K-Pg extinction survivors

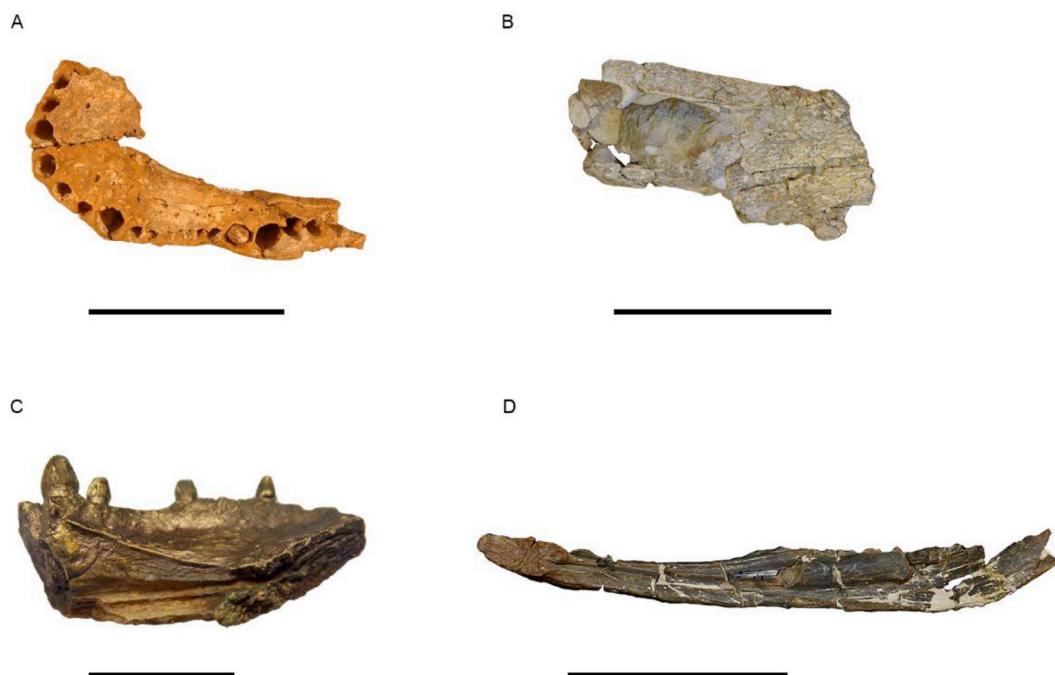


Fig. 3. Examples of the Caimaninae diversity of the South American Cenozoic. Holotype of *Eocaiman palaeocenicus* (MPEF-PV, 1933) in dorsal view (A); skull of the holotype of *E. cavernensis* (AMNH 3158) in dorsal view (B); holotype of *E. itaboraiensis* (MCT 1791-R) in medial view (C); right hemimandible of the holotype of *Necrosuchus ionensis* (AMNH 3219) in medial view (D). Scales = 10 cm (A, B and D); 1 cm (C).

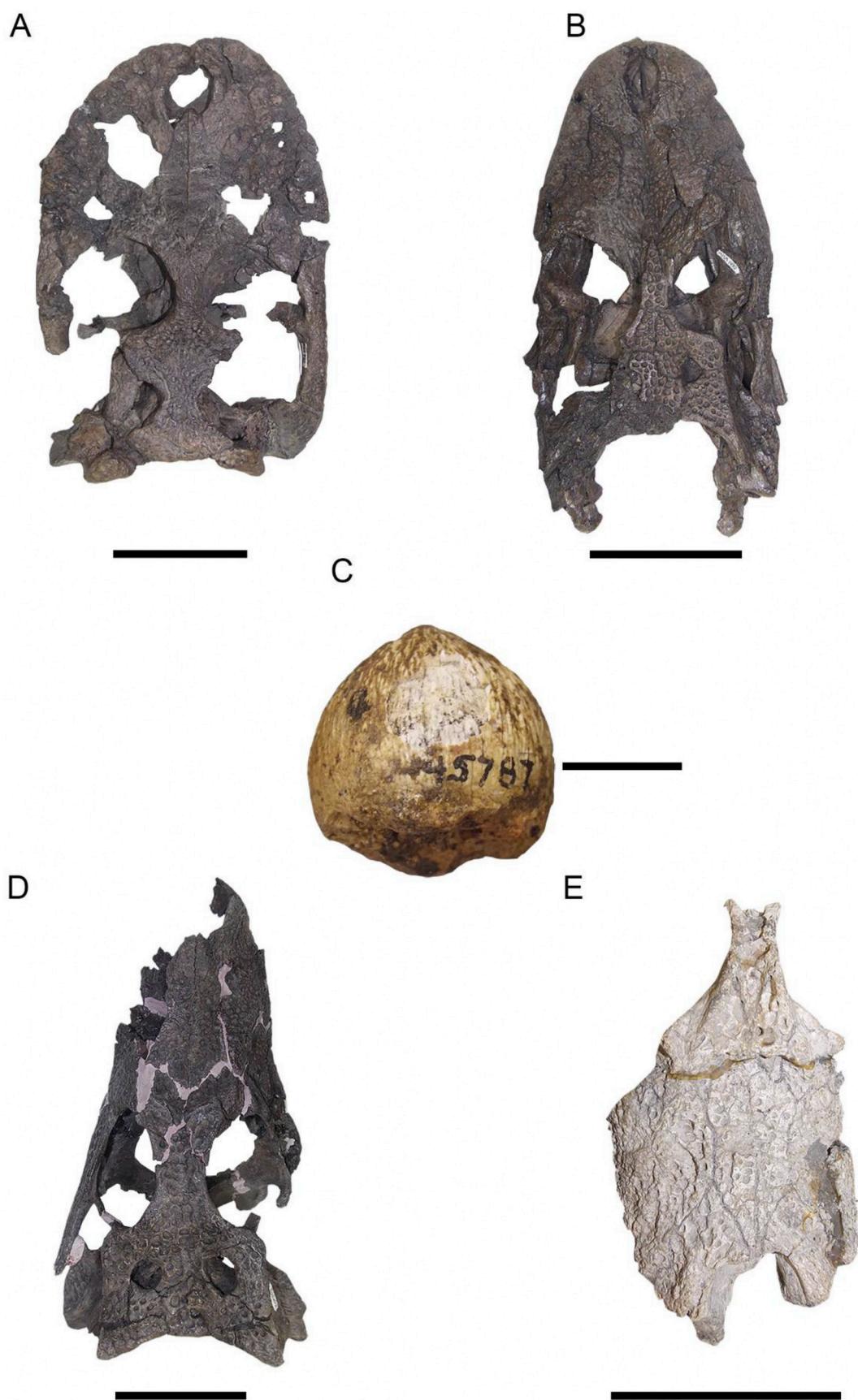


Fig. 4. The durophagous caimanines of the South American Miocene. Holotype of *Gnatusuchus pebasensis* (MUSM 990) in dorsal view (A); holotype of *Kuttanacaiman iquitosensis* (MUSM 1490) in dorsal view (B); holotype of *Balanerodus logimus* (UCMP 45787) in labial view (C); holotype of *Caiman wannlangstoni* (MUSM 2377) in dorsal view (D); rostrum of the holotype of *Caiman brevirostris* (UFAC 196) in dorsal view (E). Scales = 10 cm (A, B, D and E); 1 cm (C).



Fig. 5. Examples of the diversity of *Mourasuchus* and *Purussaurus*. Skull of the holotype of *M. arendsi* (CIAAP-UNEFM-1297) in dorsal view (A); skull of the holotype of *M. pattersoni* (MCNC-PAL-110-72V) in dorsal view (B); skull of *P. neivensis* (UCMP 39704) in dorsal view (C); skull of the holotype of *P. mirandai* (CIAAP-UNEFM-1369) in dorsal view (D). Scales = 10 cm.

(*Borealosuchus* and *Planocraniidae*, see Brochu, 1997a, 2013) have no known occurrences in South America.

Crocodylomorph fossil record in the Paleocene of South America evidences that sebecids and caimanines were well-established in the continent by this epoch, as the record of these two groups is

concentrated in central and austral portions of South America such as Argentina, Bolivia and the state of Rio de Janeiro in southeastern Brazil. The Sebecidae species recorded for the Paleocene are *Zulmasuchus querejazus* (Buffetaut and Marshall, 1991), from the early Paleocene Santa Lucía Formation of Bolivia (Buffetaut and Marshall, 1991;

