UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

Phylogenetic review of Alligatoridea (Crocodylia) and taxonomic review of the species of the Caimaninae clade

Revisão filogenética de Alligatoroidea (Crocodylia) e revisão taxonômica das espécies do clado Caimaninae

Giovanne Mendes Cidade

Tese apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Doutor em Ciências, obtido no Programa de Pós-Graduação em Biologia Comparada

Ribeirão Preto - SP

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Orientadora: Profª. Drª. Annie Schmaltz Hsiou

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I dedicate this thesis to my mother, Doria, and to my father, Pedro (*in memorian*), as a small gesture of gratitude for all love, care, dedication and support you have always given me. I love you forever.

I dedicate this thesis also to all of those who studied Alligatoroidea before me.

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“There is no knowledge that is not power”

“Não existe conhecimento que não seja poder”

- Tela de Abertura do jogo Mortal Kombat 3, Midway, 1995

“Weakness is a choice”

“A fraqueza é uma escolha”

- Diego Pimentel Venturelli

Abstract in English

Crocodylia is the crown-group that unites the most recent common ancestor of all extant crocodylomorphs and all its descendents. It is mainly divided into three clades: Crocodyloidea, Gavialoidea and Alligatoroidea. This last clade has a very large taxonomic diversity of fossil species, and although several phylogenetic analyses have already been performed for Alligatoroidea, nearly all analyses in the last two decades have been performed based on a single dataset (Brochu, 1997a, 1999), which has never been comprehensively revised, despite the fact that a handful other characters have been proposed in other studies and many fossil taxa have been created or revised. This study has performed the most comprehensive review of the phylogenetic datasets of the clade Alligatoroidea. Ten new characters are proposed, and several characters previously proposed were changed, with many new states being created and others having their texts modified. Additionally, several scoring for previously proposed characters were changed. As such, this study has assembled the largest ever phylogenetic dataset for the clade Alligatoroidea, consisting of 183 characters and 58 alligatoroid taxa, as well as 38 taxa as outgroups. The results of the phylogenetic analysis show *Leidyosuchus* and *Diplocynodon* as the basalmost alligatoroids. There are followed by the clade Globidonta, which is comprised by the Asian *Krabisuchus* and the European *Arambourgia* as successive sister-taxa to Alligatoridae. This clade in its turn if formed by a three lineage polytomy: the predominantly North American Alligatorinae, the predominantly South American Caimaninae, and the Central American *Culebrasuchus*. Regarding the evolution of ecomorphotypes in Alligatoroidea, this analysis indicates that the durophagous ecomorphotype may have arisen up to five times during the evolutionary history of the clade, although the analysis shows that most durophagous taxa are concentrated in two clades: Brachychampsidae (Alligatorinae) and Globidentosuchidae (Caimaninae). The analysis reinforces previous suggestions on the evolution of the giant predator ecomorphotype in *Purussaurus* in showing it as close to *Caiman*, suggesting that the gigantism in *Purussaurus* evolved from a small to medium-sized, generalist caimanine. Regarding the “gulp-feeder” ecomorphotype of *Mourasuchus*, further scrutiny is needed, but this analysis is more congruent with previous suggestions that it evolved from a durophagous feeding habit. A biogeographical assessment of Alligatoroidea exhibits several relevant perspectives. North America and Europe are considered as equally parsimonious places of origin for

Alligatoroidea; however, the origin of Caimaninae is still more parsimoniously seen as a dispersion from North America between the Late Cretaceous and the Paleocene. A dispersion from Europe to Asia is the more likely scenario for *Krabisuchus*. Dispersions from North America throughout the Cenozoic towards Asia and Europe are also likely scenarios. The topology of Caimaninae suggests a dispersion “back” to North America already during the Late Cretaceous to explain the occurrences of *Bottosaurus* and *Tsoabichi*, although the possibility of these two taxa being descendents of a remanescent caimanine population can also be cogitated. *Protoalligator* as a caimanine brings the possibility of a dispersion from South America towards Asia, but a more parsimonious scenario is a dispersion from North America to Asia. On Central American taxa, *Culebrasuchus* may be the result of either a dispersion from North America or South America, whereas *Centenariosuchus* is seen as a result of a dispersion from South America. Additionally, the taxonomic revision of nine species and two genera (*Melanosuchus* and *Purussaurus*) are performed, whereas the phylogenetic analysis also points to other perspectives of taxonomic revision that shall be addressed in future assessments.

Keywords: Alligatoroidea, Caimaninae, phylogeny, systematics, taxonomy

Resumo em Português

Crocodylia é o grupo-coronal que une o ancestral comum mais recente de todos os crocodilomorfos atuais e todos os seus descendentes. Este é dividido, principalmente, em três clados: Crocodyloidea, Gavialoidea e Alligatoroidea. Este último clado possui uma grande diversidade taxonômica de espécies fósseis, e embora muitas análises filogenéticas já tenham sido feitas para Alligatoroidea, quase todas as análises nas últimas duas décadas foram feitas a partir de um único conjunto de dados (Brochu, 1997a, 1999), o qual nunca foi revisado de maneira abrangente apesar do fato de que um número de caracteres já tenham sido propostos em outros estudos e muitos táxons fósseis foram criados ou revisados. Este estudo realizou a revisão mais abrangente dos conjuntos de dados filogenéticos referentes ao clado Alligatoroidea. Dez novos caracteres são propostos e muitos caracteres previamente propostos foram modificados, com muitos novos estados sendo criados e outros tendo suas redações modificadas. Adicionalmente, várias codificações de caracteres propostos previamente foram modificadas. Como tal, este estudo apresenta o maior conjunto de dados já reunido para Alligatoroidea, consistindo em 183 caracteres e 58 táxons de Alligatoroidea, além de 38 táxons como grupos externos. Os resultados da análise filogenética mostram *Leidyosuchus* e *Diplocynodon* como os aligatoroideos mais basais. Estes são seguidos pelo clado Globidonta, o qual é constituído pelo asiático *Krabisuchus* e pelo europeu *Arambourgia* como táxons-irmãos sucessivos a Alligatoridae. Este clado por sua vez é formado por uma politomia de três linhagens: o predominantemente norte-americano Alligatorinae, o predominantemente sul-americano Caimaninae, e o centro-americano *Culebrasuchus*. No que diz respeito à evolução dos ecomorfótipos em Alligatoroidea, esta análise indica que o ecomorfótipo durófago pode ter surgido até cinco vezes durante a história evolutiva do clado, embora a análise mostre que a maioria dos táxons durófagos se concentra em dois clados: Brachychampsidae (Alligatorinae) e Globidentosuchidae (Caimaninae). Esta análise reforça sugestões prévias sobre a evolução do ecomorfótipo de predador de grande de tamanho de *Purussaurus* ao mostrá-lo como próximo de *Caiman*, sugerindo que o gigantismo em *Purussaurus* evoluiu a partir de um caimaníneo generalista de pequeno a médio porte. Sobre o ecomorfótipo “gulp-feeder” de *Mourasuchus* mais pesquisas são necessárias, mas esta análise é mais congruente com sugestões prévias de que este evoluiu a partir de um hábito durófago. Uma análise biogeográfica de Alligatoroidea revela várias perspectivas relevantes. América do Norte e Europa são considerados locais de origem igualmente parcimoniosos para Alligatoroidea; porém, a origem de Caimaninae é ainda mais parcimoniosamente vista como uma dispersão vinda da América do Norte entre o Cretáceo Superior e o Paleoceno. Uma dispersão da Europa para a Ásia é o cenário mais provável envolvendo *Krabisuchus*. Dispersões a partir de América do Norte, ao longo do Cenozoico, em direção à Ásia e à Europa também se mostram como cenários com grande probabilidade. A topologia de Caimaninae sugere uma dispersão “de volta” à América do Norte já durante o Cretáceo Superior para explicar as ocorrências de *Bottosaurus* e *Tsoabichi*, embora a possibilidade de que estes dois táxons sejam descendentes de uma população remanescente de caimaníneos também possa ser cogitada. *Protoalligator* como um caimaníneo traz a possibilidade de uma dispersão da América do Sul em direção à Ásia, mas um cenário mais parcimonioso é uma dispersão de América do Norte em direção à Ásia. Sobre os táxons centro-americanos, *Culebrasuchus* pode ser o resultado de uma dispersão vinda ou da América do Norte ou da América do Sul, enquanto *Centenariosuchus* é visto como o resultado de uma dispersão vinda da América do Sul. Adicionalmente, a revisão taxonômica de nove espécies e dois gêneros (*Melanosuchus* e *Purussaurus*) são realizadas, enquanto a análise filogenética também aponta a outras perspectivas de revisão taxonômica que devem ser examinadas em estudos posteriores.

Palavras-chave: Alligatoroidea, Caimaninae, filogenia, sistemática, taxonomia

SUMMARY

LIST OF INSTITUTIONAL ACRONYMS

ACAP-FX: Association Culturelle, Archéologique et Paléontologique de l’Ouest Biterrois, Cruzy, Hérault, France.

AMNH: American Museum of Natural History, Nova York, United States.

AMU-CURS: Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela.

BMNH: British Museum of Natural History, Londres, United Kingdom.

CAMSM: Sedgwick Museum, Cambridge, United Kingdom.

CIAAP: Centro de Investigaciones Antropológicas, Arqueológicas e Paleontógicas, Universidad Nacional Experimental Francisco de Miranda (UNEFM), Coro, Venezuela.

CM: Carnegie Museum of Natural History, Pittsburgh, United States.

CNM: Canadian Museum of History, Ottawa, Canada.

DGM*: Departamento de Geologia e Mineralogia, Serviço Geológico do Brasil (CPRM), Rio de Janeiro (RJ), Brazil.

FLMNH: Florida Museum of Natural History, Gainesville, United States.

FMNH: Field Museum of Natural History, Chicago, United States.

HLMD-Me: Hessisches Landmuseum, Darmstadt, Germany.

Ingeominas-DHL: Instituto de Geología y Minería, Bogotá, Colombia.

IPS: Instituto de Paleontologia Miquel Crusafont de Sabadell, Sabadell, Spain.

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

Kr-C: “Krabi crocodilian”, Sirindhorn Museum, Kalasin Province, Thailand.

LACM: Los Angeles Natural History Museum, Los Angeles, United States.

MACN: Museo Argentino de Ciéncias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina.

MCNC-PAL: Museo de Ciéncias Naturales de Caracas, Caracas, Venezuela.

MCT*: Museu de Ciências da Terra, Serviço Geológico do Brasil (CPRM), Rio de Janeiro (RJ), Brazil.

MCZ: Museum of Comparative Zoology, Cambridge, United States.

MGB: Museu de Geología de Barcelona ‘Martorell’, Spain.

MLP: Museo de La Plata, La Plata, Argentina.

MMC: “coleção de crocodilianos da Bacia de Maoming”, School of Life Sciences, Sun Yat-sen University, Guangzhou, China.

MN: Museu Nacional, Rio de Janeiro (RJ), Brazil.

MNHN: Musée Nationale d'Histoire Naturelle, Paris, France.

MPEF-PV: Museu Paleontológico Egídio Feruglio, Trelew, Argentina.

MUL: Montanuniversität Leoben, Leoben, Austria.

MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.

NMMNH: New Mexico Museum of Natural History, Albuquerque, United States.

OR: 'El Breal de Orocual' collection of the Instituto Venezolano de Investigaciones Científicas, San António de los Altos, Venezuela.

PVL: Colección Paleontología Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina.

Rhinopolis: Association Rhinopolis, Gannat, Allier, France.

RTMP: Royal Tyrell Museum of Paleontology, Drumheller, Canada.

SMF: Senckenberg Museum, Frankfurt, Germany.

SMM: Science Museum of Minnesota, Saint Paul, United States.

SMNS: Staatliches Museum fur Naturkunde, Stuttgart, Germany.

SMNK: Staatliches Museum fur Naturkunde, Karlsruhe, Germany.

Spa: Naturhistorisches Museum Basel, Basileia, Switzerland.

STUS: Departamento de Paleontologia, "Sala de las tortugas", Universidad de Salamanca, Spain.

TMM: Texas Memorial Museum, Austin, United States.

UCMP: University of California Museum of Paleontology, Berkeley, United States.

UFAC: Universidade Federal do Acre, Rio Branco (AC), Brazil.

UMMP: University of Michigan Museum of Paleontology, Ann Arbor, United States.

USNM: United States National Museum of Natural History, Washington, United States.

YPM-PU: Yale Peabody Museum of Natural History, Yale University, New Haven, United States.

ZS: Zoologische Staatssammlung, Munique, Germany.

* Both acronyms "DGM" and "MCT" refer to the collection currently belonging to the Museu de Ciências da Terra, Rio de Janeiro, Brazil.

1. Introduction

1.1. Crocodylomorpha and Crocodylia – an overview

Crocodylians are well-known animals that are, together with birds, the only extant representative of the group Archosauria, which in the Mesozoic was the most abundant vertebrate group in the world mainly through non-avian dinosaurs. As such, crocodylians are also one of the most representative of the current "reptilian groups", which also include turtles, snakes, lizards and the tuatara. All extant crocodylians are animalivorous predators that largely employ ambush foraging techniques and that feed at virtually any prey that can capture (Busbey, 1994), with many crocodylians being large animals: species like the Australian saltwater crocodile *Crocodylus porosus* and the false gharial *Tomistoma schlegelli* reach more than 4 meters in total body length (Erickson et al., 2012).

This, along with the fact that crocodylians are also the only animals known to regularly attack human beings as prey (Brochu, 1997a; Sidelau & Britton, 2013), have guaranteed a place for crocodylians in human imagination, culture and folklore. Depictions of crocodylians in human art are abundant since pre-historical times (see Fortier, 2011). Additionally, these animals are also regularly hunted or bred as a source of leather and meat (Brochu, 1997a) or kept as pet animals. Scientific research involving crocodylians is also abundant, ranging from sex determination in reptilians (Lang et al., 1989) to cleft palate development (Ferguson, 1981, 1984, 1985), identification of antibiotical substances that can be used as antibiotics for human patiens (Kommanee et al., 2012) and research that may be applied in treatment of human cancer (Phosri et al., 2018), aside from research focused on the biology and natural history of current and extant crocodylians and their relatives.

The animals we currently know as crocodylians are, however, only part of a much larges archosaurian group that stems from the Triassic: the Crocodylomorpha (Fig. 1). This last group has a fossil record that extends from the late Triassic (Irmis et al., 2013) and may be phylogenetically defined as a stem-based group formed by the most inclusive clade containing *Crocodylus niloticus* Laurenti, 1768 but not *Rauiusuchus tiradentes* von Huene, 1942, *Poposaurus gracilis* Mehl, 1915, *Gracilisuchus stipanicicorum* Romer, 1972, *Prestosuchus chiniquensis* Huene, 1942 or *Aetosaurus ferratus* Fraas, 1977 (*sensu* Irmis et al., 2013; see also Sereno, 2005; Nesbitt, 2011).

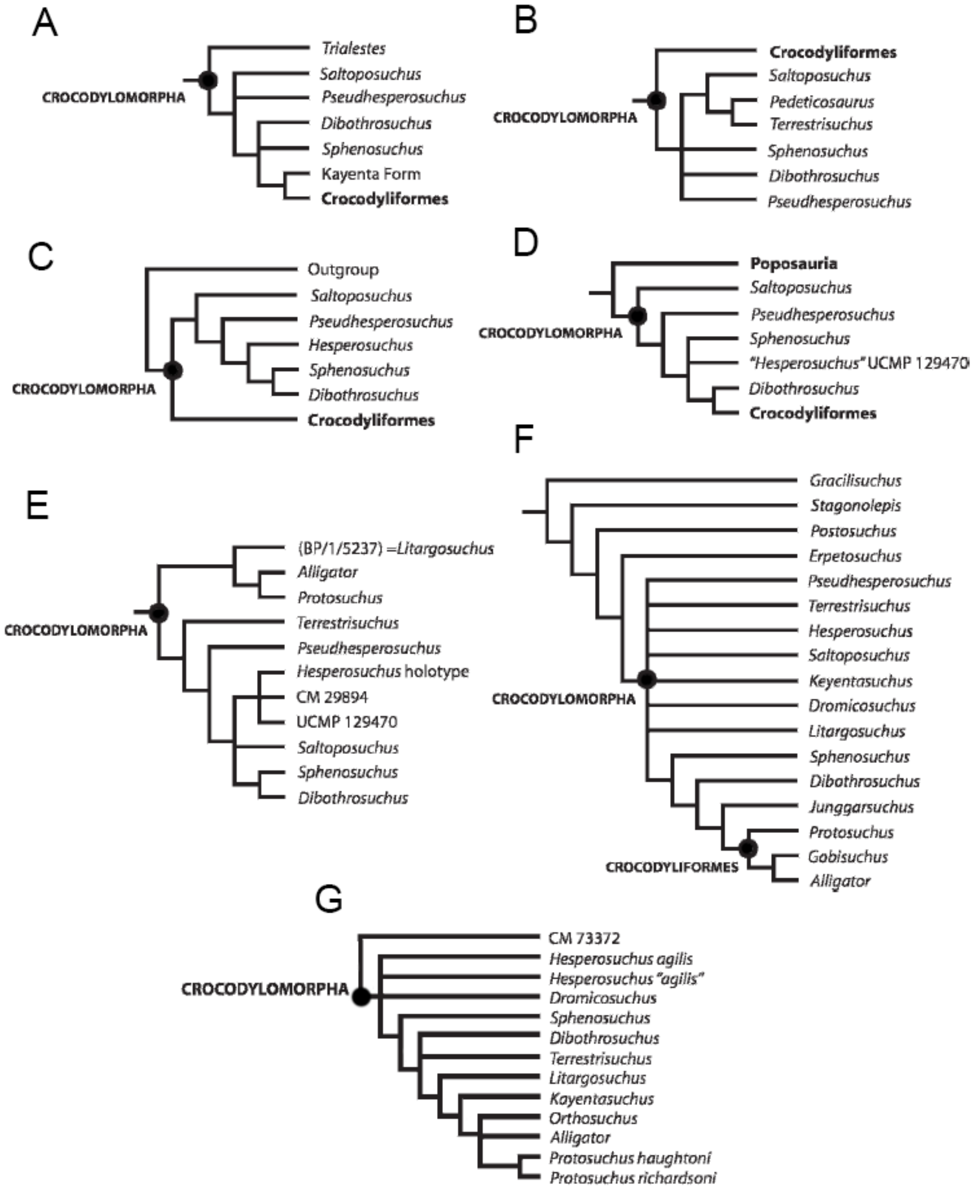

Figure 1: A compilation of alternative topologies proposed for Crocodylomorpha. Benton & Clark (1988, A); Sereno & Wild (1992, B); Wu & Chatterjee (1993, C); Parrish (1991, D); Clark et al. (2000, E); Clark et al. (2004, F); Nesbitt (2011, G). Suprageneric taxa are in bold. Taken and modified from Nesbitt (2011, figs 4 and 51).

Crocodylomorpha may be divided into two groups: Sphenosuchia Bonaparte, 1972, which is a name most frequently used to refer to the most basal crocodylomorphs (or non-crocodyliform crocodylomorphs, see below), whose members are most frequently not recovered as a monophyletic group (see Irmis et al., 2013) and Crocodyliformes Hay, 1930, a name that has been used to broadly encompass all crocodylomorphs more derived than Sphenosuchia and also (contrary to Sphenosuchia) to a consistently recovered monophyletic group. Crocodyliformes has its oldest records also in the late Triassic and is phylogenetically defined as the less inclusive clade containing *Protosuchus richardsoni* (Brown, 1933) and *Crocodylus niloticus* (*sensu* Sereno et al., 2001). With exception of the most basal forms, most crocodyliforms belong to the clade Mesoeucrocodylia Whetstone & Whybrow, 1983, whose oldest occurrences are from the early Jurassic (see Montefeltro, 2013) and which is phylogenetically defined as the clade comprised by all crocodyliforms more closely related to *C. niloticus* than to *P. richardsoni* (*sensu* Sereno et al., 2001).

Mesoeucrocodylia is mainly divided into two clades. One of them is Notosuchia, which is comprised predominantly of terrestrial forms from the continents that belonged to the austral supercontinent Gondwana. The oldest record of Notosuchia is from the middle Jurassic (Dal Sasso et al., 2017), whilst the clade is phylogenetically defined as being comprised of all crocodyliforms more closely related to *Notosuchus terrestris* than to *C. niloticus* (*sensu* Sereno et al., 2001).

The other one is Neosuchia, a clade comprised mostly by forms from the continents that belonged to the boreal supercontinent Laurasia. Contrary to Notosuchia, most neosuchians are aquatic forms, either from fresh or salty waters (in this second category a special mention goes to the very diverse Mesozoic clade Thalattosuchia Fraas, 1901). The oldest records of Neosuchia are from the early Jurassic (Tykoski et al., 2002) and the clade is phylogenetically defined as all crocodyliformes more closely related to *C. niloticus* than to *N. terrestris* (*sensu* Sereno et al., 2001).

Both Notosuchia and Neosuchia had large taxonomical diversity and morphological disparity during the Mesozoic era (see Sereno & Larsson, 2009; Mannion et al., 2019; Wilberg et al., 2019). However, after the Cretaceous-Paleogene (K-Pg) Extinction, which provoked the demise of vertebrate lineages, including all non-avian dinosaurs (Renée et al., 2013), there was an evident differential survival between the two groups. From the seven crocodyliform lineages that survived the K-Pg

Extinction and wen on through the Cenozoic era, six belong to Neosuchia (Dyrosauridae, Planocraniidae, *Borealosuchus* and the crocodylians Alligatoroidea, Crocodyloidea and Gavialoidea), while only one notosuchian clade, the predominantly South American and terrestrial Sebecidae, survived (see Brochu, 1997b, 1999, 2013; Kellner et al., 2014; Hastings et al., 2015; Cidade et al., 2019a; and below).

One of the most derived taxa within Neosuchia is Eosuchia Huxley, 1875. Originally defined as comprising all crococylomrphs that have procoelous vertebrae and a secondary choana surrounded only by the pterygoid bones (Huxley, 1875), it went on to be defined by Brochu (2003) as being the clade that comprised the last common ancestor of *Hylaeochampsa vectiana* Owen, 1874, *Crocodylus niloticus*, *Gavialis gangeticus* (Gmelin, 1789) and *Alligator mississippiensis* (Daudin, 1802) and all of its descendents. As such, the oldest record of Eusuchia is exactly that of *H. vectiana*, from the Eary Cretaceous of the Isle of Wright, United Kingdom (Owen, 1874; Brochu, 2003).

Within Eusuchia is where it is the crown-group Crocodylia Gmelin, 1789, which is currently (see Brochu, 2003, for a historical review of how the name Crocodylia was used for the group we currently know as Crocodylomorpha and then went on to be used for the crown-group) phylogenetically defined as last common ancestor of *Gavialis gangeticus*, *Alligator mississippiensis* and *Crocodylus niloticus* and all of its descendents (*sensu* Brochu, 2003; Figs 2, 3 and 4). The oldest record of Crocodylia is *Portugalosuchus azenhae*, from the Late Cretaceous (Cenomanian) of Portugal (Mateus et al., 2018) Crocodylia is currently largely divided into five phylogenetic groups: *Borealosuchus*, Planocraniidae, Gavialoidea, Crocodyloidea and Alligatoroidea. Except for Planocraniidae, which have fossil occurrences only in the Paleocene and in the Eocene (Brochu, 2013), all other clades have a fossil record that extends from the Late Cretaceous (de Kay, 1842; Lambe, 1907; Mook, 1941a; Brochu, 1997b, 1999, 2003, 2004a, 2004b, 2006; Brochu et al., 2012). Gavialoidea is the group that appears as the most basal of Crocodylia in most morphological analyses (see Brochu, 2003). Most molecular analyses, however, recover the group in a more derived position: as a crocodyloid, closely related to *Tomistoma*, while Alligatoroidea appears as the most basal crocodilian group (Gatesy et al., 2003; Man et al., 2011; Oaks, 2011; Green et al., 2014; Fig. 2). Gavialoidea is formed by marked longirostrine, putatively largely piscivorous forms. While the earliest, most basal gavialoids such as *Thoracosaurus* were inhabitants of marine and estuarine environments (Brochu, 2003), later, more derived taxa such as the South American clade Gryposuchinae (see Brochu, 2003; Vélez-Juarbe et al., 2007; Salas-Gismondi et al. 2016) and fossil forms of the *Gavialis* genus in South Asia (Martin, 2019) would go on to inhabit full freshwater environments. The only extant gavialoid species, *G. gangeticus*, which is exclusive of the Indian subcontinent, is a full freshwater taxon (Brochu, 2003).

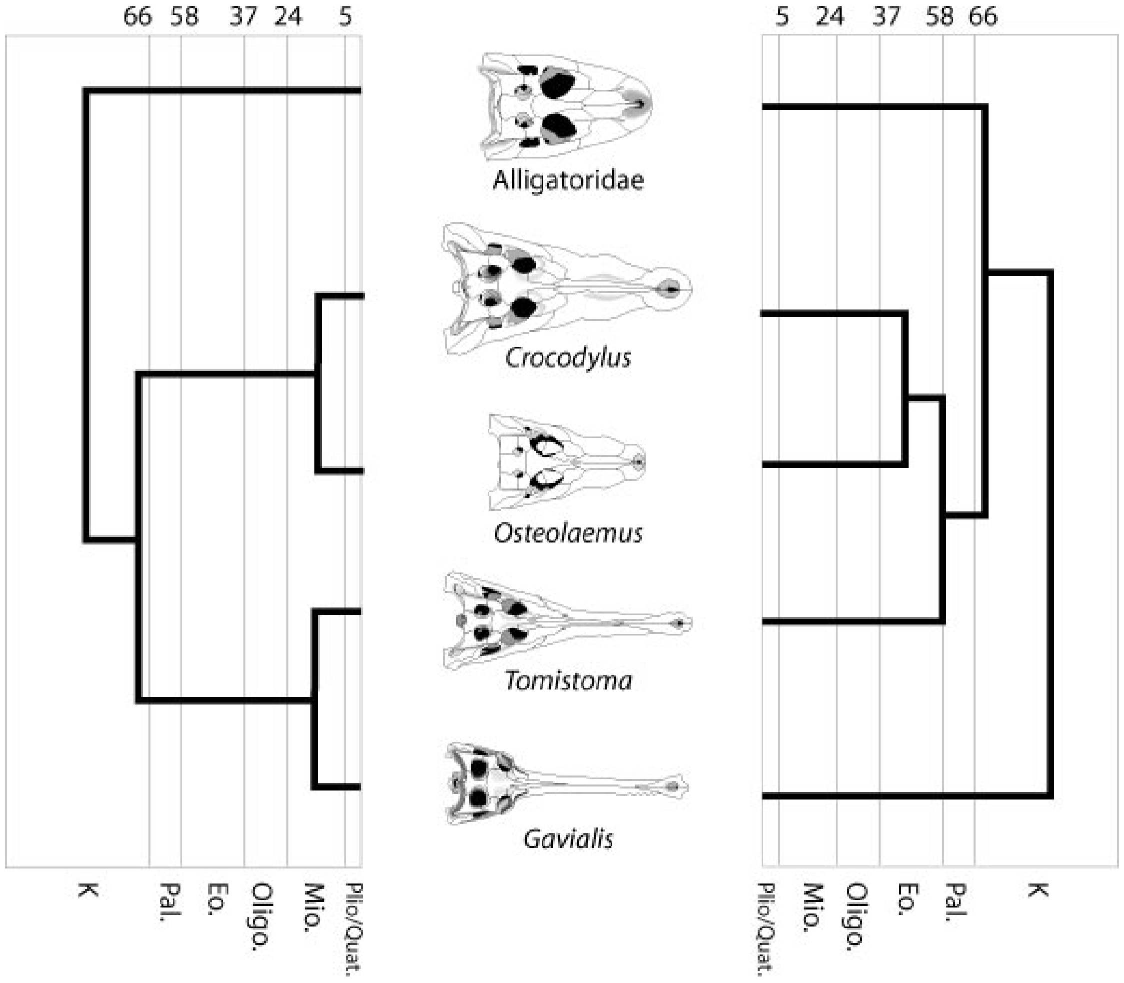

Figure 2: The divergence between most molecular analyses (left) and most morphological analyses (right) regarding the placement of Gavialoidea among Crocodylia. Taken from Brochu (2003).

Borealosuchus is semi-aqutic group that occurs from the Late Cretaceous to the Eocene and is restricted to North America (Brochu, 1997b; Brochu et al., 2012). The cranial anatomy of the group broadly resembles that of alligatoroids, and according to Brochu (2003) *Borealosuchus* is the closest proxy of what an ancestral crocodilian would look like. In fact, the species currently assigned to *Borealosuchus* were considered to belong to *Leidyosuchus* until broad-scale phylogenetic analyses (Brochu, 1997a, 1997b, 1999) showed *Leidyosuchus canadensis* to be a basal alligatoroid, while other '*Leidyosuchus*' species were recovered as basal crocodylians, thus reclassified into the new genus *Borealosuchus*.

Planocraniidae is a crocodylian clade with occurrences in the Paleocene of North America and in the Eocene of Asia, Europe of North America (see Langston, 1975; Li, 1976, 1984; Rossmann, 2000; Brochu, 2013). The group was known by the names of Pristichampsidae or Pristichampsinae (e.g. Kuhn, 1968; Rossmann, 2000a; Brochu, 2003; Brochu et al., 2012) until Brochu (2013) performed a taxonomic review based on the fact that the type species of the genus *Pristichampsus*, *P. rollinati* (Gray, 1831) was based on very fragmentary fossils and questioned the status of *Pristichampsus*, changing the most complete species to the genus *Boverisuchus* (one of the two genera of the clade, together with *Planocrania*) and adopting Planocraniidae, a family name proposed by Li (1976), as the name of the clade. Planocraniidae has been traditionally viewed as terrestrial forms, with lateromedially compressed, dorsoventrally high rostra (but not to degree seen in other terrestrial forms such as *Baurusuchus* and *Sebecus*, see Molnar, 2010; Riff & Kellner, 2011), erect limbs and serrated (ziphodont) teeth (Brochu, 2013), with movements such as galloping being proposed for the members of the group (Rossmann, 2000b). However, the degree the terrestriality of the group reached may be questioned (see Brochu, 2013) based on the fact that some similar features to those of Planocraniidae are seen in the extant caimanine *Paleosuchus*, which is more comfortable in terrestrial environment than most extant crocodylians but is still a semi-aquatic taxon. Additionally, there might be variation related to terrestriality within Planocraniidae itself, with *Boverisuchus* being proposed as more adapted to the terrestrial environment than *Planocrania* (see Brochu, 2013), although this hypothesis requires further scrutiny. Traditionally, Planocraniidae (or Pristichampsidae) have been recovered as the sister-group of Brevirostres (e.g. Brochu, 1999, 2011, 2013), the crocodylian group that united Crocodyloidea and Alligatoroidea, described below.

Crocodyloidea occurrences are known from the Late Cretaceous, with the occurrence of *Prodiplocynodon langi* Mook, 1941a in deposits of the North American state of Wyoming. In the Cenozoic, the group attains a very large diversity, morphological disparity and geographic distribution, reaching all continents except

Antarctica. Significant examples of the basals crocodyloids include *Asiatosuchus*, from the Eocene of Asia and Europe (Mook, 1940; Berg, 1966; Delfino & Smith, 2009) and possibly from the Miocene of Asia (Angielczyk & Gingerich, 1998). Another significant example is the clade Tomistominae, a group comprised mainly by longirostrine taxa that generally resemble gavialoids. The oldest records of Tomistominae are from the Paleocene of Europe (Piras et al., 2007) and from the Eocene of Africa and Europe (Owen, 1850; Mook, 1955; Brochu, 2003). Some of the most significant Tomistominae taxa are *Thecachampsa*, from the Oligocene and Miocene of North America (Piras et al., 2007; Brochu & Storrs, 2012; Weems, 2018); *Gavialosuchus,* from the Oligocene of North America and the Miocene of Europe (Toula & Kail, 1885; Erickson & Sawyer, 1996; Jouve et al., 2008); and *Charactosuchus*, from the Eocene of Jamaica (Berg, 1969; Vélez-Juarbe & Brochu, in press) and the Miocene of South America (Langston, 1965; Souza-Filho & Bocquentin-Villanueva, 1989; Souza-Filho, 1991), although the phylogenetic relationships of *Charactosuchus* have never been thoroughly assessed and as such the relationship of the genus with Tomistominae has been questioned (Vélez-Juarbe & Brochu, in press).

Records of the genus *Tomistoma* itself are as old as the Eocene, with *T. cairense* from Egypt, although the assignment of the species to this genus is challenged due to its phylogenetic placement outside the other membrs of the genus (see Brochu, 2003). Another important record is *T. lusitanica*, from the Miocene of Portugal (Vianna & Moraes, 1945; Antunes, 1961, 2017). The only extant *Tomistoma*, *T. schlegelli*, is a freshwater taxon than inhabits Southeast Asia, Malaysia and Indonesia (Brochu, 2003; Bezuijen et al., 2010, 2014). Despite the freshwater habit of the extant species, some fossil tomistomines, like *T. lusitanica* (Antunes, 1987) and some tomistomine fossils from North America (Brochu, 2003) inhabited coastal and estuarine environments; this scenario is similar to what is observed for Gavialoidea, as mentioned previously.

The most derived crocodyloids are united within the clade Crocodylinae. This group is divided in several clades. These include Mekosuchinae, a group that extends from the Eocene to the Holocene of Australia and other insular territories of Oceania (Buffetaut, 1983; Mead et al., 2002; Brochu, 2003). This group exhibits a large diversity and morphological disparity, which ranges from generalized forms to taxa with serrated teeth, roughly resembling Planocraniidae crocodylians, to small blunt-snouted forms and a possible longirostrine form (see Megirian et al. 1991; Willis et al. 1993, Salisbury

& Willis 1996; Brochu, 2003). Another significant group within Crocodylinae is Osteolaminae, an exclusively African group that comprises the extant genus *Osteolaemus* (with two species, *O. tetrapsis* and *O. osborni*), and the extinct genera *Brochuchus, Euthecodon, Rimasuchus* and *Voay* (Brochu, 2003, 2007a; Brochu et al., 2010; Conrad et al., 2013). *Osteolaemus* is a small, blunt-snouted taxon that roughly resembles the extant caimanine *Paleosuchus*. However, extinct osteolemines exhibit a more diverse morphology, including the large-sized *Voay robustus*, from the Pleistocene and Holocene of Madagascar (Brochu, 2007a) and the longirostrine *Euthecodon*, which occurs from the Miocene to Pleistocene (Forteau, 1920; Joleaud, 1920; Ginsburg & Buffetaut, 1978).

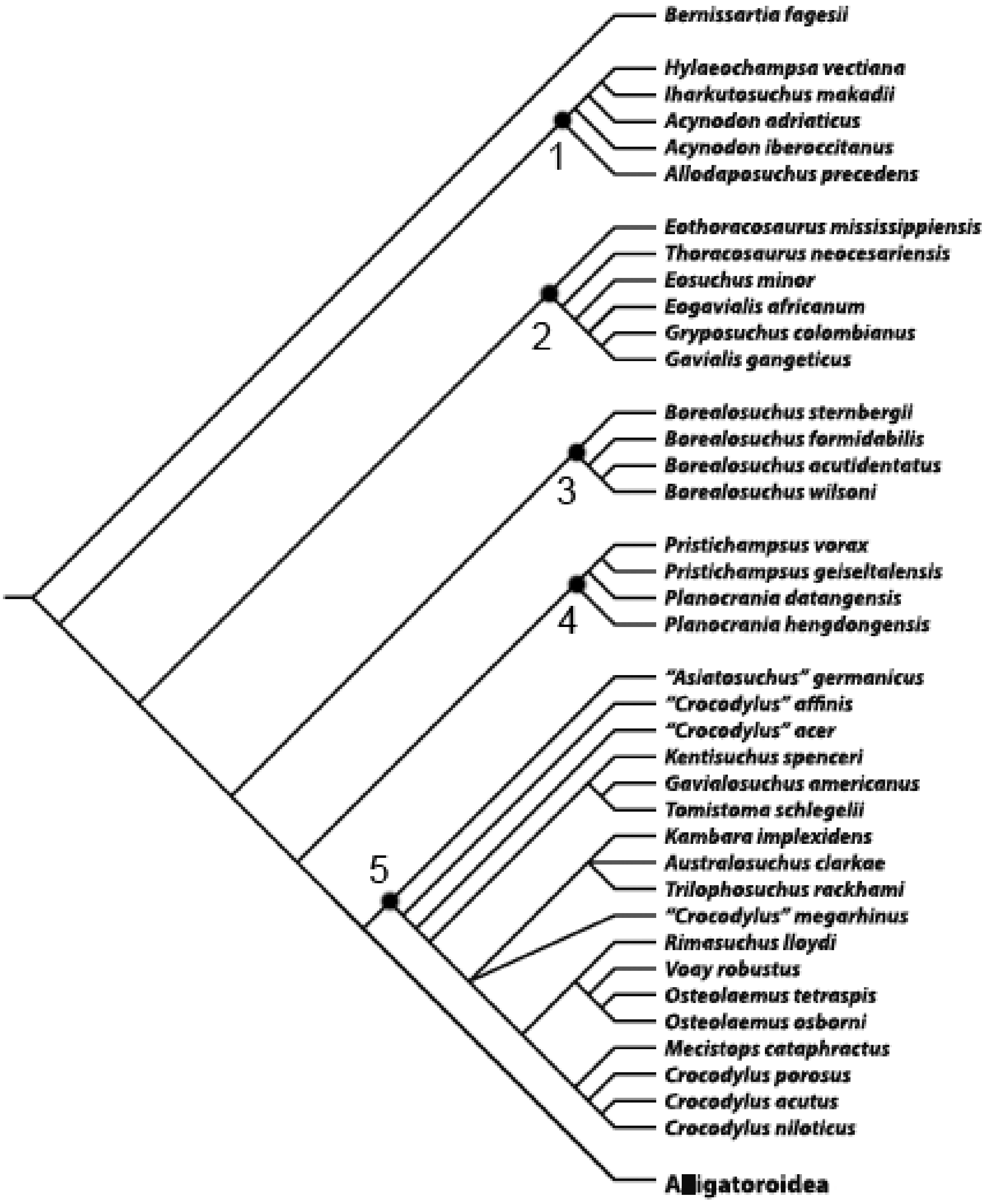

Figure 3: Phylogeny of non-alligatoroid crocodylians proposed by Brochu (2011).

Arguably, the most significant group within the clade Crocodylinae is the genus *Crocodylus*, which contains 11 to 12 extant species (and therefore, approximately half of the 23 to 26 extant crocodylians species currently recognized) and an important fossil diversity. Traditionally, many fossil species (ranging from the Cretaceous and most of the Cenozoic) had been assigned to *Crocodylus* based on plesiomorphies, most notably the presence of a notch in the maxillae as a result of the occlusion of the fourth mandibular tooth instead of a pit; however, with the advent of modern systematics, especially that based on phylogenetic reconstructions, many of such species were recognized as not belonging to *Crocodylus* (see Brochu, 2000, 2003). Modern understanding of *Crocodylus* recognizes its most ancient records as coming from the Miocene, with notable records being *C. checchiai* from the Late Miocene of Kenya (see Brochu & Storrs, 2012) and *C. palaeindicus*, from the Miocene-Pliocene Siwaliks sequence of the Indian subcontinent (see Brochu et al., 2010). Current data shows that *Crocodylus* has most likely appeared in Africa, from whence they dispersed into other continents such as Asia, Oceania and America making use of their tolerance to salt water (see Taplin & Grigg, 1989) to cross through oceanic waters that would mean a barrier for taxa without such tolerance.

Alligatoroidea also has its most ancient records in the Late Cretaceous, which come from North America. These comprise *Leidyosuchus canadensis, Albertochampsa langstoni* and *Stangerochampsa maccabei*, from Canada, *Brahychampsa*, from Canada and United States and *Bottosaurus*, from the Late Cretaceous and Paleocene of the United States (Lambe, 1907; Erickson, 1972; Wu et al., 1996, 2001; Brochu, 2004a; Cossette & Brochu, 2018). There are also fossils assigned to Alligatoroidea (genus *Tadzhikosuchus*) from the Late Cretaceous of Tadjikistan and Uzbequistan (Efimov, 1982, 1988; Nesov et al., 1989; Storrs & Efimov, 2000), but these may not actually belong to the group (C.A. Brochu, personal communication). In the Cenozoic, Alligatoroidea would spread out from North America into other continents, most notably Europe (through the genera *Arambourgia*, *Diplocynodon* and *Hassiacosuchus*), Asia (through the genera *Alligator, Krabisuchus, Protoalligator*) and South America, in this last continent through members of the clade Caimaninae.

The European alligatoroids are comprised mainly by the genera *Arambourgia*, from the Eocene of France (de Stefano, 1905; Kälin, 1940; Brochu, 2004a), *Hassiacosuchus*, from the Eocene Lagerstätte Messel pit of Germany (Weitzel, 1935; Brochu, 2004a) and *Diplocynodon*, a genus with a high number of species and specimens. *Diplocynodon* has a wide temporal and geographical distribution, with a large number of the specimens belonging to the species *D. darwini*, which comes from the Eocene Messel pit of Germany (Ludvig, 1877) and *D. muelleri*, from the Oligocene of Spain (Kälin, 1936a; Piras & Buscalioni, 2006), but also with species and/or specimens known from the Eocene of France (Martin, 2010a), Spain and the United Kingdom (Wood, 1846), Oligocene of Italy (Del Favero, 1999), and from the Miocene of Austria (Martin & Gross, 2011) and France (Pomel, 1847; Martin & Gross, 2011). While *Diplocynodon* may be seen as a "typical" semi-aquatic generalist crocodylian, both *Arambourgia* and *Hassiacosuchus* are snimals with short rostra and posterior globular teeth, which suggest adaptations to durophagy, which is seen in many alligatoroid taxa (see Brochu, 2004a, and below).

The alligatoroids of Asia are represented mainly by the genera *Protoalligator*, from the Eocene of China (Young, 1982; Wang et al., 2016), *Krabisuchus*, from the Eocene of Thailand (Martin & Lauprassert, 2010) and many occurrences assigned to the genus *Alligator*: *Alligator lucius* Li & Wang, 1987, from the middle Miocene of China; fossils assigned to the extant species *Alligator sinensis* from the Pleistocene of Taiwan (Shan et al., 2013) and as *Alligator* cf. *A. sinensis* from the late Miocene-Pleistocene of Thailand (Skutschas et al., 2014). Additionally, a fossil specimen known only as 'Maoming crocodylian', from the Eocene of China, has been phylogenetically recovered as an alligatoroid (Skutschas et al., 2014). Currently, Alligatoroidea in Asia is restricted to the critically endangered species *Alligator sinensis*, which inhabits eastern China (Pough et al., 2004; Skutschas et al., 2014).

South American caimanines includes many diverse taxa. In the Paleogene, the record comprises the genera *Necrosuchus*, *Notocaiman* and *Protocaiman*, from the Paleocene of Argentina (Simpson, 1937; Rusconi, 1937; Bona et al., 2018). The most diverse and abundant member of the Paleogene South American fauna of Caimaninae is *Eocaiman*, with records from the Paleocene of Argentina (Bona, 2007) and Brazil (Pinheiro et al., 2013), from the Eocene of Argentina (Simpson, 1933) and even from beyond the Paleogene, with a record of "*Eocaiman* sp." from the middle Miocene of Colombia (Langston, 1965). The Miocene record of Caimaninae is South America is one of the most taxonomically and morphologically diverse crocodylomorph records in the world (see Cidade et al., 2019a). Its main units, such as the early Miocene Castillo Formation (Venezuela), middle Miocene Fitzcarrald Arch and Pebas Formation (Peru), Honda Group (Colombia), and the late Miocene Ituzaingó (Argentina), Urumaco (Venezuela) and Solimões (Brazil and Bolivia) formations have yielded many caimanine genera of different sized and ecomorphotypes, such as the giant predator *Purussaurus* (Barbosa-Rodrigues, 1892; Mook, 1941b; Langston, 1965; Aguilera et al., 2006), the giant alleged gulp-feeder *Mourasuchus* (Price, 1964; Langston, 1965; Bocquentin-Villanueva, 1984; Cidade et al., 2017), the middle-size generalist predator *Acresuchus* (Souza-Filho et al., 2019) and the durophagous forms *Gnatusuchus*, *Globidentosuchus* and *Kuttanacaiman* (Scheyer et al., 2013; Salas-Gismondi et al., 2015). The Miocene of South American also contains the first records of the extant genera of Caimaninae. These include *Caiman*, through the durophagous species *C. brevirostris* (Souza-Filho, 1987; Fortier et al., 2014) and *C. wannlangstoni* (Salas-Gismondi et al., 2015) and generalist species, such as *C. australis* (Bravard, 1858, 1860; Burmeister, 1883, 1885; Bona et al., 2012), *C. gasparinae* (Bona & Carabajal, 2013) *C. lutescens* (Rovereto, 1912; Bona et al., 2012) and records of the extant species *C. latirostris* (Bona et al., 2012) and tentatively assigned to *C. yacare* (*Caiman* cf. *C. yacare*, Fortier et al., 2009). *Melanosuchus* has occurrences assigned as *Melanosuchus* sp. or *Melanosuchus* cf. *M. niger* (the holotype of *M. fisheri* Medina, 1976, posteriorly considered a *nomen dubium*; see Bona et al., 2017 and Foth et al., 2018), while *Paleosuchus* has fossils assigned to it from the Fitzcarrald Arch and the Pebas Formation of Peru (Salas-Gismondi et al., 2007, 2015). From the Pliocene onwards, the Caimaninae record of South America is restricted to fossils of the three extant genera (see Fortier & Rincón, 2012; Cidade et al., 2019). The extant genera currently comprise six species (*Caiman crocodilus*, *C. latirostris*, *C. yacare*, *Melanosuchus niger*, *Paleosuchus palpebrosus* and *P. trigonatus*), all of which are exclusive to South America except for *C. crocodilus*, which also inhabits Central America, North America (Mexico) and the Caribbean (see Medem, 1981, 1983; Thorbjarnasson, 1992; Brochu, 1999).

Caimaninae also has records in Central America, through the Miocene genera *Culebrasuchus* and *Centenariosuchus*, from the Miocene of Panama (Hastings et al., 2013, 2016), and in the Cenozoic of North America, most notably through the species *Orthogenysuchus olseni* and *Tsoabichi greenriverensis* from the Eocene of the United

States (Mook, 1924; Brochu, 1999, 2010), aside from the aforementioned records of *Bottosaurus* from the Paleocene of the same country (see Cossette & Brochu, 2018).

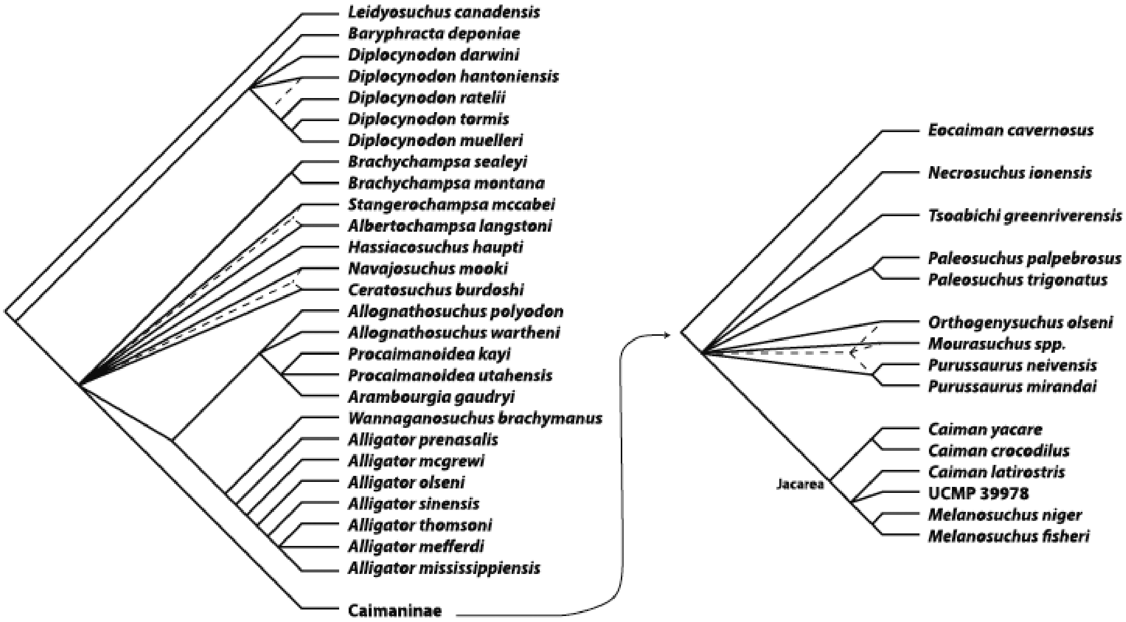

Figure 4: Phylogeny of Alligatoroidea as proposed by Brochu (2011).

However, most records of Alligatoroidea during the Cenozoic, however, belong to the clade Alligatorinae. These records include genera that are exclusive to the United States, which are *Allognathosuchus*, from the Eocene (Cope, 1872; Case, 1925. Brochu, 2004a), *Ceratosuchus*, from the Paleocene and Eocene (Schmidt, 1938; Bartels, 1984), *Navajosuchus*, from the Paleocene (Simpson, 1930; Mook, 1942; Brochu, 2004a), *Procaimanoidea*, from the Eocene (Mook, 1941c; Gilmore, 1946; Wassersug & Hetch, 1967) and *Wannaganosuchus*, from the Paleocene (Erickson, 1982). The diverse record of *Alligator* from North America is also exclusive of the United States, including many species: *A. prenasalis*, from the Oligocene (Loomis, 1904; Mehl, 1916; Brochu, 1999, 2004a); *A. mcgrewi*, from the Miocene (Schmidt, 1941); *A. mefferdi*, from the Miocene (Mook, 1946); *A. olseni*, from the Miocene (White, 1942); *A. thomsoni*, from the early Miocene (Mook, 1923). Fossils assigned to the extant species *A. mississippiensis* were found in the Miocene (Whiting et al., 2016) and in the Pleistocene (Brochu, 1999) of the United States; this species, which inhabits Southeastern United States (Sigler et al., 2007), is the only extant representative of Alligatoroidea in North America aside from the aforementioned occurrence of *C. crocodilus* in Mexico. Aside from *Alligator*, which is considered a generalist predator, all alligatorine genera have been proposed to be durophagous (Brochu, 2004a). All of these, except *Wannaganosuchus*, exhibit relatively short rostra, while all of them exhibit posterior globular teeth both in the mandible and in the maxilla.

As such, Alligatoroidea is not only one of the most diverse crocodylomorph clades of the Cenozoic but is also the one that exhibits by far the largest level of diversity of ecomorphotypes. These include not only those of generalist predator and durophagous, with each one of these being present in several taxa, but also those of giant predator (*Deinosuchus* and *Purussaurus*) and of gulp-feeder (*Mourasuchus*). Both the taxonomic and the ecomorphological diversity offer interesting areas of research that have been explored more intensely in the last four decades, when the emergence of phylogenetic systematics, molecular systematics and modern methods of morphometry, CT scan, biomechanical reconstructions and other methods have yielded several studies on these topics; a review of the phylogenetic studies on the systematics of Alligatoroidea is given below. These advances notwithstanding, many issues regarding the phylogeny, systematics, taxonomy, morphological evolution, evolution of the ecomorphotypes and paleoecology of Alligatoroidea remain to be addressed; some of these constitute the objectives of the present study, which are detailed below.

1.2. Alligatoroidea – historical on systematic and phylogenetic research

Alligatoroidea is one of the most researched groups of Crocodylia and Crocodylomorpha regarding phylogenetic analyses. The first analyses, starting in the decade of 1970 of the XX century, include phylogenies constructed from biochemical data (Gorman et al., 1971; Densmore, 1983), morphological studies based on osteological and non-ostoelogical characters (Malone, 1979; Norell, 1988, 1989; Buscalioni et al., 1992; Norell et al., 1994; Williamson, 1996; Wu et al., 1996), molecular analysis based on DNA (Gatesy et al., 1993) and combined approaches between molecular, morphological and behavioral characters (Poe, 1997).

Molecular analyses of Alligatoroidea would increase significantly in the XXI century. Although many of these studies are phylogenies of Crocodylia as a whole, including also Alligatoroidea (Gatesy et al., 2003; Oaks, 2011; Erickson et al. 2012), there have been studies focusing on alligatoroid taxa, especially on the phylogeny and delimitation between possible different species within *Caiman crocodilus* (Venegas-Anaya et al., 2008; Escobedo-Galván et al., 2011).

Regarding morphological analysis, Alligatoroidea phylogenetic studies had a major breakthrough with the work of Brochu (1997a, 1999), which was the most comprehensive analyses performed to date. The officially published version of the analysis (Brochu, 1999) contained 68 taxa (67 eusuchians and the non-eusuchian crocodyliform *Bernissartia fagesii*, from the Early Cretaceous of Belgium, as the outgroup), of which 34 were alligatoroids, and 164 characters, which was the largest dataset ever assembled at the time. Virtually all posterior morphological analysis on the phylogeny of Alligatoroidea followed the dateset of Brochu (1999): Aguilera et al. (2006); Hill & Lucas (2006); Bona (2007); Brochu (2004a, 2010, 2011); Barrios (2011); Bona et al. (2012); Hastings et al. (2013, 2016); Pinheiro et al. (2013); Scheyer et al. (2013); Fortier et al. (2014); Martin et al. (2014); Skutchas et al. (2014); Salas-Gismondi et al. (2015); Wang et al. (2016); Whiting et al. (2016); Cidade et al. (2017); Bona et al. (2018); Cossette & Brochu (2018); Souza-Filho et al. (2019). Some of these works made punctual revisions on the characters of the dataset of Brochu (1999), which mainly pertained especifically to the characters involved with the taxa they were studying (Brochu, 2004a, 2013; Bona, 2007; Barrios, 2011; Bona et al., 2012; Pinheiro et al., 2013; Salas-Gismondi et al., 2015; Cidade et al., 2017; Cossette & Brochu, 2018; Souza-Filho et al., 2019). However, there was only one comprehensive review of the original dataser of Brochu (1999): Brochu (2011, Figs. 3 and 4) assembled a dataset of 81 taxa, of which 42 are alligatoroids, with 181 characters. As such, given the widespread use of the dataset and the fact that only one comprehensive review was performed, it was considered that such comprehensive review on the dataset of Brochu (1999, 2011) needed to be performed, regarding the taxa that might be included, the content and redaction of the characters, and the scoring of the taxa for each character.

The review of the dataset is needed not only for the fact that only one comprehensive review has ever been performed on it, but mainly because since the publication of such review (2011) there has been a large number of publications regarding fossil alligatoroids that fursnished relevant data for phylogenetic and evolutionary studies on the group. There has been a significant amount of descriptions of new species (Fortier & Rincón, 2012; Bona & Carabajal, 2013; Hastings et al., 2013; Pinheiro et al., 2013; Scheyer et al., 2013; Martin et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Cidade et al., 2017; Bona et al., 2018; Souza-Filho et al., 2019), as well as inclusions of previously described species, sometimes accompanied with detailed redescriptions (Bona et al., 2012; Fortier et al., 2014; Martin et al., 2014; Wang et al., 2016; Cidade et al., 2018; Cossette & Brochu, 2018). This significant input of data in recent years is a major reason for a thorough review on the phylogeny and evolution of Alligatoroidea and of the dataset based on which most of the phylogenetic analyses have been made in the last 20 years.

Additionally, the origin and evolution of the three ecomorphotypes present in the Alligatoroidea clade that differ from that of small to medim-sized, generalist predator has been seldom discussed, aside from rather preliminary assessments on the evolution of the durophagous forms (Brochu, 2004a; Salas-Gismondi et al., 2015), of the giant size of *Purussaurus* (Souza-Filho et al., 2019) and *Deinosuchus* (Schwimmer, 2002; Brownstein, 2019), and of the gulp-feeder habit of *Mourasuchus* (Cidade et al., 2017). As such, an assessment on the origin and evolution of these distinct ecomorphotypes will be addressed in this study from the results obtained in the phylogenetic analyses.

The biogrography of the Alligatoroidea clade will also be assessed in this study from the results obtained in the analyses. This topic has also been most thoroughly assessed by Brochu (1999) but since then no other thorough phylogenetic assessments were performed, aside from punctual remarks (e.g. Brochu, 2010, 2011; Cidade et al., 2017, 2019a). As such, a new thorough asssment is necessary. The main topics to be addressed are the possible area of origin and the routes that were taken by alligatoroids to establish their distribution through four continents (North America, South America, Europe and Asia) throughout the Late Cretaceous and the Cenozoic.

Furthermore, there is a number of fossil species (mostly assigned to the Caimaninae clade) that are based on very fragmentary, incomplete holotypes or type specimens, therefore requiring taxonomic revisions regarding their validity as species, as well as their generic assignment. These include *Balanerodus logimus* (Langston, 1965), *Caiman australis* (Bravard, 1858), *C. gasparinae* Bona & Carabajal, 2013, *C. lutescens* (Rovereto, 1912), *C. venezuelensis* Fortier & Rincón, 2012, *Eocaiman* *itaboraiensis* Pinheiro et al., 2013, *Necrosuchus ionensis* Simpson, 1937, *Notocaiman stromeri* Rusconi, 1937, and the specimen UCMP-39978, formely assigned as "*Caiman* cf. *C. lutescens*" by Langston (1965). The taxonomic review of these species and the specimen UCMP-39978 will be undertaken in this study.

2. Objectives

The main objective of the thesis is:

- perform a comprehensive phylogenetic revision of the Alligatoroidea clade, focusing in a phylogenetic and taxonomic revision of its sub-clade Caimaninae, especially through the revision of the composition and of the scorings of the characters already proposed for these groups, mainly those of the most comprehensive phylogenetic work made about them to this date (Brochu, 1997a, 1999, 2011).

Within the larger scope of the main objective, the specific objectives of the project are:

- a revision of the phylogenetic placement of the Late Cretaceous North American alligatoroids *Albertochampsa*, *Brachychampsa* and *Stangerochampsa*, reporting the implications pertinent to the phylogeny, biogeography and evolution of Alligatoroidea that are related to these taxa.

- a revision of the phylogenetic placement of the taxa that have been traditionally proposed as basal caimanines, such as *Eocaiman*, *Culebrasuchus*, *Gnatusuchus*, *Kuttanacaiman* and *Globidentosuchus*. Regarding the las three taxa, the study also aims to analyze the origin and evolution of the durophagous ecomorphotype in the Alligatoroidea and Caimaninae clade. A taxonomic revision of the species *E. itaboraiensis* will also be performed.

- a revision of the phylogeny of the clade Jacarea, which is situated within the Caimaninae clade, whilst a taxonomic revision of several fragmentary fossil taxa of the Jacarea clade is also an objective, with emphasis on the species *Caiman gasparinae* Bona & Carabajal, 2013 and in the taxonomic status of the specimen UCMP 39978, formely assigned as "*Caiman* cf. *C. lutescens*" by Langston (1965).

- an assessment on the origin and evolution of the ecomorphotypes of Alligatoroidea that differ from that of small to medium-sized, generalist predator, which are the ecomorphotypes of durophagous predators (shared by several taxa), giant predator (*Deinosuchus* and *Purussaurus*) and gulp-feeder (*Mourasuchus*). Such assessment will be performed through both the phylogenetic perspectives obtained in the analyses as well as additional morphological comparisons between the pertinent taxa.

- a thorough assessment on the biogeography of the Alligatoroidea clade, to be performed based on the phylogeny obtained in the analyses. The main topics to be addressed are the possible area of origin and the routes that were taken by alligatoroids to establish their distribution through four continents (North America, South America, Europe and Asia) throughout the Late Cretaceous and the Cenozoic.

- the taxonomic review of the following fossil Caimaninae taxa, which are based on particulary fragmentary, incomplete specimens: *Balanerodus logimus* (Langston, 1965), *Caiman australis* (Bravard, 1858), *Caiman gasparinae* Bona & Carabajal, 2013, *Caiman lutescens* (Rovereto, 1912), *Caiman venezuelensis* Fortier & Rincón, 2012, *Necrosuchus ionensis* Simpson, 1937, *Notocaiman stromeri* Rusconi, 1937. Taxonomic revisions of the genera *Melanosuchus* and *Purussaurus* are also performed.

3. Materials and Methods

3.1. Taxa

3.1.1. List of visited collections and examined specimens

Museo Argentino de Ciéncias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina: *Caiman australis* (MACN-258); *C. gasparinae* (MACN-5555); *C. latirostris* (MACN-5416, MACN-5576); *C. lutescens* (MACN-13552); *Caiman* cf. *C. yacare* (MACN-5417); *Eocaiman palaeocenicus* (MACN-1914; MACN-1915; MACN-1916; MACN-1627).

Museo de La Plata, La Plata, Argentina: *Caiman gasparinae* (MLP-73-IV-15-1, holotype); *Caiman latirostris* (MLP 73-IV-15-16, MLP 73-IV-15-12); *Caiman* cf. *yacare* (MLP 73-IV-15-5, MLP 73-IV-15-6, MLP 73-IV-5-17); *Eocaiman palaeocenicus* (MLP-90-II-12-117; MLP-90-II-12-124; MLP-93-XII-10-11; MLP-93-XII-10-13; MLP-95-XII-10-20; MLP-95-XII-10-27).

Museu de Ciências da Terra, Rio de Janeiro, Brazil: *Eocaiman itaboraiensis* (MCT-1791-R, holotype; MCT-1792-R; MCT-1793-R; MCT-1794-R); *Mourasuchus amazonensis* (DGM-526-R, holotype); *Purussaurus brasiliensis* (DGM-527-R).

Universidade Federal do Acre, Rio Branco, Brazil: *Acresuchus pachytemporalis* (UFAC-2507, holotype); *Caiman brevirostris* (UFAC-196, holotype; UFAC-5388); *Purussaurus brasiliensis* (UFAC-1118; UFAC-1403).

Canadian Museum of History, Ottawa, Canada: *Leidyosuchus canadensis* (CMN-8543, plesiotype; CMN-130; CMN-139; CMN-140; CMN-153; CMN-338; CMN-377; CMN-780; CMN-808; CMN-960; CMN-975; CMN-1010; CMN-1441; CMN-1146; CMN-1508; CMN-1551; CMN-1553; CMN-1614; CMN-1705; CMN-1908; CMN-2784; CMN-8522; CMN-8523; CMN-40850; CMN-40855; CMN-40897; CMN-54608; CMN-58357; CMN-58361).

Royal Tyrell Museum of Paleontology, Drumheller, Canada: *Stangerochampsa mccabei* (RTMP.86.61.1, holotype).

Musée Nationale d'Histoire Naturelle, Paris, France: *Arambourgia gaudryi* (MNHN-QU-17155, holotype); *Diplocynodon ratelli* (MNHN-557; MNHN-12853; MNHN-13728); *D. remensis* (MNHN-F-BR-4020, holotype).

Hessisches Landesmudeum, Darmstadt, Germany: *Diplocynodon darwini* (HLMD-Me-233; HLMD-Me-236; HLMD-Me-5317; HLMD-Me-5486; HLMD-Me-5643; HLMD-Me-5923; HLMD-Me-7493; HLMD-Me-7500; HLMD-Me-7571; HLMD-Me-10262; HLMD-Me-14600a); *D. deponiae* (HLMD-Me-147); *Hassiacosuchus haupti* (HLMD-Me-4415, holotype; HLMD-Me-137; HLMD-Me-1435; HLMD-Me-5261; HLMD-Me-9119).

Senckenberg Museum, Frankfurt, Germany: *Diplocynodon darwini* (SMF-898; SMF-1158); *Diplocynodon* cf. *D. darwini* (SMF-896; SMF-900; SMF-1142); *D. deponiae* (SMF without catalogue number).

Staatliches Museum für Naturkunde, Karlsruhe, Germany: *Diplocynodon darwini* (SMNK-133; SMNK-279; SMNK-400; SMNK-649; SMNK-6517); *Diplocynodon* cf. *D. darwini* (SMNK-287); *Purussaurus* sp. (isolated tooth without catalogue number, part of the type material of *Dakosaurus amazonicus*).

Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru: *Caiman wannlangstoni* (MUSM-2377, holotype; MUSM-1983); *Gnatusuchus pebasensis* (MUSM-990, holoype; MUSM-662; MUSM-1979; MUSM-2040); *Kuttanacaiman iquitosensis* (MUSM-1490, holotype; MUSM-1942).

British Museum of Natural History, London, United Kingdom: *Diplocynodon gracilis* (BMNH-789; BMNH-790); *D. hantoniensis* (BMNH-25166, holotype; BMNH-1041; BMNH-1042; BMNH-1043; BMNH-1068; BMNH-5267; BMNH-29694; BMNH-30206; BMNH-30206a; BMNH-30215; BMNH-30217; BMNH-30314; BMNH-30392; BMNH-30393; BMNH-30394; BMNH-30396; BMNH-30402).

American Museum of Natural History, New York, United States: *Alligator mcgrewi* (AMNH-7905); *A. mefferdi* (AMNH-7016, holotype); *Brachychampsa montana* (AMNH-5032, holotype); *Eocaiman cavernensis* (AMNH-3158, holotype); *Leidyosuchus canadensis* (AMNH-5352); *Navajosuchus mooki* (AMNH-6780, holotype; AMNH-5186, holotype of *N. mexicanus*); *Necrosuchus ionensis* (AMNH-3219, holotype); *Purussaurus brasiliensis* (AMNH-3855, holotype of *Brachygnathosuchus braziliensis*); *Tsoabichi greenriverensis* (AMNH-3666).

Field Museum of Natural History, Chicago, United States: *Caiman latirostris* (FMNH-P-15029); *Ceratosuchus burdoshi* (FMNH-P-15576, holotype; FMNH-P-15436); *Leidyosuchus riggisi* (FMNH-P-15582, holotype; FMNH-P-12141; FMNH-P-15778).

Florida Museum of Natural History, Gainesville, United States: *Alligator mcgrewi* (FLMNH-26242, holotype); *A. olseni* (FLMNH-1361; FLMNH-3537; FLMNH-135596; FLMNH-143667; FLMNH-158723; FLMNH-160113; FLMNH-161099; FLMNH-161135; FLMNH-163352; FLMNH-176192; FLMNH-179878; FLMNH-203657; FLMNH-206773; FLMNH-206799; FLMNH-206805; FLMNH-206926; FLMNH-216630; FLMNH-255011; FLMNH-268789; FLMNH-278060; FLMNH-308671); *Centenariosuchus gilmorei* (FLMNH-262800, holotype; FLMNH-245503; FLMNH-281096); *Culebrasuchus mesoamericanus* (FLMNH-244434, holotype).

United States National Museum of Natural History, Washington, United States: *Allognathosuchus polyodon* (USNM-4112, holotype); *A. heterodon* (USNM-4115, holotype); *Procaimanoidea utahensis* (USNM-15996, holotype; USNM-15997); *Purussaurus neivensis* (USNM-10889, holotype); *Tsoabichi greenriverensis* (USNM-9301).

Los Angeles Natural History Museum, Los Angeles, United States: *Mourasuchus* cf. *amazonensis* (LACM-160157).

Museum of Comparative Zoology, Cambridge, United States: *Alligator olseni* (MCZ-1888, paratype; MCZ-1889; MCZ-4697; MCZ-4698; MCZ-4699); *A. prenasalis* (MCZ-1014, plesiotype; MCZ-1015, plesiotype); *Globidentosuchus brachyrostris* (MCZ-4336).

Texas Memorial Museum, Austin, United States: *Mourasuchus pattersoni* (MCNC-PAL-110-72V, postcranium of the holotype only, which is on loan at this institution); *Tsoabichi greenriverensis* (TMM 42509-1, holotype).

University of California Museum of Paleontology, Berkeley, United States: *Balanerodus logimus* (UCMP-45787, holotype); *Eocaiman* sp. (UCMP-38878; UCMP-

39023); *Mourasuchus atopus* (UCMP-38012, holotype; UCMP-40177); *Purussaurus neivensis* (UCMP-39704; UCMP-39657; UCMP-45719; UCMP-41101); UCMP-39978.

Yale Peabody Museum, New Haven, United States: *Alligator prenasalis* (YPM-PU-10782; YPM-PU-13799; YPM-PU-14063; YPM-PU-16273); *Allognathosuchus wartheni* (YPM-PU-16989); *Balanerodus logimus* (YPM-PU-23272).

Additionally, osteological specimens of all extant alligatoroid specimens were examined in the following collections: American Museum of Natural History, New York, United States; Florida Museum of Natural History, Gainesville, United States; Field Museum of Natural History, Chicago, United States; Museo Argentino de Ciéncias Naturales 'Bernardino Rivadavia', Buenos Aires; Museo de La Plata, La Plata, Argentina; Museu de Ciências da Terra, Rio de Janeiro, Brazil; Museu Nacional, Rio de Janeiro, Brazil; Senckenberg Museum, Frankfurt, Germany; University of California Museum of Paleontology, Berkeley, United States; United States National Museum of Natural History, Washington, United States; Zoologische Staatssammlung, Munich, Germany.

3.1.2. List of external groups

The external groups used in the analysis are the same used by Brochu (2011), except when noted.

3.1.2.1. Outgroup

Bernissartia fagesii

Bibliography consulted: Buffetaut (1975); Norell & Clark (1990).

3.1.2.2. Basal eusuchians

Acynodon adriaticus

Bibliography consulted: Delfino et al. (2008a)

Acynodon iberoccitanus

Bibliography consulted: Buscalioni et al. (1997); Martin (2007).

Allodapasuchus precedens

Bibliography consulted: Buscalioni et al. (2001); Delfino et al. (2008b); Martin (2010b)

Hylaeochampsa vectiana

Bibliography consulted: Clark & Norell (1992); Brochu (1997a).

Iharkutosuchus makadii

Bibliography consulted: Ösi et al. (2007)

3.1.2.3. Gavialoidea

Eogavialis africanum

Specimen analyzed: *SMNS-11785*.

Eosuchus minor

Bibliography consulted: Brochu (2006).

Eothoracosausus mississipiensis

Bibliography consulted: Brochu (2004b)

Gavialis gangeticus

Specimen analyzed: AMNH-R-88316.

Gryposuchus colombianus

Specimens analyzed: UCMP-41136; UCMP-38358; UCMP-39389.

Bibliography consulted: Langston (1965); Langston & Gasparini (1997).

The gavialoid *Thoracosaurus neocesariensis* (de Kay, 1842) was included in the dataset of Brochu (2011), but was excluded of the present analysis as its coding seemed to be erroneous, with the scoring of many characters not corresponding to the observed morphology of the species (see de Kay, 1842; Carpenter, 1983).

3.1.2.4. *Borealosuchus*

Borealosuchus acutidentatus

Bibliography consulted: Brochu (1997b)

Borealosuchus formidabilis

Bibliography consulted: Erickson (1976).

Borealosuchus sternbergii

Bibliography consulted: Gilmore (1910); Brochu (1997b).

Borealosuchus wilsoni

Specimen analyzed: AMNH-7637.

Bibliography consulted: Mook (1959).

3.1.2.5. Planocraniidae

Boverisuchus magnifrons

Bibliography consulted: Brochu (2013).

Boverisuchus vorax

Bibliography consulted: Langston (1975); Brochu (2013).

Planocrania datagensis

Bibliography consulted: Brochu (2013)

Planocrania hengdongensis

Bibliography consulted: Brochu (2013)

3.1.2.6. Crocodyloidea

Asiatosuchus germanicus

Bibliography consulted: Berg (1966)

Australosuchus clarkae

Bibliography consulted: Willis & Molnar (1991).

Crocodylus acer

Bibliography consulted: Mook (1921a).

Crocodylus acutus

Specimen analyzed: AMNH-R-9659.

Crocodylus affinis

Bibliography consulted: Mook (1921b).

Crocodylus megarhinus

Bibliography consulted: Mook (1927)

Crocodylus niloticus

Specimen analyzed: AMNH-R-10081.

Crocodylus porosus

Specimen analyzed: AMNH-R-66378.

Kambara implexidens

Bibliography consulted: Sallisbury & Willis (1996)

Kentisuchus spenceri

Bibliography consulted: Brochu (2007b)

Mecistops cataphractus

Specimen analyzed: AMNH-R-29300.

Osteolaemus osborni

Specimen analyzed: AMNH-R-160900.

Osteolaemus tetrapsis

Specimen analyzed: AMNH-R-74420; AMNH-R-160901.

Prodiplocynodon langi

Bibliography consulted: Mook (1941a).

Rimasuchus lloidy

Bibliography consulted: Fourtau (1920).

Thecachampsa americana

Bibliography consulted: Sellards (1915); Mook (1921c);

Tomistoma schlegelli

Specimen analyzed: AMNH-15177

Trilophosuchus rackhami

Bibliography consulted: Willis (1993).

Voay robustus

Specimens analyzed: AMNH-3101 and AMNH-3104.

Bibliography consulted: Brochu (2007a).

3.1.3. Lists of taxa used or consulted for the internal group or taxonomic reviews

3.1.3.1. Internal groups used in the phylogenetic analysis

Acresuchus pachytemporalis (Fig. 5)

Specimen analyzed: UFAC-2507, holotype (Fig. 5).

Bibliography consulted: Souza-Filho et al. (2019).

Figure 5: Skull of the holotype of *Acresuchus pachytemporalis* (UFAC-2507) in dorsal view. Taken from Souza-Filho et al. (2019). Scale bar = 5 cm.

The holotype is from the Solimões Formation, late Miocene of Brazil.

Albertochampsa langstoni (Fig. 6)

Specimen analized: SMM-P67.15.3, holotype.

Bibliography consulted: Erickson (1972).

Figure 6: Skull of the holotype of *Albertochampsa langstoni* (SMM-P67.15.3) in dorsal view. Scale bar = 5 cm.

The holotype is from the Oldman (or Dinosaur Park) Formation, Late Cretaceous of Canada.

Alligator sinensis (Fig. 7)

Specimens analyzed: AMNH-R-23898; AMNH-R-23907 (Fig. 7); AMNH-R-139672; AMNH-R-139673; AMNH-R-142620.

Figure 7: A specimen of *Alligator sinensis* (AMNH-R-23907) in dorsal view. Scale bar = 5 cm.

Alligator mississippiensis (Fig. 8)

Specimens analyzed: AMNH-R-7128; AMNH-R-40582; AMNH-R-43314; AMNH-R-46842; AMNH-R-71621 (Fig. 8); AMNH-R-75041; AMNH-R-142506; UCMP-131080; UCMP-131699; UCMP-142041.

Alligator thomsoni (Fig. 9)

Specimens analyzed: *AMNH-1736, holotype* (Fig. 9); *AMNH-1738*; *AMNH-1739*; *AMNH-1742*; *AMNH-1743*; *AMNH-11328*; *AMNH-11529*; *AMNH-19244*; *AMNH-19245*.

Bibliography consulted: Mook (1923)

The holotype is from the Trojan Quarry, Miocene of the United States (see Skinner et al., 1977).

Figure 8: A specimen of *Alligator mississippiensis* (AMNH-R-71621) in dorsal view. Scale bar = 5 cm.

Figure 9: Holotype of *Alligator thomsoni* (AMNH-1736) in dorsal view. Skull length from the posterior end of the quadrates to the tip of the snout: 36.3 cm (Mook, 1923).

Alligator prenasalis (Fig. 10)

Specimens analyzed: MCZ-1014, plesiotype (Fig. 10); MCZ-1015, plesiotype; YPM-PU-10782; YPM-PU-13799; YPM-PU-14063; YPM-PU-16273.

Bibliography consulted: Mook (1932)

Figure 10: Skull of the plesiotype of *Alligator prenasalis* (MCZ-1014) in dorsal view. Scale bar = 5 cm.

The plesiotypes and other specimens are from the Brule and Chadron formations, from the Oligocene of South Dakota, United States (Brochu, 1997a).

Alligator mefferdi (Fig. 11)

Specimens analyzed: AMNH-7016, holotype (Fig. 11); *FLMNH-115627*.

Bibliography consulted: Mook (1946).

Figure 11: Holotype of *Alligator mefferdi* (AMNH-7016) in dorsal view. Scale bar = 5 cm.

The holotype is from the Miocene Ash Hollow Formation, from Nebraska, United States. The other consulted specimen is from the Moss Acres Racetrack Site, from the Miocene of Florida, United States (see Snyder, 2007).

Alligator olseni (Fig. 12)

Specimens analyzed: *MCZ-1887, holotype* (Fig. 12); MCZ-1888, paratype; MCZ-1889; MCZ-4697; MCZ-4698; MCZ-4699; FLMNH-1361; FLMNH-3537; FLMNH-135596;

FLMNH-143667; FLMNH-158723; FLMNH-160113; FLMNH-161099; FLMNH-161135; FLMNH-163352; FLMNH-176192; FLMNH-179878; FLMNH-203657; FLMNH-206773; FLMNH-206799; FLMNH-206805; FLMNH-206926; FLMNH-216630; FLMNH-255011; FLMNH-268789; FLMNH-278060; FLMNH-308671.