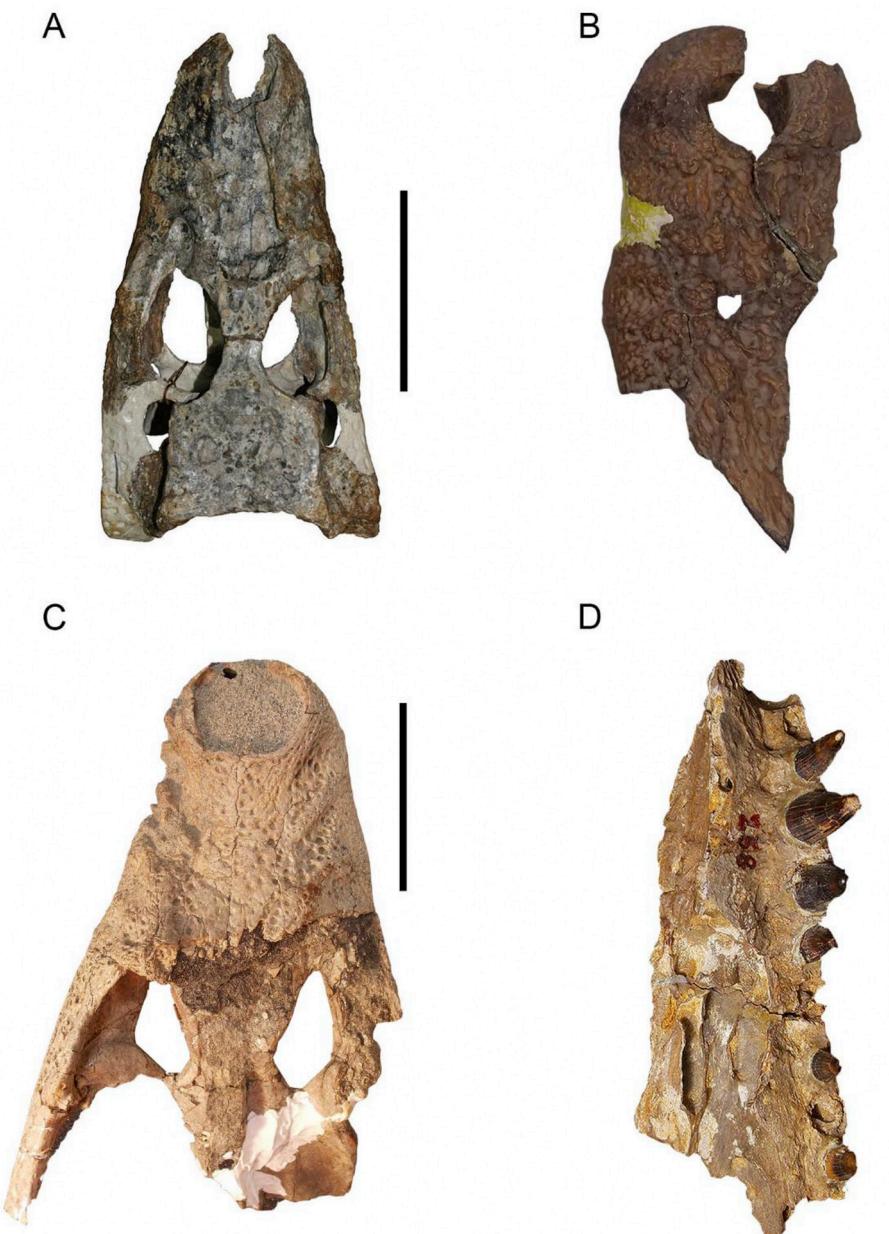


Fig. 6. Examples of the diversity of small to medium-sized generalist crocodylians of the South American Miocene. Skull assigned to *Melanosuchus* sp. (MCZ 243, holotype of *M. fisheri*) in dorsal view (A); rostrum of the holotype of *Caiman gasparinae* (MLP-73-IV-15-1) in dorsal view (B); partial skull assigned to *Caiman* sp. (UCMP 39978) in dorsal view (C); left maxilla of *Caiman australis* (MACN PV 258) in ventral view (D). Scales = 10 cm.

(Paolillo and Linares, 2007), *Lorosuchus nodosus* Pol and Powell (2011), from the middle/late Paleocene Rio Loro Formation of Argentina (Pol and Powell, 2011, Fig. 2-A), *Bretesuchus bonapartei* Gasparini et al. (1993), from the late Paleocene Maíz Gordo Formation of Argentina (Gasparini et al., 1993, Fig. 2-B), and *Sahitisuchus fluminensis* Kellner et al. (2014), from the middle/late Paleocene Itaboráí Basin of the Rio de Janeiro state of Brazil (Kellner et al., 2014, Fig. 2-F). *Bretesuchus* and *Zulmasuchus* were considered to belong not to Sebecidae but to Bretesuchidae by some authors (e.g. Gasparini et al., 1993; Paolillo and Linares, 2007). However, we follow Pol and Powell (2011) in considering all South American notosuchians of the Cenozoic as belonging to Sebecidae until more robust phylogenetic analyses eventually reveal Bretesuchidae as a stable clade. Additionally, *Z. querejazus* was originally described as belonging to *Sebecus*, but we follow the taxonomy of Paolillo and Linares (2007), which erected the new genus *Zulmasuchus* for this species. *Lorosuchus* is an interesting case as it represents the only sebecid known to date to be a semi-aquatic rather than a terrestrial

animal (Pol and Powell, 2011). Additionally, Pol and Powell (2011) obtained in a constrained phylogenetic analysis a topology only two steps longer that places *Lorosuchus* not as a sebecid, but as the sister-taxon of Neosuchia. As the authors noted, this perspective, if eventually confirmed, would make of *Lorosuchus* an additional lineage to survive the K-Pg extinction.

The Caimaninae species recorded in this epoch are represented by *Eocaiman palaeocenicus* Bona (2007) (Fig. 3-A), *Necrosuchus ionensis* Simpson (1937b) (Simpson, 1937b; see also Brochu, 2011, Fig. 3-D) and *Protocaiman peligrensis* Bona et al. (2018) from the Salamanca Formation of Argentina; *Notocaiman stromeri* Rusconi (1937) from the middle Paleocene Las Violetas Formation of Argentina (Bona and Barrios, 2015) and *Eocaiman itaboraiensis* Pinheiro et al. (2013), from the middle/late Paleocene Itaboráí Basin of Brazil (Fig. 3-C). However, Fortier (2011) considers *Notocaiman* as being from the early Eocene Rio Chico Formation of Argentina. The recently described *Protocaiman peligrensis* is an interesting form and it exhibits the most complete skull



Fig. 7. Examples of the diversity of longirostrine crocodylians of the South American Miocene. Gryposuchinae gavialoids: skull of the holotype of *Gryposuchus croizati* (MCNC-URU-2002-77) in dorsal view (A); holotype of *Hesperogavialis cruxenti* (CIAAP-UNEFM-320) in ventral view (B); holotype of *Ikanogavialis gameroi* (UCV-VF-1165) in dorsal view (C). Putative tomistomine crocodyloids: holotype of *Charactosuchus fieldsi* (UCMP 39646) in dorsal view (D). Scales = 10 cm.

table of a caimanine from the Paleocene. It exhibits large supratemporal fenestrae that resemble more of *Culebrasuchus mesoamericanus* Hastings et al. (2013), from the early Miocene of Panama and basal alligatoroids (Bona et al., 2018) than the relatively small fenestrae seen in most caimanines, in which the margins of the fenestrae are also largely overhung by the bones surrounding it (Brochu, 1997b, 1999, 2011). Accordingly, *P. peligrensis* is recovered as one of the most basal caimanines by Bona et al. (2018). Furthermore, Maury (1935) commented (but not illustrated) about a mandible from the Itaboráí Basin of Brazil that could be assigned to *Caiman* cf. *C. latirostris* (Daudin, 1802). However, the absence of illustrations and of any reassessment of this specimen turns this record doubtful until reassessment is performed (see Fortier, 2011). Additionally, the Itaboráí Basin is considered here as being from the middle/late Paleocene, since it is the age followed by the papers which proposed the two species (Pinheiro et al., 2013 and Kellner et al., 2014, respectively), but other works considered the unit

as being of early Eocene in age (see Woodburne et al., 2014; Carneiro and Oliveira, 2017).

The Dryosauridae record in South America is exclusive of the Paleocene, and it differs from those of Sebecidae and Caimaninae as it is concentrated in the north (Colombia and the Brazilian state of Pernambuco, in the northeast of country) and central portions of the continent (Bolivia). The species from the Paleocene of the Brazilian state of Pernambuco is *Guarinisuchus munizi* Barbosa et al. (2008), from the early Paleocene Maria Farinha Formation (Barbosa et al., 2008). The dyrosaurid *Hyposaurus derbianus* Cope (1886) was described from an unknown locality of the Brazilian state of Pernambuco (see Cope, 1886; Barbosa et al., 2008; Riff et al., 2012; Sena et al., 2017); even though the fact that it is from Pernambuco makes possible that *H. derbianus* is from the Maria Farinha Formation (Barbosa et al., 2008), this ultimately cannot be assured and thus the locality and age of this species remain unknown. The Colombian species are all from the

middle/late Paleocene Cerrejón Formation: *Cerrejonisuchus improcerus* Hastings et al. (2010) (Fig. 1-A), *Acherontisuchus guajiraensis* Hastings et al. (2011) (Fig. 1-B) and *Anthracosuchus balrogus* Hastings et al. (2015) (Fig. 1-C). While most dyrosaurids are longirostrine, *Anthracosuchus* is markedly brevirrostrine (Fig. 1), which suggests an adaptation of this taxon to sub-surface predation, as in modern *Gavialis*, instead of the surface-based predation proposed for other dyrosaurids (see Hastings et al., 2015).

The occurrences of Bolivian Dyrosauridae are from a locality near the Titicaca lake (Argollo et al., 1987) and of the Santa Lucía Formation (Buffetaut, 1991); neither of these were assigned to a genus or species. The Bolivian occurrences may be linked to a Late Cretaceous seaway that connected the north of South America to that region (see Hastings et al., 2015), even though the Colombian dyrosaurids *Cerrejonisuchus* and *Acherontisuchus* are proposed to be freshwater taxa (Hastings et al., 2011). Regarding Dyrosauridae arrival in South America, Hastings et al. (2015) propose two independent dispersal events from Africa: one in the Late Cretaceous, that originated the Colombian and Bolivian occurrences, and another in the Paleocene, from which *Guarinisuchus munizi* of the Paleocene of northeast Brazil is derived. However, the species *Acherontisuchus guajiraensis* and *Hyposaurus derbianus* were not included in the biogeographic analysis of these authors. The eventual inclusion of these two taxa in biogeographic considerations may reveal a more complex scenario.