Bibliography consulted: White (1942).

The holotype is from the Alachua Formation, lower Miocene of Florida, United States.

Figure 12: Skull of the holotype of *Alligator olseni* (MCZ-1887) in dorsal view. Scale bar = 5 cm.

Alligator mcgrewi (Fig. 13)

Specimens analyzed: FLMNH-26242, holotype (Fig. 13); AMNH-7905.

Bibliography consulted: Schmidt (1941).

Figure 13: Skull of the holotype of *Alligator mcgrewi* (FLMNH-26242) in dorsal view. Scale bar = 5 cm.

The holotype is from the lower Miocene Runningwater Formation, from Nebraska, United States. The other consult specimen is also from the lower Miocene of Nebraska, in a locality at Dawes County.

Allognatosuchus polyodon (Fig. 14)

Specimens analyzed: USNM-4112, holotype (Fig. 14); *AMNH-6049*; *AMNH-23444*; *UMMP-100453*; *UMMP-102013*.

Bibliography consulted: Mook (1921d); Brochu (2004a).

Figure 14: Holotype of *Allognathosuchus polyodon* (USNM-4112) in medial view. Scale bar = 5 cm.

The holotype is from the Bridger Formation, Eocene of Wyoming, United States.

Allognatosuchus wartheni (Fig. 15)

Specimens analyzed: *AMNH-5157*; *MCZ-1032*; *MCZ-1627*; *TMM-42170-1*; *UMMP-V-65778*; *UMMP-V-8923*; *UMMP-V-16833*; *YPM-PU-8449*; YPM-PU-16989 (Fig. 15).

Bibliography consulted: Case (1925); Bartels (1983).

The holotype (UMMP-8925), which was consulted only through bibliography (Case, 1925), is from the Eocene ("Wasatch Eocene") of the Wighorn Basin, Wyoming, United States. The specimen consulted directly (YPM-PU-16989) is from the Paleocene of the Willwood Formation, which is also in the Wighorn Basin (see Brochu, 1997a).

Figure 15: Specimen of *Allognathosuchus wartheni* (YPM-PU-16989) in dorsal view. Scale bar = 5 cm.

Arambourgia gaudryi (Fig. 16)

Specimens analized: MNHN-QU-17155, holotype (Fig. 16).

The holotype and only known specimen is from Oligocene deposits known as Phosphats (or Phosphorites) of Quercy, in southwestern France (Brochu, 1997a; see also Remy, 1972).

Figure 16: Holotype of *Arambourgia gaudryi* (MNHN-QU-17155) in dorsal view. Scale bar = 5 cm.

Botttosaurus harlani (Fig. 17)

Bibliography consulted: Cossette & Brochu (2018)

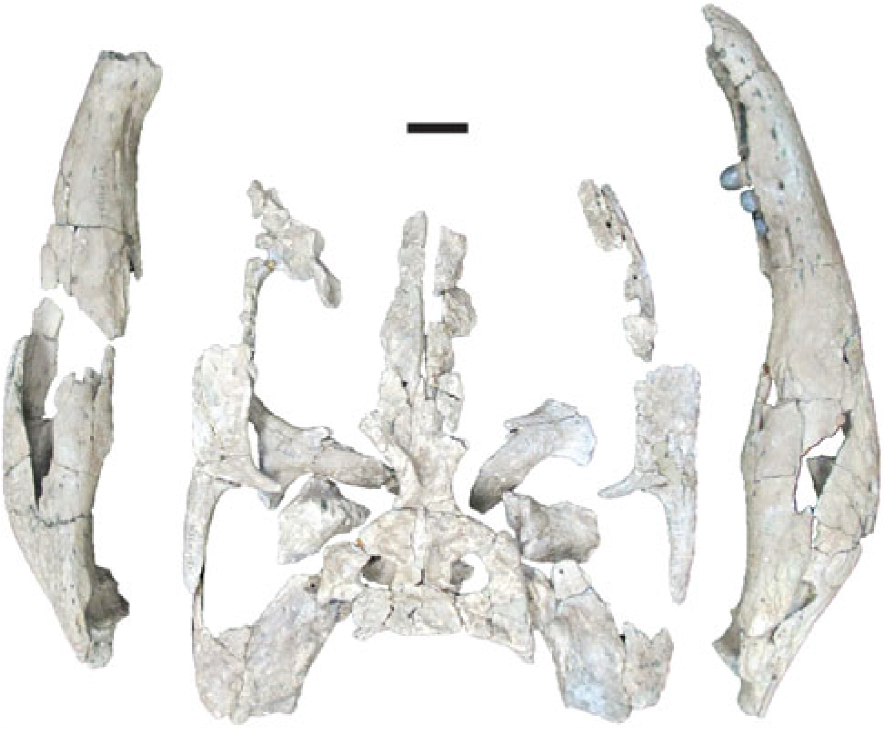

Figure 17: Specimen of *Bottosaurus harlani* (NJSM-11265) in dorsal view. Taken from Cossette & Brochu (2018). Scale bar = 5 cm.

The species is known from several depoists across the Late Cretaceous and the Paleocene of New Jersey, United States (Cossette & Brochu, 2018).

Brachychampsa montana (Fig. 18)

Specimens analyzed: AMNH-5032, holotype (Fig. 18); UCMP-133901; *SMM-P92.4.3*; *SMM-P87.10.2C*; *YPM-PU-56582*.

Bibliography consulted: Norell et al. (1994).

Figure 18: Holotype of *Brachychampsa montana* (AMNH-5032) in dorsal view. Scale bar = 5 cm.

The holotype is from the Late Cretaceous Hell Creek Formation of Montana, United States. The other specimen consulted directly (UCMP-133901) is also from the Hell Creek Formation, but from the state of North Dakota.

Brachychampsa sealeyi (Fig. 19)

Bibliography consulted: Williamson (1996).

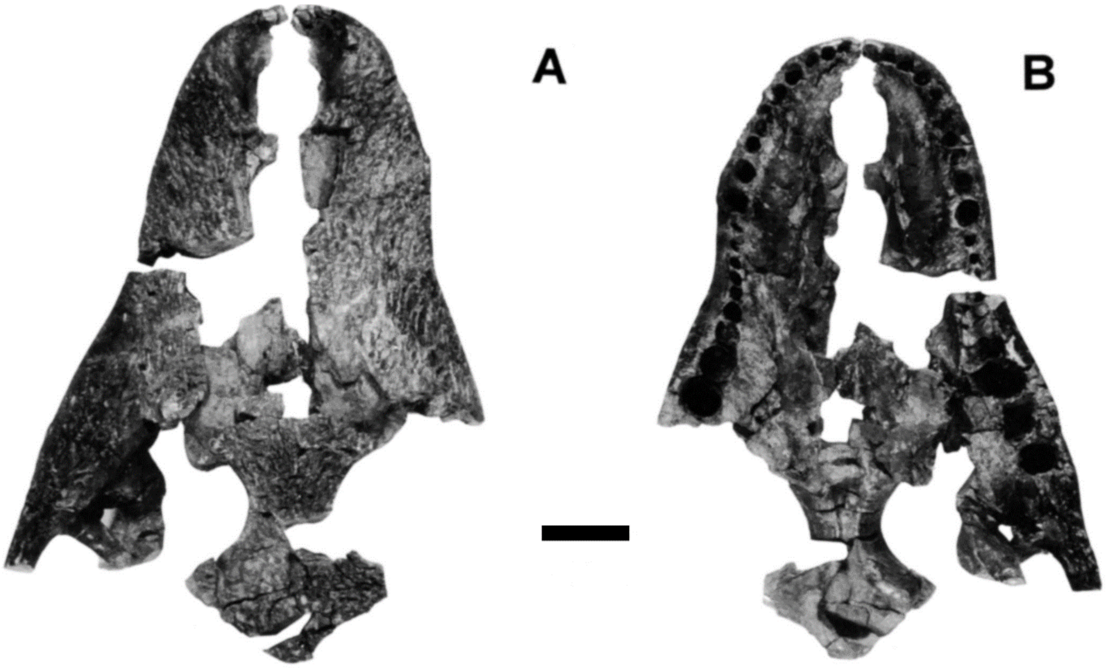

Figure 19: Skull of the holotype of *Brachychampsa sealeyi* (NMMNH-P-25050) in dorsal (A) and ventral (B) views. Taken from Williamson (1996). Scale bar: 2 cm.

The holotype and only known specimen is from the Late Cretaceous Menefee Formation of New Mexico, United States.

Caiman brevirostris (Fig. 20)

Specimens analyzed: UFAC-196, holotype (Fig. 20); UFAC-5388.

Bibliography consulted: Souza-Filho (1987); Fortier et al. (2014).

The holotype and the referred specimen are from the late Miocene Solimões Formation of Brazil.

Figure 20: Part of the skull of the holotype of *Caiman brevirostris* (UFAC-196) in dorsal view. Modified from Cidade et al. (2019a). Scale bar = 10 cm.

Caiman crocodilus (Fig. 21)

Specimens analyzed: AMNH-R-43291, AMNH-R-73048, AMNH-R-137179, FMNH-69840, FMNH-69842, FMNH-69843, FMNH-69846, FMNH-69848, FMNH-69852, FMNH-69854, FMNH-69855, FMNH-69861, FMNH-69865, FMNH-73697, FMNH-73700, FMNH-73704 (Fig. 21), FMNH-73722, FMNH-73725, FMNH-73731, FMNH-73737, FMNH-73744, FMNH-73747, MCT-148-RR, MCT-155-RR, MCT-300-RR, MN-67, MN-1030, MN-1031, MN-25188, MN-25461, UCMP-42483, UCMP-42842, UCMP-42844, UCMP-119115, UCMP-123093, UCMP-123095, UCMP-123096, UCMP-123097, UCMP-123098, UCMP-132075, UCMP-132076; FMNH-69812, *holotype of C. crocodilus apaporiensis*; FMNH-69813, FMNH-69814, FMNH-69817, FMNH-69818, FMNH-69819, FMNH-69821, FMNH-69823, FMNH-69824, FMNH-69825, FMNH-69827, FMNH-69828, FMNH-69830, FMNH-69831, FMNH-69832 (all paratypes of *C. crocodilus apaporiensis*).

Figure 21: Specimen of *Caiman crocodilus* (*C. crocodilus chiapasius*, FMNH-73704) in dorsal view. Scale bar = 5 cm.

Caiman latirostris (Fig. 22)

Specimens analyzed: AMNH-R-28367, AMNH-R-143183, MACN-30566, MACN-30567, MACN-30572, MACN-30610, MACN-30612, MCT-156-RR, MCT-157-RR, MN-69, MN-1019, MN-1041, MN-1254, MN-1255 (Fig. 22), MN-1256, MN-1257, MN-1455, MN-2078, MN-2333, MN-2340, MN-2395, MN-9756, MN-11254, MN-2395, MN-24588.

Figure 22: Specimen of *Caiman latirostris* (MN-1255) in dorsal view. Scale bar = 5 cm.

Caiman wannlangstoni (Fig. 23)

Specimens analyzed: MUSM-2377, holotype (Fig. 23); MUSM-1983.

Bibliography consulted: Salas-Gismondi et al. (2015).

Figure 23: Skull of the holotype of *Caiman wannlangstoni* (MUSM-2377) in dorsal view. Taken from Cidade et al. (2019a). Scale bar = 10 cm.

The holotype and all specimens consulted (directly or through bibliography) are from the Pebas Formation, middle Miocene of Peru.

Caiman yacare (Fig. 24)

Specimens analyzed: AMNH-R-97305, MACN-30540, MACN-30542, MACN-30558, MACN-30593, MACN-30595, MACN-30601, MACN-30602, MACN-30637, MACN-8267, MLP-604 (Fig. 24), MN-68, MN-1259, MN-9754, MN-9755, MN-12126, MN-12127, MN-25436, MN-25437, USMP-342487.

Figure 24: Specimen of *Caiman yacare* (MLP-604) in dorsal view. Scale bar = 5 cm.

Caimaninae sp. nov. (Fig. 25)

Biblliography consulted: Langston (1965).

Specimen analyzed: UCMP-39978 (Fig. 25).

Figure 25: Caimaninae sp. nov. (UCMP-39978) in dorsal view. Taken from Cidade et al. (2019a). Scale bar = 10 cm.

The specimen is from the Honda Group, middle Miocene of Colombia.

Centenariosuchus gilmorei (Fig. 26)

Specimens analyzed: FLMNH-262800, holotype (Fig. 26); FLMNH-245503; FLMNH-281096.

Bibliography consulted: Hastings et al. (2013, 2016).

Figure 26: Part of the skull of the holotype of *Centenariosuchus gilmorei* (FLMNH-262800) in dorsal view. Scale bar = 5 cm.

The holotype and specimens consulted are from the early Miocene Cucaracha Formation of Panama.

Ceratosuchus burdoshi (Fig. 27)

Specimens analyzed: FMNH-P-15576, holotype (Fig. 27); FMNH-P-15436; *TMM-42291-4*.

The holotype is from the Paleocene DeBeque Formation, from Colorado, United States.

Figure 27: Skull of the holotype of *Certatosuchus burdoshi* (FMNH-P-15576) in dorsal view. Scale bar = 5 cm.

Culebrasuchus mesoamericanus (Fig. 28)

Specimens analyzed: FLMNH-244434, holotype (Fig. 28).

Bibliography consulted: Hastings et al. (2013).

Figure 28: Part of the skull of the holotype of *Culebrasuchus mesoamericanus* (FLMNH-244434) in dorsal view. Scale bar = 10 cm.

The holotype and only known specimen is from the early Miocene Culebra Formation of Panama.

Diplocynodon darwini (Fig. 29)

Specimens analyzed: HLMD-Me-233; HLMD-Me-236; HLMD-Me-5317; HLMD-Me-5486; HLMD-Me-5643; *HLMD-Me-5648*; HLMD-Me-5923; *HLMD-Me-7435a*; HLMD-Me-7493; HLMD-Me-7500 (Fig. 29); HLMD-Me-7571; *HLMD-Me-9747;* HLMD-Me-10262; HLMD-Me-14600a; SMF-898; SMF-1158; SMNK-133; SMNK-279; SMNK-400; SMNK-649; SMNK-6517.

Figure 29: Specimen of *Diplocynodon darwini* (HLMD-Me-7500) in medial view. Scale bar = 8 cm.

All specimens are from the Eocene Messel Pit, located near the village of Messel, in Hesse, Germany.

Diplocynodon deponiae (Fig. 30)

Specimens analyzed: *SMF-Me-899, holotype*; HLMD-Me-147 (Fig. 30); *HLMD-Me-8080*; SMF without catalogue number.

Bibliography consulted: Delfino & Smith (2012).

The holotype and all consulted specimens are from the Eocene Messel Pit.

Figure 30: Specimen of *Diplocynodon deponiae* (HLMD-Me-147) in dorsal view. Scale bar = 7 cm.

Diplocynodon elavericus (Fig. 31)

Bibliography consulted: Martin (2010a).

Figure 31: Skull of the holotype of *Diplocynodon elavericus* (Rhinopolis B3) in dorsal view. Scale bar = 1 cm.

The holotype and only known specimen comes from a Late Eocene locality at Domérat, Allier, France (see Martin, 2010a for details).

Diplocynodon hantoniensis (Fig. 32)

Specimens analyzed: BMNH-25166, holotype (Fig. 32); BMNH-1041; BMNH-1042; BMNH-1043; BMNH-1068; BMNH-5267; BMNH-29694; BMNH-30206; BMNH-30206a; BMNH-30215; BMNH-30217; BMNH-30314; BMNH-30392; BMNH-30393; BMNH-30394; BMNH-30396; BMNH-30402; *CAMSM-TN-904; CAMSM-TN-907; CAMSM-TN-917.*

Bibliography consulted: Owen (1850); Piras & Buscalioni (2006).

Figure 32: Skull of the holotype of *Diplocynodon hantoniensis* (BMNH-25166) in dorsal view. Scale bar = 10 cm.

The holotype and all directly analyzed specimens come from the early Oligocene Lower Headon Beds, located in Hampshire, England (see Brochu, 1997a).

Diplocynodon muelleri (Fig. 33)

Specimens analyzed: *MGB-9289*; *MGB-9292*; *MGB-9294*; *MGB-9351-1*; *MGB-9360*; *MGB-9406*; *MGB-9420*; *MGB-9424*; *MGB-9426-1*; *MGB-9428*; *MGB-9429*; *MGB-9431*; *MGB-9433*; *MGB-9438*; *MGB-9440*; *MGB-9441*; *MGB-20823*; *MGB-25924*; *MGB-27150*; *MGB-28126*; *MGB-28127*; *MGB-28128*; *MGB-28129*; *MGB-28130*; *MGB-4157-2*; *MGB-4157-3*.

Bibliography consulted: Kälin (1936a); Piras & Buscalioni (2006).

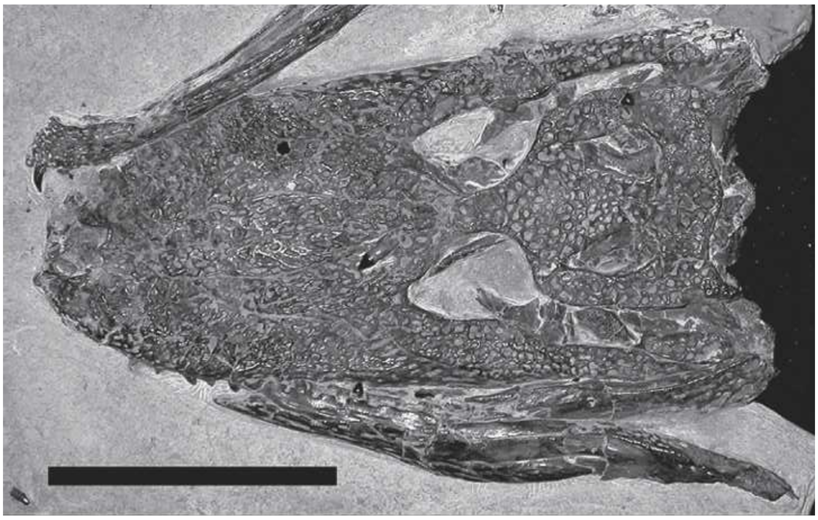

Figure 33: Skull of the holotype of *Diplocynodon muelleri* (Spa-4-T2) in dorsal view. Taken from Piras & Buscalioni (2006). Scale bar = 5 cm.

The holotype of the species (only consulted through bibliography) is from the early Oligocene Calcaries de Tàrraga Formation, in Lleida, Spain.

Diplocynodon ratelii (Fig. 34)

Specimens analyzed: *MNHN-539* (Fig. 34); *MNHN-541*; MNHN-557; MNHN-12853; MNHN-13728.

Bibliography consulted: Brinkman & Rauhe (1998).

The specimens directly consulted come from an early Miocene locality in Saint Gérand-le-Puy, in the Allier Department, France.

Figure 34: Skull of the holotype of *Diplocynodon ratelii* (MNHN-539) in dorsal view. Scale bar = 10 cm.

Diplocynodon remensis (Fig. 35)

Specimens analyzed: MNHN-F-BR-4020, holotype.

Bibliography consulted: Martin et al. (2014).

Figure 35: Holotype of *Diplocynodon remensis* (MNHN-F-BR-4020) in dorsal view. Taken from Martin et al. (2014). Scale bar = 2 cm.

The holotype and all referred specimen of the species are from the late Paleocene Châlons-sur-Vesles Formation, Marne Department, in Champagne-Ardenne, north-eastern France.

Diplocynodon tormis (Fig. 36)

Specimens analyzed: *STUS-7211*.

Bibliography consulted: Buscalioni et al. (1992).

Figure 36: Skull of the holotype of *Diplocynodon tormis* (IPS-9001) in dorsal view. Modified from Buscalioni et al. (1992). Scale bar = 1 cm.

The holotype, only consulted through bibliography, is from the Eocene Duero Basin, Areniscas de Cabrerizos Formation of Spain.

Diplocynodon ungeri (Fig. 37)

Bibliography consulted: Martin & Gross (2011).

The holotype and all referred specimens consulted (all through bibliography) are from the middle Miocene Eibiswald Formation, located in Styria, Austria.

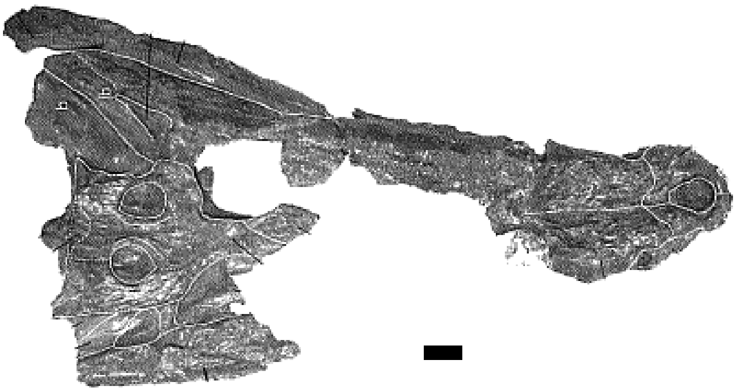

Figure 37: Specimen of *Diplocynodon ungeri* (MUL-21) in dorsal view. Taken from Martin & Gross (2011). Scale bar = 2 cm.

Eocaiman cavernensis (Fig. 38)

Specimen analyzed: AMNH-3158, holotype (Fig. 38).

Bibliography consulted: Simpson (1933); Bona (2007); Pinheiro et al. (2013).

Figure 38: Part of the skull of the holotype of *Eocaiman cavernensis* (AMNH-3158) in dorsal view. Scale bar = 10 cm.

The holotype an only known specimen from the Eocene Sarmiento Formation, Argentina.

Eocaiman palaeocenicus (Fig. 39)

Specimens analyzed: *MPEF-PV-1933, holotype* (Fig. 39); MACN-1914; MACN-1915; MACN-1916; MACN-1627; MLP-90-II-12-117; MLP-90-II-12-124; MLP-93-XII-10-11; MLP-93-XII-10-13; MLP-95-XII-10-20; MLP-95-XII-10-27.

Bibliography consulted: Bona (2007); Pinheiro et al. (2013).

Figure 39: Anterior portion of the mandibles of the holotype of *Eocaiman palaeocenicus* (MPEF-PV-1933) in dorsal view. Scale bar = 10 cm.

The holotype and all referred specimens are from the Paleocene Salamanca Formation, Argentina.

Globidentosuchus brachyrostris (Fig. 40)

Specimen analyzed: MCZ-4336.

Bibliography consulted: Scheyer et al. (2013); Hastings et al. (2016); Bona et al. (2017); Foth et al. (2018).

The holotype (Fig. 40) and the referred specimen are from the late Miocene Urumaco Formation, Venezuela.

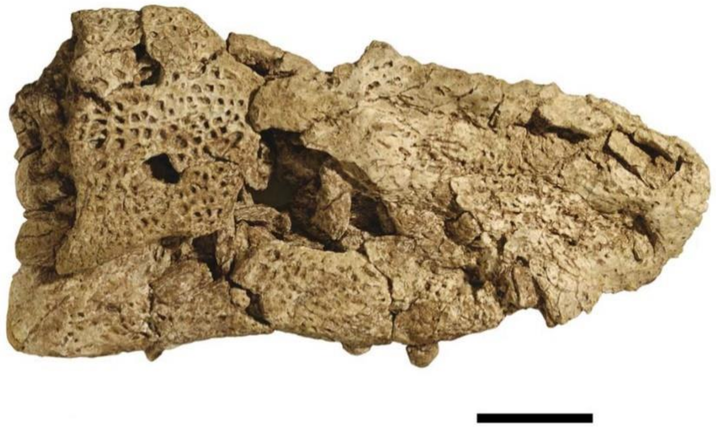

Figure 40: Skull of the holotype of *Globidentosuchus brachyrostris* (AMU-CURS-222) in dorsal view. Taken from Hastings et al. (2016). Scale bar = 5 cm.

Gnatusuchus pebasensis (Fig. 41)

Specimens analyzed: MUSM-990, holoype (Fig. 41); MUSM-662; MUSM-1979; MUSM-2040.

Bibliography consulted: Salas-Gismondi et al. (2015).

Figure 41: Skull of *Gnatusuchus pebasensis* in dorsal view (MUSM-990, holotype) in dorsal view. Scale bar = 10 cm.

The holotype and all referred specimens are from the middle Miocene Pebas Formation, Peru.

Hassiacosuchus haupti (Fig. 42)

Specimens analyzed: HLMD-Me-4415, holotype (Fig. 42); HLMD-Me-137; HLMD-Me-1435; HLMD-Me-5261; *HLMD-Me-8008*; HLMD-Me-9119.

Bibliography consulted: Weitzel (1935); Brochu (2004a).

Figure 42: Skull of *Hassiacosuchus haupti* (HLMD-Me-4415, holotype) in dorsal view. Scale bar = 5 cm.

The holotype and all referred specimens are from the Eocene Messel Pit, Germany.

Krabisuchus siamogallicus (Fig. 43)

Specimens analyzed: *Kr-C-012, holotype* (Fig. 43); *Kr-C-006*; *Kr-C-007*; *Kr-C-010*; *Kr-C-012*; *Kr-C-015*; *Kr-C-017*; *Kr-C-020*; *Kr-C-021*; *Kr-C-022*; *Kr-C-025*; *Kr-C-028*; *Kr-C-032*; *Kr-C-038*; *Kr-C-043*; *Kr-C-065*; *Kr-C-066*.

Bibliography consulted: Martin & Lauprasert (2010).

The holotype and all referred specimens (see Martin & Lauprasert, 2010, for details) are from the late Eocene Krabi Basin, southern Thailand.

Figure 43: Holotype of *Krabisuchus siamogallicus* (Kr-C-012) in dorsal view. Scale bar = 5 cm.

Kuttanacaiman iquitosensis (Fig. 44)

Specimens analyzed: MUSM-1490, holotype; MUSM-1942.

Bibliography consulted: Salas-Gismondi et al. (2015).

Figure 44: Skull and articulated mandibles of *Kuttanacaiman iquitosensis* (MUSM-1490, holotype) in dorsal view. Scale bar = 10 cm.

The holotype and referred specimens analyzed in this study are from the middle Miocene Pebas Formation, Peru.

Leidyosuchus canadensis (Fig. 45)

Specimens analyzed: CMN-8543, plesiotype (Fig. 45); CMN-130; CMN-139; CMN-140; CMN-153; CMN-338; CMN-377; CMN-780; CMN-808; CMN-960; CMN-975; CMN-1010; CMN-1441; CMN-1146; CMN-1508; CMN-1551; CMN-1553; CMN-1614; CMN-1705; CMN-1908; CMN-2784; CMN-8522; CMN-8523; CMN-40850; CMN-40855; CMN-40897; CMN-54608; CMN-58357; CMN-58361; AMNH-5352.

Bibliography consulted: Lambe (1907); Wu et al. (2001).

Figure 45: Skull of *Leidyosuchus canadensis* (CMN-8543, plesiotype) in dorsal view. Scale bar = 10 cm.

The plesiotype is from the Late Cretaceous Upper Judith River Group, Canada.

Melanosuchus niger (Fig. 46)

Specimens analyzed: AMNH-R-101419; AMNH-R-58130 (Fig. 46), FLMNH-62641; FLMNH-1045123; FMNH-45653, MCT-286-RR, MN-61, MN-63, MN-64, MN-66, MN-81, MN-82, MN-1034, MN-3174; SMF-30102; SMF-30113; USNM-257785; ZS-

3; ZS-11; ZS-13; ZS-14; ZS-35; ZS-46; ZS-52; ZS-57; ZS-64; ZS-69; ZS-75; ZS-77; ZS-79; ZS-89.

Figure 46: Specimen of *Melanosuchus niger* (AMNH-R-58130) in dorsal view. Scale bar = 10 cm.

Mourasuchus amazonensis (Fig. 47)

Specimens analyzed: DGM-526-R, holotype (Fig. 47).

Bibliography consulted: Price (1964); Cidade et al. (2019b).

Figure 47: Skull of the holotype of *Mourasuchus amazonensis* (DGM-526-R. Taken from Cidade et al. (2019b). Scale bar = 20 cm.

The holotype is from the late Miocene Solimões Formation, Brazil.

Mourasuchus arendsi (Fig. 48)

Specimens analyzed: *CIAAP-1297, holotype* (Fig. 48).

Bibliography consulted: Bocquentin-Villanueva (1984); Scheyer & Delfino (2016); Cidade et al. (2018, 2019c).

Figure 48: Skull of the holotype of *Mourasuchus arendsi* (CIAAP-1297) in dorsal view. Taken from Cidade et al. (2018). Scale bar = 10 cm.

The holotype and the referred specimens consulted in Scheyer & Delfino (2016) are from the late Miocene Urumaco Formation, Venezuela. The referred specimens consulted in Cidade et al. (2019c) are from the late Miocene Solimões Formation of Brazil, except AMNH-14441, which alternatively may be from the late Miocene Cobija Formation of Bolivia.

Mourasuchus atopus (Fig. 49)

Specimen analyzed: UCMP-38012, holotype (Fig. 49).

Bibliography consulted: Langston (1965).

Figure 49: Left maxilla of the holotype of *Mourasuchus atopus* (UCMP-38012) in ventral view. Scale bar = 5 cm.

The holotype is from the middle Miocene Honda Group, Colombia.

Mourasuchus pattersoni (Fig. 50)

Specimen analyzed: MCNC-PAL-110-72V, holotype (Fig. 50).

Bibliography consulted: Langston (2008); Cidade et al. (2017).

Figure 50: Skull of the holotype of *Mourasuchus pattersoni* (MCNC-PAL-110-72V) in dorsal view. Taken from Cidade et al. (2017). Scale bar = 20 cm.

The holotype is from the late Miocene Urumaco Formation, Venezuela.

Navajosuchus mooki (Fig. 51)

Specimens analyzed: AMNH-6780, holotype (Fig. 51); AMNH-5186, holotype of *N. mexicanus.*

Bibliography consulted: Simpson (1930).

Figure 51: Skull of the holotype of *Navajosuchus mooki* (AMNH-6780) in dorsal view. Scale bar = 5 cm.

The holotype and referred specimen directly analyzed are from the Paleocene Nacimiento Formation, in New Mexico, United States.

Paleosuchus palpebrosus (Fig. 52)

Specimens analyzed: AMNH-R-137170, AMNH-R-137174, AMNH-R-145071, AMNH-R-93812, AMNH-R-97326, AMNH-R-97328, FLMNH-75023, FMNH-69867, FMNH-69869 (Fig. 52), FMNH-69871, FMNH-69874, MCT-269-RR, MCT-291-RR, MN-317, MN-2356.

Figure 52: Specimen of *Paleosuchus palpebrosus* (FMNH-69869) in dorsal view. Scale bar = 5 cm.

Paleosuchus trigonatus (Fig. 53)

Specimens analyzed: AMNH-R-58136, AMNH-R-66391, AMNH-R-129259; AMNH-R-129260, FMNH-81980, MN-65, MN-2491, MN-9757, USNM-213705, USNM-234047, USNM-300660 (Fig. 53), USNM-302052, USNM-317555, USNM-317556, USNM-562714.

Figure 53: Specimen of *Paleosuchus trigonatus* (USNM-300660) in dorsal view. Scale = 5 cm.

Procaimanoidea kayi (Fig. 54)

Specimens analyzed: *CM-9600, holotype* (Fig. 54).

Bibliography consulted: Mook (1941c).

Figure 54: Skull of the holotype of *Procaimanoidea kayi* (CM-9600) in dorsal view. Scale bar = 5 cm.

The holotype is from the Eocene Bridger Formation, in Wyoming, United States.

Procaimanoidea utahensis (Fig. 55)

Specimens analyzed: USNM-15996, holotype; USNM-15997 (Fig. 55)

Bibliography consulted: Gilmore (1946).

The holotype and the referred specimen are from the Eocene Uinta Basin, in Utah, United States.

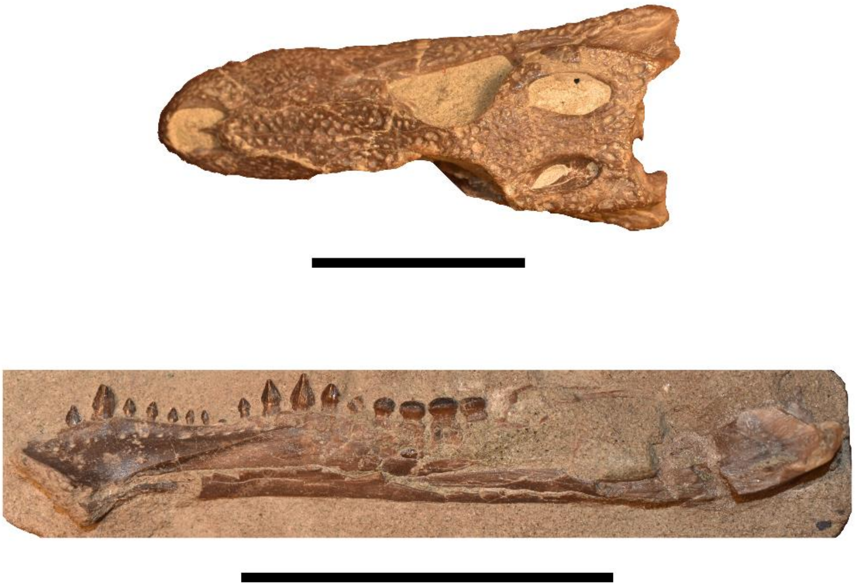

Figure 55: Skull of the holotype (USNM-15996, above) and a referred right mandible in medial view (USNM-15997) of *Procaimanoidea utahensis*. Scale bar = 5 cm.

Protoalligator huningensis (Fig. 56)

Bibliography consulted: Young (1982); Wang et al. (2016).

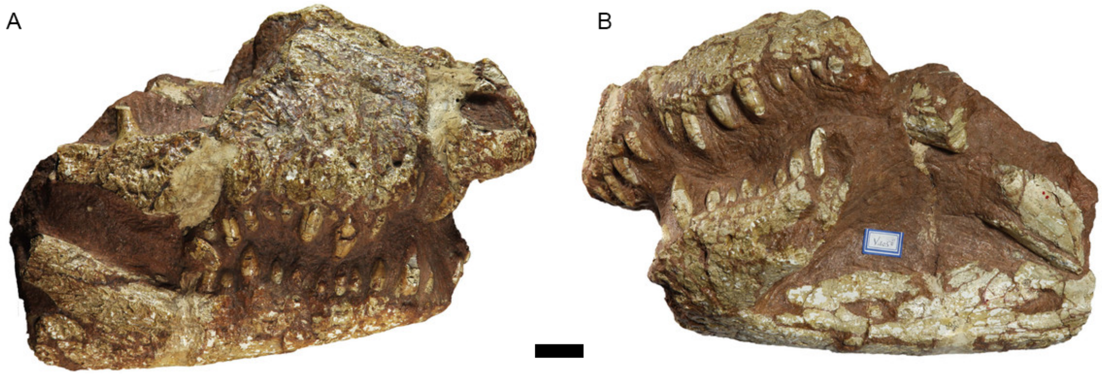

Figure 56: Holotype of *Protoalligator huningensis* (IVPP-V-4058) in dorsolateral (A) and ventromedial (b) views. Scale bar = 2 cm.

The holotype and only known specimen is from the Wanghudun Formation, middle Paleocene, in the Anhui Province of China.

Purussaurus brasiliensis (Fig. 57)

Specimens analyzed: DGM-527-R; UFAC-1118; UFAC-1403 (Fig. 57); AMNH-3855, holotype of *Brachygnathosuchus braziliensis.*

Bibliography consulted: Barbosa-Rodrigues (1892); Price (1967); Bocquentin-Villanueva et al. (1989); Aureliano et al. (2015).

Figure 57: Skull of *Purussaurus brasiliensis* (UFAC-1403) in dorsal view. Scale bar = 20 cm.

All specimens are from the late Miocene Solimões Formation of Brazil. The holotype, consulted only from bibliography (Barbosa-Rodrigues, 1892), is most likely from the Solimões Formation as well, but it is now lost (see Price, 1967).

Purussaurus mirandai (Fig. 58)

Specimens analyzed: *CIAAP-1369, holotype* (Fig. 58).

Bibliography consulted: Aguilera et al. (2006).

The holotype and all referred specimens analyzed through the literature are from the late Miocene Urumaco Formation, Venezuela.

Figure 58: Skull of the holotype of *Purussaurus mirandai* (CIAAP-1369) in dorsal view. Taken from Cidade et al. (2019). Scale bar = 10 cm.

Purussaurus sp. nov. (Fig. 59)

Specimens analyzed: UCMP-39704 (Fig. 59); UCMP-45719.

Bibliography consulted: Langston (1965).

Figure 59: Specimen UCMP-39704 in dorsal view. Taken from Cidade et al. (2019a). Scale bar = 10 cm.

Both specimens are from the middle Miocene Honda Group of Colombia.

Stangerochampsa mccabei (Fig. 60)

Specimens analyzed: RTMP.86.61.1, holotype (Fig. 60).

Bibliography consulted: Wu et al. (1996).

Figure 60: Skull of the holotype of *Stangerochampsa mccabei* (RTMP.86.61.1) in dorsal view. Scale bar = 5 cm.

The holotype and only known specimen is from the Late Cretaceous Judith River Group, Canada.

Tsoabichi greenriverensis (Fig. 61)

Specimens analyzed: TMM-42509-1, holotype (Fig. 61); AMNH-3666; *SMNK-2333*; *SMNK-23334*; USNM-9301.

Bibliography consulted: Brochu (2010).

The holotype and all specimens directly analyzed are from the early Eocene Green River Formation, in Wyoming, United States.

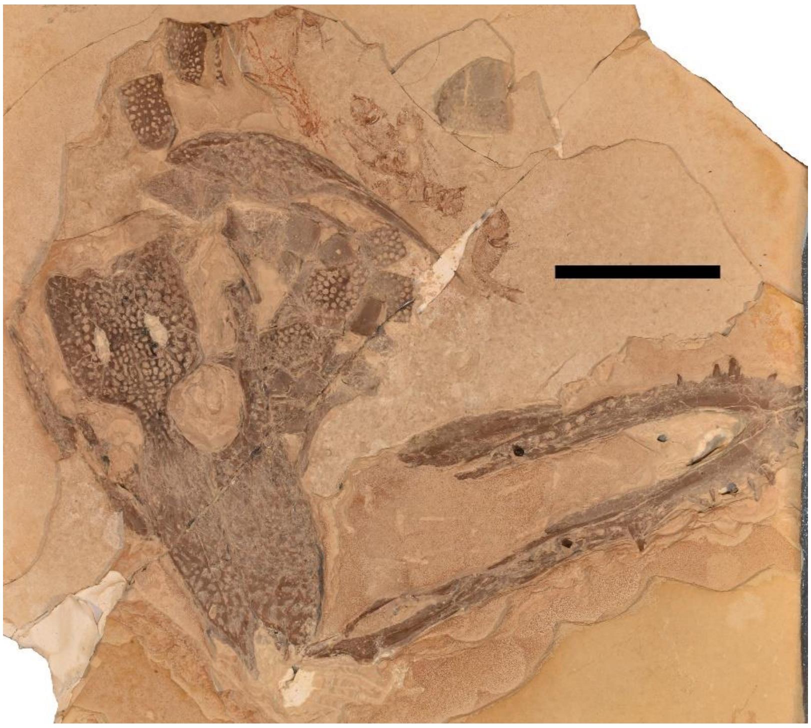

Figure 61: Holotype of *Tsoabichi greenriverensis* (TMM-42509-1) in dorsal view. Scale bar = 5 cm.