The fossil record of caimanines and sebecids continues through Eocene in South America, but Dyrosaurids are absent from the continent in this epoch, although its record continues in Africa (Hastings et al., 2011, 2015). Whether Dyrosaurids were already extinct in South America in the Eocene or this absence is the result of scarcity of estuarine and marine deposits during this epoch (see Fortier, 2011) in the continent, it cannot be established now; eventual future collecting efforts in the Eocene localities of South America would be useful to address this issue. After the Eocene, there are no records of Dyrosauridae anywhere in the world (Hastings et al., 2015). All Sebecidae and Caimaninae species for the Eocene of South America come from Argentina, being the sebecids *Ayllusuchus fernandezi* Gasparini (1984), from the early Eocene Lumbra Formation (Gasparini, 1984, Fig. 2-C), *Sebecus icaeorhinus* Simpson (1937a), from the early Eocene Casamayor Formation (Simpson, 1937a; Colbert, 1946; Molnar, 2010, 2013; Pol et al., 2012, Fig. 2-E) and *Ilchunaia parca* Rusconi (1946), from the late Eocene Divisadero Largo Formation. The single caimaninae species is *Eocaiman cavernensis* Simpson (1933), from the late Eocene deposits of the Sarmiento Formation (Simpson, 1933; Fortier, 2011; Bona and Barrios, 2015, Fig. 3-B).

Additionally, an isolated ziphodont tooth from the Guabirota Formation of the south of Brazil has been assigned to Sebecidae (Licciano and Weinschütz, 2010). The authors considered the Guabirota Formation as being a “Miocene/Pliocene –Pleistocene” unit. This would make of the tooth a possible occurrence of sebecids after the middle Miocene (after which all unequivocal records of the clade cease, see below), along with two isolated teeth from the late Miocene Solimões Formation that have been assigned to Sebecidae (see Price et al., 1977; and below). However, more recent research on the fauna of the Guabirota Formation (Sedor et al., 2017) proposed a late middle Eocene age for the unit. This perspective is followed by this study, but since many different ages have already been proposed for the Guabirota Formation (see Sedor et al., 2017), further research may reveal another age for this occurrence.

Another interesting record from the Eocene is the species *Cunampia simplex* Rusconi (1946), also from the Divisadero Largo Formation of Argentina. This species was initially described as a bird (Rusconi, 1946), but a later revision by Agnolin and Pais (2006) showed that the remains assigned to it belong to an indeterminate mesoeucrocodylian crocodyliform and that *C. simplex* is a *nomen dubium* given the absence of autapomorphies. The Oligocene is the Cenozoic epoch with scarcest crocodylomorph fossil record in South America. The most important

record is *Caiman tremembensis* Chiappe (1988), from the Tremembé Formation of the southeast of Brazil. However, this species is based on incomplete material (a left dentary, a fragment of a humerus and isolated vertebrae and osteoderms). Fortier et al. (2014) state that *C. tremembensis* is a Caimaninae but exhibits no diagnostic features and consider it a *nomen dubium*. Other records include those of the Mugrosa Formation of Colombia reported by Stirton (1953), which consist of a partial tooth assigned to *Sebecus* and two teeth assigned to Crocodylidae, though are considered as being “indeterminate crocodyliforms” (Fortier, 2011). Additionally, Moraes-Santos et al. (2011) described some remains assigned to “Gavialoidea indet.” from the late Oligocene-early Miocene Pirabas Formation, from the Brazilian state of Pará, in the north of the country. This record is the earliest for Gavialoidea in South America. The species *Thoracosaurus bahiensis* Marsh (1869), a possible gavialoid from the Early Cretaceous Recôncavo Basin of Brazil, was based only on teeth that actually can be recognized as belonging to a crocodylomorph but not to a more specific group within it (Souza et al., 2015). As such, Souza et al. (2015) consider *T. bahiensis* a *nomen dubium*.

The occurrence of gavialoids in South America from the late Oligocene/early Miocene is better explained by a dispersion from Africa or from Asia through Africa during the Oligocene (see Scheyer and Moreno-Bernal, 2010), although a vicariant scenario (corroborated by the presence of a probable gavialoid tooth in the Eocene of Antarctica, see Willis and Stilwell, 2000) is also possible (see Riff et al., 2010).

However incomplete the Oligocene fossil record is, it still exhibits caimanine and sebecid fossils while dyrosaurids are absent, showing that the crocodylomorph fauna of South America during the Paleogene was consistently formed by caimanines and sebecids (two groups whose occurrences persist into the Neogene), while the Dyrosauridae record is restricted to the Paleocene in the continent.

Additionally, the fact that South American Paleogene caimanine and sebecid records are concentrated in the current territory of Argentina, with many occurrences in the Chubut province, in the south of the country, yields interesting biogeographic considerations. Patagonia currently has a dry, cold climate, which are features that preclude the existence of crocodylians in any given area (Markwick, 1998; Brochu, 1999). However, climate in Patagonia during the Paleogene is described warm and humid, with abundant vegetation and watercourses (Baez and Gasparini, 1977; Gasparini et al., 1986; Albino, 1993; Gasparini, 1996). Such climate is more in accordance with crocodylian physiology, and the Paleocene-Eocene records of *Eocaiman*, *Necrosuchus*, *Notocaiman* and *Sebecus* also correspond to a peak in global crocodylomorph diversity occurred in this transition, which coincides with the peaks in estimated average annual temperature in the globe (Brochu, 2011).

Likewise, decrease in temperature and aridity and dryness growth registered in Patagonia during the Paleogene (Barreda and Palazzi, 2010; Madden et al., 2010) may have caused the extinction of crocodylomorphs in the area. Fossil crocodylomorphs are not registered in the south of Argentina after the Eocene records of *Eocaiman* and *Sebecus* (see Barrios, 2011). Curiously, however, the early Miocene Santa Cruz Formation from the south of Patagonia is considered to have had “warmer and more humid conditions” than in the present day, due to fossil occurrences of reptilian groups such as the *Tupinambis* lizard (Fernicola and Albino, 2012). However, crocodylomorph remains are absent from this formation, which takes Kay et al. (2012) to speculate on the existence of dispersal barriers in the dry mid-latitudes that did not allow crocodylomorphs to reach Patagonia. Accordingly, an increase in aridity, as well as thermal seasonality, were also reported by Pinheiro et al. (2013) as a possible explanation for the extinction of *Eocaiman* in the Itaboraí Basin, in southeastern Brazil. The Oligocene record of a caimanine for the Tremembé Formation, however (see above), denounces that the climatic conditions were already suitable again to crocodylians in the area during the Oligocene.

A summary of the Paleogene crocodylomorph occurrences in the

Paleocene		
Caimaninae	<i>Eocaiman itaboraiensis</i>	Itaborai Basin, Brazil
	<i>E. palaeocenicus</i>	Salamanca Formation, Argentina
	<i>Necrosuchus ionensis</i>	Salamanca Formation, Argentina
	<i>Notocaiman stromeri</i>	Las Violetas Formation, Argentina
Dyrosauridae	<i>Protocaiman peligrensis</i>	Salamanca Formation, Argentina
	<i>Acherontisuchus guajiraensis</i>	Cerrejón Formation, Colombia
	<i>Anthracosuchus balrogus</i>	Cerrejón Formation, Colombia
	<i>Cerrejonisuchus improcerus</i>	Cerrejón Formation, Colombia
Sebecidae	<i>Guarinisuchus munizi</i>	Maria Farinha Formation, Brazil
	<i>Bretesuchus bonapartei</i>	Maiz Gordo Formation, Argentina
	<i>Lorosuchus nodosus</i>	Rio Loro Formation, Argentina
	<i>Sahitisuchus fluminensis</i>	Itaborai Basin, Brazil
Caimaninae	<i>Zulmasuchus querejazus</i>	Santa Lucia Formation, Bolivia
	<i>Eocaiman cavernensis</i>	Sarmiento Formation, Argentina
	<i>Ayllusuchus fernandezii</i>	Lumbrera Formation, Argentina
	<i>Sebecus icaeorhinus</i>	Casamayor Formation, Argentina
Eocene		
Sebecidae	<i>Sebecus sp.</i>	Mugrosa Formation, Colombia
	<i>Hypsosaurus derbianus</i>	unkown locality, Pernambuco state, Brazil
Oligocene		
Sebecidae	<i>Sebecus sp.</i>	Mugrosa Formation, Colombia
Uncertain age		
Dyrosauridae	<i>Hypsosaurus derbianus</i>	unkown locality, Pernambuco state, Brazil

Fig. 8. Table of the crocodylomorph occurrences at a genus level at the best in the Paleogene of South America.

level of genus and species in South America is available in Fig. 8.

2.2. Crocodylomorpha of the Neogene and the Pleistocene

The Miocene epoch is by far the most diverse of the fossil crocodylomorphs in South America. Records of the group in the Miocene are formed not only by caimanines (Figs. 3–6) and sebecids (Fig. 2), but also by two newcomer lineages at the continent: Crocodyloidea (*Charactosuchus* and *Brasiliosuchus*) and Gavialoidea (Fig. 7), through five genera of the Gryposuchinae clade (*sensu* Vélez-Juarbe et al., 2007). There is, however, one record from the Early Cretaceous of Brazil that has been assigned to Crocodyloidea: Maury (1925) assigned, without illustrations, an isolated tooth from the Itapecuru Formation, of the Early Cretaceous (see Carvalho et al., 2003) as “*Crocodylus* sp.”.

However, according to Fortier (2011), the description given is not precise and the tooth could belong to any neosuchian. This, along with the fact that the fossil record of *Crocodylus* begins worldwide only in the Miocene, and specifically in South America in the Pliocene (Brochu, 2000; Fortier, 2011; Scheyer et al., 2013; and below), leads us to consider this record as doubtful. As such, the first record of Crocodyloidea in South America can be assigned to the Miocene.