Wannaganosuchus brachymanus (Fig. 62)

Specimens analyzed: *SMM-P76.28.247, holotype* (Fig. 62); *SMM-P2002.4.IC*; *YMP-PU-16988*; *YMP-PU-17558*; *YMP-PU-20612*; *YMP-PU-23943*.

Bibliography consulted: Erickson (1982).

Figure 62: Skull of the holotype of *Wannganosuchus brachymanus* (SMM-P76.28.247) in dorsal view. Scale bar = 5 cm.

The holotype is from the Paleocene locality “Wanngan Creek Quarry”, from the “Bullion Creek (Tongue River) Formation” as stated by Erickson (1982), in North Dakota, United States.

3.1.3.2. List of Alligatoroidea taxa used in taxonomic reviews or for general comparisons

Caiman australis

Specimen analyzed: MACN-258.

Bibliography consulted: Bravard (1858, 1860); Burmeister (1883, 1885); Rovereto (1912); Rusconi (1933); Bona et al. (2012).

The specimen is from the late Miocene layer “conglomerado osífero” (“bony conglomerate”), Ituzaingó Formation, Argentina.

Caiman crocodilus apapporiensis (Fig. 63)

Specimens analyzed: FMNH-69812, holotype (Fig. 63); FMNH-69813, FMNH-69814, FMNH-69817, FMNH-69818, FMNH-69819, FMNH-69821, FMNH-69823, FMNH-69824, FMNH-69825, FMNH-69827, FMNH-69828, FMNH-69830, FMNH-69831, FMNH-69832 (all paratypes).

Figure 63: Skull of *Caiman crocodilus apaporiensis* (FMNH-69812, holotype) in dorsal view. Scale bar = 5 cm.

Caiman gasparinae

Specimens analyzed: MLP-73-IV-15-1, holotype; MACN-5555.

Bibliography consulted: Bona & Carabajal (2013); Bona et al. (2012).

The holotype and referred specimen are from the late Miocene “conglomerado osífero”, Ituzaingó Formation, Argentina.

Eocaiman itaboraiensis

Specimens analyzed: MCT-1791-R, holotype; MCT-1792-R; MCT-1793-R; MCT-1794-R.

Bibliography consulted: Pinheiro et al. (2013).

The holotype and all referred specimens are from the Paleocene Itaboraí Basin, in Rio de Janeiro, Brazil.

Melanosuchus sp. (MCNC-243)

Bibliography consulted: Medina (1976); Bona et al. (2017); Foth et al. (2018).

The specimen is from the late Miocene Urumaco Formation, Venezuela.

MMC-001 (Maoming crocodylian, Fig. 64)

Bibliography consulted: Skutschas et al. (2014).

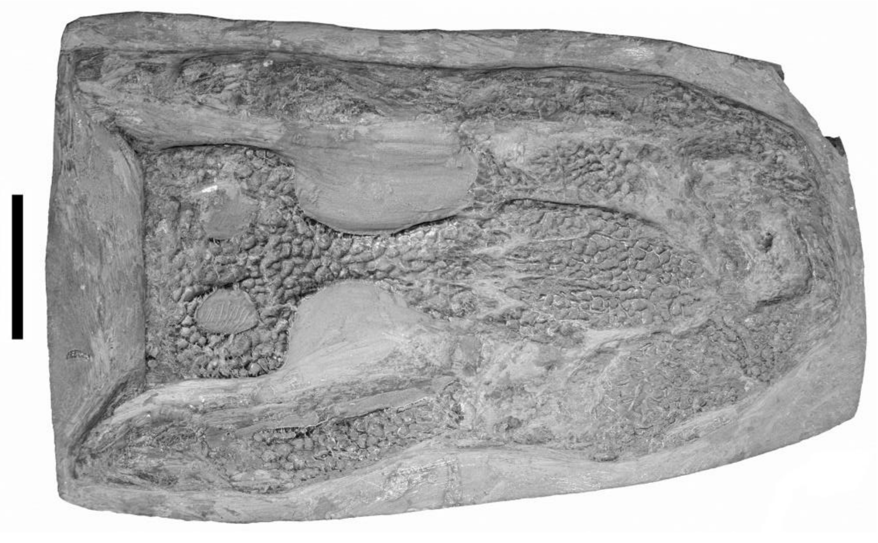

Figure 64: Specimen MMC-001 (Maoming crocodylian) in dorsal view. Taken from Skutschas et al. (2014). Scale bar = 3 cm.

The specimen, consulted only from bibliography, is from the late Eocene Youganwo Formation, Maoming Basin, in the Guangdong Province of China.

Necrosuchus ionensis

Specimen analyzed: AMNH-3219, holotype.

Bibliography consulted: Simpson (1937); Brochu (2011).

The holotype and only known specimen is from the Paleocene Salamanca Formation, Argentina.

Notocaiman stromeri

Specimens analyzed: *PVL-752, holotype*.

Bibliography consulted: Rusconi (1937).

The holotype and only known specimen is from the Paleocene Las Violetas Formation (but see Cidade et al., 2019a for controversies regarding the stratigraphic origin of the species), Argentina.

Protocaiman peligrensis (Fig. 65)

Bibliography consulted: Bona et al. (2018).

Figure 65: Holotype of *Protocaiman peligrensis* (MLP-80X-10-1) in dorsal view. Taken from Bona et al. (2018). Scale bar = 5 cm.

The holotype and only known specimen is from the Paleocene Salamanca Formation, Argentina.

Purussaurus neivensis (Fig. 66)

Specimens analyzed: USNM-10889, holotype (Fig. 66).

Bibliography consulted: Mook (1941b).

Figure 66: Part of the occluded left maxilla and left dentary of the holotype of *Purussaurus neivensis* (USNM-10889) in lateral view. Scale bar = 5 cm.

The holotype is from the middle Miocene Honda Group, Colombia.

3.2. Characters

3.2.1. Characters considered for inclusion in the analysis

A survey was performed through the publications regarding phylogenetic analyses of Alligatoroidea to determine which characters already proposed for the group or for the Eusuchia clade as a whole would be revised by this study in order to include them or not in the phylogenetic analyses performed in this study itself.

All 181 characters proposed by Brochu (2011) for Eusuchia were considered for inclusion in the analysis, as it is the most comprehensive dataset for that clade and for Alligatoroidea itself to have been published to date. A complete list of these characters is at the Appendix 1. Of these 181 characters, 171 was analyzed directly from the text proposed by Brochu (2011), while the remaining ten were analyzed based on modifications already proposed by later authors: one by Aguilera et al. (2006) and nine by Salas-Gismondi et al. (2015). These modified characters are available at the Appendix 2.

Additionally, characters proposed by the following publications were also considered to be included in the analysis: one character from Bona (2007), later modified by Pinheiro et al. (2013); six characters from Barrios (2011); three from Bona et al. (2012); eight from Brochu (2013); two from Salas-Gismondi et al. (2015); and one from Cidade et al. (2017). The characters of these publications are available at the Appendix 2. As such, a total of 202 characters were initially considered for inclusion in the analysis of this study.

3.2.2. Criteria used for the selection of characters to be used in the analysis

The 202 characters surveyed were preliminarly analyzed for their definitive inclusion in the phylogenetic analysis of this study based on two broad criteria: whether the characters were informative; and whether the characters were coherent with the morphology observed in the concerned taxa. Out of the 202 characters initially considered, 173 were deemed valid for inclusion in the phylogenetic analysis.

Out of the 181 characters of Brochu (2011), 161 will be used in the present analysis. From the other 21 characters, 12 were excluded for not being informative: the characters 21, 30, 107 and 136 only had one of the character states scored. In the others, the least scored character state was present only in one taxon. This happened either for binary characters (20, 37, 98, 100, 161 and 170) or for polymorphic characters (95 and 178). In these last two, both character states '1' and '2' were scored only once each. These facts render these characters uninformative and as such they were not employed in the present analysis (see Appendix 1 for the characters that were excluded from the analysis). Eight (08) other characters were excluded due to individual variation observed in living alligatoroids. These are listed below, with their original numbers as per the original publication (see also Appendix 1).

65. Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis; anterior tip acute (0) or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis; anterior tip very blunt (1)

Significant individual variation was observed regarding this character in extant caimanines.

68. Articular–surangular suture simple (0) or articular bears anterior lamina dorsal to lingual foramen (1) or articular bears anterior lamina ventral to lingual foramen (2) or bears laminae above and below foramen (3)

Variation was found in three extant Caimaninae species: *Caiman latirostris* (originally scored as 2) presents individuals with no lamina, whereas both species of *Paleosuchus* (originally scored as 0) exhibit individuals either with the dorsal or the ventral lamina. As the variation seen in *Paleosuchus* denotes a variability between three states (0, 1 and 2), it was considered the exclusion of this character from the analysis to avoid the use of such a variable feature among fossil taxa that are frequently known from a single specimen, without the possibility of evaluation of individual variation.

112. Maxilla has linear medial margin adjacent to suborbital fenestra (0) or bears broad shelf extending into fenestra, making the lateral margin of the fenestrae concave (1)

Significant variation in this character was observed in extant caimanines, between both states.

113. Anterior face of palatine process rounded or pointed anteriorly (0) or notched anteriorly (1)

Both species of *Paleosuchus* were originally scored as 1 for this character, but observation of the specimens revelated both to be polymorphic for it. As, aside from *Paleosuchus*, the only taxa that are scored as 1 for this character are the crocodyloid *Kentisuchus spenceri* and the alligatoroid *Brachychampsa montana*, the polymorphism renders this character *de facto* uninformative for the present analysis, which focus on the Alligatoroidea clade. This fact, together with the doubt it puts regarding fossil the scoring of fossil taxa for this character, led to its exclusion from the analysis.

119. Pterygoid ramus of ectopterygoid straight, posterolateral margin of suborbital fenestra linear (0) or ramus bowed, posterolateral margin of fenestra concave (1)

This character was excluded from the analysis due to the significant variation seen in most extant caimanines, except in *Caiman niger* and *Paleosuchus trigonatus*, in which there is also variation, but to significantly lesser degree.

129. Prefrontals separated by frontals and nasals (0) or prefrontals meet medially (1)

Fernández-Blanco et al. (2018) detected significant ontogenetic variation regarding this character in *Caiman yacare* and individual variation in *C. latirostris*. These perspectives are corroborated in this analysis, and individual variation in *C. crocodilus* has also been noted by Brochu (2013) and in this analysis. As such, this character has been excluded from the analysis.

146. Postorbital–squamosal suture orientated ventrally (0) or passes medially (1) ventral to skull table

This character was excluded from the analysis due to its variability in living crocodylians (C.A. Brochu, personal communication). A similar approach was performed by Guest (2014).

151. Frontoparietal suture concavoconvex (0) or linear (1) between supratemporal fenestrae

Significant variation between the two states of this character was found in the extant caimanines *Caiman crocodilus, C. yacare* (originally scored as state 0), *C. latirostris* (originally scored as state 1) and variation in a lesser degree was found both species of *Paleosuchus* and in *Alligator mississippiensis* (all originally scored as state 1). No variation was found in *Caiman niger* (state 1) and *Alligator sinensis* (state 0), but regarding the latter our sample of adult specimens was small (five individual), and analysis of larger samples are required for more well-supported conclusions.

Nevertheless, the variation found is significant and thus the character was excluded from the analysis.

From the changes proposed to the characters of Brochu (2011), the change proposed by Aguilera et al. (2006) to the character 128 was incoporated. From the nine changes proposed by Salas-Gismondi et al. (2015), four (04) were incorporated: those proposed for characters 47, 80, 131 and 157. The other five changes (proposed for characters 49, 71, 128, 129 and 138) were either not incorporated or inspired further changes made by the analysis of this study; these perspectives are thoroughly presented in the next section, in which the changes in the characters used in the analysis that are proposed by this study itself are more deeply discussed.

The character proposed by Bona (2007), with the changes proposed by Pinheiro et al. (2013) (see Appendix 2), was considered for inclusion in the analysis. However, the proposed derived state of this character was considered as an additional state of the previously proposed character 50 of Brochu (2011), which was already included in previous versions of the dataset (e.g. Brochu, 1999). As such, the text of character 50 of Brochu (2011) was changed accordingly in this study (see below).

From the six (06) new characters proposed by Barrios (2011) analyzed (see Appendix 2), four were incorporated (104, 106, 108 and 109), whilst two (02) were not (105 and 107). Some of the incorporated characters were eventually changed.

Character 105 was not introduced because an intraspecific variation was found regarding some extant crocodylians. For example, whilst *Alligator mississippiensis* and *Gavialis gangeticus* are scored as having a straight suture between the palatine and the pterygoid (state 0), a specimen of *G. gangeticus* (AMNH-R-88316) shows a concave-convex suture (state 1), whereas an *A. mississippiensis* specimen (AMNH-R71621) has a strongly curved suture (state 3). Additionally, whilst *Caiman crocodilus* is scored as having a slighlt curved suture (state 2), the suture of one specimen (AMNH-R-43291) is straighter than that seen in a *Crocodylus acutus* specimen (AMNH-R-9659), which is scored as having a straight suture (state 0). Similarly, a specimen of *Paleosuchus trigonatus* (AMNH-R-66391) exhibits a suture that may be considered as deeply curved (state 3), wheres this taxon is scored by Barrios (2011) as having an only slightly curved suture (state 2). As such, given the intraspecific variation and the fact that the differences between the states cannot be well defined and thus may not be discreet, this character was not used in the present analysis.

Character 107 was not incorporated for two reasons: firstly, it is not an informative character as the derived morphology (pterygoid excluded from the posterior margin of the suborbital fenestra) is present only in *Caiman yacare*. Furthermore, this species exhibits intraspecific variation: some specimens analyzed in this study (examples are MACN-30542 and MACN-30558) exhibit the pterygoid reaching the posterior margin of the suborbital fenestrae. Given the lack of information potential and intraspecific variation, this character was also not used in the analysis.

From the three characters of Bona et al. (2012), two (165 and 167) were incorporated. Character 166 was not because the only taxon scored for it was *Mourasuchus amazonensis*, based on the drawing of the holotype (Price, 1964); as the character is not informative and as the morphology could not be analyzed directly in the holotype as its dorsal portion cannot be visualized (Cidade et al., 2019b), the character was not used.

From the eight new characters proposed by Brochu (2013) analyzed (see Appendix 2) four were incorporated (182, 183, 185 and 187). From the other four, three (186, 188 and 189) were not informative: in two (186 and 189), the least scored character was scored only once, whilst in 188 only the state “0” was scored. Regarding character 184, which deals with the amount of paired midline scale rows, the author himself (Brochu, 2013) states that there is “considerable” intraspecific variation and that further work is needed to clarify this issue; in this way, this character was not considered in the present analysis.

From the two new characters proposed by Salas-Gismondi et al. (2015; see Appendix 2), one (Character 198) was incorporated into the analysis, albeit with modifications (see in the next section), while Character 199 was not used as it is considered that the morphological difference approached by it is already covered by the Character 51 of Brochu (2011; see below).

The new character proposed by Cidade et al. (2017; see Appendix 2) was analyzed and incorporated.

3.2.3. List of characters used in the analysis, with changes made on the original characters and new characters created for this analysis

The original publications of the characters are presented after the enunciations (see also Appendix 1 and 2). New characters are presented as such in the same. New states are marked in bold; new states elaborated during the project but already published (in Cidade et al., 2017 and Souza-Filho et al., 2019) are marked in bold italics.

These are the characters that were used in the phylogenetic analysis. A complete list of the characters in telegraphic form is in Appendix 3. The complete matrix of scored characters is in Appendix 4.

1. Ventral tubercle of proatlas more than one half (0) or no more than one half (1) the width of the dorsal crest. From Brochu (2011), character 1.

2. Fused proatlas boomerang-shaped (0), strapshaped (1), or massive and block-shaped (2). From Brochu (2011), character 2.

3. Proatlas with prominent anterior process (0) or lacks anterior process (1). From Brochu (2011), character 3.

4. Proatlas has tall dorsal keel (0) or lacks tall dorsal keel; dorsal side smooth (1). From Brochu (2011), character 4.

5. Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0), or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1). From Brochu (2011), character 5.

6. Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1). From Brochu (2011), character 6.

7. Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end. From Brochu (2011), character 7.

8. Atlantal ribs lack (0) or possess (1) large articular facets at anterior ends for each other. From Brochu (2011), character 8.

9. Axial rib tuberculum wide, with broad dorsal tip (0) or narrow, with acute dorsal tip (1). From Brochu (2011), character 9.

10. Axial rib tuberculum contacts diapophysis late in ontogeny, if at all (0) or early in ontogeny (1). From Brochu (2011), character 10.

11. Anterior half of axis neural spine orientated horizontally (0) or slopes anteriorly (1). From Brochu (2011), character 11.

12. Axis neural spine crested (0) or not crested (1). From Brochu (2011), character 12.

13. Posterior half of axis neural spine wide (0) or narrow (1). From Brochu (2011), character 13.

14. Axis neural arch lacks (0) or possesses (1) a lateral process (diapophysis). From Brochu (2011), character 14.

15. Axial hypapophysis located toward the centre of centrum (0) or toward the anterior end of centrum (1). From Brochu (2011), character 15.

16. Axial hypapophysis without (0) or with (1) deep fork. From Brochu (2011), character 16.

17. Hypapophyseal keels present on 11th vertebra behind atlas (0), 12th vertebra behind atlas (1), or tenth vertebra behind atlas (2). From Brochu (2011), character 17.

18. Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1). From Brochu (2011), character 18.

19. Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0) or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1). From Brochu (2011), character 19.

20. Anterior sacral rib capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0), or anterior margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1). From Brochu (2011), character 22.

21. Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1). From Brochu (2011), character 23.

22. Deltoid crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1). From Brochu (2011), character 24.

23. Scapulocoracoid synchondrosis closes very late, **if at all,** in ontogeny (0) or relatively early in ontogeny (1). Modified from Brochu (2011), character 25.

Remarks. This change clarifies that the closure of the scapulocoracoid synchondrosis not necessarily happens in taxa with the state 0 (see Brochu, 1995). This, however, does not change the informative potential of the character.

24. Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1). From Brochu (2011), character 26.

25. Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1). From Brochu (2011), character 27.

26. M. teres major and M. dorsalis scapulae insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon; single insertion scar (1). From Brochu (2011), character 28.

27. Olecranon process of ulna narrow and subangular (0) or wide and rounded (1). From Brochu (2011), character 29.

28. Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2). From Brochu (2011), character 31.

29. Anterior end of interclavicle flat (0) or rod-like (1). From Brochu (2011), character 32.

30. Iliac anterior process prominent (0) or virtually absent (1). From Brochu (2011), character 33.

31. Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation (wasp-waisted;

2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4). From Brochu (2011), character 34.

32. Supraacetabular crest narrow (0) or broad (1). From Brochu (2011), character 35.

33. Limb bones relatively robust, and hindlimb much longer than forelimb at maturity (0) or limb bones very long and slender (1). From Brochu (2011), character 36.

34. Dorsal osteoderms not keeled (0) or keeled (1). From Brochu (2011), character 38.

35. Dorsal midline osteoderms rectangular (0) or nearly square (1). From Brochu (2011), character 39.

36. Four (0), six (1), eight (2), or ten (3) contiguous dorsal osteoderms per row at maturity. From Brochu (2011), character 40.

37. Nuchal shield grades continuously into dorsal shield (0) or differentiated from dorsal shield; four nuchal osteoderms (1) or differentiated from dorsal shield; six nuchal osteoderms with four central and two lateral (2) or differentiated from dorsal shield; eight nuchal osteoderms in two parallel rows (3). From Brochu (2011), character 41.

38. **Ventral armour: absent (0) or comprised by single ventral osteoderms (1) or comprised by paired ventral ossifications that suture together (2)**. Modified from Brochu (2011), character 42.

Remarks. The text of the character was changed to make clearer that it refers to either the absence of the ventral armour or to the fact that the ventral armour is formed by osteoderms or ossifications that suture to one another. It does not change the character *per si*.

39. Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth, without process (1). From Brochu (2011), character 43.

40. Ventral scales have (0) or lack (1) follicle gland pores. From Brochu (2011), character 44.

41. Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two parallel enlarged rows (2). From Brochu (2011), character 45.

42. Median pelvic keel scales form two parallel rows along most of tail length (0) or form single row along tail (1) or merge with lateral keel scales (2). From Brochu (2011), character 46.

43. Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0), or fourth alveolus larger than third, and alveoli are separated (1), or 3 and 4 are nearly the same size and separated (2). From Salas-Gimsondi *et al*. (2015), character 47, modified from Brochu (2011), character 47.

Remarks. State 2 was proposed by Salas-Gismondi et al. (2015) and is only present in *Gnatusuchus pebasensis*. However, in two specimens of this species analyzed in this study (MUSM 1979 and MUSM 2040), the fourth alveolus is actually slightly larger than the third, suggesting that there might be individual variation regarding this feature in the species. Nevertheless, the scoring of “2” for *G. pebasensis* was kept as it was considered that the morphology of the species is still closer to what is described by that state than to that described by state 1.

44. Two or three anterior dentary teeth strongly procumbent (0), **only first anterior tooth strongly procumbent (1)** or anterior teeth project anterodorsally (2). Modified from Brochu (2011), character 48.

Remarks. Brochu (1997a) proposed this character originally separating only between “two or three anteriormost” procumbent alveoli seen in noneusuchian taxa and the the anterodorsal projection of the same alveoli seen in most eusuchian taxa. There are, however, three alligatoroid taxa that exhibit only the first alvelolous as procumbent: *Leiodyosuchus canadensis, Eocaiman cavernensis* and *“Eocaiman” itaboraiensis* (Fig. 67), which is treated as a new state as the procumbent morphology is restricted to the first alveolous. However, as pointed out by several previous authors, vitamin D deficiencies may result in anomalies that can make all dentary teeth procumbent

(Müller, 1924; Kälin, 1936b; Brochu, 1997a), which is typical in captive animals (Brochu, 1997a). Wild individuals rarely exhibit it, although it can happen as a result of mandibular injuries (Müller, 1924; Brochu, 1997a). Nevertheless, these facts make this character more suitable to individual variation, and as such a larger sample of specimens for of the mentioned taxa may reveal a different morphology to be the standard for those species. For the time being, however, the known specimens show the presence of procumbent anterior teeth for the taxa scored with states 0 or 1.

Figure 67: First anterior alveolus and/or tooth strongly procumbent of *Leidyosuchus canadensis* (CMN-8523, A), "*Eocaiman*" *itaboraiensis* (MCT-1791-R, B) and *Eocaiman cavernensis* (AMNH-3158, C). Scale bars = 1 cm.

45. Dentary symphysis extends to fourth or fifth alveolus (0) or sixth to eighth alveolus (1) or behind eighth alveolus (2) ***or symphysis very short, extending to the level of the first alveolous (3),*** **or symphysis very long, extending behind sixth alveolous with a lateromedial expansion of the dentary area lateral to the symphysis (4)**. Modified from Cidade et al. (2017), character 49, modified from Brochu, character 49.

Remarks. State 3 refers to the extremely short mandibular symphysis of *Mourasuchus* (Langston, 1965; Cidade et al., 2018; Fig. 68-B), which is limited to the level of the first mandibular alveolous. This change was already used in Cidade et al. (2017). State 4 refers to the unusually long, lateromedially extensive "shovel-like" mandibular symphysis of *Gnatusuchus pebasensis* (Salas-Gismondi et al., 2015; Fig. 68-A).

Salas-Gismondi et al. (2015) proposed three other states to this character (see Appendix 2) but these were not used in the present analysis as they are informative only for gavialoids. Future analysis that focus on Crocodylia as a whole, however, shall consider them in addition to the states proposed here.

Figure 68: Mandibular symphyses of *Gnatusuchus pebasensis* (MUSM-662, taken from Salas-Gismondi et al., 2015, A) and *Mourasuchus amazonensis* (DGM-526-R, B). Scale bars = 5 cm.

46. Dentary slightly curved between 4th and 10th alveoli (0), or deeply curved between 4th and 10th alveoli (1), **or linear to the 10th alveolous and elevated after the 11th alveolous (2) or linear throughout the tooth row** (3). Modified from Brochu (2011), Character 50, fused with Pinheiro et al. (2013), Character 124, which is adapted from Bona (2007).

Remarks. Bona (2007) proposed a new character (later rephrased by Pinheiro et al., 2013) which would distinguish the two species of *Eocaiman* known by then – *E. cavernensis* (Fig. 69-A) and *E. palaeocenicus* – by having the dentary at a higher level between the 10th and 11th alveolous than at the 4th alveolous, whereas most other alligatoroids would have these two portions at the same level of height. However, it is considered here that this morphology is within the scope of Character 50 of Brochu (2011), which concerns the level of dorsoventral curvature observed in crocodylians. As such, while the state 1 of the character of Bona (2007) – which is the state 0 in the rephrased version of Pinheiro et al. (2013) – can be allocated in the states 0 and 1 of the present character (from which they would be distinguished by a slight or a deep curvature, a difference not approached in the characters of Bona, 2007 and Pinheiro et al., 2013), the state 1 of Bona (2007), which is the morphology seen in *E. cavernensis* and *E. palaeocenicus*, represents a new state of this character (state 2). The state 3 of the present character is the same state 2 of Brochu (2011), rephrased only to emphasize that a taxon must have the dentary linear (i.e., without curvatures) throughout the entire dentary bone to fit in this state (Fig. 69-B), without curvatures between the 4th and 11th alveolous (states 0 and 1) or after the 11th alveolous (state 2).

Pinheiro et al. (2013) proposed that state 2 was also present in "*Eocaiman*" *itaboraiensis*, but this feature is not exhibited by any of the three specimens of "*E*". *itaboraiensis* that are mandibular remains. This is one of the features that prompted a taxonomic revision of the species, which is presented posteriorly.

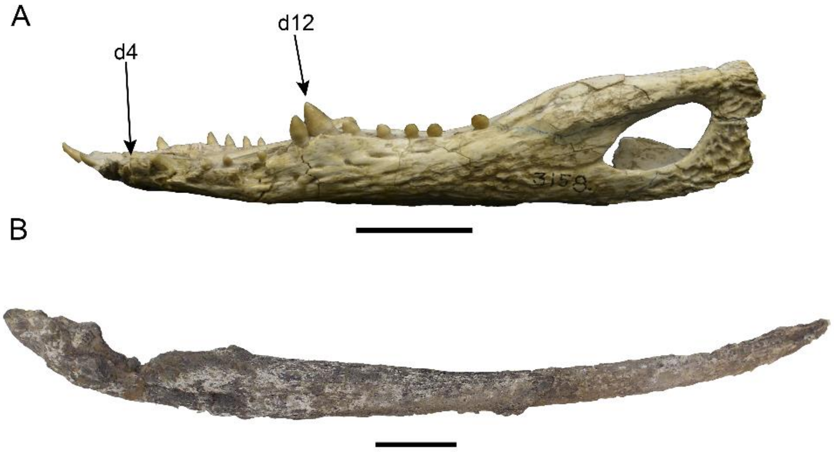

Figure 69: Dentary linear to the 10th alveolous and elevated after the 11th alveolous in *Eocaiman cavernensis* (AMNH-3158, A) and dentary linear throughout the tooth row in *Mourasuchus arendsi* (CIAAP-1297, B). **d4** = fourth dentary tooth; **d12** = twelfth dentaru tooth Scale bars = 5 cm.

47. Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, (2) 11 or 12, or (3) no differentiation, or (4) behind 14, or **(5) 12 and a series behind it, or (6) 17 and a series behind it, or (7) 5, 6 and 7, after which alveoli are smaller and approximately of the same size (8) 9 and a series behind it**. Modified from Brochu (2011), Character 51.

Remarks. Four new states were created for this character. State 5 regards the morphology seen in *Kuttanacaiman iquitosensis* and *Caiman wannlangstoni* and state 6 that of *Procaimanoidea utahensis*. State 7 regards the morphology seen in *Mourasuchus amazonensis* and *M. atopus*, and which is probably shared with the other two species of the genus (*M. arendsi* and *M. pattersoni*), but the morphology of the dentary teeth in both this species cannot be currently visualized (see Cidade et al., 2017, 2018). State 8 regards the morphology present in *Caiman brevirostris*.

Character 199 of Salas-Gismondi et al. (2015) (see Appendix 2) was considered redundant to this character: the taxa belonging to the state of the referred character have several different morphologies regarding the size of the remaining dentary teeth, which are covered by character 51. Regarding the taxa scored with the state 1 by Salas-Gismondi et al. (2015), *Mourasuchus* and *Purussaurus*, the interpretation of this study differs. The morphology of the former is considered a new state of this character (7), whereas that of the latter could only be observed in *P. brasiliensis* and is considered as belonging to state 0 because, although the first four alveoli are indeed the largest in the species, the difference between those and the 13th and 14th alveoli was not deemed to be distinct from that seen in the other taxa with state 0.

There is a polymorphism regarding this character in both species of *Paleosuchus*. In some specimens of these, the 13th alveolous is as large or larger than the 11th and the 12th (Cidade et al. 2019d; see the taxonomic review of *Necrosuchus ionensis* below). As such, both species were scored as polymorphic between states 0 and 2 in this character.

48. Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1). From Brochu (2011), character 52.

Remarks. Wang et al. (2016) state that "*there is no evident* foramen intermandibularis oralis *near the symphysis or on the medial surface of splenial body*" of *Protoalligator huningensis*. The pictures offered by these authors and in the original description by Young (1982) offer little opportunity for double-checking, so the scoring was maintained. This is important as it may be one of the characters putting *Protoalligator* in the Caimaninae clade (see below).

49. Mandibular ramus of cranial nerve V exits splenial anteriorly only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1) or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2). From Brochu (2011), character 53.

50. Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove (1) or splenial excluded from mandibular symphysis; anterior tip of splenial passes dorsal to Meckelian groove (2) or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide V within symphysis (3), or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within symphysis and forms narrow V (4), **or splenial excluded from mandibular symphysis; anterior tip of splenial does not approach Meckelian groove (5)**. Modified from Brochu (2011), character 54.

Remarks. The new state regards the morphology seen in *M. amazonensis* and *M. atopus* (Fig. 70), in which the anterior tip of the splenial not only does not participate in the mandibular symphysis as it is not close to the Meckelian groove, as it happens in states 1 and 2, thus constituting a new morphology. Whether it is present in the other species of *Mourasuchus* is unknown, since the feature cannot be currently observed in them (Cidade et al., 2017, 2018).

Figure 70: Left mandible of *Mourasuchus atopus* (UCMP-38012) in medial view showing the anterior end of the splenial (**sp at**). Scale bar = 5 cm.

51. Coronoid bounds posterior half of foramen intermandibularis medius (0) or completely surrounds foramen intermandibularis medius at maturity (1) or obliterates foramen intermandibularis medius at maturity (2). From Brochu (2011), character 55.

52. Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1). From Brochu (2011), character 56.

53. Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1). From Brochu (2011), character 57.

54. Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1). From Brochu (2011), character 58.

55. Process of splenial separates angular and coronoid (0) or no splenial process between angular and coronoid (1). From Brochu (2011), character 59.

56. Angular–surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) **or passes along ventral margin of external mandibular fenestra late in ontogeny (1) or passes along dorsal margin of external mandibular fenestra late in ontogeny (2)**. Modified from Brochu (2011), character 60.

Remarks. The new state (2) regards the morphology seen in *Alligator mcgrewi* (Fig. 71), in which the angular-surangular suture terminates anteriorly in the dorsal margin of the external mandibular fenestra. The state 1 is the same as proposed by Brochu (2011) with the omission of the word "broadly" to describe the presence of the suture in the ventral (and dorsal, in the case of state 2) margin of the external mandibular fenestra, as in the opinion of the author the location of the suture is not necessarily "broad" into the ventral or dorsal margins of the fenestra in either of states 1 or 2.

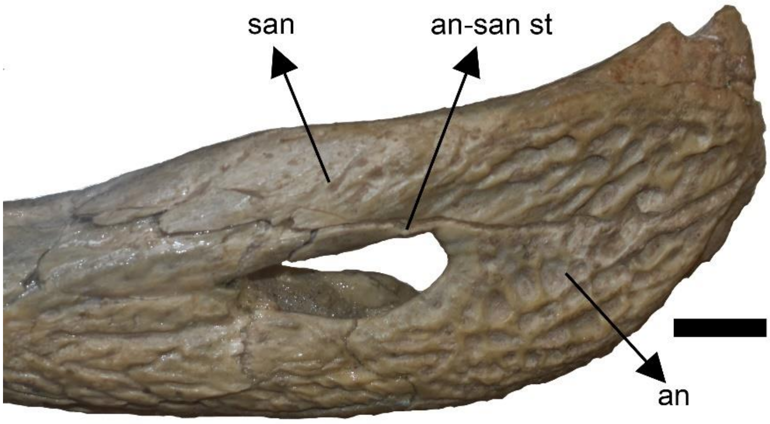

Figure 71: Posterior portion of the left mandible of *Alligator mcgrewi* (FLMNH-26242) in lateral view. **an** = angular; **an-san st** = angular-surangular suture; **san** = surangular. Scale bar = 1 cm.

57. Anterior processes of surangular unequal (0) or subequal to equal (1). From Brochu (2011), character 61.

58. Surangular with spur bordering the dentary tooth row lingually for at least one alveolus length (0) or lacking such spur (1). From Brochu (2011), character 62.

Remarks. *Caiman crocodilus* and *C. yacare* had their stated changed from “0” to “1” because in the specimens analyzed there are no processes like those present in *Gavialis gangeticus*, for example. In some specimens of both species there is a small anterior process that reaches or approaches the posterior limit of the toothrow with in maximum reaching, if anything, a very small portion of the medial margin of the toothrow, but far to the degree seen in the taxa with state 0.

59. External mandibular fenestra absent (0) or present (1) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (2) **or present, dorsoventrally compressed and anteroposteriorly expanded (3)**. Modified from Brochu (2011), character 63.

Remarks. The new state regards the morphology seen in *Mourasuchus arendsi* and *M. pattersoni*, in which the external mandibular fenestra is dorsoventrally compressed and anteroposteriorly expanded (Fig. 72). In *Necrosuchus ionensis* and in most specimens of both species of *Paleosuchus*, the external mandibular fenestra is relatively small and bent. This morphology is not treated as a separate state given the variability in the absence of detailed studies about its ontogeny and development in *Paleosuchus* but may be a sign of the affinity between this taxon and *Necrosuchus*, which has been proposed by previous phylogenetic studies (Cidade et al., 2019d).

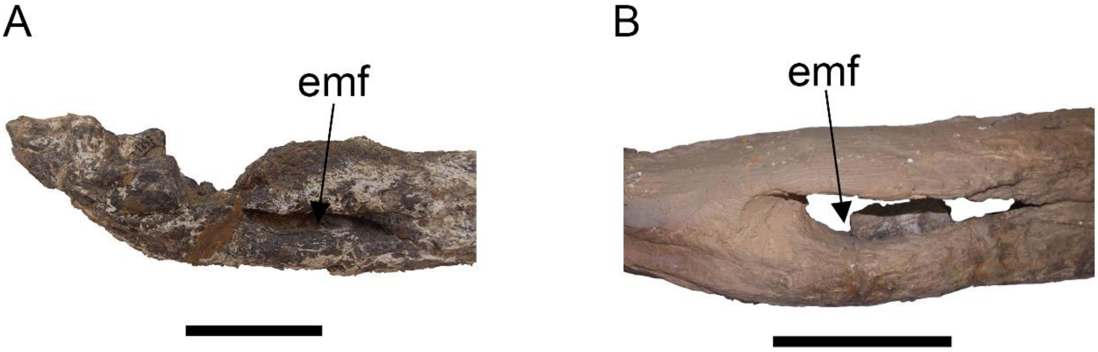

Figure 72: Posterior portion of the right mandibles of *Mourasuchus arendsi* (CIAAP-1297) and *M. pattersoni* (MCNC-PAL-110-72V) in lateral view, showing the morphology of the external mandibular fenestra (**emf**). Scale bars = 10 cm (A) and 5 cm (B).

60. Surangular–dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) **or at or close to the posterodorsal corner (1)**. Modified from Brochu (2011), character 64.

Remarks. The original text of state 1 referred to the suture intersecting the fenestra only “at the posterodorsal corner”, but observation of the taxa led to the perspective that a more accurate description of the derived state of this character would be the suture “intersecting at or approaching the posterodorsal corner” of the external mandibular fenestra. This change does not alter the content of the character *per si*: the scoring of the taxa remained largely the same of previous published versions of the character (Brochu, 2011; Cidade et al., 2017), only with occasional changes.

61. Surangular–angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1). From Brochu (2011), character 66.

62. Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1). From Brochu (2011), character 67.

63. Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1). From Brochu (2011), character 69.

Remarks. Whiting et al. (2016) found *Alligator prenasalis* to be polymorphic for this character, a conclusion also reached by the present study. *A. olseni* was also scored as polymorphic for this character following Whiting et al. (2016).

64. Foramen aereum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1). From Brochu (2011), character 70.

65. Retroarticular process projects posteriorly (0) or projects posterodorsally (1). From Brochu (2011), character 71.

66. Surangular extends to posterior end of retroarticular process (0) or pinched off anterior to tip of retroarticular process (1). From Brochu (2011), character 72.

67. Surangular–articular suture orientated anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa. From Brochu (2011), character 73.

68. Sulcus between articular and surangular (0) or articular flush against surangular (1). From Brochu (2011), character 74.

69. Dorsal projection of hyoid cornu flat (0) or rodlike (1). From Brochu (2011), character 75.

70. Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1). From Brochu (2011), character 76.

71. Lingual osmoregulatory pores small (0) or large (1). From Brochu (2011), character 77.

72. Tongue with (0) or without (1) keratinized surface. From Brochu (2011), character 78.

73. Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or **posteriormost** teeth laterally compressed (1), **or all teeth posterior to the fifth alveolous compressed (2)** or all teeth compressed (**3**). Modified from Brochu (2011), character 79.

Remarks. The new state (2) accommodates the morphology seen in *M. amazonensis* and *M. atopus*. As in previous characters, whether *M. arendsi* and *M. pattersoni* share the state cannot be currently observed (Cidade et al., 2017, 2018), but it is probable given the shape of the rostrum shared between all species of *Mourasuchus*. Additionally, in the text of state 1 “posterior” was changed to “posteriormost” to more clearly depict the observed morphology that corresponds to the state.

74. Maxillary and dentary teeth with smooth carinae (0), or serrated (1), **or with pseudo-serrations (2)** or with neither carinae nor serrations (3). Modified from Salas-Gismondi et al. (2015), character 80, modified from Brochu (2011), character 80.

Remarks. Souza et al. (2016) classified the serrations present in *Purussaurus* as pseudo-serrations (false ziphodonty) following Prasad & de Broin (2002), which would be distinct from “true” serrations found in proper ziphodont taxa. Implanted teeth with this morphology were observed in *P. mirandai* and in *Purussaurus* sp. nov. (UCMP-39704). *P. brasiliensis* was not scored for this character as no implanted teeth in which the feature could be observed was found; Aureliano et al. (2015) assign a clearly pseudo-serrated tooth to *P. brasiliensis*, but this is isolated.

75. Naris projects anterodorsally (0) or dorsally (1). From Brochu (2011), character 81.

76. **External naris bisected by nasals (0) or not bisected (1)**. Modified from Brochu (2011), character 82.

Remarks. This character was changed from an evaluation of the presence or absence of a septum bisecting the external naris and of whether the nasals contact anteriorly the external naris and the premaxillae (see Appendix 1, Character 82) to just the evaluation of the presence or absence of the septum. This is due to the fact that whether the nasals reached the external naris or are separated from it by the premaxillae was found to be subject to individual variation in *Caiman yacare* by Fernández-Blanco et al. (2018), which was also encountered in the present analysis. Furthermore, the same variation was found in a significant level in *C. crocodilus*, *C. niger* and to a lesser degree *Paleosuchus palpebrosus* – a small variation is also detected in *C. latirostris* and *P. trigonatus*, but these were not considered significant. As such, evaluation about the presence or absence of contact between the nasals and the external naris were excluded from the present analysis.

77. Naris circular or keyhole-shaped (0) or wider than long (1) or ***longer than wide*** (2) or anteroposteriorly long and prominently teardrop-shaped (3). From Cidade et al. (2017), character 83, modified from Brochu (2011), character 83.

Remarks. State 2 described the morphology present in the caimanines *Purussaurus* and *Kuttanacaiman*, in which a large external naris is longer than wide.

78. External naris of reproductively mature males (0) remains similar to that of females **or (1) develops bony excrescence related to the ghara**. Modified from Brochu (2011), character 84.

Remarks. The change in this character does not modify its content, but only clarifies that state 1 refers to the presence of a bony excrescence that appears as a result of the presence of the ghara and not to the presence of the ghara itself, which is a structure formed by epitelian and conjunctive tissues only (Martin & Bellairs, 1977). This change clarifies that fossil taxa may be scored for this character, which is the case of

Gryposuchus croizati (see Riff & Aguilera, 2008), which was not used in the present analysis.

79. External naris (0) opens flush with dorsal surface of premaxillae or (1) circumscribed by thin crest. From Brochu (2011), character 85.

80. Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1) ***or surrounded by a dorsoventrally developed rim (2).*** From Cidade et al. (2017), character 86, modified from Brochu (2011), character 86.

Remarks. The new state (2) refers to the presence in *Mourasuchus atopus* and *M. arendsi* of a developed rim surrounding the external naris. The structure is not related to the notch described in state 1 *per si*, but the presence of the rim precludes the presence of the notch in a single taxon as they are in the same position. The eventual finding of a taxon that exhibits both structures shall make them to be considered as different characters, but for the time being they may be accommodated into a single character.

81. Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny. From Brochu (2011), character 87.

82. Incisive foramen small, less than half the greatest width of premaxillae (0) **or large, with more than or approximately half the greatest width of premaxillae (1)** or large, and intersects premaxillary–maxillary suture (2). Modified from Brochu (2011), character 88.

Remarks. A more accurate description of state 1 is the incisive foramen being more than or approximately of the greatest width of the premaxillae, and not only more than the greatest width as metioned originally, since in many taxa the foramen is not actually larger than the greatest width of the premaxillae and yet this difference does not merit a distinct state in itself. The scorings of the taxa have remained largely the same, save for occasional changes.

83. Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0) or abuts premaxillary tooth row (1) **or has anterior margin tapering anteriorly and projecting itself between first premaxillary teeth (2)**. Modified from Brochu (2011), character 89.

Remarks. The change in state 2 is only to give a more accurate description of the morphology to which it corresponds. In the original text, state 2 speaks of an incisive foramen that “projects between first premaxillary teeth” (see Appendix 1, Character 89) but upon observing taxa with state 2 a more accurate description is that, in those, the incisive foramen has a anterior margin that tapers anteriorly and thus projects itself between the first premaxillary teeth, and thus the text of state 2 was modified accordingly.

84. Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1). From Brochu (2011), character 90.

85. Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1). From Brochu (2011), character 91.

86. All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between seventh and eighth maxillary teeth; all other dentary teeth occlude lingually (1) or dentary teeth occlude in line with maxillary tooth row (2) **or occlusion pits between fifth to the seventh or the eight teeth; all other dentary teeth occlude lingually (3)**. Modified from Brochu (2011), character 92.

Remarks. The new state (3) regards the morphology seen in several species of *Diplocynodon*: *D. deponiae, D. ratelli, D. hantoniensis* and *D. tormis* (Fig. 73). In some specimens (and occasionally in one of the tooth rows of some specimens), the occlusion pit between the fifth and sixth bone is not present (Fig. 73-B); the other pits are constantly present. In *D. tormis*, an occlusion pit between the eight and ninth dentary teeth was also observed (Fig. 73-A). Nevertheless, it was considered that *D. tormis* should be scored in state 3, although future assessments may consider this morphology as a separate state.

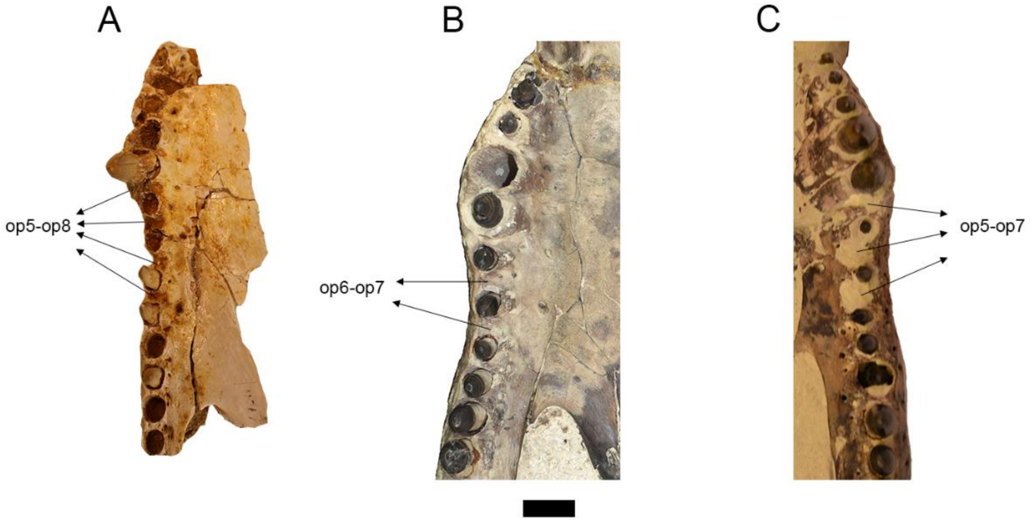

Figure 73: Patterns of maxillary occlusion pits in *Diplocynodon* between the fifth and the ninth maxillary alveoli: *D. tormis* (STUS-7211, A) and *D. hantoniensis* (BMNH-25166, B and CAMSM-TN-907, C). Scale bars = 2 cm.

87. Largest maxillary alveolus **among the first ten alveoli** is no. 3 (0), no. 5 (1), no. 4 (2), nos. 4 and 5 are same size (3), no. 6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6), **nos. 3 and 4 are same size (7)**. Modified from Brochu (2011), character 93.

Remarks. The text was changed to clarify that the character refers only to the first ten alveoli of the maxillae. This was stated in the description of the character by Brochu (1997a) but was not mentioned in the text of the character itself, hence the change. The new state (7) refers to the morphology seen in *Purussaurus* sp. nov. (UCMP-39704; Fig. 74-A). Caimaninae taxa *Caiman gasparinae* (Fig. 74-B) and *C. australis* also seem to have state 7, but in the former the maxillary tooth row is not complete and in the later teeth seem to have been artificially implanted onto the maxilla, including the third and fourth alveolous (see Rusconi, 1933), which leaves doubt about the actual size of the alveoli.

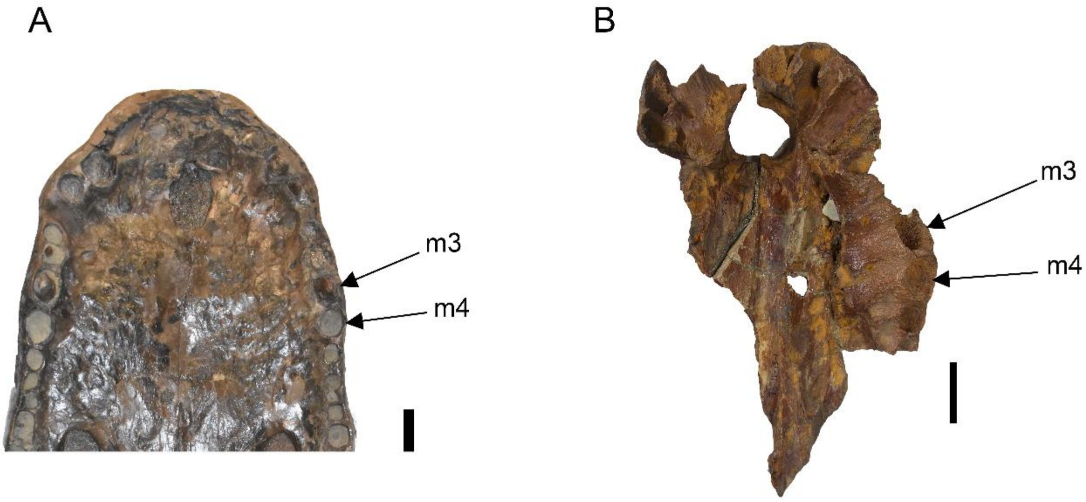

Figure 74: Rostra of *Purussaurus* sp. nov. (UCMP-39704, A) and *Caiman gasparinae* (MLP-73-IV-15-1, B) in ventral view, showing the similar sizes of third (m3) and fourth (m4) maxillary alveoli. Scale bar = 5 cm.

88. Maxillary tooth row curved medially or linear (0) or curves laterally broadly (1) posterior to first six maxillary alveoli. From Brochu (2011), character 94.

89. Canthi rostralii absent or very modest at maturity (0) **or very prominent at maturity, with or without a depression lateral to it (1) or very prominent at maturity, with a developed fossa lateral to it (2)**. Modified from Brochu (2011), character 96.

Remarks. A new state (2) was created for this character regarding a morphology seen in *Purussaurus brasiliensis* (Fig. 75-B) and *P. mirandai* (Fig. 75-A), in which the *canthi rostralii* are developed to a degree that a fossa is formed lateral to them. Such fossae are proposed by Aureliano et al. (2015) to provide a space for dissipation of the biting force in *Purussaurus*. Other taxa with developed *canthi rostralii*, like *Caiman niger* (Fig. 75-C) and *Purussaurus* sp. nov. (UCMP-39704; Fig. 75-D), exhibit a small depression lateral to these structures that are considered here as homologous to the developed fossae of *P. brasiliensis* and *P. mirandai*. However, the small depressions are not considered here as a separate state as they are seen as correlated to the presence of the developed *canthi rostralii* themselves.

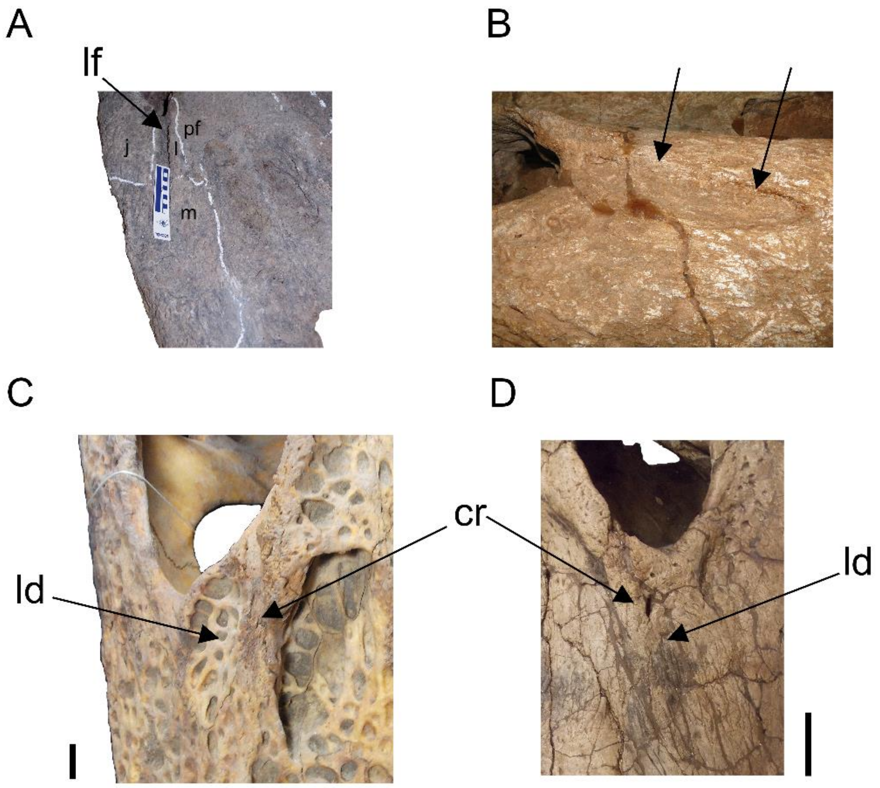

Figure 75: *Canthi rostralii* with developed lateral fossa (**lf**) in *Purussaurus mirandai* (CIAAP-1369, A) and *P. brasiliensis* (UFAC-1403, B), and with only a slight lateral depression (**ld**) in *Caiman niger* (C) and *Purussaurus* sp. nov. (UCMP-39704, D). Scale bars = 10 cm (A), 1 cm (C) and 5 cm (D). Skull length from posterior end of quadrate to the tip of the snout in UFAC-1403 (B): 140 cm.

90. Preorbital ridges absent or very modest (0) or very prominent (1) at maturity. From Brochu (2011), character 97.

91. Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary–maxillary suture (1). From Brochu (2011), character 99.

92. Surface of maxilla within narial canal imperforate (0) or with a linear array of pits (1). From Brochu (2011), character 101.

93. Medial jugal foramen small (0) or very large (1). From Brochu (2011), character 102.

94. Maxillary foramen for palatine ramus of cranial nerve V small or not present (0) or very large (1). From Brochu (2011), character 103.

95. Ectopterygoid abuts maxillary tooth row (0) or maxilla broadly separates ectopterygoid from maxillary tooth row (1). From Brochu (2011), character 104.

96. Maxilla terminates in palatal view anterior to lower temporal bar (0) or comprises part of the lower temporal bar (1). From Brochu (2011), character 105.

97. Penultimate maxillary alveolus less than (0) or more than (1) twice the diameter of the last maxillary alveolus. From Brochu (2011), character 106.

98. Dorsal half of prefrontal pillar narrow (0) or expanded anteroposteriorly (1). From Brochu (2011), character 108.

99. Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1). From Brochu (2011), character 109.

100. Prefrontal pillar solid (0) or with large pneumatic recess (1). From Brochu (2011), character 110.

101. Medial process of prefrontal pillar wide (0) or constricted (1) at base. From Brochu (2011), character 111.

102. Anterior ectopterygoid process tapers to a point (0) or forked (1). From Brochu (2011), character 114.

103. Palatine process extends (0) or does not extend (1) significantly beyond anterior end of suborbital fenestra. From Brochu (2011), character 115.

104. Palatine process generally broad anteriorly (0) or in form of thin wedge (1). From Brochu (2011), character 116.

105. Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1). From Brochu (2011), character 117.

Remarks. “*Caiman*” sp. nov. (UCMP-39978) exhibits what appears to be state 1, but it was left unscored because what appears to be the lateral process may be a taphonimical effect of the sediment that filled the fossil dorsal to the pertinent area. *Alligator mississippiensis* was scored as polymorphic for this character following Whiting et al. (2016).

106. Palatine–pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra. From Brochu (2011), character 118.

107. Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing shelf (1). From Brochu (2011), character 120.

108. Anterior border of the choana is comprised of the palatines (0) or choana entirely surrounded by pterygoids (1). From Brochu (2011), character 121.

109. Choana projects posteroventrally (0) or anteroventrally (1) at maturity. From Brochu (2011), character 122.

110. Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form neck surrounding aperture (2) or everted from flat surface to form neck surrounding aperture (3). From Brochu (2011), character 123.

111. Posterior rim of internal choana not deeply notched (0) or deeply notched (1). From Brochu (2011), character 124.

112. Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2). From Brochu (2011), character 125.

113. Ectopterygoid–pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1). From Brochu (2011), character 126.

114. Ectopterygoid extends (0) or does not extend (1) to posterior tip of lateral pterygoid flange at maturity. From Brochu (2011), character 127.

115. Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) **or prefrontal with anterior expansion separating the lacrimal from the nasals (2) or lacrimal broadly**

separated from the nasals (3). Modified from Aguilera *et al*. (2006), from Brochu (2011), character 128, and from Brochu (1999), character 93.

Remarks: states 2 and 3 of this character were modified not regarding their content, but with the aim of providing a more accurate explanations about the morphologies observed in each of them. In the taxa with state 2 there is an anterior expansion of the prefrontal that separates the lacrimal from the nasals, and not necessarily a posterior process of the maxillae between the prefrontal and the lacrimal as stated originally (Appendix 1, Character 128). State 3, present only in *Purussaurus,* was rephrased to speak only of a broad separation between the lacrimal and the nasals; Aguilera et al. (2006) phrased it originally to denote the presence of an anterior process of the prefrontal separating the lacrimal from the nasal. However, it is not possible to affirm whether the separation between the lacrimals and the nasals in *Purussaurus* is due to an anterior expansion of the prefrontal or a posterior expansion of the maxillae, hence the change in the text to limit it on the separation between the bones. Eventual studies on ontogenetic development of the skull in *Purussaurus* may clarify this issue.

116. Lacrimal longer than prefrontal (0), or prefrontal longer than lacrimal (1), or lacrimal and prefrontal both elongate and nearly the same length (2). From Brochu (2011), character 130.

117. **Anterior tip of frontal visible in dorsal view forms simple acute point** (0), or forms broad, complex sutural contact either with the nasals or prefrontals (1). Modified from Salas-Gimsondi *et al*. (2015), character 131, and from Brochu (2011), character 131.

Remarks. The text of state 1 was changed only to clarify that the character refers to the anterior extremity of the frontal that is visible in dorsal view, and not any part of the bone that can be located underneath the prefrontals or the nasals and thus not visible dorsally.

118. Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1). From Brochu (2011), character 132.

119. Postorbital bar massive (0) or slender (1). From Brochu (2011), character 133.

120. Postorbital bar bears process that is prominent, dorsoventrally broad, and divisible into two spines (0) or bears process that is short and generally not prominent (1). From Brochu (2011), character 134.

121. Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1). From Brochu (2011), character 135.

122. Margin of orbit flush with skull surface (0) or dorsal edges of orbits **highly** upturned (1) **or dorsal edges of orbits lowly upturned (2)** or orbital margin telescoped **(3)**. Modified from Brochu (2011), character 137.

Remarks. The new state (2) regards the morphology seen in *Paleosuchus* (Fig. 76-B) and *Centenariosuchus* (Fig. 76-C), in which the dorsal edges of the orbits are upturned only slightly, in contrast to the high upturning seen in most caimanines and is represented by state 1 (Fig. 76-A). *Paleosuchus* and *Centenariosuchus* were considered in previous analyses (e.g. Cidade et al., 2017) as belonging to the state 1 together with other caimanines.

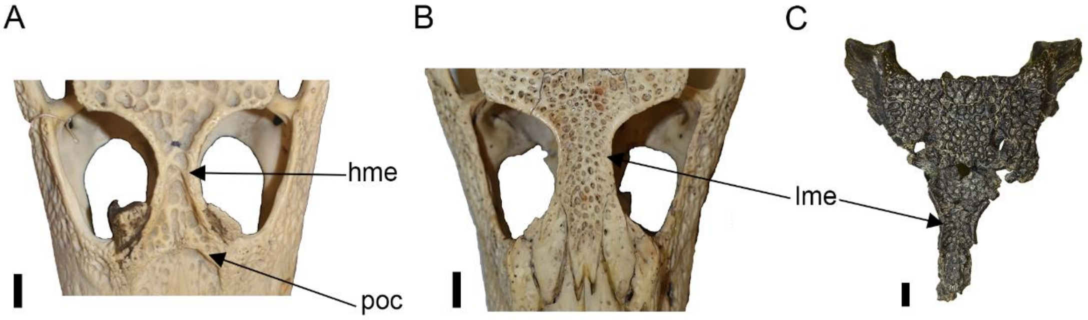

Figure 76: Differences in upturning of the dorsal edges of the orbits: high medial elevation (**hme**) in *Caiman crocodilus* (FMNH-73704, A) and low medial elevation (**lme**) in *Paleosuchus palpebrosus* (FLMNH-75023, B) and *Centenariosuchus gilmorei* (FLMNH-262800, C). Additionally: the presence of the preorbital crest (**poc**) in A and its absence in B. Scale bars = 1 cm.

123. **Lateral margin of orbit (medial margin of the jugal): smooth (0)** or with prominent notch (1). Modified from Brochu (2011), character 138.

Remarks. The original redaction of state 0 (Appendix 1, Character 138) refer to the structure in question as “the ventral margin of the orbit”, with no mention of the jugal. However, observing the taxa directly and the description given by Brochu (1997a), a more clear description is to refer to the area in question as the lateral margin of the orbit or the medial margin of the jugal, since it is in this area that a proeminen notch can be seen in some taxa such as *Gavialis gangeticus*. The content and scope of the character was not changed.

124. Palpebral forms from single ossification (0) **or from two ossifications (1) or from three ossifications (2)**. Modified from Brochu (2011), character 139.

Remarks. Originally, this character distinghuished only between palpebrals formed by single ossifications (state 0) or multiple ossifications (state 1, see Appendix 1, Character 139). However, according to Brochu (1997a), between the taxa with multiple ossifications there is a difference regarding the number: in *Osteolaemus* the palpebrals are formed by two ossifications, whereas in *Paleosuchus* those are formed by three. Given this, the multiple ossifications state was split to accommodate these two different morphologies.

125. Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1). From Brochu (2011), character 140.

126. Quadratojugal spine low, near posterior angle of infratemporal fenestra (0) or high, between posterior and superior angles of infratemporal fenestra (1). From Brochu (2011), character 141.

127. Quadratojugal forms posterior angle of infratemporal fenestra (0) or jugal forms posterior angle of infratemporal fenestra (1) or quadratojugal–jugal suture lies at posterior angle of infratemporal fenestra (2). From Brochu (2011), character 142.

128. Postorbital neither contacts quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3). From Brochu (2011), character 143.

129. Quadratojugal bears long anterior process along lower temporal bar (0) or bears modest process, or none at all, along lower temporal bar (1). From Brochu (2011), character 144.

130. Quadratojugal extends to superior angle of infratemporal fenestra (0) **or does not extend to superior angle of infratemporal fenestra (1)**. Modified from Brochu (2011), character 145.

Remarks. State 1 of this character originally regarded the quadratojugal not reaching the superior angle of the infratemporal fenestra by being prevented by a participation of the quadrate in the fenestra (Appendix 1, Character 145). However, in many taxa that present the state 2 of Character (143) – *Purussaurus* sp. nov. (UCMP-39704), *Acresuchus* and extant caimanines –, the quadratojugal is prevented from reaching the superior angle of the fenestra by the postorbital, and not by the quadrate, and as such the text was changed to refer only to the quadratojugal not reaching the superior angle of the infratemporal fenestra, regardless of which bone prevents it. One could argue that characters 143 and 145 would be at least partially dependend on each other based on the fact that the postorbital that contacts the quadratojugal in the former is the same that prevents it from reaching the superior angle of the infratemporal fenestra in the latter. However, in many other taxa that exhibit the state 2 of Character 143, the quadratojugal can be considered to reach the superior angle of the infratemporal fenestra – *Hassiacosuchus, Allognatosuchus wartheni, Arambourgia, Alligator, Stangerochampsa* and *Brachychampsa montana*.

131. Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1). From Brochu (2011), character 147.

132. Squamosal–quadrate suture extends dorsally along posterior margin of external auditory meatus (0) or extends only to posteroventral corner of external auditory meatus (1). From Brochu (2011), character 148.

133. Posterior margin of otic aperture smooth (0) or bowed (1). From Brochu (2011), character 149.

134. Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2). From Brochu (2011), character 150.

135. Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) ***or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae small, with a circular or nearly circular shape*** (1) or supratemporal fenestra closes **or nearly closes** during ontogeny (2) ***or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae large, significantly longer than wide, with an oval shape (3)***. Modified from Cidade et al. (2017), character 151, and from Brochu (2011), character 152.

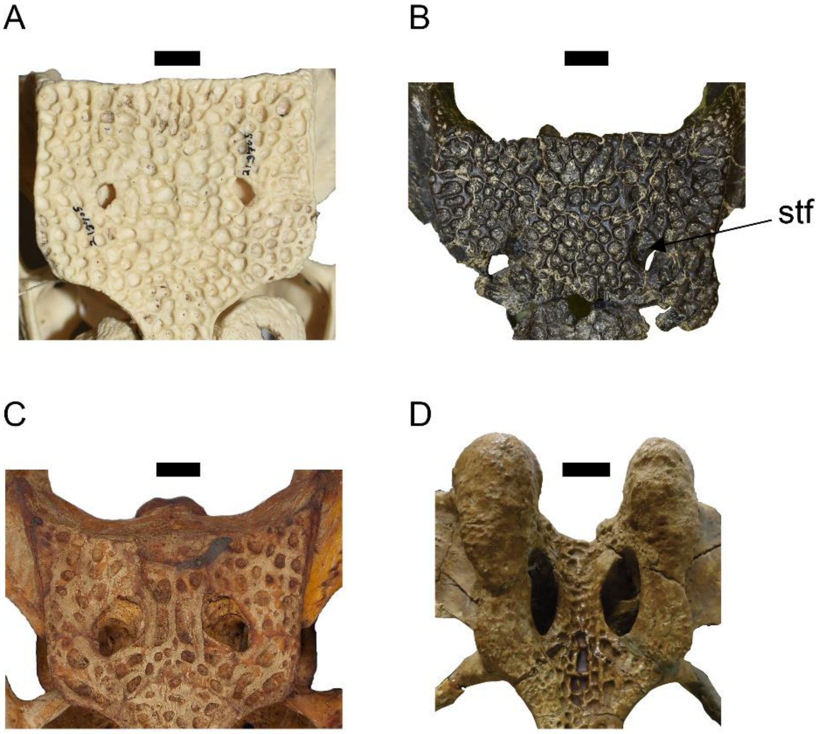

Figure 77: Diversity of the morphology of the supratemporal fenestra (**stf**). *Paleosuchus trigonatus* (USNM-213705, A), *Centenariosuchus gilmorei* (FLMNH-

262800, B), *Caiman latirostris* (MN-2333, C) and *Acresuchus pachytemporalis* (UFAC-2507, D; taken from Souza-Filho et al., 2019). Scale bars = 1 cm (A, B and C), 5 cm (D).

Remarks. The new state (3) regards the morphology seen in *Acresuchus* (Fig. 77-D) and *Purussaurus*, in which the dorsal margins of the supratemporal fenestrae are overhung by the bones surrounding it, as in most caimanines (state 1), but in which the fenestrae are large and with an oval shape, in contrast with most caimanines in which the fenestrae are small, with a circular or nearly circular in shape. The text of state 1 was modified accordingly to distinguish it from the new state (see Fig. 77-C). State 2 was modified to refer to taxa in which the supratemporal fenestra closes or nearly closes during ontogeny. This change is performed by two reasons: while most mature *Paleosuchus* specimens exhibit closed fenestra, the closure does not occur in all specimens (Fig. 77-A); additionally, *Centenariosuchus gilmorei* (Fig. 77-B) exhibits fenestrae that are nealy closed and exhibit a resemblance to those of *Paleosuchus* when not closed, but as there are no other specimens aside from the holotype of *C. gilmorei* to confirm whether the fenestrae closed or not in this taxon, the text of state 2 was modified to confirm to the scoring of *C. gilmorei* as having the same morphology as *Paleosuchus*.

136. Shallow fossa at anteromedial corner of supratemporal fenestra (0) or no such fossa; anteromedial corner of supratemporal fenestra smooth (1). From Brochu (2011), character 153.

137. Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1). From Brochu (2011), character 154.

138. Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0) or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1) or parietal and squamosal meet along posterior wall of supratemporal fenestra (2). From Brochu (2011), character 155.

139. Skull table surface slopes ventrally from sagittal axis (0) or planar (1) at maturity. From Brochu (2011), character 156.

140. Posterolateral margin of squamosal horizontal or nearly so (0) or upturned to form a discrete eminence (1) or producing a high transversely oriented eminence at the posterior margin, late in ontogeny (2) or ***highly upturned throughout the entire lateral margin, with a dorsoventral expansion in the posterior portion of the eminence (3) or highly upturned throughout the entire lateral margin, with a dorsoventral and lateromedial expansion in the posterior portion of the eminence (4)***. From Souza-Filho et al. (2019), character 156, modified from Salas-Gismondi et al. (2015) and Brochu (2011), character 157.

Remarks. Two new states were created for this character. The state 3 regards the morphology seen in the alligatoroids *Acresuchus* (Fig. 77-D) and *Ceratosuchus* (Fig. 78-C), whilst state 4 regards the morphology seen in the crocodyloid *Voay robustus* (see Souza-Filho et al., 2019; Fig. 78-D). Examples of state 1 are *Crocodylus rhombifer* (Fig. 78-A) and *Mourasuchus arendsi* (Fig. 78-B).

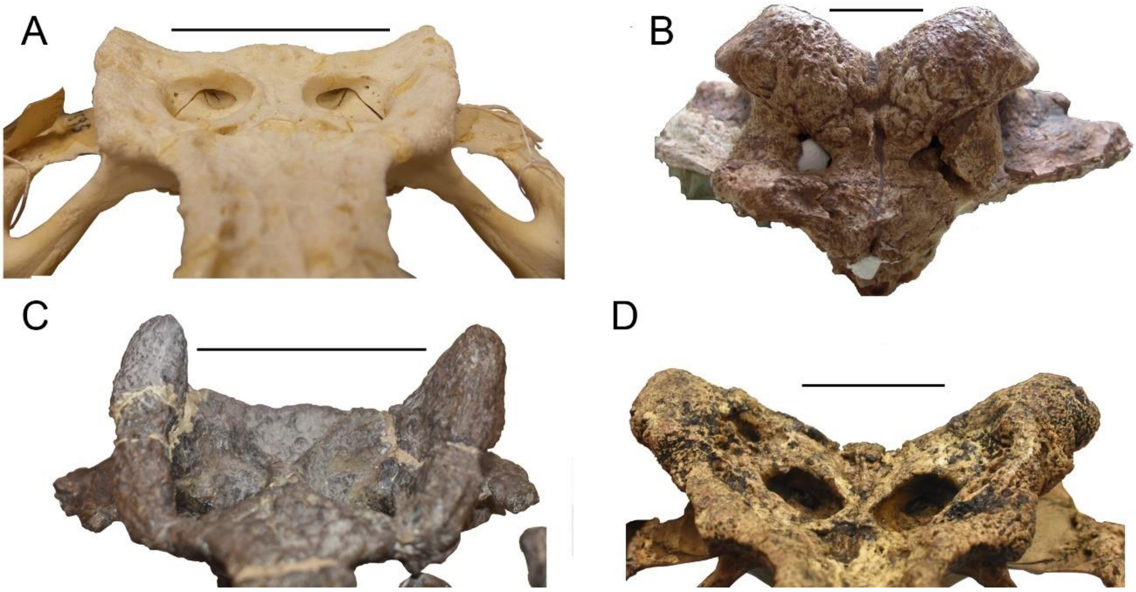

Figure 78: Diversity of the morphology of the squamosal eminences. *Crocodylus rhombifer* (AMNH R-6178, A), *Mourasuchus arendsi* (UFAC-1431, B), *Ceratosuchus burdoshi* (FMNH-P15576, C) *Voay robustus* (AMNH-3101, D). Scale bar = 5 cm.

141. Mature skull table with broad curvature; short posterolateral squamosal rami along paroccipital process (0) or with nearly horizontal sides; significant posterolateral squamosal rami along paroccipital process (1). From Brochu (2011), character 158.

142. Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paraoccipital process. From Brochu (2011), character 159.

143. Supraoccipital exposure on dorsal skull table **medium (0), absent, or with minimal exposure (1),** large (2), or large such that parietal is excluded from posterior edge of table (3). Modified from Brochu (2011), character 160.

Remarks. The content and scope of this character were not changed, but modifications are made in the first two states in order to clarify the morphologies to which they refer. State 0 was changed from “small” to “medium” to specify that the morphology seen in this state is intermediary (in size) between those seen in states 1 (absent or minimal) and states 2 and 3 (large). The state 1 was modified from “absent” to “absent, or with minimal exposure” because in at least some specimens of the taxa that exhibit state 1, the supraoccipital is not entirely absent of exposure in the skull table in dorsal view, having instead a minimal exposure. As such exposure does not approximates that of state 0, it was not considered that it could merit a separate state, so it was decided to maintain this morphology within the range of state 1.

144. Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1). From Brochu (2011), character 162.

145. Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall anterior to trigeminal foramen. From Brochu (2011), character 163.

146. Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1). From Brochu (2011), character 164.

147. Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process **of the pterygoid** (1). Modified from Brochu (2011), character 165.

Remarks. The original text of state 1 referred to an ascending process of the palatine bone (Appendix 1, Character 165). However, upon observing taxa and according to the original description of the character (Brochu, 1997a), the ascending process is actually of the pterygoid bone, to the text of the state was changed accordingly.

148. Capitate process of laterosphenoid orientated laterally (0) or anteroposteriorly (1) toward midline. From Brochu (2011), character 166.

149. Parietal with recess communicating with pneumatic system (0) or solid, without recess (1). From Brochu (2011), character 167.

150. Significant ventral quadrate process on lateral braincase wall (0) or quadrate–pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1). From Brochu (2011), character 168.

151. Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid at maturity. From Brochu (2011), character 169.

152. Posterior pterygoid processes tall and prominent (0) or small and project posteroventrally (1) or small and project posteriorly (2). From Brochu (2011), character 171.

153. Basisphenoid thin (0) or anteroposteriorly wide (1) ventral to basioccipital. From Brochu (2011), character 172.

154. Basisphenoid not broadly exposed ventral to basioccipital at maturity; pterygoid short ventral to median eustachian opening (0) or basisphenoid exposed as broad sheet ventral to basioccipital at maturity; pterygoid tall ventral to median eustachian opening (1). From Brochu (2011), character 173.

155. Exoccipital with very prominent boss on paroccipital process; process lateral to cranioquadrate opening short (0) or exoccipital with small or no boss on paroccipital

process; process lateral to cranioquadrate opening long (1). From Brochu (2011), character 174.

156. Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal. From Brochu (2011), character 175.

157. Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust process ventrally and participate in basioccipital tubera (1) or send slender process **lateral to the** basioccipital tubera (2). Modified from Brochu (2011), character 176.

Remarks. The original text of state 2 (Appendix 1, Character 176) described the slender process “ventrally to (in the sense of ‘towards the ventral portion’) basioccipital tubera”. However, observing the taxa and the original description of the character (Brochu, 1997a, figs. 115 and 116), a more accurate description of the morphology observed in state 2 is that the slender processes are located lateral to the basioccipital tubera, and so the text was changed accordingly.

158. Quadrate foramen aereum on mediodorsal angle (0) or on dorsal surface (1) of quadrate. From Brochu (2011), character 177.

159. Quadrate lacks (0) or bears (1) prominent, mediolaterally thin crest on dorsal surface of ramus. From Brochu (2011), character 179.

160. Attachment scar for posterior mandibular adductor muscle on ventral surface of quadrate ramus forms modest crests (0) or prominent knob (1). From Brochu (2011), character 180.

161. Quadrate with small, ventrally reflected medial hemicondyle (0) or with small medial hemicondyle; dorsal notch for foramen aereum (1) or with prominent dorsal projection between hemicondyles (2) or with expanded medial hemicondyle (3). From Brochu (2011), character 181.

162. Orbits equal or sub equal than infratemporal fenestrae (0) ***or orbits larger than infratemporal fenestrae (1) or orbits smaller than infratemporal fenestrae (2)***. From Souza-Filho et al. (2019), character 181, modified from Cidade et al. (2017), character 181, and Bona *et al*. (2012), character 165. Rephrased.

Remarks. Originally (see Appendix 2), this character splitted the taxa with orbits larger than the infratemporal fenestrae in two distinct states distinguished by the supratemporal fenestrae being small or oblitared, in one of the states, or larger than the orbits, in the other. However, since the size of the supratemporal fenestrae are already the object of another character, it was decided to limit these character to a comparison of the side of the infratemporal fenestrae in relation to the orbits, and so the text was changed accordingly and the two previous states are treated as one.

163. Prefrontal-frontal not thickened or thickened forming a flange (0) or thickened forming a marked knob (1) at the anterior-medial margin of the orbits. From Bona *et al*. (2012) character 167.

164. Anterior extremity of the frontal long and reaching or exceeding the anterior margins of the orbits (0), or short, not reaching the anterior margins of the orbits (1). From Barrios (2011) character 104, translated from Spanish.

165. Posterior margin of the skull table transversely straight to slightly concave (0) or deeply concave (1). From Barrios (2011) character 108, translated from Spanish.

166. Jugal lateromedially slender and dorsoventrally low (0), or jugal lateromedially wide and dorsoventrally low, with a blade-like shape (1) or jugal lateromedially wide and dorsoventrally high, with a cylindrical shape (2). From Cidade et al. (2017), character 188.