The Miocene record is also unique by exhibiting at least six different crocodylomorph ecomorphotypes, which occupied each a different ecological niche: terrestrial predator (sebecids; Fig. 2), the durophagous caimanines (*Gnatusuchus*, *Kuttanacaiman*, *Globidentosuchus*, *Balanerodus*, *Caiman wannlangstoni* Salas-Gismondi et al., 2015 and *C. brevirostris* Souza-Filho, 1987, Fig. 4), semi-aquatic giant predator (*Purussaurus*; Fig. 5), semi-aquatic gulp-feeder (*Mourasuchus*; Fig. 5), the

small to medium-sized generalist caimanines (*Caiman*, *Melanosuchus* and *Paleosuchus*; Fig. 6) and the longirostrine piscivorous (crocodyloids *Characotosuchus* and *Brasilosuchus* and gryposuchine gavialoids; Fig. 7). It is also notable the large size reached by several of these taxa. *Purussaurus brasiliensis* Barbosa-Rodrigues (1892) has an estimated body length of 12.5 m (Aureliano et al., 2015), while that of *Mourasuchus pattersoni* Cidade et al. (2017) is 6.6 m (Langston, 2008). The larger specimen of *Gryposuchus croizati* Riff and Aguilera (2008) is estimated to have had 9 and 10 m (Riff and Aguilera, 2008), while *Barinasuchus arveloi* Paolillo and Linares (2007) is estimated to have had between 6 to just over 10 m (Molnar and Vasconcellos, 2016).

The reasons behind such high taxonomic diversity and morphological disparity among South American Miocene crocodylomorphs, as already pointed out by several authors (Cozzuol, 2006; Latrubblesse et al., 2010; Riff et al., 2010; Scheyer and Moreno-Bernal, 2010; Scheyer et al., 2013; Souza et al., 2016; Cidade et al., 2017) are numerous. Those include the very fact that most of the important geological units that bear crocodylomorph fossils (except for the Ituzaingó Formation of Argentina) are in the northern portion of the continent, in an equatorial zone, either in or near the area of the current Amazon rainforest. These include early Miocene Castillo Formation of Venezuela, early/middle Miocene Castilletas Formation and middle Miocene Honda Group of Colombia, Fitzcarrald Arch, and Pebas Formation of Peru and Socorro Formation of Venezuela, and late Miocene formations Solimões, of Brazil and Bolivia, Urumaco of Venezuela, Cobija and Yecua of Bolivia, and Pisco of Peru. As such, the fossils recorded from these units document a fauna that inhabited an equatorial area with hot-humid climate suitable to crocodylomorph physiology, which generated high level of a primary productivity, including a variety of prey items for each crocodylomorph ecomorphotype according to their different diets (mollusks, insects, crustaceans, fish, anurans, turtles and mammals, amongst others).

Additionally, the presence of large water systems in the area during the Miocene (the middle Miocene Pebas system and the late Miocene Acre system, Hoorn et al., 2010), which contained an array of different aquatic systems, including rivers, lakes, streams and swamps (see Hoorn et al., 2010; Latrubblesse et al., 2010) offered a variety of different habitats that could be inhabited by the different ecomorphotypes. It is possible, for example, that *Mourasuchus* preferred to inhabit margins of lakes, swamps and quiet rivers due to its gulp-feeding habit (see Cidade et al., 2017), with the same scenario being possible for the durophagous caimanines, given their habit of foraging in the margins for mollusks and arthropods. Meanwhile, the piscivorous gavialoids and crocodyloids would prefer to inhabit areas more within water bodies, given their preferred prey.

Purussaurus was a semi-aquatic crocodylian but which, given its large size, could make incursions to the land to capture prey, although not reaching the level of terrestriality of sebecids, which had many adaptations to a terrestrial lifestyle such as a high rostrum and erected limbs (see Colbert, 1946; Langston, 1965; Molnar, 2010, 2013). The small to medium-sized caimanines, which had a generalist feeding habit like that of their extant relatives (see Medem, 1981, 1983) would also have a slightly more generalist habitat, preferring the margins of water bodies but with regular incursions into the water bodies themselves and out to the land. Additionally, current equatorial ecosystems are well-known for being more biodiverse than temperate ones given not only to their hot and humid climates, but also for being more stable throughout geological time than temperate areas, which allows new species to originate, evolve and endure for a much longer time in their original habitats if compared to the temperate areas (Fischer, 1960; Mittelbach et al., 2007; Souza et al., 2016).

This scenario, present for current equatorial ecosystems (such as those of the Amazon rainforest) was present in the Miocene ecosystems of the same area. From the Paleocene to the Miocene, the current Amazonian environment maintained itself relatively stable in terms of temperature (Hoorn et al., 2010), while drastic geomorphological

changes would only occur with the elevation of the northern portion of the Andes chain from the middle to the late Miocene (Hoorn et al., 2010) which would cause the extinction of many crocodylomorph taxa present in the Miocene (see below). In summary, the environmental stability of the northern portion of South America played a key role in allowing the huge diversity of crocodylomorphs of the Miocene of South America to originate, diversify, evolve and endure until drastic environmental changes caused much of its diversity to disappear.

The sebecids of the Miocene of South America are represented by the species *Langstonia huilensis* (Langston, 1965) (Fig. 2-D) from the middle Miocene units Honda Group of Colombia (Langston, 1965; Langston and Gasparini, 1997) and Fitzcarrald Arch of Peru (Salas-Gismondi et al., 2007), and *Barinasuchus arveloi*, from the middle Miocene Parangula Formation of Venezuela and Fitzcarrald Arch of Peru (Paolillo and Linares, 2007). *L. huilensis* was originally described as belonging to *Sebecus*, but we follow the taxonomy of Paolillo and Linares (2007), which erected the new genus *Langstonia* for this species. A record of *Langstonia* cf. *L. huilensis* for the Honda Group was described by Busbey (1986). These middle Miocene records represent the last unequivocal records of Sebecidae not only in South America but in the whole world. Two isolated teeth from the late Miocene Solimões Formation of Brazil have been assigned to Sebecidae (Price et al., 1977). However, the authors did not illustrate nor assigned a catalogue number to the material, which according to them was housed either at the MCT in Brazil or at the AMNH in the United States. The teeth could not be located at the MCT, and a consult to the AMNH about whether they would be there was not answered until the publication of this review. Only a reanalysis of the teeth can determine whether they belong to Sebecidae or not, but it is possible to speculate that the teeth may also belong to *Purussaurus*. The teeth of this taxon also exhibit serrated carinae, although these are classified in a “pseudo-ziphodont” morphology in contrast to the true ziphodont found in Sebecidae (see Souza et al., 2016). An assignment to *Purussaurus*, which has a large fossil record in the late Miocene, would also be more congruent with the late Miocene age of the occurrence, rather than the assignment to Sebecidae.

The extinction of the Sebecidae in the Amazon area during the middle Miocene could be surprising at a first glance since it was in the middle Miocene that the giant lake of the Pebas system started to disintegrate into smaller water bodies, which would gradually go on to establish the modern Amazon river basin (Hoorn et al., 2010). However, these changes were driven by the orogeny of the northern portion of the Andes mountain chain, and the environmental changes caused by the elevation of the Andes were certainly detrimental to many fauna and flora components, including terrestrial sebecids. The other crocodylomorphs, which were aquatic, may have survived as the fluvio-lacustrine system that succeeded Pebas, the Acre system (Hoorn et al., 2010) still had water bodies significant in size, even if smaller than those of its predecessor. Alternatively, it is possible that large water bodies such as the Pebas system may have already caused a decline in the populations of sebecids by decreasing the terrestrial environment that could be available to them. As such, the sebecids may have already been in decline by the middle Miocene and thus geomorphological changes occurred in the transition to the late Miocene may have accelerated and provoked the ultimate demise of the group.

The Caimaninae record in the Miocene of South America is large and diverse. It includes the most ancient fossil occurrences of the three extant caimanine genera. *Paleosuchus* is represented by “*Paleosuchus* sp.” occurrences from the middle Miocene units Fitzcarrald Arch (Salas-Gismondi et al., 2007) and Pebas Formation (Salas-Gismondi et al., 2015), both from Peru. *Melanosuchus* is currently represented by some specimens from the late Miocene; one of them (MCZ 243; Fig. 6-A) being from the late Miocene Urumaco Formation of Venezuela, which represents the holotype of the species *Melanosuchus fisheri* Medina (1976). This species, however, was considered a *nomen dubium* by Bona et al. (2017a). These authors considered that the holotype specimen of

M. fisheri could be assigned to *Melanosuchus* sp. while Foth et al. (2017) assigns it as *Melanosuchus* cf. *M. niger* (Spix, 1825). This work follows the former. The other specimen (MCZ 4336) assigned to *M. fisheri* by Medina (1976) was considered by Foth et al. (2017) to belong to *Globidentosuchus brachyrostris* Scheyer et al. (2013), a species that had already been described for the Urumaco Formation (see below). Another specimen from the Urumaco Formation (AMU CURS 234) is also assigned as *Melanosuchus* sp. by Bona et al. (2017a), after being presented as a caimanine with affinities to *M. fisheri* by Scheyer and Delfino (2016). The other occurrences of *Melanosuchus* are from the late Miocene Solimões Formation of Brazil (Lacerda et al., 2017; Souza-Filho et al., 2017).