167. Iris (0) greenish/yellowish or (1) brown. From Brochu (2013), character 182.

168. Two or more (0) or one (1) row of postoccipital osteoderms. From Brochu (2013), character 183.

169. Ectopterygoid maxillary ramus forms less than (0) or more than (1) two-thirds of lateral margin of suborbital fenestra. From Brochu (2013), character 185.

170. Palatine–maxillary suture intersects suborbital fenestra at its anteromedial margin (0) or nearly at its anteriormost limit (1). From Brochu (2013), character 187.

171. **Shape of the posteriormost five to six dentary teeth: exclusively pointed to slightly blunt (0); with the presence of globular teeth (1); with the presence of large globular teeth (2); with the presence of molariform multicusped (3)**. Modified from Salas-Gismondi et al. (2015), character 198.

Remarks. Originally, this character regarded the teeth posterior to the 11th-12th alveoli concerning whether those would be pointed to slighlt blunt (Fig. 79-A), molariform multicusped, absent, globular with at least four being subequal or globular but different in size. A different approach was decided for this character in several aspects. Firstly, it was decided to concentrate the character about the shape of the posteriormost teeth, regardless of how many teeth any particular taxon has, due to the tendency in alligatoroids to have blunt or globular posteriormost teeth. As such, the state of “absent” teeth was not used. Additionally, the difference in size between globular teeth has a different approach: we distinguish between regular globular teeth (state 1, Fig. 79-C and D) and globular teeth with particularly large sizes (state 2, Fig. 79-B), as seen in the alligatoroids *Ceratosuchus*, *Hassiacosuchus*, *Wannaganosuchus*, *Notocaiman* (not included in the analysis), *Allognatosuchus wartheni* and *Brachychampsa sealeyi*. The state regarding molariform multicusped teeth, which in this dataset is present only in the basal eusuchian *Iharkutosuchus makadii* (Ösi et al., 2007), was maintained.

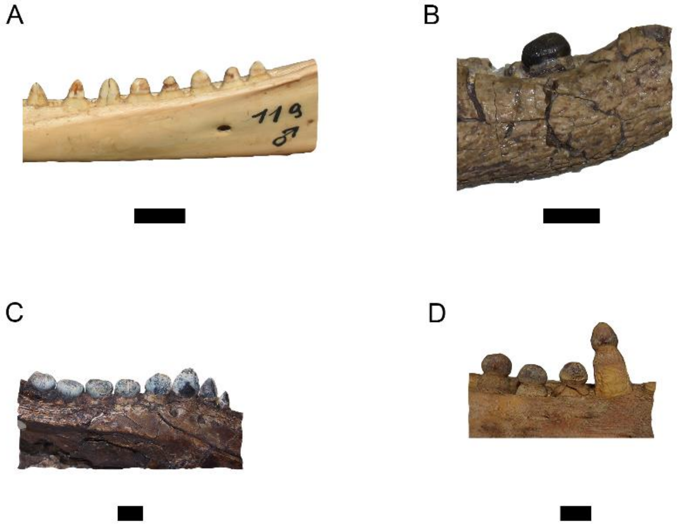

Figure 79: Diversity of posterior mandibular teeth in Alligatoroidea: pointed to slightly blunt (*Caiman crocodilus apaporiensis*, FMNH-69832, A), large and globular (*Allognathosuchus wartheni*, YPM PU-16989, B) and globular (*Kuttanacaiman*

iquitosensis, MUSM-1942, C; *Caiman niger,* MN-64, D). Modified from Cidade et al. (2019e). Scale bar = 1 cm.

172. **Preorbital crest absent** (0) or present (1). Modified from Barrios (2011), character 109, translated from Spanish.

Remarks. *Alligator mississippiensis, A. sinensis* and *Crocodylus affinis* were scored as polymorphic for this character following Brochu (1997a). Examples of both states are *Caiman crocodilus* (Fig. 76-A) and *Paleosuchus palpebrosus* (Fig. 76-B), respectively.

173. **Maxilla with strong festooning and dorsoventrally low (0), or with strong festooning and dorsoventrally high (1) or with rounded lateral margins (2) or with slight festooning (3) or no festooning, maxilla dorsoventrally flattened (4) or no festooning, maxilla making part of rostrum with tubular shape (5)**. Modified from Barrios (2011), character 106.

Remarks. Originally, Barrios (2011) conceived this character as distinguishing only between absence of festooning, presence of slight festooning and strong festooning (see Appendix 2). However, morphological variation regarding the maxilla of eusuchians and alligatoroids in particular exhibit a larger degree not restricted to the festooning. In *Paleosuchus* (Fig. 80-B) and *Procaimanoidea utahensis,* the maxilla is distinguished for being dorsoventrally high. In *Gnatusuchus, Wannaganosuchus* (Fig. 80-C) and *Brachychampsa sealeyi* the maxilla is lateromedially expanded and has its lateral margins rounded. Barrios (2011) considered all taxa without festooning as belonging to a single state, but here those are splitted between two states: one for those in which the maxilla is dorsoventrally flattened (state 4), which includes *Mourasuchus* (Fig. 80-E) and *Caiman australis* (the last one not included in the analysis), and anoth for the taxa in which the maxilla is elongated and slightly dorsoventrally high, making part of a tubular rostrum, which includes gavialoids (Fig. 80-F) and the crocodyloid *Tomistoma schlegelli*. This last state may be considered roughly equivalent to the “longirostrine” morphology, but taxa typically considered as longirostrine, such as the crocodyloid

Mecistops cataphractus, are considered here as belonging to state 0. Additionally, Barrios (2011) considered as taxa with slight festooning (state 3 of this character) *Alligator mississippiensis*, *Crocodylus acutus*, *Purussaurus* and *Paleosuchus*. However, as stated previously, *Paleosuchus* is treated here as belonging to new state 1, whereas *A. mississippiensis* and *C. acutus* are considered as belonging to state 0, together with other taxa such as *C. niloticus* (Fig. 80-A), with state 3 being restricted to *Purussaurus* (Fig. 80-D).

Type specimens of state characters: *Crocodylus niloticus*, AMNH-R-10081 (0); *Paleosuchus palpebrosus*, FMNH-69869 (1); *Wannaganosuchus brachymanus*, SMM-P76.28.247 (2); *Purussaurus mirandai*, CIAAP-1369 (3); *Mourasuchus amazonensis*, DGM-526-R (4); *Gavialis gangeticus*, AMNH-R-88316 (4).

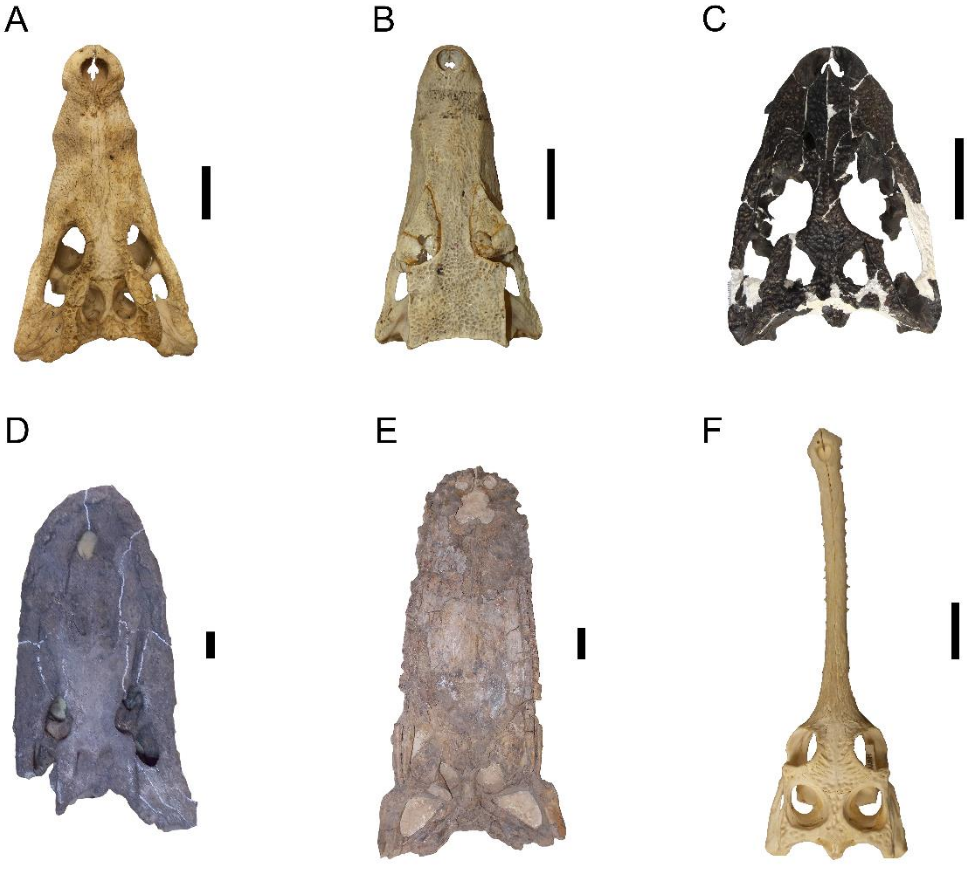

Figure 80: The type specimens of the states of Character 173: 0 *Crocodylus niloticus*, AMNH-R-10081 (A); 1 *Paleosuchus palpebrosus*, FMNH-69869 (B); 2

Wannaganosuchus brachymanus, SMM-P76.28.247 (C); 3 *Purussaurus mirandai*, CIAAP-1369 (D); 4 *Mourasuchus amazonensis*, DGM-526-R (E); 5 *Gavialis gangeticus*, AMNH-R-88316 (F). Scale bars = 10 cm (A, D and E), 5 cm (B, C and F)

174. **Secondary choana circular (0) or compressed lateromedially and anteroposteriorly (1). New character.**

Remarks. Plesiomorphically in Eusuchia and Alligatoroidea, the secondary choana is circular (Fig. 81-A and B), whereas in most caimanines it is compressed lateromedially and anteroposteriorly (Fig. 81-C), except in *Gnatusuchus* and *Paleosuchus palpebrosus*, in which it is circular. *Paleosuchus trigonatus* is scored as polymorphic for this character.

Figure 81: Diversity of size and shape of the secondary choana in Alligatoroids: small, circular choana of *Leidyosuchus canadensis* (CMN-8543); large, circular choana of *Brachychampsa montana* (UCMP-133901); small, compressed choana of *Caiman niger* (MN-81, C). Scale bar = 1 cm.

175. **Secondary choana small (0) or large (1). New character.**

Remarks. Plesiomorphically in Eusuchia, the secondary choana has a small size. (Fig. 81-A and C). This is preserved in most eusuchians examined in this study, except for the planocraniid *Boverisuchus vorax* and the alligatoroids *Albertochampsa*, *Alligator* *sinensis, A. mefferdi, Brachychampsa montana* (Fig. 81-B), *Diplocynodon elavericus* and *Procaimanoidea*, in which the secondary choana is large.

176. **Pattern of size in the maxillary teeth and alveoli: anteriormost with increasing size, those in the middle-length slightly smaller, and posteriormost with the same size or larger than those of middle-length (0); anteriormost with increasing size, those in the middle-length strongly smaller, and posteriormost with larger than those of middle-length (1); anteriormost with increasing size, followed by progressively smaller teeth and alveoli (2); teeth and alveoli approximately of the same size (3); anteriormost teeth and alveoli small, followed by progressively larger teeth and alveoli (4). New character.**

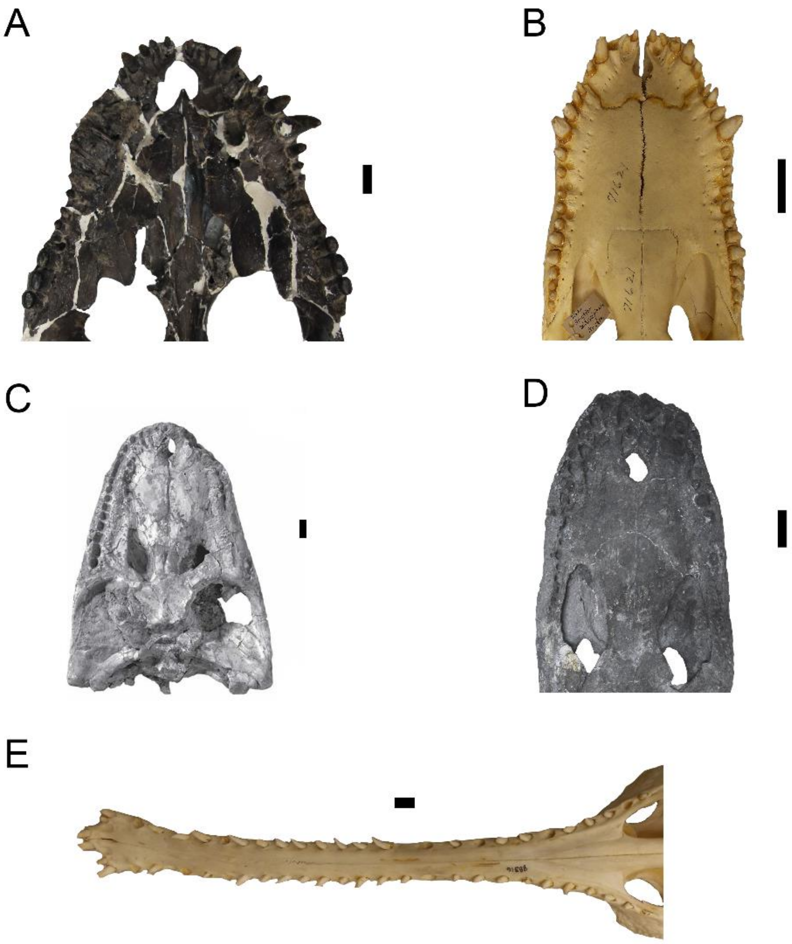

Figure 82: The type specimens of the states of Character 176: 0: *Alligator mississippiensis*, AMNH-R-71621 (B); 1: *Wannaganosuchus brachymanus*, SMM-P76.28.247 (A); 2: *Purussaurus mirandai*, CIAAP-1369 (D, taken from Scheyer &

Delfino, 2016); 3: *Gavialis gangeticus*, AMNH-R-88316 (E); 4: *Acynodon iberoccitanus*, ACAP-FX1 (C). Scale bars = 1 cm (A, C and E), 5 cm (B) and 10 cm (D).

Remarks. In most eusuchians, the size of the maxillary teeth and alveoli throughout the bone has the following pattern: a first set formed by the anteriormost gradually grow until the fourth or fifth alveolous, followed by a second set of three to five teeth that are slightly smaller that the largest teeth of the first series, which is then followed by a third set of teeth that are either of the same size or larger than those of the second set (Fig. 82-B). Variations of this pattern include the following: taxa in which the second set of teeth is strongly smaller in size than the first and the third, which comprises the alligatoroids *Brachychampsa*, *Stangerochampsa*, *Wannaganosuchus* (Fig. 82-A) and the outgroup *Bernissartia fagesii*. Maxillary teeth homodont are accommodated in state 3, which includes the basal eusuchian *Iharkutosuchus*, gavialoids (Fig. 82-E), the planocraniid *Boverisuchus magnifrons*, the crocodyloids *Tomistoma schlegelli* and *Mecistops cataphractus*, and the alligatoroid *Mourasuchus*. State 2 is seen only in the planocraniid *Boverisuchus vorax* and the alligatoroid *Purussaurus mirandai* (Fig. 82-D), whereas state 4 is seen only in the basal eusuchian *Acynodon iberoccitanus* (Fig. 82-C).

Type specimens of state characters: *Alligator mississippiensis*, AMNH-R-71621 (0); *Wannaganosuchus brachymanus*, SMM-P76.28.247 (1); *Purussaurus mirandai*, CIAAP-1369 (2); *Gavialis gangeticus*, AMNH-R-88316 (3); *Acynodon iberoccitanus*, ACAP-FX1 (4).

177. **Mid-length portion of the palatines lateromedially compressed (0) or expanded (1). New character.**

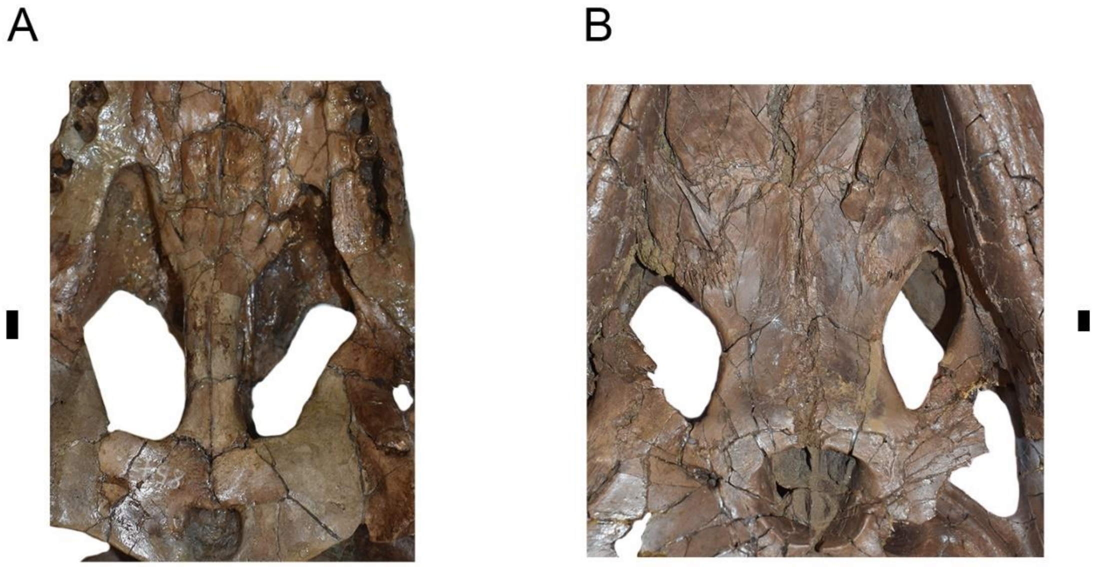

Figure 83: Mid-length portion of the palatines lateromedially compressed (*Leidyosuchus canadensis*, CMN-8543, A) and expanded (*Brachychampsa montana*, UCMP-133901, B). Scale bars = 1 cm.

Remarks. Plesiomorphically within Eusuchia, the mid-length portion of the palatine bones is lateromedially expanded. However, there is considerable diversity within the clade between this morphology and palatines in which the mid-length portion is lateromedially compressed. Among alligatoroids, palatines with the mid-length portion lateromedially compressed (state 0) are found in basal forms (*Leidyosushcus*, Fig. 83-A, and *Diplocynodon*), in some alligatorids (*Allognatosuchus, Procaimanoidea, Hassiacosuchus, Navajosuchus* and *Alligator prenasalis*) and in some caimanines (*Eocaiman cavernensis, Kuttancaiman, Mourasuchus atopus* and *M. pattersoni*), whereas palatines with the mid-length portion expansed (state 1) are found in most caimanines and in the alligatorines *Albertochampsa, Brachychampsa* (Fig. 83-B), *Ceratosuchus, Stangerochampsa* and in most species of *Alligator*.

178. **Medial portion of the quadrate oriented dorsally (0) or medially (1). New character.**

Remarks. The plesiomorphic morphology of the medial portion of the quadrate in Eusuchia and Alligatoroidea is it oriented dorsally (Fig. 84-B), whereas in the caimanine *Gnatusuhcus pebasensis* (Fig. 84-A) the medial portion of the bone is oriented medially.

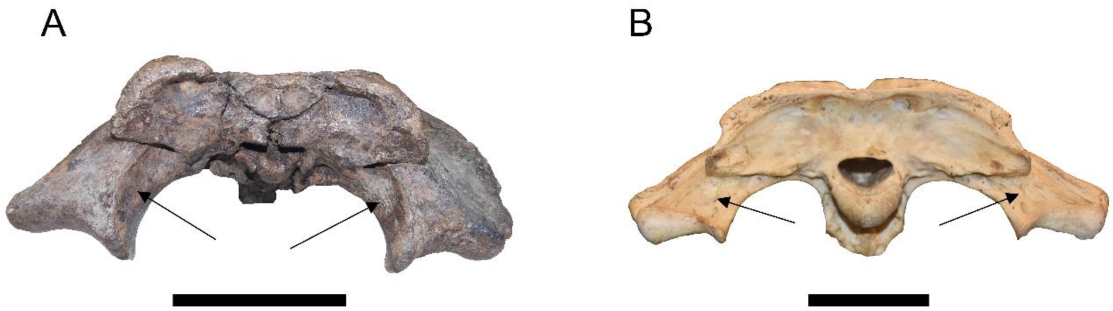

Figure 84: Arrows indicating the medial portion of the quadrate oriented medially (*Gnatusuchus pebasensis*, MUSM-990, A) and dorsally (*Caiman crocodilus apaporiensis*, FMNH-69812, B). Scale bar = 5 cm.

179. **Retroarticular process anteroposteriorly long (0) or short (1). New character.**

Remarks. In most eusuchians and alligatoroids, the retroarticular process of the articular is anteroposteriorly long (Fig. 85-B), which is also the plesiomorphic state in the Eusuchia clade. However, in some alligatorines (*Allognatosuchus wartheni*, *Krabisuchus*, *Navajosuchus*, Fig. 85-A) and in some caimanines (*Bottosaurus harlani*, *Mourasuchus arendsi* and *M. atopus*) the retroarticular process is remarkably anteoposteriorly short. The alligatorine *Hassiacosuchus haupti* exhibited polymorphism in this character and was scored accordingly.

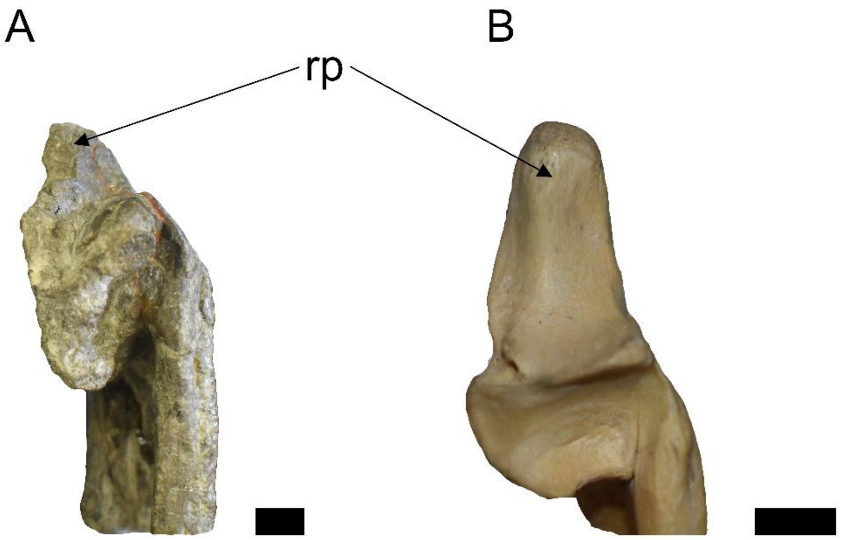

Figure 85: Retroarticular process anteroposteriorly short (*Navajosuchus mooki*, AMNH-6780, A) and long (*Alligator mississippiensis*, UCMP-131699, B). Scale bar = 1 cm.

180. **Anteroposteriorly length of the maxilla in dorsal view: long (0) or short (1). New character.**

Remarks. The anteroposteriorly length of the maxillae in dorsal view varies remarkably in proportion among Eusuchians, especially due to the differences in size between the forms. The correlation between this feature and the total length of the skull (and of the body as a whole) is strong; however, upon observing the diversity of morphologies among the maxillae of alligatoroids and eusuchians as a whole, the presence of remarkably short maxillae in a number of taxa was deemed to be a phylogenetically relevant character. In many taxa, the maxillae exhibit a remarkable short anteroposterior length in dorsal view, including the basal eusuchians *Acynodon*, *Allodaposuchus* and *Iharkutosuchus*, the basal alligatoroids *Krabisuchus* (Fig. 43) and *Arambourgia* (Fig. 16), the alligatorines *Allognatosuchus* (Fig. 15), *Hassiacosuchus* (Fig. 42) and *Alligator mcgrewi* (Fig. 13), and in the caimanines *"Caiman" brevirostris* (Fig. 20, see also Fortier et al., 2014), *"Caiman" wannlangstoni* (Fig. 23), *Globidentosuchus* (Fig. 40), *Gnatusuchus* (Fig. 41), *Kuttanacaiman* (Fig. 44) and the specimen UCMP-39978

(Caimaninae sp. nov., Fig. 25). Short maxillae have been associated with a durophagous feeding habit (see Salas-Gismondi et al., 2015).

181. **Laterocaudal bridge sectioning the trigeminal foramen: absent (0) or present (1). New character.**

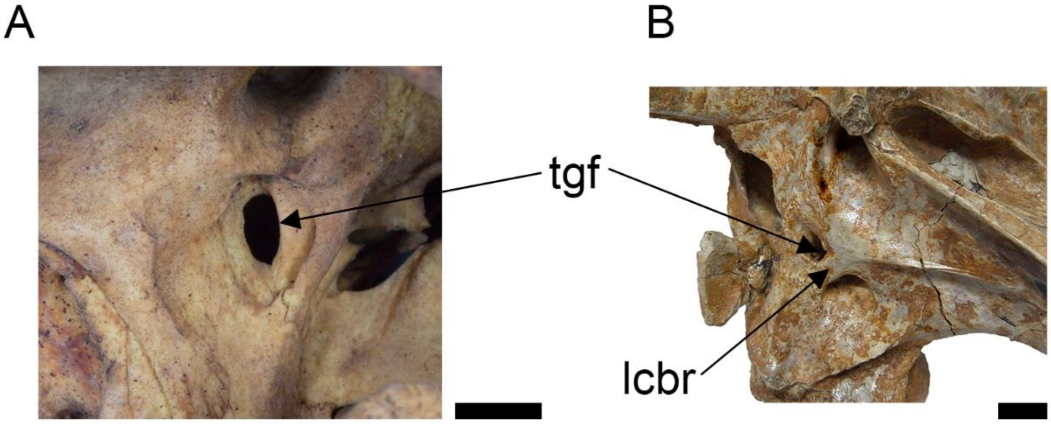

Figure 86: Trigeminal foramen (tgf) without (*Caiman latirostris*, MN-1019, right side) and with the lateocaudal bridge (*Mourasuchus arendsi*, UFAC-2515, left side; modified from Cidade et al., 2019c). Scale bar = 1 cm.

Remarks. In most eusuchians, the trigeminal foramen does not exhibit any osseous structure sectioning its opening (see Holliday & Witmer, 2009). In *Mourasuchus arendsi* (see Cidade et al., 2019c), the foramen is sectioned by the laterocaudal bridge, a structure formed by a ventral expansion of the quadrate and a dorsal expansion of the laterosphenoid. Remnants of the same structure can be observed in specimens assigned as *Mourasuchus* cf. *M. amazonensis* (Cidade et al., 2019b). In some individuals of the extant crocodyloid *Crocodylus palustris*, an analogous structure formed only by a ventral of the caudal bridge of the laterosphenoid (Cidade et al., 2019c), but this species is not included in this analysis.

182. **Osteoderms with low spines (0) or with high spines (1). New character.**

Remarks. The osteoderms of most eusuchians have low medial spines in their dorsal portions. *Mourasuchus pattersoni* exhibit osteoderms with high spines (‘horns’; see Langston, 2008; Fig. 87). The position of these osteoderms in the body is unknown, but the existence of the high spines is a derived morphology in itself and was deemed to be approached as different character. According to Langston (2008), osteoderms similar to *M. pattersoni* are found in the alligatoroid *Akanthosuchus* and in the basal neosuchian *Pinacosuchus* (see also Gilmore, 1942; O’Neill et al., 1981; Hill & Lucas, 2006), but neither was included in the present analysis.

Figure 87: An isolated osteodem with high spine of *Mourasuchus pattersoni* (MCNC-PAL-110-72V). Scale bar = 1 cm.

183. **Median crest of the parietal: absent or low (0) or high (1). New character.**

Remarks. In most eusuchians, the dorsal surface of the parietal bone is either flat or bears a low median crest (see Fig. 77). In the basal eusuchian *Acynodon adriaticus* (Delfino et al., 2008a) and in the caimanine alligatoroid *Mourasuchus arendsi* (Cidade et al., 2019c), the medial crest of the parietal is high, even though the degree of elevation varies (Fig. 88). This same morphology is also seen in specimens assigned as *Mourasuchus* cf. *M. amazonensis* (Cidade et al., 2019b).

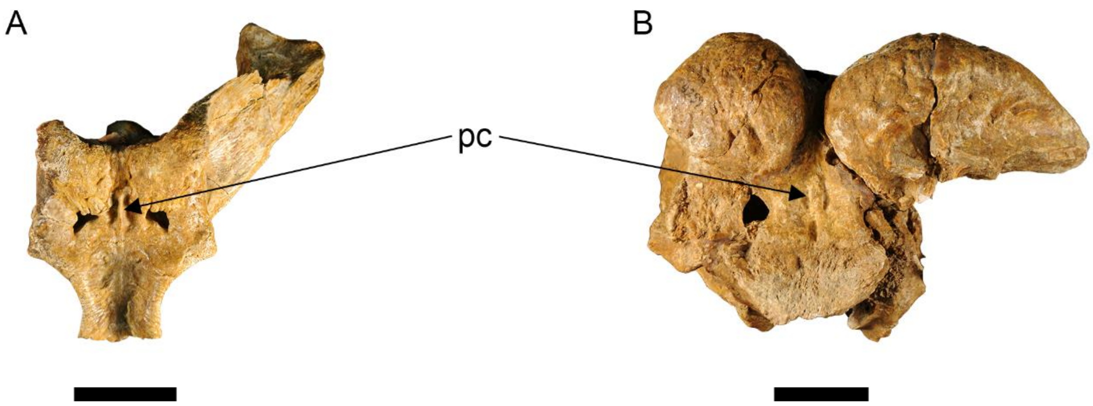

Figure 88: The high parietal crests present in *Mourasuchus arendsi*: a more elevated structure in UFAC-2515 (A) and a less elevated one in UFAC-4259 (B). Taken from Cidade et al. (2019c). Scale bar = 5 cm.

Additional changing: Anterior foramen for palatine ramus of cranial nerve VII ventrolateral (0) or **lateral** (1) to basisphenoid rostrum. From Brochu (2011), character 161.

Remarks. Originally, state 1 of this character presents the anterior foramen as ventral to the basisphenoid rostrum. However, upon the observation of specimens and of Brochu (1997a), this structure is located lateral to the basisphenoid rostrum in the taxa that are scored with state 1.

3.3. Methods of phylogenetic analysis

The scoring of the characters was stored and modified in the software Mesquite, version 3.2 (Maddison & Maddison, 2017). The analysis was performed in the software Tree Analysis Using New Technology (TNT), version 1.5 (Goloboff et al., 2008; Goloboff & Catalano, 2016).

The analysis was performed with non-additive and non-odered characters. The first analysis used a number of replications of 9,000, with 20 trees saved per replication, the random seed as ‘0’; the swapping algorithm was the Tree Bissection Reconnection (TBR), the trees were collapsed after the search and the existing trees were replaced. From the trees obtained in the first analysis, a second analysis was performed with the “trees from the RAM” option of the software, in which the trees continued to be collapsed after the search.

Posteriorly to the main analysis, a Pcr Prune analysis (Goloboff & Szumik, 2015; see also Pol & Escapa, 2009) was also performed in TNT to identify the unstable taxa that were generating polytomies and a semi-strict consensus obtained from the pruning of such taxa from the strict consensus. A 50% majority consensus was also performed from the original strict consensus with the TNT software.

3.4. Use of type specimens for state characters

As an experimental approach, this study proposes the use of “type specimens” for state characters in order to diminish ambiguity and improve the understanding of most complex characters to reserches when first seeing them. The type specimen of the character state may be named by the researcher who proposed the character or by a later reasercher who uses it, if he or she deems it necessary to make the character state more easy to understand to readers by allowing them to observe an actual specimen that “represents” the character stata, thus facilitating the understanding of it from the use of visual resource. The type specimens for state characters are not supposed to be mandatory, and they are neither “state bearing” specimens, in the sense that holotypes, lectotypes etc. are name-bearing specimens of species, for example. As such, an eventual reconsideration that concludes that the type specimen does not represent the character state would not make the character state invalid; the type specimen is to be an auxiliary instrument only. Additionally, any other specimen must not necessarily have the exact same morphology of the time specimen to be assigned to the state; the type specimen serves as a guide to aid in the assignment of other specimens to that particular state.

In this study, in characters 173 (modified from Barrios (2011), character 106) and 176 (new character), the type specimens for character states are used.

4. Results

4.1. Phylogenetic Analysis

The analyses resulted in a strict consensus of 256 most parsimonious trees, with 715 steps each. 97423 trees were generated in the first analysis. The ensemble consistency index is 0.376, and the ensemble retention index is 0.788.

Th strict consensus topology for the clade Eusuchia as a whole, excluding Alligatoroidea, is at Figure 89. The detailed topology of the clade Alligatoroidea is at Figure 90. The semi-strict consensus of the Pcr Prune analysis is in Figure 91) and the 50% majority consensus in is Figure 92) The description, synapomorphies and, whenever applied, nomenclature, definition and discussion of the clade Alligatoroidea and the clades within it as recovered by this study are given below.

Clade Alligatoroidea Gray, 1844

Definition: *Alligator mississippiensis* and all crocodylians closer to it than to *Crocodylus niloticus* or *Gavialis gangeticus* (sensu Brochu, 2003).

Synapomorphies: alveoli for dentary teeth 3 and 4 nearly same size and confluent (Character 43-0); anterior processes of surangular subequal to equal (Character 57-1); foramen aereum set in from margin of retroarticular process (Character 64-1); maxilla broadly separating ectopterygoid from maxillary tooth row (Character 95-1); quadratojugal spine high, between posterior and superior angles of infratemporal fenestra (Character 126-1); foramen aereum on dorsal surface of quadrate (Character 158-1).

Leidyosuchus canadensis appears as the basalmost alligatoroid, a topology that is recovered by the vast majority of analysis performed from the dataset of Brochu (1999) and that includes this taxon (e.g. Brochu, 1999, 2004a, 2010, 2011; Barrios, 2011; Bona et al., 2012; Hastings et al., 2013; Pinheiro et al., 2013; Fortier et al., 2014;

Skutchas et al., 2014; Salas-Gismondi et al., 2015; Wang et al., 2016; Whiting et al., 2016; Cidade et al., 2017; Cossette & Brochu, 2018; Souza-Filho et al., 2019).

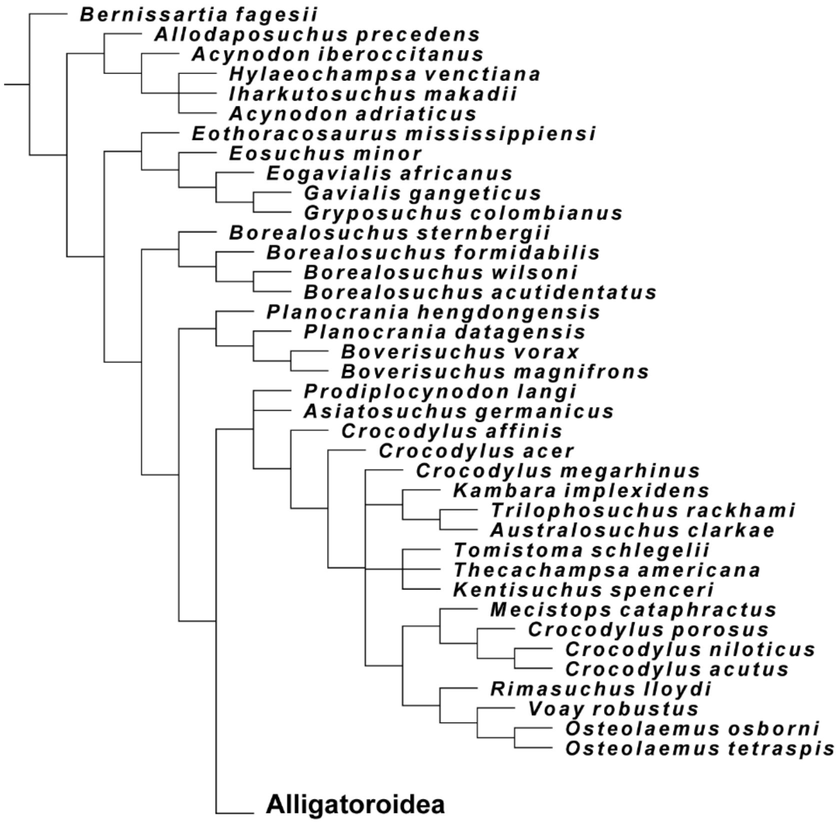

Figure 89: Topology of the Eusuchia clade obtained in the analysis of this study. Strict consensus of 256 most parsimonious trees, with 715 steps each. Ensemble consistency index = 0.376. Ensemble retention index = 0.788.

Unnamed clade: ***Diplocynodon remensis* + *Diplocynodon sensu stricto* + Globidonta**

Synapomorphies: ventral armour comprised by paired ventral ossifications that suture together, (Character 38-2); dentary symphysis extending to fourth or fifth alveolus, (Character 45-0); squamosal–quadrate suture extends only to posteroventral corner of external auditory meatus (Character 132-1); parietal and squamosal approaching each other on posterior wall of supratemporal fenestra without actually making contact (Character 138-1).

Figure 90: Topology of the Alligatoroidea clade obtained in the analysis of this study. Strict consensus of 256 most parsimonious trees, with 715 steps each. Ensemble consistency index = 0.376. Ensemble retention index = 0.788.

Diplocynodon as the second most basal clade of Alligatoroidea following *Leidyosuchus,* is also recovered by most of these analyses (Brochu, 1999, 2004a, 2010, 2011; Bona et al., 2012; Pinheiro et al., 2013; Fortier et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Wang et al., 2016; Cidade et al., 2017), except for the analyses that include *Deinosuchus,* from the Late Cretaceous of North America, which consistently appears as a basal alligatoroid, predominantly in a placement between *Leidyosuchus* and *Diplocynodon* (Aguilera et al., 2006; Scheyer et al., 2013; Martin et al., 2014; Hastings et al., 2016). *Deinosuchus* was not included in the present analysis as the genus is now undergoing a taxonomic review, after which it shall be included in the dataset of this analysis.

The analysis recovered *Diplocynodon remensis* as the sister-taxon of a clade including the remaining *Diplocynodon* species, which in its turn is the sister-taxon of the clade Globidonta. The placement of *D. remensis* differs from that of Martin et al. (2014), which recovered it together with the other species of *Diplocynodon* in the analysis that did not include what they deem the "less complete species of *Diplocynodon*", *D. ungeri* and *D. elavericus*. When those are included, the authors recovered all *Diplocynodon* and *Dinosuchus* in a polytomy. However, a topology somewhat similar to the present study was recovered in a strict consensus of an analysis with extended implied weight of Rio et al. (2019), which shows *D. remensis* as the basalmost alligatoroid, whereas Leidyosuchus canadensis as sister-taxon to the remaining *Diplocynodon*.

The placement of *D. remensis* obtained in this analysis is most likely explained by this taxon sharing with *Leidyosuchus canadensis* the fourth dentary tooth occluding in notch, rather than in a pit, between the premaxilla and the maxilla (Character 85-0), a plesiomorphy among crocodylia (see Brochu, 2003), whilst more derived alligatoroids share the fourth dentary tooth occluding in a pit (see Character 85-1, and below). This separate placement of *D. remensis* from the other *Diplocynodon* species would invite a taxonomic revision regarding the generic assignment of this species; however, such review is not performed in this study, as *Diplocynodon* is a group with a large number of species and specimens which requires detailed taxonomic review regarding its actual diversity (see also in the 'Discussion' below).

The clade formed by the other species of *Diplocynodon* is named in this analysis as *Diplocynodon sensu stricto*; a similar scenario involving *Allognatosuchus* led Brochu (1999) to use the appellation "*Allognathosuchus sensu stricto*" for one given clade.

Unnamed clade: *Diplocynodon sensu stricto* + Globidonta

Synapomorphies: dentary tooth 4 occluding in a pit between premaxilla and maxilla; no notch early in ontogeny (Character 85-1); lateral edges of palatines flaring posteriorly, producing shelf (Character 107-1); anterior tip of frontal visible in dorsal view forming broad, complex sutural contact either with the nasals or prefrontals (Character 117-1).

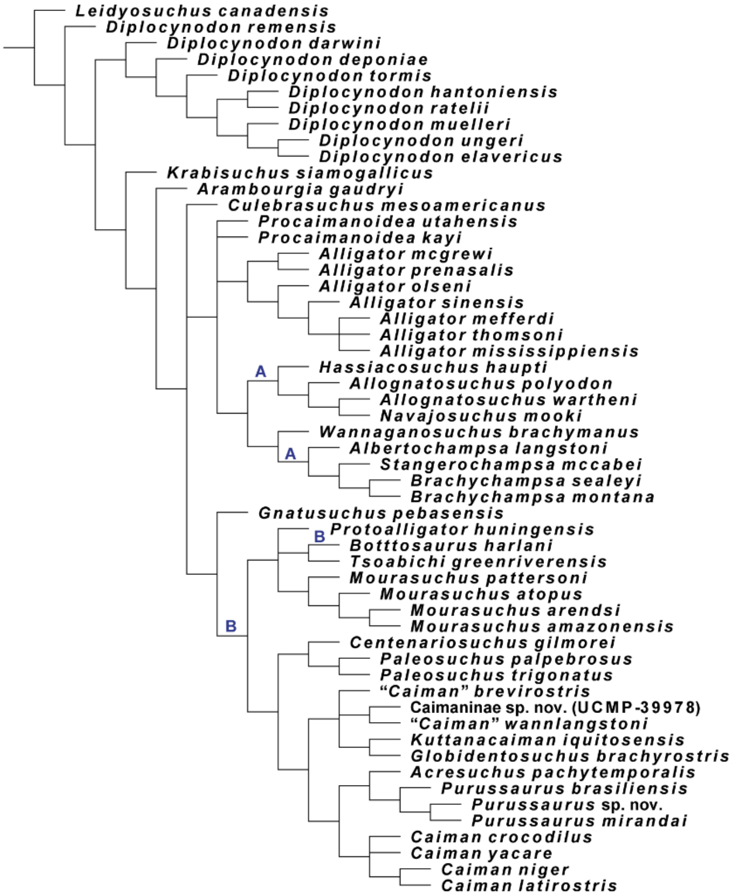

Figure 91: Topology of the semi-strict consensus of the Pcr Prune analysis. A = possible placements of *Ceratosuchus burdoshi*; B = possible palcements of the clade *Eocaiman*, which includes *E. cavernensis* and *E. palaeocenicus*.

Clade *Diplocynodon sensu stricto*

Synapomorphies: axial hypapophysis located toward the centre of centrum (Character 15-0); dorsal margin of iliac blade rounded rounded with smooth border, and posterior tip of blade very deep (Character 31-4); surangular pinched off anterior to tip of retroarticular process (Character 66-1).

Unnamed clade: *Diplocynodon deponiae* + (*D. tormis* + (((*D. muelleri* + (*D. ungeri* + *D. elavericus*)) + (*D. hantoniensis* + *D. ratelii*))))

Synapomorphies: dentary teeth with occlusion pits between fifth to the seventh or the eight teeth; all other dentary teeth occlude lingually (Character 86-3); squamosal–quadrate suture extending dorsally along posterior margin of external auditory meatus (Character 132-0).

Unnamed clade: *Diplocynodon tormis* + (((*D. muelleri* + (*D. ungeri* + *D. elavericus*)) + (*D. hantoniensis* + *D. ratelii*)))

Synapomorphy: naris projecting dorsally (Character 75-1).

Unnamed clade: ((*Diplocynodon muelleri* + (*D. ungeri* + *D. elavericus*)) + (*D. hantoniensis* + *D. ratelii*))

Synapomorphy: quadrate–pterygoid suture linear from basisphenoid exposure to trigeminal foramen (Character 150-1).

Unnamed clade: *Diplocynodon muelleri* + (*D. ungeri* + *D. elavericus*)

Synapomorphies: surangular truncated and not continuing dorsally towards dorsal tip of lateral wall of glenoid fossa (Character 62-1); squamosal–quadrate suture extends only to posteroventral corner of external auditory meatus (Character 132-1).

Unnamed clade: *Diplocynodon ungeri* + *D. elavericus*

Synapomorphies: palatine process does not extend significantly beyond anterior end of suborbital fenestra (Character 103-1); lateral edges of palatines paralleling posteriorly (Character 107-0).

Unnamed clade: *Diplocynodon hantoniensis* + *D. ratelii*

Synapomorphies: premaxillary surface lateral to naris with deep notch (Character 80-1); orbits equal or sub equal than infratemporal fenestrae (Character 162-0).

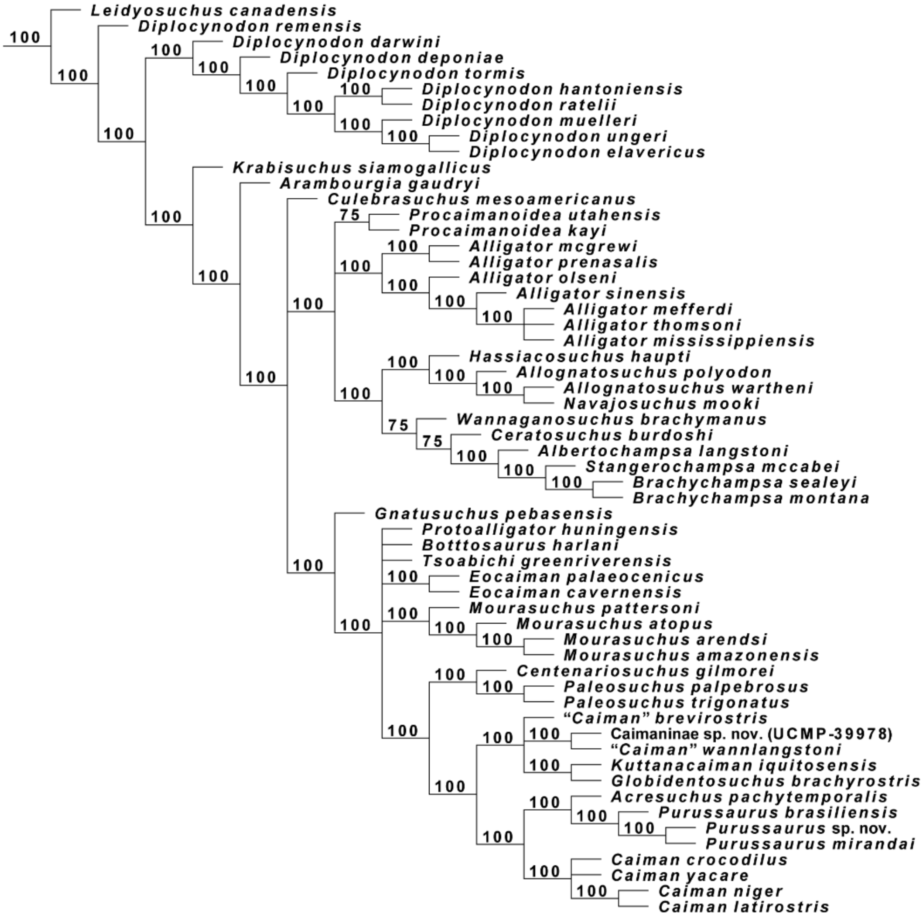

Figure 92: Topology of the 50% majority consensus obtained in this analysis. Numbers represent the percentage that each clade was recovered among the total number of trees.

Clade Globidonta Brochu, 1999

Definition: *Alligator mississippiensis* and all crocodylians more closely related to it than to *Diplocynodon ratelii* (sensu Brochu, 1999).

Synapomorphies: dorsal midline osteoderms nearly square (Character 35-1); fourth dentary alveolus larger than third, and alveoli are separated (Character 43-1); dentary deeply curved between 4th and 10th alveoli (Character 46-1); largest dentary alveolus immediately caudal to fourth being the 13th or the 14th (Character 47-0); largest maxillary alveolus among the first ten alveoli is the 4th (Character 87-2); choana projects anteroventrally at maturity (Character 109-1); frontoparietal suture on skull table entirely (Character 134-2).

Krabisuchus siamogalicus appears as the basalmost globidontan. This differs from the two previous analyses that included the taxon: Martin & Lauprasert (2010) recovered it as an alligatorine alligatorid, whereas Skutschas et al. (2014) recovered it as an alligatorid, but as part of a large polytomy. The last analysis also included a specimen, a partial skull only visible in dorsal view from the Eocene of the Guangdong Province of China, the 'Maoming crocodylian' (MMC-001), which was also recovered as an alligatorid within the large polytomy. This specimen is not included in the present analysis due to its incompleteness and absence of status as a distinct taxon. The presence of *Krabisuchus* as a sister-taxon of the remaining globidotans arises interesting biogeographic questions, which are addressed posteriorly.

Unnamed clade: *Arambourgia* + Alligatoridae

Synapomorphies: prefrontal with anterior expansion separating the lacrimal from the nasals (Character 115-2); prefrontal longer than lacrimal (Character 116-1).

The placement of *Arambourgia gaudryi* from Eocene of France as the sister-taxon of Alligatoridae is different from all other topologies ever published involving the taxon, in which it appears either as an alligatorine alligatorid (Brochu, 1999, 2010, 2011, 2013; Hastings et al., 2013; Scheyer et al., 2013; Salas-Gismondi et al., 2015; Whiting et al., 2016; Cidade et al., 2017; Cossette & Brochu, 2018; Souza-Filho et al., 2019) or as an alligatorid at least (Skutschas et al., 2014). Many previous analyses have also recovered *Arambourgia* within the same clade as *Procaimanoidea*, from the Eocene of the United States (Brochu 2004a, 2010, 2011, 2013; Scheyer et al.,2013; Skutchas et al., 2014; Hastings et al., 2016; Wang et al., 2016; Cidade et al., 2017; Cossette & Brochu, 2018; Souza-Filho et al., 2019), but in this analysis *Procaimanoidea* is in the clade Alligatorinae.

Clade Alligatoridae Gray, 1844

Definition: last common ancestor of *Alligator mississippiensis* and *Caiman crocodilus* and all of its descendents (sensu Brochu, 1999).

Synapomorphies: naris projects dorsally (Character 75-1); medial process of prefrontal pillar expanded anteroposteriorly (Character 99-1); supraoccipital exposure on dorsal skull table large such that parietal is excluded from posterior edge of table (Character 143-3).

Alligatoridae is recovered as consisting of three clades in a polytomy: Alligatorinae, Caimaninae and *Culebrasuhcus*. The split between Alligatorinae and Caimaninae is recurrent, but *Culebrasuchus* has been recovered in previous analyses either as a basal caimanine (Hastings et al., 2013; Cidade et al., 2017; Souza-Filho et al., 2019) or amont the species of *Alligator* (Salas-Gismondi et al., 2015). The placement of *Culebrasuchus* in a polytomy in this analysis, as well as the discrepancy between its placement in previous assessments, are likely due to the relative incompleteness of the species' holotype and only known specimen (see Hastings et al., 2013) and to the fact that Culebrasuchus exhibits some features that shared with basal alligatoroids and alligatorines, like character the supratemporal fenestrae with fossa, with the dermal bones of skull roof not overhanging the rim at maturity (Character 135-0) and the exoccipitals terminating dorsal to the basioccipital tubera (Character 157-0), whereas at the same time sharing with caimanines features such as the supraoccipital exposure on dorsal skull table being large such that parietal is excluded from posterior edge of table (Character 143-3). Future assessments and/or more complete findings on *Culebrasuchus* will better establish its phylogenetic placement, likely either as an Alligatorinae or as Caimaninae.

Clade Alligatorinae Kälin, 1940

Definition: *Alligator mississippiensis* and all crocodylians closer to it than to *Caiman crocodilus* (sensu Brochu, 1999)

Synapomorphies: surangular pinched off anterior to tip of retroarticular process (Character 66-1); supraoccipital exposure on dorsal skull table absent, or with minimal exposure (Character 143-1); secondary choana small large (Character 175-1).

Alligatorinae appears as a predominantly North American clade, in agreement with all previous analyses. However, in this analysis this scenario is more accentuated, with only one taxon from Asia (the extant *Alligator sinensis*) and one from Europe (*Hassiacosuchus*, from the Eocene of Germany), even though *Alligator lucius*, from the middle Miocene of China, was not included in this analysis, which may yield a relatively more complex biogeographic scenario depending on its eventual phylogenetic placement. A thorough assessment on the biogeography of Alligatorinae is provided in the "Discussion" below.

Both species of *Procaimanoidea* are recovered within Alligatorinae, as in most previous analyses (Brochu, 1999, 2010, 2011, 2013; Hastings et al., 2013; Scheyer et al., 2013; Salas-Gismondi et al., 2015; Whiting et al., 2016; Cidade et al., 2017; Cossette & Brochu, 2018; Souza-Filho et al., 2019), although not closely related to *Arambourgia*, as explained above. However, both species of *Procaimanoidea* are not united in a clade, as in most of previous analyses cited above (e.g. Brochu 2004a, 2010, 2011, 2013; Scheyer et al.,2013; Skutchas et al., 2014; Hastings et al., 2016; Wang et al., 2016; Cidade et al., 2017; Cossette & Brochu, 2018; Souza-Filho et al., 2019), bur rather both of them appear as independent lineages in a four-lineage polytomy in Alligatoridae. Nevetheless, the 50% majority consensus tree shows both species of *Procaimanoidea* united as a clade in 75% of the trees (Fig. 92), which points to a likelihood that they are recovered as a clade in future analyses.

Clade *Alligator* Cuvier, 1807

Synapomorphies: lingual foramen for articular artery and alveolar nerve perforating surangular/angular suture (Character 63-1); external naris bisected by nasals (Character 76-0).

Alligator mcgrewi and *A. prenasalis* are recurrently recovered as the basalmost species of *Alligator* (Brochu, 2011, 2013; Scheyer et al., 2013; Wang et al. 2016; Whiting et al., 2016; Cidade et al., 2017; Souza-Filho et al., 2019). Only Cossette & Brochu (2018) recovered both as a separate clade within Alligatorinae and separated from the remaining species of *Alligator*, with a lineage consisted of *Wannganosuchus* and another of *Arambourgia* and *Procaimanoidea* separting those clades. As such, the topology of this study, recovering *A. mcgrewi* and *A. prenasalis* as a clade within *Alligator*, but as the sister-group of the remaining *Alligator* has not been recovered in any previous assessment.

Unnamed Clade: *Alligator mcgrewi* + *A. prenasalis*

Synapomorphies: naris projecting anterodorsally (Character 75-0); secondary choana small (Character 175-0).

Unnamed Clade: *Alligator olseni* + (*A. sinensis* + (*A. mefferdi* + *A. mississippiensis* + *A. thomsoni*))

Synapomorphies: sides of scapular blade being subparallel; minimal dorsal flare at maturity (Character 21-1); dorsal margin of iliac blade rounded, with modest dorsal indentation (Character 31-1); external mandibular fenestra present and very large; most of foramen intermandibularis caudalis visible in lateral view (Character 59-2); dorsal edges of orbits highly upturned (Character 122-1).

Unnamed Clade: *Alligator sinensis* + (*A. mefferdi* + *A. mississippiensis* + *A. thomsoni*)

Synapomorphies: deltoid crest of scapula very wide at maturity, with broad margin (Character 22-1); dentary slightly curved between 4th and 10th alveoli (Character 46-0); splenial excluded from mandibular symphysis; anterior tip of splenial passing dorsal to Meckelian groove (Character 50-2).

Unnamed Clade: *Alligator mefferdi* + *A. mississippiensis* + *A. thomsoni*

Synapomorphies: prefrontal pillar with large pneumatic recess (Character 100-1).

This clade has been recovered in most analyses that included the same species of *Alligator* as this one (Brochu, 2011, 2013; Scheyer et al., 2013; Wang et al. 2016; Cidade et al., 2017; Cossette & Brochu, 2018; Souza-Filho et al., 2019). This raises perspectives on the taxonomy of the two fossil species of the clade, as discussed posteriorly.

Clade Brachychampsidae, tax. nov.

Definition: a node-based group containing the most recent common ancestor of *Brachychampsa montana* and *Wannaganosuchus brachymanus* and all of its descendents (new definition).

Synapomorphies: largest dentary alveolus immediately caudal to fourth being the 13th or 14th and a series behind it (Character 47-1); posteriormost five to six dentary teeth: with the presence of large globular teeth (Character 171-2).

Brachychampsidae in this topology is a polytomy with four lineages: *Ceratosuchus*, *Wannaganosuchus*, Allognathosuchinae and Brachychampsinae, the latter two also being new taxa (see below). Brachychampsidae is defined with *Wannaganosuchus brachymanus* as a specifier alongside *Brachychampsa montana*, as opposed to any taxon of Allognathosuchinae, due to the alternative scenarios observed in the 50% majority consensus (Fig. 92) and in the Pcr Prune analysis (Fig. 91). In the former, the clade here is defined as Brachychampsidae is recovered by 75% of the trees as having *Wannaganosuchus* as the basalmost taxon, followed by *Ceratosuchus* and the sister-taxon of Brachychampsinae. In the latter, *Ceratosuchus* is pruned, and the semi-strict consensus shows *Wannaganosuchus* as the sister-taxon of Brachychampsinae. These two semi-strict consensa evidence a plausibility of *Wannaganosuchus* forming a clade with Brachychampsinae, and because of this the name Brachychampsidae is chose to be based on this potential closer affinity between these two taxa between each other than between those and Allognathosuchinae.

Clade Brachychampsinae, tax. nov.

Definition: a node-based group containing the most recent common ancestor of *Albertochampsa langstoni* and *Brachychampsa montana* and all of its descendents (new definition).

Synapomorphy: dorsal premaxillary processes long, extending beyond third maxillary alveolus (Character 84-1).

Brachychampsinae is a clade formed exclusively by taxa from the Late Cretaceous of North America (see Gilmore, 1911; Erickson, 1972; Williamson, 1996; Wu et al., 1996; Brochu, 2004a). In all three scenarios considered by this study (strict consensus, 50% majority consensus, Pcr Prune analysis), Brachychampsinae appears as a clade within Brachychampsidae (see Figs. 90, 91 and 92).

Unnamed clade: *Stangerochampsa* + *Brachychampsa*

Synapomorphy: palatine–maxillary suture intersects suborbital fenestra nearly at its anteriormost limit (Character 170-1).

Clade *Brachychampsa* Gilmore, 1911

Synapomorphies: dorsal midline osteoderms rectangular (Character 35-0); largest maxillary alveolus among the first ten alveoli is the 5th (Character 87-1); supraoccipital exposure on dorsal skull table large (Character 143-2).

Clade Allognathosuchinae Rusconi, 1934

Definition: a node-based group containing the most recent common ancestor of *Allognathoushcus wartheni* and *Hassiacosuchus haupti* and all of its descendents (new definition).

Synapomorphy: surangular–dentary suture intersecting external mandibular fenestra at or close to the posterodorsal corner (Character 60-1).

Allognathosuchinae includes *Allognathosuchus*, from the Eocene of the United States (Case, 1925; Brochu, 2004a), *Hassiacosuchus*, from the Eocene of Germany (Weitzel, 1935; Wasserhug & Hetch, 1967) and *Navajosuchus*, from the Paleocene of the United States (Simspon, 1930; Mook, 1942; Brochu, 2004a). The last two taxa were already considered as synonymous to *Allognathosuchus* (see Brochu, 2004a). The fact that the two species assigned to *Allognathosuchus*, *A. polyodon* and *A. wartheni*, indicates the possibility of a taxonomic revision. However, this is refrained from being performed in this study due to the necessity of a thorough taxonomic revision of the species that can be assigned to *Allognathosuchus* and of the specimens that can be assigned to each species (this is discussed in more detail in the "Discussion" below).

Allognatosuchinae appears within Brachychampsidae in the strict consensus (Fig. 90), but as a sister-taxon of that Brachychampsidae in the 50% majority consensus (Fig. 92) and in the semi-strict consensus of the Pcr Prune analysis (Fig. 91).

Unnamed Clade: *Allognathosuchus polyodon* + (*A. wartheni* + *Navajosuchus*)

Synapomorphy: surangular–articular suture bowed strongly laterally within glenoid fossa (Character 67-1).

Unnamed Clade: *Allognathosuchus wartheni* + *Navajosuchus*

Synapomorphy: retroarticular process anteroposteriorly short (Character 179-1).

Clade Caimaninae Brochu, 1999

Definition: a stem-based group including *Caiman crocodilus* and all crocodylians more closely related to it than to *Alligator mississippiensis* (sensu Brochu, 1999, following Norell, 1988)

Synapomorphies: dentary slightly curved between 4th and 10th alveoli (Character 46-0); splenial lacking anterior perforation for mandibular ramus of cranial nerve V (Character 48-1); dermal bones of skull roof overhanging rim of supratemporal fenestra near maturity; fenestrae small, with a circular or nearly circular shape (Character 135-

1); medial parietal wall of supratemporal fenestra bearing foramina (Character 137-1); exoccipitals sending slender process lateral to the basioccipital tubera (Character 157-2).

Caimaninae appears as a well-established clade of predominantly South American taxa, as in previous analyses. Its most basal form is *Gnatusuchus pebasensis*, from the middle Miocene of Peru (Salas-Gismondi et al., 2015), which is the sister-taxon of the remaining caimanines. Other taxa that appeared in previous analysis as basal within Caimaninae, such as *Culebrasuchus* (Hastings et al., 2013), *Globidentosuchus* (Scheyer et al., 2013) and *Eocaiman* (Brochu, 1999) are recovered respectively as a non-caimanine and non-alligatorine alligatorid (see above), a globidentosuchid and a more derived caimanine (see below).

Unnamed clade: *Bottosaurus* + *Eocaiman* + *Mourasuchus* + *Protoalligator* + *Tsoabichi* + Crown-group Caimaninae

Synapomorphies: splenial excluded from mandibular symphysis; anterior tip of splenial passing dorsal to Meckelian groove (Character 50-2); surangular–angular suture lingually meets articular dorsal to tip (Character 61-1); dorsal edges of orbits highly upturned (Character 122-1).

All taxa included in this clade have been previously recovered as derived caimanines in previous analyses (see Brochu, 1999, 2004a, 2010, 2011; Hastings et al., 2013; Scheyer et al., 2013; Salas-Gismondi et al., 2015; Cidade et al., 2017; Souza-Filho et al., 2019), with the exception of *Protoalligator huningensis*, from the Paleocene of China which, in the only previous analysis that included it, was recovered as a globidontan in large polytomy (Wang et al., 2016). The presence of an Asian form within a typically South American clade raises complex biogeographic questions, as will be approached in the “Discussion” below.

The Pcr Prune semi-strict consensus, upon pruning *Eocaiman* from the analysis, shows a clade formed by *Protoalligator, Mourasuchus* and a clade formed by *Bottosaurus* and *Tsoabichi* as a sister-group of the crown-group Caimaninae (Fig. 91).

This suggests an affinity between the only two North American caimanines, as well as an affinity of the Asian *Protoalligator* with them, which represents a considerably simpler biogeographic scenario than if considering them with South American ancestors (see “Discussion” below). The 50% majority consensus showed no differences with the strict consensus.

Other caimanine species not included in this analysis may have affinities with taxa of this clade. *Necrosuchus ionensis*, from the Paleocene of Argentina, has been recovered as having affinities with *Tsoabichi* in previous studies (Cidade et al. 2019d), whereas *Caiman gasparinae*, from the Miocene of Argentina, has been recovered as close to *Mourasuchus* in a previous analysis (Cidade et al. 2019d). Both *N. ionensis* and *C. gasparinae* are considered here as valid species (see “Taxonomic Revisions” below) but were excluded from the analysis due to their high degree of incompleteness. Future assessments shall consider their inclusion to evaluate their phylogenetic positions. Regarding *N. ionensis*, Cidade et al. (2019d) also suggested a possible affinity with *Paleosuchus*, recovered in this analysis as a member of the crown-group Caimaninae (see below).

Clade *Eocaiman* Simpson, 1933

Synapomorphy: dentary linear to the 10th alveolous and elevated after the 11th alveolous (Character 46-2).

Eocaiman included only the species *E. cavernensis* and *E. palaeocencius*. The species *Eocaiman itaboraiensis* is considered in this study as a new genus (see “Taxonomic Revision” below) within Alligatoroidea but was not included in the analysis due to its high degree of incompleteness.

Clade *Mourasuchus* Price, 1964

Synapomorphies: dentary linear throughout the tooth row (Character 46-3); external mandibular fenestra present, dorsoventrally compressed and anteroposteriorly expanded

(Character 59-3); maxilla with no festooning, maxilla dorsoventrally flattened (Character 173-4).

The topology shows *Mourasuchus pattersoni* as the basalmost taxon, followed by *M. atopus* as the sister-taxon of a clade formed by *M. amazonensis* and *M. arendsi*. This differs from the previous analyses that included all taxa (Cidade et al., 2017, 2018; Souza-Filho et al., 2019), which recovered a clade formed by *M. arendsi* and *M. atopus* and another by *M. amazonensis* and *M. pattersoni*. This is due to the fact that characters that had been scored based solely on drawings on the holotypes of *M. amazonensis* (see Price, 1964) and *M. arendsi* (see Bocquentin-Villanueva, 1984) were left unscored in the present analysis, which scored only characters that could be seen directly on specimens or through photographs.

Unnamed clade: *Mourasuchus atopus* + (*M. amazonensis* + *M. arendsi*)

Synapomorphy: premaxillary surface lateral surrounded by a dorsoventrally developed rim (Character 80-2).

Unnamed clade: *Mourasuchus amazonensis* + *M. arendsi*

Synapomorphy: mid-length portion of the palatines lateromedially expanded (Character 177-1).

Clade Crown-Group Caimaninae

Synapomorphies: incisive foramen having anterior margin tapering anteriorly and projecting itself between first premaxillary teeth (Character 83-2); mid-length portion of the palatines lateromedially expanded (Character 177-1).

Brochu (1999) referred to the clade formed by the most recent common ancestor of all living caimanines and all of its descendents as “crown-group Caimans”, a terminology used in later studies (e.g. Cidade et al., 2017; Souza-Filho et al., 2019).

However, crown-group Caimaninae is considered here a more accurate name and is adopted. It appears with two clades: one formed by *Centenariosuchus* and *Paleosuchus*, and another with the new name Caimanini.

Unnamed clade: *Centenariosuchus + Paleosuchus*

Synapomorphies: dorsal edges of orbits being lowly upturned (Character 122-2); supratemporal fenestra closing or nearly closing during ontogeny (Character 135-2).

The affinity between *Centenariosuchus* and *Paleosuchus* is different from previous strict consensa analyses including the former taxon. Hastings et al. (2013) recovered it as part of a derived polytomy of the crown-group Caimaninae, without a precise placement, whereas Salas-Gismondi et al. (2015) recovered it as sister-taxon to the clade Jacarea and Cidade et al. (2017) recovered it as a sister-taxon of a clade formd by *Mourasuchus* and *Purussaurus*.

Clade *Paleosuchus* Gray, 1862

Synapomorphies: premaxilla has four teeth early in posthatching ontogeny (Character 81-1); medium upraoccipital exposure on dorsal skull table (Character 143-0).

Clade Caimanini, tax. nov.

Definition: a node-based group containing the most recent common ancestor of *Caiman latirostris* and *Caiman wannlangstoni* and all of its descendents (new definition).

Synapomorphy: preorbital crest present (Character 172-1).

Caimanini is a new taxon created to unite some of the most derived caimanines. In this analysis, it is split into the clades Globidentosuchidae, Purussauria and *Caiman*, with the last two forming a clade and having Globidentosuchidae and their sister-taxon.

Clade Globidentosuchidae, tax. nov.

Definition: a node-based group containing the most recent common ancestor of *Caiman wannlangstoni* and *Globidentosuchus brachyrostris* and all of its descendents (new definition).

Synapomorphies: dentary symphysis extends to sixth to eighth alveolus (Character 45-1); largest dentary alveolus immediately caudal to fourth is the 12th and a series behind it, or (Character 47-5); anteroposteriorly length of the maxilla in dorsal view short (Character 180-1).

Globidentosuchus was previously recovered as a basal caimanine (Scheyer et al., 2013; Cidade et al., 2017) but here appears as a derived taxon within the clade. In fact, the union of the taxa present in this clade was not recovered in any previous analyses. The presence of "*Caiman*" *brevirostris* and "*Caiman*" *wannlangstoni* in Globidentosuchidae invites a taxonomic review of both taxa at the generic level, with possible new genera being assigned for each of the species. The new genus of "*Caiman*" *wannlangstoni* can also include the new species represented by the specimen UCMP-39978 (see below). Most of the taxa included in Globidentosuchinae – "*Caiman*" *brevirostris*, "*Caiman*" *wannlangstoni*, *Globidentosuchus* and *Kuttanacaiman* have been considered as durophagous taxa, due to features such as long mandibular symphysis, large posterior teeth with globular crowns and anteroposteriorly short rostra. Incidentally, these characters or features related to them constitute the synapomorphies of Globidentosuchidae.

Unnamed clade: "*Caiman*" *wannlangstoni* + Caimaninae sp. nov. (UCMP-39978)

Synapomorphy: canthi rostralii very prominent at maturity, with or without a depression lateral to it (Character 89-1).

Affinities between "*Caiman*" *wannlangstoni* and the specimen UCMP-39978 (Caimaninae sp. nov.) were suggested by Salas-Gismondi et al. (2015) and are corroborated by the two taxa forming a clade in this analysis. UCMP-39978 was previously considered as having affinities with *Caiman lutescens* (see Langston, 1965), but taxonomic reviews determined it cannot be assigned to this taxon (see Bona et al., 2012, and below).

Unnamed clade: *Globidentosuchus* + *Kuttanacaiman*

Synapomorphy: margin of orbit flush with skull surface (Character 122-0).

Unnamed clade: *Caiman* + Purussauria

Synapomorphies: coronoid completely surrounds foramen intermandibularis medius at maturity (Character 51-1); superior edge of coronoid sloping strongly anteriorly (Character 52-0).

Clade Purussauria, tax. nov.

Definition: a node-based group containing the most recent common ancestor of *Acresuchus pachytemporalis* and *Purussaurus mirandai* and all of its descendents (new definition).

Synapomorphies: external mandibular fenestra present and very large; most of foramen intermandibularis caudalis visible in lateral view (Character 59-2); dermal bones of skull roof overhanging rim of supratemporal fenestra near maturity; fenestrae large, significantly longer than wide, with an oval shape (Character 135-3).

Purussaurusia is created for accommodating the well-known giant caimanine *Purussaurus* and the recently described *Acresuchus*, which has been considered as something of a “transitional form” between a generalized caimanine and the giant ecomorphotype represented by *Purussaurus* (Souza-Filho et al., 2019).

Clade *Purussaurus* Barbosa-Rodrigues, 1892

Synapomorphies: naris longer than wide (Character 77-2); orbits equal or sub equal than infratemporal fenestrae (Character 162-0); posterior margin of the skull deeply concave (Character 165-1); maxilla with slight festooning (Character 173-3).

Unnamed clade: *Purussaurus mirandai* + *Purussaurus* sp. nov.

Synapomorphies: incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (Character 83-0); posterolateral margin of squamosal upturned to form a discrete eminence (Character 140-1).

Clade *Caiman* Spix, 1825

Synapomorphy: lacrimal longer than prefrontal (Character 116-0).

Includes the species *Caiman crocodilus*, *C. latirostris*, *C. yacare* and *C. niger* (formely considered *Melanosuchus niger*, see below). Brochu (1999) and later studies referred to this clade as Jacarea Gray, 1844, which is defined as the most recent common ancestor of those four species and all of its descendents. However, since *Caiman* is the only genus of this clade following the taxonomic revision of *C. niger*, the name Jacarea is not used.

Caiman crocodilus and *C. yacare* are not recovered forming a clade, in opposition to nearly all of the previously published analyses. However, as *C. crocodilus* may be a species complex currently comprising several cryptic species that may be effectively split in the future (see Escobedo-Galván et al., 2015), phylogenetic relationships of this clade might considerably change considering these possible taxonomic revisions.

Unnamed clade: *Caiman latirostris* + *C. niger*

Synapomorphies: ventral collar scales in two parallel enlarged rows (Character 41-2); canthi rostralii very prominent at maturity, with or without a depression lateral to it (Character 89-1).

4.2. Taxonomic Revisions

4.2.1. *Balanerodus logimus*

The holotype of *Balanerodus logimus* (UCMP-45787) is an isolated tooth crown with a globular shape and marked longitudinal crenulations (Langston, 1965; Fig. 93-A). Upon proposing *B. logimus* as a distinct species, Langston (1965) recognized that the holotype tooth and the 118 associated teeth had resemblances to the alligatoroid *Allognathosuchus* Mook, 1921 and the crocodylid *Bottosaurus* Agassiz, 1849 but argued that *Balanerodus logimus* was different from *Allognatosuchus* for having more “perfect rounded” crowns, absence of a tendency toward flattening of the top of the tooth and more developed mesial and distal carinae. From *Bottossaurus*, *Balanerodus logimus* would be distinct by presenting a pronounced division between crown and root.

However, the posterior upper and lower teeth of most alligatoroid species have blunt crowns, distinct from the acute crowns seen in the anterior and middle teeth. Posterior teeth with distinctive globular crowns similar to *B. logimus* can be seen not only in *Allognathosuchus* (see Case, 1925; Brochu, 2004a; Fig. 93-B) but also in the posterior upper and lower teeth of the extant *Caiman niger* (Fig. 93-G) and *Caiman latirostris* (Fig. 93-H) and also of the extinct caimanines *Gnatushchus*, *Kuttanacaiman*, (Fig. 93-C), “*Caiman*” *wannlangstoni*, (Fig. 93-D) and allegedelly in *Purussaurus* (see Salas-Gismondi *et al*., 2015), and the extinct basal alligatoroids *Brachychampsa* (see Brochu, 2004a; Fig. 93-E), *Albertochampsa* (see Erickson, 1972), *Stangerochampsa* (see Wu et al., 1996) and the extinct alligatorids *Procaimanoidea utahensis* (Fig. 93-F) and *P. kayi* (see Mook, 1941c). Except from *Gnatusuchus*, which can be distinguished from the holotype of *Balanerodus logimus* for not having carinae (see Salas-Gismondi *et al*., 2015), the globular teeth of the other taxa exhibit crowns that are largely similar to the holotype of *B. logimus*, without any systematically relevant differences. The crowns of the posteriormost teeth are even more globular than the first posterior teeth, but some of these most globular crowns (for example in *Allognatosuchus wartheni* Case, 1925) are different from the holotype of *B. logimus* in which they are anteroposteriorly expanded and dorsoventrally compressed. In *Bottosaurus harlani*, distinctly, the most posterior teeth are globular but more lateromedially compressed than the holotype of *B. logimus*, which bears more resemblance to the more anterior posteriormost teeth of *Bottosaurus harlani*, which are less lateromedially compressed (see Cossette & Brochu, 2018). However, the enamel of *Bottosaurus harlani* teeth display apical wrinkling (Cossette & Borchu, 2018), which are absent in *B. logimus* and thus distinguishes this last species from the former. Thereby, it is probable that UCMP-45787 was the crown of a posterior maxillary or mandibular tooth, but not of one of the posteriormost teeth, if the morphology of most extant and extinct alligatoroid species is considered.

As the holotype of *Balanerodus logimus* does not present any distinct characteristics (autapomorphies) if compared to other fossil and extant alligatoroids, including some taxa that were named before it – *Allognathosuchus*, *Purussaurus*, *Caiman niger* and *C. latirostris* –, this species is considered by this study to be a *nomen dubium*, being assigned to no lower taxonomic level than Alligatoroidea indet.

The other 118 isolated teeth referred to *B. logimus* by Langston (1965) were not directly analyzed by this work, but as these are described as having the same general structure to the holotype (Langston, 1965, p. 114–115), these can be assigned to Alligatoroidea indet. as well; the same assignment is here proposed by the *B. logimus* tooth described by Salas-Gimsondi et al. (2007). The specimen assigned to *B. logimus* by Langston & Gasparini (1997) comprised by a right maxilla with two teeth from the Honda Group (middle Miocene, Colombia), was also not directly analyzed in this work, and its new taxonomic assignment shall be assessed in an eventual specific study of the specimen. Nevertheless, these issues do not change the status of *B. logimus* as a *nomen dubium* due to the absence of distinctive characters of the name-bearing specimen (the holotype) in comparison with previously described alligatoroids.

This taxonomic review has been published in Cidade et al. (2019e).