The *Caiman* genus has the richest Miocene record of all extant genera, with five fossil specimens recorded. These are *C. wannlangtoni* (from the middle Miocene Pebas Formation of Peru and late Miocene Urumaco Formation of Venezuela; Salas-Gismondi et al., 2015; Scheyer and Delfino, 2016; the holotype is in Fig. 4-C; the Urumaco occurrence is the specimen AMU CURS 49, previously considered as *C. lutescens* by Aguilera, 2004 and Sánchez-Villagra and Aguilera, 2006), *C. brevirostris* (from the late Miocene formations Solimões, Brazil, and Urumaco of Venezuela; Souza-Filho, 1987; Aguilera, 2004; Scheyer and Moreno-Bernal, 2010; Fortier et al., 2014; Scheyer and Delfino, 2016, Fig. 4-D), *C. australis* (Bravard, 1858) (Fig. 6-D), *C. gaspariniae* Bona and Carabajal (2013) (Fig. 6-B) and *C. lutescens* (Rovereto, 1912) (from the late Miocene Ituzaingó Formation of Argentina; Bravard, 1858; Rovereto, 1912; Rusconi, 1933; Bona and Carabajal, 2013; Bona et al., 2013a). The UCMP 39978 specimen (Fig. 6-C) from the Honda Group, was assigned by Langston (1965) as *Caiman* cf. *C. lutescens*, but a revision of *C. lutescens* by Bona et al. (2013a) showed that the specimen could not be attributed to this species. Salas-Gismondi et al. (2015) and Scheyer and Delfino (2016) argued that the specimen has affinities to *C. wannlangtoni*, but the proper taxonomic assignment of UCMP 39978 still requires further research; for the meantime, it can be considered as *Caiman* sp. Additionally, *C. wannlangtoni* may not belong to *Caiman* according to a recent phylogeny (Cidade et al., 2017). However, this perspective must be reassessed by future works.

There are also fossil records of the extant species *C. latirostris* from the late Miocene Ituzaingó Formation of Argentina (Bona et al., 2013a) and Urumaco Formation of Venezuela (Scheyer and Delfino, 2016, through specimen MCNC URU 145 72V, previously considered as belonging to *Caiman lutescens* by Aguilera, 2004), aside from a record of *Caiman* cf. *C. latirostris* from the late Miocene Palo Pintado Formation of Argentina (Bona et al., 2014) and specimens assigned as *Caiman* cf. *C. yacare* (Daudin, 1802) from the Ituzaingó Formation (Bona et al., 2013a) and the late Miocene Solimões Formation of Brazil (Fortier et al., 2009). Additionally, there are also records attributed to *Caiman* sp. for the early Miocene Castillo Formation of Venezuela (Solórzano et al., 2018), the middle Miocene units Honda Group of Colombia (Langston, 1965), Socorro Formation of Venezuela (Scheyer et al., 2013), and the late Miocene units Ituzaingó Formation of Argentina (Gasparini and Baez, 1975; Gasparini, 1981) and Solimões Formation of Brazil (Fortier, 2011; Lacerda et al., 2017), aside from the description of teeth with *Caiman* affinities from the middle Miocene Fitzcarrald Arch of Peru (Salas-Gismondi et al., 2007) and an alligatorid with *Caiman* affinities recorded by Spillman (1949) for the Solimões Formation of Peru.

Aside from the extant genera, the Caimaninae fossil record of the Miocene exhibits highly peculiar fossil genera that held ecological niches that are absent in extant crocodylians. The species *Gnatusuchus pebasensis* Salas-Gismondi et al. (2015) (Fig. 4-A), *Kuttanacaiman iquitosensis* Salas-Gismondi et al. (2015) (Fig. 4-B), both of the middle Miocene Pebas Formation of Peru (Salas-Gismondi et al., 2015), *Balanerodus logimus* Langston (1965) (from the middle Miocene units Honda Group of Colombia and Fitzcarrald Arch of Peru; Langston, 1965; Langston and Gasparini, 1997; Salas-Gismondi et al., 2007, Fig. 4-C) and *Globidentosuchus brachyrostris* (from the late Miocene Urumaco

Formation of Venezuela; Scheyer et al., 2013; Hastings et al., 2016; Scheyer and Delfino, 2016; Bona et al., 2017a; Foth et al., 2017) are considered, together with the aforementioned fossil species *C. wannlangtoni* and *C. brevirostris*, as eminent durophagous taxa, which used of highly globular teeth, along with other features, to feed predominantly of hard-shelled prey such as mollusks and arthropods (Langston, 1965; Fortier et al., 2014; Salas-Gismondi et al., 2015). Aside from the aforementioned records of the species themselves, there are also records of *Globidentosuchus* cf. *G. brachyrostris* from the Urumaco Formation (Scheyer and Delfino, 2016).

The *Purussaurus* genus is a large-bodied apex predator that fed on large mammals, turtles, fishes and other crocodylians. It comprises three species: *P. neivensis* (Mook, 1941) (from the middle Miocene Honda Group and Pebas Formation; Mook, 1941; Langston, 1965; Langston and Gasparini, 1997; Salas-Gismondi et al., 2015, Fig. 5-C), *P. mirandai* Aguilera et al. (2006) (from the late Miocene Urumaco Formation; Aguilera et al., 2006; Scheyer and Delfino, 2016, Fig. 5-D) and *P. brasiliensis* (from the late Miocene Solimões Formation of Brazil; Barbosa-Rodrigues, 1892; Price, 1967; Bocquentin-Villanueva et al., 1989; Souza et al., 2010; Aureliano et al., 2015). Additionally, there is also an occurrence of *Purussaurus* cf. *P. mirandai* in the Urumaco Formation (Scheyer and Delfino, 2016). There are also records of *Purussaurus* sp. for the early Miocene Castillo Formation of Venezuela (Solórzano et al., 2018), the early/middle Miocene Castilletes Formation of Colombia (Moreno-Bernal et al., 2016) and for the middle Miocene units Pebas Formation and Fitzcarrald Arch of Peru (Salas-Gismondi et al., 2007, 2015) and Socorro Formation of Venezuela (Scheyer et al., 2013), as well as the late Miocene Urumaco Formation of Venezuela (Scheyer and Delfino, 2016), Solimões Formation of Brazil (Scheyer and Moreno-Bernal, 2010; Souza et al., 2016) and Cobija Formation of Bolivia (Rusconi, 1931; Carrasco, 1986; Leytón and Pacheco, 1989; Fortier, 2011). Furthermore, Moreno (2006) suggested the presence of *Purussaurus*, based on a maxillary fragment and large teeth, in the early Miocene Barzalosa Formation of Colombia.

The peculiar, “duck-faced” genus *Mourasuchus* was also a large crocodylian whose feeding habits were originally described as being a “filter-feeding” activity (see Langston, 1965; Riff et al., 2010; Bona et al., 2013b), but a recent work described it alternatively as “gulp-feeding” (Cidade et al., 2017) proposing that *Mourasuchus* fed preferably on large amounts of small-sized prey that were grasped at once with the ventral portion of the rostrum. It consists of four species: *M. atopus* (Langston, 1965) (from the middle Miocene Honda Group of Colombia and Pebas Formation of Peru (Langston, 1965; Langston and Gasparini, 1997; Salas-Gismondi et al., 2015); *M. amazonensis* Price (1964) (from the Solimões Formation of Brazil; Price, 1964; Souza-Filho and Guilherme, 2011a); *M. arendsi* Bocquentin-Villanueva (1984) (from the late Miocene Urumaco Formation of Venezuela, Ituzaingó Formation of Argentina, Solimões Formation of Brazil and either the Solimões or the Cobija Formation of Bolivia; see below; Bocquentin-Villanueva, 1984; Souza-Filho and Guilherme, 2011b; Scheyer and Delfino, 2016; Cidade et al., 2018a, Fig. 5-A) and *M. pattersoni* (Urumaco Formation; Cidade et al., 2017, Fig. 5-B). Occurrences of *Mourasuchus* sp. have also been recorded for early/middle Miocene Castilletes Formation of Colombia (Moreno-Bernal et al., 2016) and for the middle Miocene units Pebas Formation and Fitzcarrald Arch of Peru (Salas-Gismondi et al., 2007, 2015) and Socorro Formation of Venezuela (Scheyer et al., 2013), and the late Miocene Formations Solimões of Brazil (Souza-Filho and Kischlat, 1995; Oliveira and Souza-Filho, 2001; Scheyer and Moreno-Bernal, 2010; Souza et al., 2016), Urumaco of Venezuela (Scheyer and Delfino, 2016) and Yecua of Bolivia (Tineo et al., 2014). Most specimens that were assigned in the past to *M. nativus* Gasparini (1985) can now be assigned to *M. arendsi* as the former species has been considered a junior synonym of the latter (Scheyer and Delfino, 2016). These include not only the holotype and the referred specimen of *M. nativus* from the late Miocene Ituzaingó Formation of Argentina, originally described by Gasparini (1985), but specimens from the late Miocene

units Urumaco Formation of Venezuela (see Scheyer et al., 2013) and from the Solimões Formation of Brazil (see Cidade et al., 2013) and maybe Bolivia (the specimen AMNH 14441, which has an uncertain origin and may also be from the late Miocene Cobija Formation of Bolivia, which is correlated to the Solimões Formation; see Cidade et al., 2016) as well.

Another interesting caimanine record for the Miocene consists of two specimens assigned as *Eocaiman* sp. for the middle Miocene Honda Group of Colombia by Langston (1965), which makes *Eocaiman* the only Caimaninae genus to have occurrences from the Paleocene to the Miocene.

Putative crocodyloids of the South American Miocene are comprised by the *Charactosuchus* and *Brasiliosuchus* genera. The South American *Charactosuchus* is represented by the species *Ch. fieldsi* Langston (1965) (from the middle Miocene Honda Group and late Miocene Solimões Formation of Brazil; Langston, 1965; Langston and Gasparini, 1997; Souza-Filho, 1993, Fig. 7-D). “*Ch. sansaoi*” from the late Miocene Solimões Formation of Brazil has been mentioned as a valid species (Riff et al., 2010), but because this name was presented only in a conference abstract (Souza-Filho, 1991), it is not actually a valid name. There is also a record of *Charactosuchus* sp. for the Solimões Formation of Brazil (Fortier, 2011). *Brasiliosuchus* is represented only by the species *B. mendesi* Souza-Filho and Bocquentin-Villanueva (1989), from the late Miocene Solimões Formation of Brazil and Urumaco Formation of Venezuela (Souza-Filho and Bocquentin-Villanueva, 1989; Souza-Filho et al., 1993; Aguilera, 2004; Scheyer and Moreno-Bernal, 2010). Souza-Filho et al. (1993) considered *Brasiliosuchus* to be a junior synonym of *Charactosuchus*. However, as the work of Souza-Filho et al. (1993) is a conference abstract, *Brasiliosuchus* remains as a valid genus, with its only species being *B. mendesi*. Additionally, Salas (2003) recorded an ‘unidentified longirostrine tomistominae crocodylian’ (“Tomistominae indet.” according to Riff et al., 2010) for the late Miocene near-shore marine Pisco Formation of Peru, while Carrasco (1986) assigned cranial fossils to *Gavialosuchus* sp. for the late Miocene Solimões Formation of Bolivia. However, these materials could not be thoroughly reassessed for this contribution and as such their taxonomic assignments must be seen with caution until reassessments are made, especially the latter, as *Gavialosuchus* is so far restricted to North America (see below).

Brasiliosuchus and the South American species of *Charactosuchus* have never been inserted in phylogenetic analyses (Brochu, 2003; Vélez-Juarbe and Brochu, in press). However, *Charactosuchus* has been considered as a tomistominae crocodyloid (Steel, 1973), while Vélez-Juarbe and Brochu (in press) argue that the genus cannot be assigned to Tomistominae or to Crocodyloidea based on the currently known specimens, referring it as “Crocodyliformes incertae sedis”. If the perspective of *Charactosuchus* (and consequently *Brasiliosuchus*, as stated above) as tomistomines is correct, *Charactosuchus* and *Brasiliosuchus* would be part of the first dispersion of crocodyloids into the American continents, of which the genera *Thecachampsia* and *Gavialosuchus*, which have records from the Oligocene to the Pliocene of North America (Brochu, 1997b; Myrick, 2001; Piras et al., 2007) are part of. A possible link between North American tomistomines and South American forms could be the *Charactosuchus kugleri* species Berg (1969), from the Eocene Chapelton Formation of Jamaica (Estes and Báez, 1985; Piras et al., 2007), which allows the hypothesis that South American forms are derived from North American or Central American/Caribbean ancestors. However, a thorough phylogenetic analysis involving all putative tomistomines of the American continents, which has not been performed to date (Brochu, 2003), is imperative for a better assessment of these biogeographical issues. The arrival of tomistomines in North America has been interpreted as a dispersal from European forms (Piras et al., 2007), although a vicariant event between these two continents (Piras et al., 2007) or a dispersal from African forms cannot be ruled out. Remains from the late Miocene Urumaco Formation of Venezuela have been assigned to *Thecachampsia* (Aguilera, 2004), but Scheyer and Moreno-Bernal (2010) have argued that these are gavialoids. Later,

however, Scheyer et al. (2013) tentatively assigned a specimen comprised by a cranium and rostrum (AMU CURS 034) of the middle Miocene Socorro Formation of Venezuela to *Thecachampsia*. Further studies of these specimens are required to settle their taxonomic status.

The Miocene South America gavialoids, which are also part of the clade *Gryposuchinae sensu* Vélez-Juarbe et al. (2007), may be broadly split into two groups according to the current paleoecological understanding about the group: the taxa that inhabited freshwater environments (*Gryposuchus* and *Hesperogavialis*) and those that inhabited coastal/estuarine environments (*Aktiogavialis*, *Ikanogavialis*, *Piscogavialis* and *Siquisiquesuchus*) (Salas-Gismondi et al., 2016, 2018). *Gryposuchus* is comprised by the species *G. jessei* Gürich (1912) (from the late Miocene Solimões Formation of Brazil and Urumaco Formation of Venezuela; Gürich, 1912; Aguilera, 2004; Sánchez-Villagra and Aguilera, 2006; Scheyer and Moreno-Bernal, 2010; Souza et al., 2018), *G. colombianus* Langston (1965) (from the middle Miocene Honda Group of Colombia and late Miocene Urumaco Formation of Venezuela; Langston, 1965; Langston and Gasparini, 1997; Aguilera, 2004), *G. pachakamue* Salas-Gismondi et al. (2016) (from the middle Miocene Pebas Formation of Peru; Salas-Gismondi et al., 2016), *G. croizati* (from the late Miocene Urumaco Formation of Venezuela; Riff and Aguilera, 2008, Fig. 7-A) and *G. neogaeus* (Burmeister, 1885) (from the late Miocene Ituzaingó Formation; Burmeister, 1885; Rusconi, 1935; Gasparini, 1968; Bona et al., 2017b).

There is also an occurrence assigned to *Gryposuchus* cf. *G. colombianus* for the middle Miocene Fitzcarrald Arch of Peru (Salas-Gismondi et al., 2007). Additionally, records of *Gryposuchus* sp. were mentioned for the early Miocene Castillo Formation of Venezuela (Solórzano et al., 2017), middle Miocene Pebas Formation of Peru (Salas-Gismondi et al., 2015), middle/late Miocene Tranquitas Formation of Argentina (Gasparini and Baez, 1975; Fortier, 2011) and for the late Miocene formations Urumaco of Venezuela (Aguilera, 2004), Solimões of Brazil (Riff and Oliveira, 2008; Souza et al., 2016) and Peru (Spillman, 1949). *Hesperogavialis* is comprised solely by the *H. cruxenti* species Bocquentin-Villanueva and Buffetaut (1981), from the late Miocene Urumaco Formation of Venezuela (Bocquentin-Villanueva and Buffetaut, 1981, Fig. 7-B), aside from other occurrences of the genus (*Hesperogavialis* sp.) from the same unit and from the Solimões Formation of Brazil (Riff et al., 2010; Fortier, 2011).

The estuarine gavialoid species are the following: *Siquesiquesuchus venezuelensis* Brochu and Rincón (2004) from the early Miocene Castillo Formation of Venezuela; *Piscogavialis jugaliperforatus* Kraus (1998) from the late Miocene Pisco Formation of Peru, *Aktiogavialis caribesi* Salas-Gismondi et al. (2018) from the late Miocene Urumaco Formation Venezuela and *Ikanogavialis gameroi* Sill (1970), whose holotype is also from the Urumaco Formation (Sill, 1970, Fig. 7-C), but for which there is also an occurrence for the middle Miocene Socorro Formation of Venezuela (Scheyer et al., 2013). There is also a possible occurrence assigned to *Ikanogavialis* sp. from the early Miocene Barzalosa Formation of Colombia (Moreno, 2006). Additionally, Moreno-Bernal et al. (2016) record fossils assigned as “Gavialoidea indeterminate” for the early Miocene Jimol Formation and for the early/middle Miocene Castilletas Formation, both in Colombia.

Sharing of crocodylomorph taxa between the Miocene units located near or in the area of the current Amazon can be expected due to the relative geographical closeness between them. However, sharing of taxa such as *Caiman*, *Mourasuchus*, and *Gryposuchus* between the Amazonian units and the Ituzaingó Formation of Argentina deserves considerations. Several authors have suggested the existence of one or more connections between these two areas during the Miocene (Bocquentin and Souza-Filho, 1990; Räsänen et al., 1995; Latrubesse et al., 2010; Riff et al., 2010) based on the sharing of these and other continental vertebrates between them. Proposed connections are drainage basins that would occur through swamp areas between the two regions (see Riff et al., 2010), which would exist after the regression of the Paranian Sea but before an uplift of the Andes Chain (especially of the Bolivian

Altiplano) during the middle-late Miocene (Cozzuol, 2006; Hoorn et al., 2010; Riff et al., 2010).

After the late Miocene, only the extant caimanine genera *Caiman*, *Melanosuchus* and *Paleosuchus* would remain from the crocodylomorph taxa with fossil record until that period. All the other crocodylians, including gavialoids, the crocodyloids *Charactosuchus* and *Brasiliosuchus* and most caimanines (including *Purussaurus*, *Mourasuchus* and the durophagous taxa) were extinct. The extinction of these taxa in the area of the current Amazon river basin has been traditionally linked (Riff et al., 2010; Scheyer et al., 2013; Souza et al., 2016) to the continuous elevation of the northern portion of the Andes Chain, which, through the late Miocene, ended with the large lakes with the Acre system and started shaping the current Amazon river drainage basin (Hoorn et al., 2010), thus reducing the space and food resources available to semi-aquatic crocodylians. This reduction of space and resources would be especially harsh on large (*Purussaurus*, *Mourasuchus*, *Gryposuchus*) and specialized crocodylians (*Mourasuchus*, gavialoids, *Charactosuchus* and *Brasiliosuchus* and the durophagous caimanines *Caiman brevirostris* and *Globidentosuchus*), due to high food demands in the first group and adaptation inability for environmental changes in the second. Consequently, smaller, generalist taxa such as the extant caimanines had more survival chances.

A similar event (related to the elevation of the Andes affecting the river basins) might have happened in the south of the continent, in the Ituzaingó Formation area, in what is now Argentina, although in this case a climate cooling during the Pliocene might have had a role in the extinction as well (Souza et al., 2013). There, *Mourasuchus* and *Gryposuchus* were extinct after the late Miocene, but *Caiman latirostris* continued to have records in Argentina throughout the Pliocene and Pleistocene and inhabits the country today, together with *C. yacare* (Bona and Barrios, 2015; see below).

From the Pliocene onwards, the surviving South American crocodylomorph fauna would be enriched by the crocodyloid genus *Crocodylus*, represented in the Pliocene by the species *C. falconensis* (Scheyer et al., 2013) from the early Pliocene San Gregorio Formation of Venezuela and from a posterior fragment of a right mandibular ramus assigned to *Crocodylus* sp. from the late Pliocene Ware Formation of Colombia described by Moreno-Bernal et al. (2016). Additionally, Moreno-Bernal et al. (2016) assigned two specimens from the late Pliocene Ware Formation of Colombia as “Crocodylidae indeterminate”. Although it is not a strictly Pliocene unit, Barrios (2013) also reported the presence of *Caiman latirostris* for the Plio-Pleistocene Piquete Formation of Argentina.

The records of *Crocodylus* in the Pliocene of South America suggest that the genus arrived in the continent between the late Miocene and the Pliocene. The continent from which the South American *Crocodylus* dispersed may either be Africa or North America. The most probable origin of *Crocodylus* in the American continents as a whole is from an African ancestor dispersed through the Atlantic Ocean at least in the late Miocene or earlier, as it is congruent with estimations of molecular analyses (Meredith et al., 2011; Oaks, 2011), with the phylogenetic proximity between the American extant and extinct *Crocodylus* with the extant African species *C. niloticus* Laurenti, 1768 (Meredith et al., 2011; Oaks, 2011; Scheyer et al., 2013), and with recent described fossils assigned to *Crocodylus* from the late Miocene Puente Ixcán locality of Mexico (Carbot-Chanona, 2017). This dispersion represents the second crocodyloid displacement into American continents in the Cenozoic. An origin from Asia or Oceania for the American *Crocodylus* is also possible, but less likely (see Brochu et al., 2007). Regarding South American *Crocodylus* specifically, it cannot be currently known whether they are descendants of ancestors that came from North America or directly from Africa. The last hypothesis is more probable given the closer geographical proximity between Africa and South America; regardless of these two hypotheses, however, it is noteworthy that the North and South American *Crocodylus*, when considered as a whole, are more likely originary from African ancestors. This would imply that

Crocodylus arrived in South America in a time in which the continent was already separated of Africa by a large Atlantic Ocean, but this may not represent a significant barrier given the salt tolerance present in extant *Crocodylus* (Taplin and Grigg, 1989). A dispersion from North America would also require displacements through salt water, albeit in a much shorter distance (see Iturrealde-Vinent, 2006). Additionally, a dispersion between North and South America in the late Miocene or Pliocene could also be accomplished through gradual displacement between islands and archipelagos (“island-hopping”) situated between the continents at the time (see Iturrealde-Vinent, 2006), similarly to what is suggested for the possible dispersion of caimanines from North to South America between the late Cretaceous and the Paleocene (see Brochu, 1999, 2010, 2011, and above).

The crocodylomorph fossil record for the Pleistocene may be considered good “quantitatively, but not qualitatively” as stated by Fortier (2011) in the sense that the vast majority of the fossils known to date belong to the extant species or can be assigned only to the genus-level at best. The only record different from the extant taxa at a species level is *Caiman venezuelensis* Fortier and Rincón (2012), from the Pleistocene asphalt deposit “El Breal de Orocual” of Venezuela. All extant caimanine genera have fossil records in the Pleistocene, with occurrences of “*Caiman* sp.” for “El Breal de Orocual” (Fortier and Rincón, 2012), for the “La Carolina” locality of Equator (Hoffstetter, 1970), for several localities in Brazil (Fortier, 2011; Eduardo et al., 2018), and for the Arroyo Feliciano Formation of Argentina (Noriega et al., 2004; Fortier, 2011).

There are records of “*Melanosuchus* sp.” for the Rio Madeira Formation of the Brazilian state of Rondonia (Andrade et al., 2010), and of “*Paleosuchus* sp.” (Hirooka, 1997, 2003) from the Baxuxi caves of the Brazilian state of Mato Grosso. Also, from the Rio Madeira Formation there is a record assigned to Crocodylidae (Fortier et al., 2006) which represents the most significant known crocodyloid record for the Pleistocene of South America to date. At specific level, there are records of *Caiman latirostris* for the Jandaíra Formation of the Brazilian state of Rio Grande do Norte (Mariño et al., 2005) and for the Upper Chaco Formation in the Salta Province of Argentina (Patterson, 1936). This last record is considered as being from the “Plio-Pleistocene” by Bona and Barrios (2015), but other authors (Fortier, 2011) still consider it as being from the Pleistocene. A more in-depth review of the crocodylian occurrences of the Pleistocene of South America is available in Fortier and Rincón (2012).

In summary, the crocodylomorph fossil record of the Pleistocene does not differ significantly from the current crocodylian diversity seen in South America. This fact shows that, by this epoch, the fauna had already stabilized into its current structure. This present fauna is comprised by six caimanine species and two crocodyloid species. These are distributed among the genera *Caiman* (*C. crocodilus*, (Linnaeus, 1758), *C. latirostris* and *C. yacare*), *Melanosuchus* (*M. niger*), *Paleosuchus* (*P. palpebrosus* (Cuvier, 1807) and *P. trigonatus* (Schneider, 1801)) and *Crocodylus* (*C. acutus* Cuvier, 1807 and *C. intermedius* Graves, 1819) (Medem, 1981, 1983).

A summary of the Neogene crocodylomorph occurrences in the level of genus and species in South America from early to middle/late Miocene deposits is available in Fig. 9, and from the late Miocene to the Pleistocene in Fig. 10. Pleistocene entries in the table, however, are restricted to the only fossil taxon that is different from the extant crocodylian species in the continent at the specific level (*Caiman venezuelensis*), given the extensive Pleistocene record of crocodylians in South America and the fact that most of which identifiable only to the generical level or to extant species (see Fortier and Rincón, 2012).

3. Discussion

3.1. Conclusions

The first records of the fossil crocodylomorph fauna of the Cenozoic

Miocene		
early Miocene		
Gavialoidea	<i>Gryposuchus</i> sp.	Castillo Formation, Venezuela
	<i>Siquisquischus venezuelensis</i>	Castillo Formation, Venezuela
	<i>Caiman</i> sp.	Castillo Formation, Venezuela
Caimaninae	<i>Purussaurus</i> sp.	Castillo Formation, Venezuela
early/middle Miocene		
Caimaninae	<i>Mourasuchus</i> sp.	Castilletes Formation, Colombia
	<i>Purussaurus</i> sp.	Castilletes Formation, Colombia
middle Miocene		
Caimaninae	<i>Balanerodus logimus</i>	Fitzcarrald Arch, Peru; Honda Group, Colombia
	<i>Caiman wannlangstoni</i>	Pebas Formation, Peru
	<i>Caiman</i> sp.	Honda Group, Colombia; Socorro Formation, Venezuela
	<i>Eocaiman</i> sp.	Honda Group, Colombia
	<i>Gnatusuchus pebasensis</i>	Pebas Formation, Peru
	<i>Kuttanacaiman iquitosensis</i>	Pebas Formation, Peru
	<i>Mourasuchus atopus</i>	Honda Group, Colombia; Pebas Formation, Peru
	<i>Mourasuchus</i> sp.	Fitzcarrald Arch, Peru; Pebas Formation, Peru; Socorro Formation, Venezuela
	<i>Paleosuchus</i> sp.	Fitzcarrald Arch, Peru; Pebas Formation, Peru
	<i>Purussaurus neivensis</i>	Honda Group, Colombia; Pebas Formation, Peru
	<i>Purussaurus</i> sp.	Fitzcarrald Arch, Peru; Pebas Formation, Peru; Socorro Formation, Venezuela
Crocodyloidea	<i>Charactosuchus fieldsi</i>	Honda Group, Colombia
	<i>Gryposuchus colombianus</i>	Honda Group, Colombia
	<i>Gryposuchus</i> cf. <i>G. colombianus</i>	Fitzcarrald Arch, Peru
Gavialoidea	<i>G. pachakamue</i>	Pebas Formation, Peru
	<i>Gryposuchus</i> sp.	Pebas Formation, Peru
	<i>Ikanogavialis gameroi</i>	Socorro Formation, Venezuela
	<i>Barinasuchus arveloi</i>	Fitzcarrald Arch, Peru; Parángula Formation, Venezuela
Sebecidae	<i>Langstonia huilensis</i>	Fitzcarrald Arch, Peru; Honda Group, Colombia
	<i>Langstonia</i> cf. <i>L. huilensis</i>	Honda Group, Colombia
middle/late Miocene		
Gavialoidea	<i>Gryposuchus</i> sp.	Tranquitas Formation, Argentina

Fig. 9. Table of the crocodylomorph occurrences at a genus level at the best in the units assigned to the early Miocene, early/middle Miocene, middle Miocene and middle/late Miocene of South America.

of South America are from the second half of the 19th century, especially from Argentina (Bravard, 1858, 1860; Burmeister, 1883, 1885; Ambrosetti, 1887; Scalabrini, 1887) and the Brazilian Amazonia (Gervais, 1876; Barbosa-Rodrigues, 1892). From these works, three proposed species remain valid to this day: *Caiman australis*, *Gryposuchus neogaeus* and *Purussaurus brasiliensis* (see Bravard, 1858; Burmeister, 1885; Barbosa-Rodrigues, 1892). The 20th century saw a major breakthrough in our knowledge of the fauna, and there is no doubt through this revision that this knowledge has significantly advanced in the last decade particularly.

Currently, we can distinguish three phases in the evolution of the South American Cenozoic crocodylomorph fauna: the first one is in the Paleogene, which is dominated by sebecids and alligatoroid caimanines, with dyrosaurids restricted to the Paleocene. The second phase is the Miocene, in which a mega-diverse crocodylomorph fauna with a plethora of species and at least six ecomorphotypes (terrestrial predator, semi-aquatic large predator, small to medium-sized semi-aquatic generalist predator, gulp-feeder, durophagous, piscivorous longirostrine) inhabited the large aquatic systems of the Amazon area while also reaching the area of the current Argentina. The third phase

late Miocene	
<i>Caiman australis</i>	Ituzaingó Formation, Argentina
<i>C. brevirostris</i>	Solimões Formation, Brazil; Urumaco Formation, Venezuela
<i>C. gasparinæ</i>	Ituzaingó Formation, Argentina
<i>C. latirostris</i>	Ituzaingó Formation, Argentina; Urumaco Formation, Venezuela
<i>Caiman cf. C. latirostris</i>	Palo Pintado Formation, Argentina
<i>C. lutescens</i>	Ituzaingó Formation, Argentina
<i>C. wannlangstoni</i>	Urumaco Formation, Venezuela
<i>Caiman cf. C. yacare</i>	Ituzaingó Formation, Argentina; Solimões Formation, Brazil
<i>Caiman sp.</i>	Ituzaingó Formation, Argentina; Solimões Formation, Brazil
<i>Globidentosuchus brachyostrois</i>	Urumaco Formation, Venezuela
<i>Globidentosuchus cf. G. brachyostrois</i>	Urumaco Formation, Venezuela
<i>Melanosuchus sp.</i>	Solimões Formation, Brazil; Urumaco Formation, Venezuela
<i>Mourasuchus amazonensis</i>	Solimões Formation, Brazil
<i>M. arendsi</i>	Ituzaingó Formation, Argentina; Solimões Formation, Brazil; Urumaco Formation, Venezuela; undefined Formation, Bolivia
<i>M. pattersoni</i>	Urumaco Formation, Venezuela
<i>Mourasuchus sp.</i>	Solimões Formation, Brazil; Urumaco Formation, Venezuela; Yecua Formation, Bolivia
<i>Purussaurus brasiliensis</i>	Solimões Formation, Brazil
<i>P. mirandai</i>	Urumaco Formation, Venezuela
<i>Purussaurus cf. P. mirandai</i>	Urumaco Formation, Venezuela
<i>Purussaurus sp.</i>	Cobija Formation, Bolivia; Solimões Formation, Brazil
	Urumaco Formation, Venezuela
<i>Brasiliosuchus mendesi</i>	Solimões Formation, Brazil; Urumaco Formation, Venezuela
<i>Charactosuchus fieldsi</i>	Solimões Formation, Brazil
<i>Charactosuchus sp.</i>	Solimões Formation, Brazil
<i>Gavialosuchus sp.</i>	Solimões Formation, Bolivia
<i>Aktiogavialis caribesi</i>	Urumaco Formation, Venezuela
<i>Gryposuchus colombianus</i>	Urumaco Formation, Venezuela
<i>G. croizati</i>	Urumaco Formation, Venezuela
<i>G. jessei</i>	Solimões Formation, Brazil; Urumaco Formation, Venezuela
<i>G. neogaetus</i>	Ituzaingó Formation, Argentina
<i>Gryposuchus sp.</i>	Solimões Formation, Brazil and Peru; Urumaco Formation, Venezuela
<i>Hesperogavialis cruxenti</i>	Urumaco Formation, Venezuela
<i>Hesperogavialis sp.</i>	Solimões Formation, Brazil
<i>Ikanogavialis gameroi</i>	Urumaco Formation, Venezuela
<i>Piscogavialis jugaliperforatus</i>	Pisco Formation, Peru
Pliocene	
<i>Crocodylus falconensis</i>	San Gregorio Formation, Venezuela
<i>Crocodylus sp.</i>	Ware Formation, Colombia
Pliocene/Pleistocene	
<i>Caiman latirostris</i>	Piquete Formation, Argentina
Pleistocene*	
<i>Caiman venezuelensis</i>	El Breal de Orocuá asphalt deposit, Venezuela

Fig. 10. Table of the crocodylomorph occurrences at a genus level at the best in the late Miocene, Pliocene, and Pleistocene of South America. As the Pleistocene record is very large but at the same time all occurrences at a genus level and most occurrences at a specific level belong to the extant taxa, only the single record distinct from extant taxa at a specific level was included (*Caiman venezuelensis*). More information about the Pleistocene record is available at the text and in Fortier and Rincón (2012).

(from the Pliocene to this day) is due to geomorphological changes in the continent between middle Miocene and late Miocene/Pliocene, especially related to orogeny of the Andes chain, which led to environmental changes that caused extinction of much of the fauna, except the extant genera *Caiman*, *Melanosuchus* and *Paleosuchus*. The arrival of *Crocodylus* in the continent, not earlier than the Pliocene and probably from Africa or North America, completed the current

crocodylian fauna of South America.

3.2. Perspectives

All these advances in our knowledge notwithstanding, many unsolved questions, challenges and knowledge gaps remain to be filled. The inclusion of South American occurrences of *Charactosuchus* in

phylogenetic analyses is a very important issue to be assessed. This must shed light not only on whether this genus is a tomistomine crocodyloid or not but also on the biogeographic origin of the group which, for the time being, remains as perhaps the biggest biogeographical enigma involving crocodylomorphs from the Cenozoic of South America.

Accordingly, another important issue is whether the fossils that have been assigned for the tomistomines *Thecachampsia*, for the Miocene of Venezuela (Aguilera, 2004; Scheyer et al., 2013) and *Gavialosuchus*, for the Miocene of Bolivia (Carrasco, 1986) really belong to these groups, to *Charactosuchus*, to gavialoids or to any other group. Regardless of the outcome, a revision of the taxonomy of these groups shall bring interesting perspectives about the crocodylomorph fauna of the South American Cenozoic. For example, a confirmation of the assignment of these fossils to *Thecachampsia* and *Gavialosuchus*, which are taxa exclusive to North America (see Piras et al., 2007), would bring interesting biogeographic questions about tomistomine crocodylians.

Another issue to be tackled is the predominance of Miocene fossils in the record; this must be improved by a larger collecting effort in the units from the Paleogene and from the Pliocene that have already yielded fossils in the past. Some units of the Paleogene, such as the Salamanca, Las Violetas, Río Loro, Divisadero Largo, Casamayor, Sarmiento and Lumbreña formations of Argentina, Santa Lucía of Bolivia and the María Farinha and Tremembé formations of Brazil, are particularly interesting for future fieldworks as fossils from these units have been described in the 20th century but little research has been done in them in this century (e.g. Barbosa et al., 2008; Sena et al., 2017). Fieldworks in the Itaboráí Basin itself cannot be done anymore as the outcrops are now covered with water (Croft, 2016), but there are still rock fragments around the area that may bear fossils and can be prospected (C. Rangel, personal communication, 2018). The only Paleogene Formations whose fossils have been intensely described in recent years is the Cerrejón Formation of Colombia (Hastings et al., 2010, 2011, 2015), which has been revealing a most interesting dyrosaurid fauna and from which hopefully much more may come.

Paleogene fossils have immensurable importance as they may help to answer some of the most important questions involving South American crocodylomorphs South America: how long dyrosaurids remained in the continent; when crocodyloids and gavialoids arrived in South America; whether there were more semi-aquatic sebecids, such as *Lorusuchus*, which is their phylogenetic placement and what they say about the evolution of sebecids; and how was the origin and evolution of the highly distinct caimanine ecomorphotypes of *Purussaurus*, *Mourasuchus* and the durophagous caimanines, especially the highly specialized *Gnatusuchus* (see Salas-Gismonti et al., 2015). Although some ideas have been offered for the origin and evolution of these three ecomorphotypes (see Cidade, 2016; Cidade et al., 2018b), the fossil record of Paleogene caimanines that may be more basal forms of these taxa is an essential gap to be filled for the understanding of the evolution of these taxa.

The absence of crocodylomorph fossils for the Pliocene, despite the number of fossiliferous units that can be assigned to this epoch, is a problem recognized by Fortier (2011), but the description of *Crocodylus falconensis* from the Pliocene San Gregorio Formation of Venezuela (Scheyer et al., 2013) brings a new hope that our knowledge on the Pliocene crocodylomorph fauna of South America can be significantly improved in the future. This perspective is important because the Pliocene represents the gap between the hyper-diverse Miocene fauna and the extant crocodylomorph fauna, and a better understanding of it is very important for a thorough comprehension of this transition and, most notably, for the understanding about how *Crocodylus* arrived in South America if the Pliocene is confirmed as the oldest time in which fossils of this genus are found in the continent.

The Pleistocene also offers an interesting ground for work. Despite the fact that most of the crocodylomorph remains of the epoch can be assigned to the extant genera and species, when they can be assigned to

these lower taxonomic levels at all, the abundance of Pleistocene deposits, caves and other fossiliferous places with crocodylian remains (see Fortier, 2011; Fortier and Rincón, 2012; Castro et al., 2014) hints that conducting more fieldwork may yield a much richer and diverse fauna for the epoch than the one currently known for it. The Pleistocene is also important as making part of the transition to the extant crocodylian fauna, and a deeper knowledge about Pleistocene crocodylomorphs is as essential for a thorough understanding of the Cenozoic fauna as that of the crocodylomorphs of any other Cenozoic epoch, no matter how recent Pleistocene is when compared to the others.

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Appendix A. Supplementary data

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