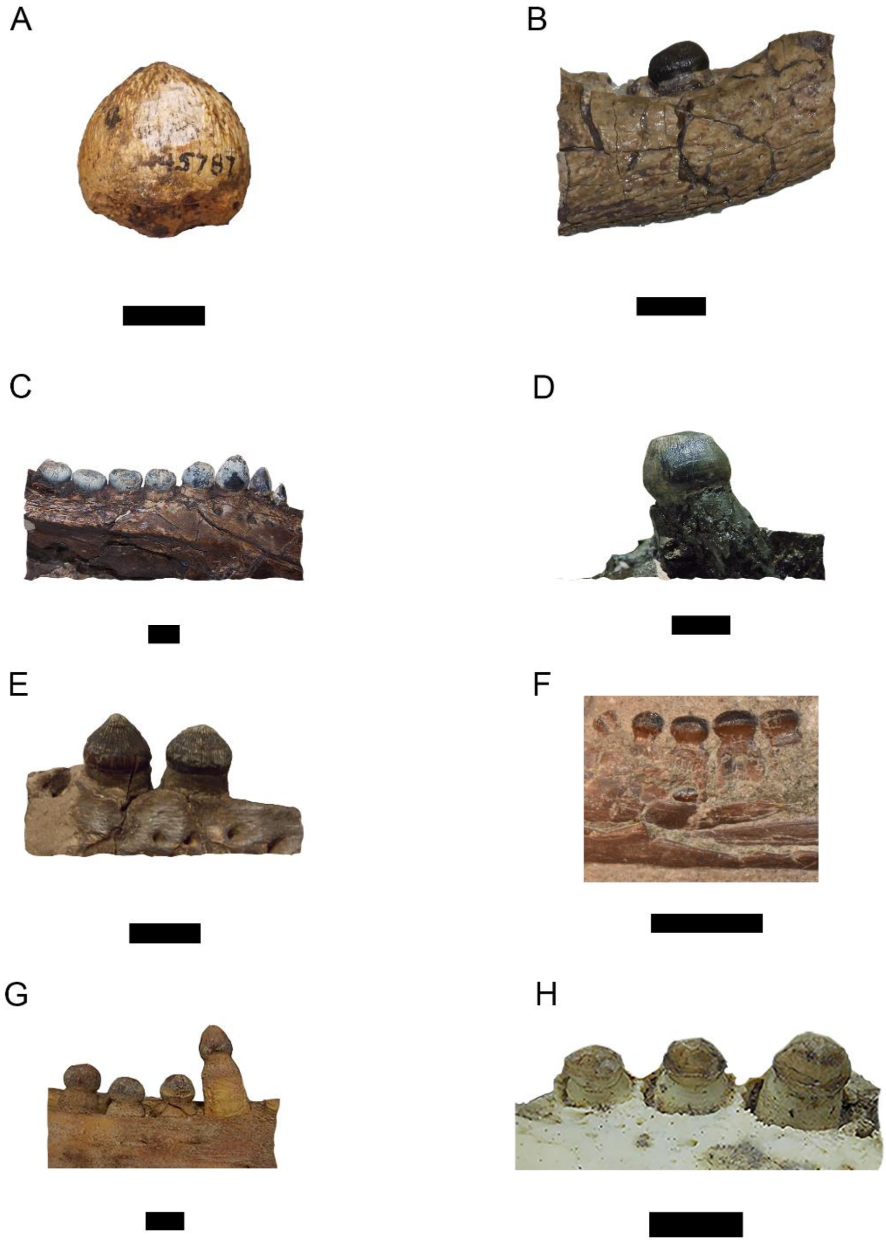

Figure 93: Comparison between the holotype of *Balanerodus logimus* (UCMP-45787, A) and similarly globular teeth in Alligatoroidea: *Allognathosuchus wartheni* (YPM PU-16989), right dentary tooth in lateral view; *Kuttanacaiman iquitosensis*, left dentary teeth in medial view (MUSM-1942, C); *Caiman wannlangstoni*, right maxillary tooth in lateral view (MUSM-2377, D); *Brachychampsa montana*, right maxillary teeth in medial view (AMNH-5032, E); *Procaimanoidea utahensis*, posterior right dentary teeth in medial view (USNM-15997, F); *Caiman niger*, posterior right dentary teeth in lateral view (MN-64, G); *Caiman latirostris*, posterior left maxillary teeth in medial view (MACN-30612, H). Taken from Cidade et al. (2019e). Scale bars = 1 cm.

4.2.2. *Caiman australis*

The species *Crocodilis australis* was proposed by Bravard (1858) based on an unknown number of cranial fragments, isolated teeth and 'placas huesosas' (which most likely refer to osteoderms). Unfortunately, the author did not name a holotype or a syntype, neither clarified whether the fossils constituted a single specimen or several specimens and also did not provide illustrations of the fossils. Posteriorly, the same author would quote the name *Crocodilus australis* is a litagraphic catalogue about fossil species in Argentina (Bravard, 1860; see Buffetaut, 2016, for a copy of the original catalogue). However, neither of these are official publications and thus cannot be considered for nomenclatural acts; consequently, *Crocodilus australis* Bravard, 1858 is a *nomen nudum*.

Posteriorly, Burmeister (1883), due to the little availability of Bravard's 1858 publication, reprinted the latter, but with some changes: while Bravard (1858) refers only to cranial fragments, teeth and osteoderms as belonging to *C. australis*, Burmeister (1883) mention all of these but also a vertebra, which was not mentioned by Bravard (1858). Later, Burmeister (1885) published another volume dedicated to a critical analysis of the fossils described by Bravard (1858). In this work, the author described a left maxilla (MACN-258, the same specimen later identified as the "type" of the species by Rovereto, 1912 and as the "holotype" of the species by Bona et al., 2012), isolated teeth and an isolated vertebra as belonging to *C. australis,* while assigning an osteoderm (that was also apparently part of the material assigned by Bravard (1858) to *C. australis*) to the gavialoid *Gryposuchus neogaeus,* a species that Burmeister described in the same work (1885). In terms of nomenclatural validity, as the publication of Burmeister (1883) may be considered official and as it makes use of the name *Crocodilus australis,* it is possible to consider this a nomenclatural act for a *nomen novum*, and as such *C. australis* Burmeister, 1883 is an available name. However, this name is a junior primary homonym of *Crocodilus australis* Krefft, 1867, a name proposed for the extant crocodyloid *Crocodylus johnstoni* Krefft, 1873, and as such is a permanently invalid name.

Posterior authors who studied the South American fossil *Crocodilus australis,* however, seemed to be unaware of this synonymy. Ambrosetti (1887) created the new genus *Proalligator* to place *Crocodilus australis* in it, while also describing associated right premaxilla and maxilla that he argues to belong to the same individual of the left maxilla described by Burmeister (1885) and a mandibular fragment and isolated teeth and osteoderms that he assigns to *P. australis*, but does not state whether they belonged to the same individual of the left maxilla of Burmeister (1885).

Scalabrini (1887), upon reviewing the record of fossil crocodylians in Argentina, referred to the species described by Bravard (1858) as "*Crocodilus meridionalis* Bravard", apparently due to a lapsus (according to Rusconi, 1933), only mentioning the presence of 'dientes y placas" ("teeth and osteoderms", presumably) that had been described by Burmeister (1885) as pertaining to that species. The author also proposed other two species: *Crocodilus paranensis* and *Alligator paranensis*. Whether the materials in which these last two species were based had any relation to *Crocodilus australis* cannot be known, as Scalabrini (1887) does not specity whether those specimens belonged to the material once assigned to *C. australis* by Burmeister (1885) or not. Posterior works would diverge in this matter: Rovereto (1912) considered *Crocodilus meridionalis*, *Crocodilus paranensis* and *Alligator paranensis* as synonyms of *C. australis* (Bravard, 1858). Rusconi (1933) and Bona et al. (2012) consider only *C. meridionalis* and *A. paranensis* as synonyms of *C. australis*, while Bona & Carabajal (2013) and Bona et al. (2012) consider specimens assigned to *Crocodilus paranensis* as actually belonging to the species *Caiman gasparinae*, described by Bona & Carabajal (2013). As such, we consider *Crocodilus meridionalis* Scalabrini, 1887 as a synonym of *Crocodilus australis* Burmeister, 1883, *Alligator paranensis* Scalabrini, 1887 as a *nomen nudum*, and *Crocodilus paranensis* Scalabrini, 1887 as a species unrelated to *C. australis*.

Rovereto (1912) reclassified the species as *Alligator australis* and stated that the maxilla described by Burmeister (1885) was the "type" of the species, which is the first mention of a "type" of any kind for the species. Additionally, he also described an incomplete left premaxilla and two fragments (one anterior and another posterior) of a right mandible that he assigns to *A. australis*, but it is not known whether these last specimens were part of the material studied by previous authors.

Rusconi (1933) reclassified it as *Proalligator australis* and redescribed the "type" and the specimens described by Rovereto (1912), aside from assigning another premaxilla and another mandibular material to the species. Patterson (1936) considered

Crocodilus australis Bravard, 1858 as a *nomen nudum*, but considered the species valid when described by Burmeister (1885) and classified it into the genus *Proalligator* – thus *Proalligator australis* (Burmeister, 1885). This proposal was followed by Langston (1965), who also suggested that the "type" described by Rovereto (1912) constituted either "the holotype or the neotype" of *P. australis*.

Finally, Bona et al. (2012) reclassified it as *Caiman australis* (Burmeister, 1885) and named the specimen MACN-258 (the isolated left maxillae called the "type" of the species by Rovereto, 1912, Fig. 94) as the "holotype" of the species. This act, however, is erroneous, as if one considers as the species valid the one described by Burmeister (1883), it is not known whether the specimen belonged to the type material; and, even if one considers as valid the species as described by Burmeister (1885), MACN-258 would be either a lectotype or part of the holotype, but not the holotype.

Considering these issues, a taxonomic review of the species *Caiman australis* was deemed as necessary. The first step in this review was to undertake an analysis of the "holotype" (Fig. 94) as only specimen assigned to the species by Bona et al. (2012) in order to establish whether the specimen would constitute a distinct taxon or not; all remaining taxonomic issues to be solved would stem from this initial perspective.

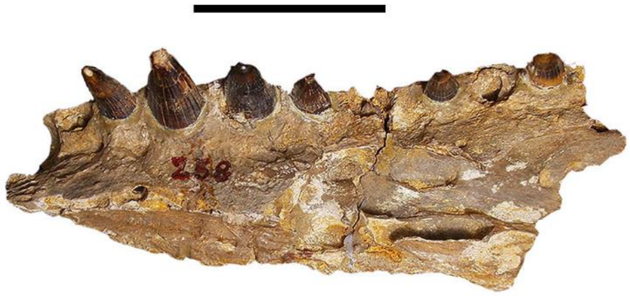

Figure 94: *Caiman australis*: specimen MACN-258, an isolated left maxilla in ventral view. Modified from Cidade et al. (2019a). Scale bar = 10 cm.

MACN-258 is an isolated nearly complete left maxilla (Fig. 94). The specimen is narrow, indicating that the whole rostrum of the individual would be longer than wide (Bona et al., 2012). The dorsal surface is ornamented with scarce elevations and grooves, but also exhibits several eroded portions. The medial suture with the nasal and the posterior sutures with the jugal, lacrimal and presumably the prefrontal are preserved. The anterior suture with the premaxilla is partially preserved, being progressively eroded from the lateral to the medial margin of the contact between the bones. The specimen preserves nine alveoli. All of the preserved alveoli exhibit fully erupted teeth except for the first, sixth and eighth alveoli, which preserve only very recently erupted teeth crowns. However, the teeth seemed to have been glued into the alveoli, as pointed out by Rusconi (1933); in fact, remains of the glue are still in the base of the implanted teeth. The third and fourth preserved alveoli are the largest of the maxilla; however, given the artificial implantation of the teeth, it is not known whether the two alveoli had the same size or if one of them was larger, a feature that has systematic importance as detailed below. The first four preserved alveoli are rounded in shape while the last five preserved alveoli and teeth are slightly lateromedially compressed.

The overall shape of the specimen distinguishes it from several crocodylomorph taxa of the Cenozoic of South America, such as Sebecidae, Gavialoidea and the crocodyloids *Brasilosuchus* and *Charactosuchus*. The fact that the third and fourth alveoli are both the largest in the maxilla would distinguish *Caiman australis* from the remaining Crocodyloidea, in which the largest maxillary alveolous is either the fifth or both the fourth and the fifth (see Brochu, 2011 and Cidade et al., 2017). This feature would also distinguishes this taxon from most Alligatoroidea, in which the fourth alveolous is the largest, while both the fourth and fifth are the largest in *Leidyosuchus* and *Diplocynodon*, the fifth is the largest in *Brachychampsa*, and the third is the largest in *Culebraushcus*, *Gnatusuchus* and *Globidentosuchus* (see Brochu, 2011 and Cidade et al., 2017). The only taxa of Brevirostres (clade formed by Alligatoroidea and Crocodyloidea *sensu* Brochu, 2003) to also exhibit the third and fourth alveolus as the largest of the maxilla are *Caiman gasparinae*, which is also from the 'mesopotamiense' late Miocene of Argentina (Bona & Carabajal, 2013), and *Purussaurus* sp. nov. (UCMP-39704), from the middle Miocene of Colombia (see Langston, 1965, and below). However, *C. australis* may be distinguished from *Purussaurus* by the overall morphology of the skull, as mentioned previously (see Langston, 1965; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006; Aureliano et al., 2015), and from *C. gasparinae* by the narrowness of the maxilla and by the small size and the lateromedial compression of the alveoli. Both these last features can be seen in the maxillae on both species of the extant *Paleosuchus*, with a narrow maxilla being more frequent in *P. trigonatus* (Carvalho, 1951; Medem, 1958). However, *Paleosuchus* can be differed from the fact that none of the *Paleosuchus* specimens analyzed in this study exhibit maxilla as dorsoventrally flattened and with as extreme a reduction of the festooning as in *C. australis*.

However, as it is possible that the third or the fourth alveolous may be the largest, further systematic considerations are needed. First, the specimen can be classified as an alligatoroid independently of whether of these two alveoli are the largest or whether both are of the same size, as any of these characters is almost exclusively found in Alligatoroidea within Crocodylia. Brochu (2011) scores the basal gavialoid *Thoracosaurus neocesariensis* as having the third maxillary alveolous as the largest of the bone, but as mentioned previously the overall morphology of *C. australis* is very distinct from gavialoids and is closer to *Paleosuchus*, a caimanine alligatoroid. Regarding the alligatoroids that have the third or the fourth alveolous as the largest of the maxilla, mentioned previously, *C. australis* (the specimen MACN-258) differs from all of those by the long, narrow, dorsoventrally flattened form of the rostrum, as mentioned previously.

Regarding generic assignment, our review finds no basis for the assignment of MACN-258 to any other currently valid genus, since it differs from all of them, including *Paleosuchus*. As such, another generic name must be used, and the most coherent decision is to assign it to the *Proalligator* genus, which was already erected to house the species to which the specimen belonged and is the oldest available name for a distinct genus involving the species. The specific epithet to be used is another issue: *australis* Burmeister, 1883 is permanently invalid as it is a junior homonym of *Crocodilus australis* Krefft, 1867. Currently, research is underway as to whether the name *meidionalis* proposed by Scalabrini (1887) – even if such a proposal was based on a mistake, as it appears likely to have been – may be used as an alternative name for the species described by Burmeister (1883). If this is not the case, a new specific name shall be created.

4.2.3. *Caiman gasparinae*

The holotype of *Caiman gasparinae* (MLP-73-IV-15-1) is a rostral fragment associated with an incomplete skull table (see Figs. 74 and 95, and Bona & Carabajal, 2013). The only other specimen referred to the species in the original description is an incomplete right premaxilla (MACN-5555). In the original diagnosis of the species, Bona & Carabajal (2013, p. 4) state that *C. gasparinae* distinghuishes itself from other Crocodylia taxa for the following features: “large, broad-snouted caiman with a low rostrum; narial opening oriented dorsally and broadly distanced from the anterior margin of premaxilla; interpremaxillary suture long with respect to the intermaxillary suture; occipital surface of the braincase with the poorly developed *crista tuberalis* exposing the carotid foramen in lateral view; the carotid foramen is bounded by the *crista tuberalis* only posteriorly”.

Caiman gasparinae may be considered a caimanine alligatoroid for having the exposure of the supraoccipital in dorsal view large such that it excludes the parietal from the posterior margin of the skull table, a character found only in Caimaninae among Crocodylia. Another character, the dermal bones of skull roof overhanging the rim of small, nearly circular supratemporal fenestra, is also typical of caimanines, although this character is also found in *Diplocynodon deponiae* and in osteolemine crocodyloids among Crocodylia (see Brochu, 2011). Among these five characters, the first three are not considered here as diagnostic for *Caiman gasparinae* as they are present in several other crocodylian species, extinct and extant. A broad-snout and low rostrum is present is all extant Caimaninae species, except those of the *Paleosuchus* genus and in the subspecies *C. crocodilus apapporiensis* (vide Medem, 1958; Escobedo-Galván et al., 2015). As for a “large size”, Bona & Carabajal (2013) estimate the skull length of *C. gasparinae* in 45 cm. The authors did not state the methodology used in the estimation, but a 45 cm skull length is within the range of the extant caimanine *Caiman niger* (see Foth et al., 2013), which can be indeed considered a ‘large’ size, but that is then not exclusive to *C. gasparinae*. The second character, “narial opening oriented dorsally and broadly distanced from the anterior margin of premaxilla”, can also be found in all extant and most fossil caimanines, with exception of *Tsoabichi greenriverensis* (Brochu, 2010) and *Caiman wannlangstoni* (Salas-Gismondi et al., 2015). Regarding the third character “interpremaxillary suture long with respect to the intermaxillary suture”, in fact sutures with a similar size to that seen in *C. gasparinae* can be seen in other caimanines such as *Globidentosuchus* (Scheyer et al., 2013) and *Mourasuchus* (see Cidade et al., 2017). Whereas *C. gasparinae* may be distinguished from *Mourasuchus* based on the overall morphology of the two taxa (see Cidade et al., 2017 for the overall morphology of *Mourasuchus*), the same is not true for *Globidentosuchus*, and as such this character may not be useful for taxonomic differentiation.

Regarding the last two characters ("occipital surface of the braincase with the poorly developed *crista tuberalis* exposing the carotid foramen in lateral view. The carotid foramen is bounded by the *crista tuberalis* only posteriorly"), comparisons made between *Caiman gasparinae* and the extant (*Caiman crocodilus*, *C. latirostris*, *C. yacare*, *C. niger*, *Paleosuchus palpebrosus* and *P. trigonatus*) and some fossil caimanines (C. *brevirostris*, *C. wannlangstoni*, *Gnatusuchus pebasensis*, *Kuttanacaiman iquitosensis*, *Mourasuchus arendsi*, *M. pattersoni* and *Purussaurus brasiliensis*) did not found the two characters in any other taxon besides *C. gasparinae*. As such, those two characters may be considered autapomorphies of the species, but this must be seen with some caution as the area in question is not preserved in several fossil caimanines, whereas in others the area is deteriorated and in some cases the area could not be seen in species for which only photos were available.

Figure 95: Rostrum of the holotype of *Caiman gasparinae* (MLP-73-IV-15-1) in dorsal view. Modified from Cidade et al. (2019a). Scale bar = 10 cm.

However, there is another character that distinguishes *Caiman gasparinae* from all other caimanines and, in fact, from all other alligatoroids: the fact that the third and the fourth maxillary alveoli are of the same size and are the largest of the bone (Fig. 74). As discussed previously, *Caiman australis* (MACN-258) seems to share this character with *Caiman gasparinae*, but in the former the teeth seem to have been artificially implanted (see Rusconi, 1933), which may have distorced the original morphology of the specimen. In most alligatoroids, the largest maxillary alveolus is either the fourth or the third alveolus (see Brochu, 1997a, 2011, and above).

As such, *Caiman gasparinae* Bona & Carabajal, 2013 is considered here as a valid species, with the following diagnosis: a caimanine alligatoroid that differs from other caimanines for having the third and the fourth maxillary alveoli of the same size and as the largest of the maxilla, the occipital surface of the braincase with a poorly developed *crista tuberalis* exposing the carotid foramen in lateral view, and the carotid foramen being bounded by the *crista tuberalis* only posteriorly.

4.2.4. *Caiman lutescens*

Caiman lutescens was proposed as "*Alligator lutescens*" by Rovereto (1912) based on the large size exhibited by several isolated cranial and postcranial fossils from the late Miocene Ituzaingó Formation of Argentina. As the author did not name a holotype, the whole lot of specimens present in the original description may be considered the syntype of *C. lutescens*. Posteriorly, Rusconi (1933) reclassified the species as *Xenosuchus lutescens* and named one of the specimens of the syntype, an articulated left premaxilla and incomplete left maxillar (MACN-5416; Fig. 96) as the lectotype of the species. Posteriorly, Patterson (1936) would consider *X. lutescens* as a junior synonym of *Caiman paranensis* (Scalabrini, 1887), while Langston (1965) considered the species described by Rovereto (1912) as valid, while reclassifying it in *Caiman* – hence the species being known as *C. lutescens* thenceforth.

Figure 96: MACN-5416, lectotype of *Caiman lutescens*. Scale bar = 5 cm.

Later, Gasparini (1973, 1981) considered *C. lutescens* as a junior synonym of *C. latirostris* (Spix, 1825). Bona et al. (2012), however, while also considering the lectotype MACN-5416 (Fig. 96) as belonging to *C. latirostris* (therefore also considering *C. lutescens* a junior synonym of *C. latirostris*), also considered *C. lutescens* as a valid species, calling the specimen MACN-13551 (Fig. 97), an incomplete posterior portion of the skull originally described by Rovereto (1912) as one of the specimens of *C. lutescens*, as the "holotype" of the species.

This work follows Gasparini (1973, 1981) in considering *Caiman lutescens* as a junior synonym of *C. latirostris* as the lectotype of the former species (MACN-5416) indeed does not show morphological differences in comparison with the latter. Regarding the specimen MACN-13551, it cannot be considered the holotype of *C. lutescens* (as proposed by Bona et al., 2012) since the type specimen of the species is the lectotype, named by Rusconi (1933), and also by the fact that a holotype could only be named or be present in the original description of the species, and not being named posteriorly. While MACN-13551 was part of the syntype described by Rovereto (1912), from the naming of the lectotype on all the other specimens of the syntype lose prerogative regarding being a name-bearing specimen.

Figure 97: Specimen MACN-13551 (Caimaninae indet.) in dorsal view.

From these findings, a new taxonomic assignment to the specimen MACN-13551 is needed. This overall morphology of the specimen is similar to that of most caimanines. One feature in particular deserves mention: the frontal of MACN-13551 is very short, with its anterior margin not reaching what would be the anterior margins of the orbits (the orbits are incomplete in the specimen, see Fig. 97). However, this feature is also present in other caimanines: *Acresuchus pachytemporalis* (see Souza-Filho et al., 2019), *Purussaurus mirandai* (see Aguilera et al., 2006), *Purussaurus* sp. nov. (UCMP-39704, see Langston, 1965), *Mourasuchus atopus* (see Langston, 1965), *Globidentosuchus brachyrostris* (see Scheyer et al., 2013; Bona et al., 2017), and the specimen MCNC-243, holotype of *Melanosuchus fisheri* (*Caiman* sp. according to this study, see below). MACN-13551 can be distinguished from *Acresuchus*, *Purussaurus* and *Mourasuchus* for the absence of high hypertrophies ("horns") in the squamosal bones (see Cidade et al., 2017, 2019c; Souza-Filho et al., 2019). In *G. brachyrostris* and MCNC-243, the hypertrophies are also absent, and as such there are no systematically important differences between those and MACN-13551. As a result, as MACN-13551 is considered here as belonging to an indeterminate Caimaninae.

An interesting point to be raised in a possible proximity between MACN-13551 and *Caiman gasparinae*, which is also from the Ituzaingó Formation. Additionally, both exhibit similar coloration and ornamentation pattern, although these features are not systematically relevant. The only difference between the specimen and the species is in the shape of the supra-temporal fenestrae: while those of *C. gasparinae* are large with a circular to oval shape, the fenestra of MACN-13551 are small, with an oval shape. The shape and relative size of the fenestra varies individually and with ontogeny in living caimanines: generally, these structures are significantly large after the hatch, from which they become progressively smaller relative to the size of the skull table as the ontogeny progresses (Brochu, 1997a). As such, the difference seen between MACN-13551 and *C. gasparinae* is not systematically relevant. However, *C. gasparinae* also does not preserve the frontal entirely (see Bona & Carabajal, 2013), which further hinders comparison between it and the specimen. As such, MACN-13551 is better seen as an indeterminate caimanine, although the finding of more complete material that can be assigned as close to MACN-13551 (or of *C. gasparinae*) may reveal whether the species to which MACN-13551 belonged is closer to *Globidentosuchus*, *Caiman niger* or *C. gasparinae*.

4.2.5. *Caiman niger* and MCNC-243

The extant black caiman (Fig. 46), which inhabits predominantly the Amazon Basin in the north of South America, was originally named by Spix (1825) as *Caiman niger*, posteriorly becoming *Melanosuchus niger* upon the erection of the new genus by Gray (1862). The species went on to be called by several names (see Carvalho, 1951) until the name *M. niger* became established around the middle of the XX Century (see Carvalho, 1951; Langston, 1965). The emergence of phylogenetic systematics has generated doubs about the generic assignment of the species. In all morphological analysis of extant and extinct alligatoroids, *Melanosuchus niger* was found as close to the genus *Caiman*, and particularly to the species *Caiman latirostris* (Brochu, 1999, 2010, 2011; Hastings et al., 2013; Scheyer et al., 2013; Fortier et al., 2014; Cidade et al., 2017; Souza-Filho et al., 2019). Molecular analyses also show an affinity between *M. niger* and *Caiman*, although in most of these *M. niger* appears as the sister-taxon of a *Caiman* clade (e.g., Oaks, 2011). Given these results, it is here considered that there is no need for a different genus for this species, and as such *Melanosuchus* Gray, 1862 is considered as a junior synonym of *Caiman* Spix, 1825, and hence the black caiman is named as *Caiman niger*, which is a return to its original appellation.

Figure 98: Secimen MCNC-243 (holotype of *Melanosuchus fisheri*, here assigned as *Caiman* sp.) in dorsal view.

A fossil species was proposed to belong to *Melanosuchus*: *M. fisheri* Medina, 1976, from the late Miocene Urumaco Formation of Venezuela. This species, however, was posteriorly considered a *nomen dubium* (see Bona et al., 2017 and Foth et al., 2018), with its holotype (MCNC-243; Fig. 98) being assigned either as "*Melanosuchus* sp." (Bona et al., 2017) or "*Melanosuchus cf. M. niger*" (Foth et al., 2018), while the only other known specimen (MCZ-4336) was assigned to *Globidentosuchus brachyrostris* (Bona et al., 2017; Foth et al., 2018). This new assignment of MCZ-4336 is followed by this study. Regarding MCNC-243, given the generic reassignment of *M. niger* into *Caiman*, a reeaxamination of the taxonomic status of the specimen is necessary. The fact that MCNC-243 probably represents a juvenile individual (see Bona et al., 2017; Foth et al., 2018) difficultes a definitive assessment of its traits, but features present in the specimen such as supertemporal fenestrae not obliterated, circular and with the dorsal rim overhung of the bones surrounding it (Character 135-1), a circular external naris (Character 77-0) and the presence of proeminent *canthi rostralli* without a depression lateral to ti (Character 89-1) allows an preliminary assignment of the specimen as *Caiman* sp., with affinities with the species *C. latirostris* and *C. niger*.

4.2.6. *Caiman venezuelensis*

The holotype and only known specimen of *Caiman venezuelensis* (OR-1677; (Figs. 99 and 100) is an incomplete left premaxilla and a very small portion of the left maxilla. It preserves the third, fourth and fifth alveoli, part of the second alveolus, the occlusal pit for the fourth mandibular alveolus. Only the tooth of the fifth alveolus is preserved, and only the posterolateral portion of the incisive foramen is preserved. The suture with the right premaxilla is preserved and is large, extending anteriorly until the anterior margin of the fourth alveolus.

The presence of a pit for the occlusion of the fourth mandibular tooth between the premaxilla allows an assignment of OR-1677 to Alligatoroidea (see Brochu, 1997a, 1999), while the fact non-caimanine alligatoroid fossils are not known from the either the Pliocene or Pleistocene of South America (see Fortier & Rincón, 2012) allows as assignment of it to Caimaninae. Among Caimaninae taxa, the specimen can be clearly distinguished from the peculiar *Purussaurus* (see Aguilera et al., 2006; Aureliano et al., 2015) and *Mourasuchus* (see Langston, 1965; Cidade et al., 2017), which have very derived morphologies in the premaxillae; from *Paleosuchus*, which has only four premaxillary teeth (Brochu, 1997a, 1999); and from *Caiman niger* for not presenting the vomer ventrally exposed in the posterior portion of the maxilla (see Brochu, 1999). OR-1677 may be distinguished from *Caiman latirostris* for exhibiting the perforation for the fourth mandibular tooth posteriorly to the fifth premaxillary alveolous, which does not occur in that species (Bona et al., 2012). Regarding the extant species of *Caiman* and the fossil Caimaninae species that preserve premaxillae, the holotype of *C. venezuelensis* differs for having the premaxilla significantly narrow, longer than wide, with a large contact between both premaxillae posteriorly to the incisive foramen. The only exceptions among these are some specimens of the subspecies *Caiman crocodilus apaporiensis* Medem, 1955: all specimens analyzed in this study also exhibit premaxilla significantly longer than wide. Additionally, some specimens of *C. crocodilus apaporiensis* (the holotype FMNH-69812, FMNH-69813, FMNH-69821, FMNH-69824 and, in FMNH-69828, only in the left premaxillae; Figs. 99 and 100) exhibit a large contact between both premaxillae posteriorly to the incisive foramen. The fact that this second character is exhibited by some of the largest studies specimens of *C. crocodilus apaporiensis* in this study suggests that this trait appear late in ontogeny in this subspecies, although a mere individual variation is also possible; the difference in size between the premaxillae of FMNH-69828 supports this last hypothesis. This issue must be assessed by thorough ontogenetic studies on the subspecies.

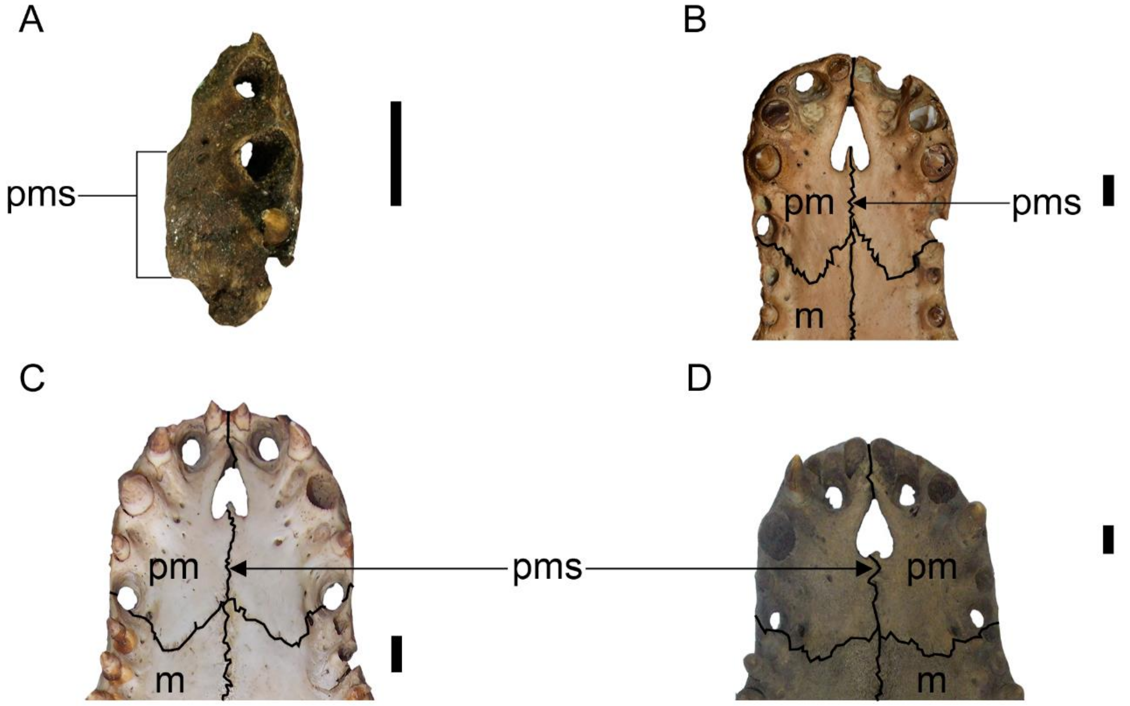

Figure 99: Comparison between the holotype of *Caiman venezuelensis* in ventral view and extant *Caiman*: *C. venezuelensis* (OR-1677, holotype, A); *C. crocodilus apaporiensis*, premaxillae (FMNH-69812, holotype, B); *C. crocodilus*, premaxillae (MCT-148-RR, C); *C. yacare*, premaxillae (MACN-30595, D). Taken from Cidade et al. (2019e). m = maxilla, pm = premaxilla, pms = suture between both premaxillae. Scale bars = 1 cm.

These two shared characters between *C. crocodilus apaporiensis* and OR-1677 represent two of the proposed diagnostic characters proposed by Fortier & Rincón (2012) for *C. venezuelensis* (as 'premaxilla nearly twice as long than wide in ventral view, with near parallel sides' and 'premaxillae in close contact medially in ventral view in half of their [length], forming a narrow and long wall', respectively). Although narrow and significantly longer than wide premaxillae as that of the holotype of *C. venezuelensis* can be seen only in the specimens of *C. crocodilus apaporiensis*, premaxillae nearly twice as long than wide in ventral view (but not as narrow as in *C. venezuelensis*) can be observed in other Caimaninae taxa, such as in *C. crocodilus* specimens not assigned to *C. crocodilus apaporiensis* (MCT 148-RR, MCT-155-RR, MCT-300-RR, MN-25461), and in *C. yacare* (MACN-30595; Fig. 99), *C. niger* (MN-63, MN-81, MN-3174, MCT-286-RR) and *Paleosuchus palpebrosus* (MCT-291-RR).

Additionally, premaxillae in close contact medially in ventral view in half of their length can also be seen in at least one specimen of *C. crocodilus* that is not assigned to *C. crocodilus apaporiensis* (MCT-148-RR; Fig. 3–C) and in one of *Paleosuchus* sp (MCT-270-RR).

Regarding the other three diagnostic characters proposed by Fortier & Rincón (2012), a 'linear premaxillae suture posterior to the incisive foramen' is also seen in several specimens of *C. crocodilus apaporiensis* (FMNH-69812, FMNH-69813, FMNH-69819, FMNH-69824, FMNH-69828, FMNH-69831, FMNH-69832), *C. crocodilus* non-*apaporiensis* (MN-1031, AMNH-43291, MCT-148-RR, MCT-155-RR, MCT-300-RR, Fig. 99) and *C. yacare* (MN-68, MN-1259, MN-9755, AMNH-R-97305, MACN-30542, MACN-30593, MACN-30602, MACN-30637), but also in at least one specimen of *C. latirostris* (MCT-156-RR), *C. niger* (AMNH-R-58130) and *Paleosuchus* sp (MCT-268-RR). Furthermore, 'tooth row relative to the last four premaxillary form a straight line rather than curved, in ventral view' is very evident in all specimens of *C. crocodilus apaporiensis* analyzed in this study except for FMNH 69819, which is a hatchling and thus exhibits early staged of development, and is also seen in several specimens of *C. crocodilus* non-*apaporiensis* (AMNH-43291, MCT-148-RR, MCT-155-RR, MN-25461; Fig. 99) *C. yacare* (MN-1259, MN-9755, AMNH-R-97305, MACN-30542, MACN-30558, MACN-30593, MACN-30595, MACN-30601, MACN-30602; Fig. 99), and also in some specimens of *C. niger* (MN-64 and MN-3174). In some specimens of *Paleosuchus palpebrosus* (MN-317, AMNH-R-93812, MCT-269-RR, MCT-291-RR), *P. trigonatus* (MN-65, MN-2491, MN-9757, AMNH-R-66391) and *Paleosuchus* sp. (MCT-268-RR and MCT-270-RR), the three last premaxillary teeth (which are homologous to the last three premaxillary teeth of other caimanines, in spite of the fact that *Paleosuchus* has only four premaxillary teeth as opposed to five in the others – see Brochu, 1997a) also form a straight line in ventral view.

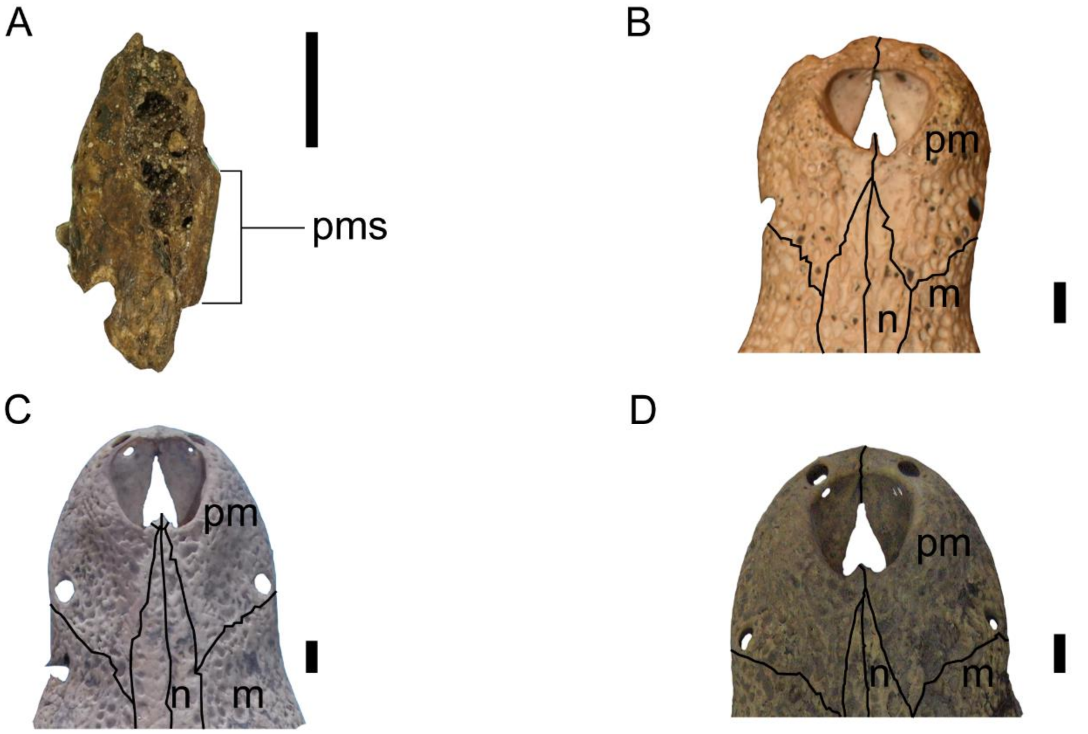

Figure 100: Comparison between the holotype of *Caiman venezuelensis* in dorsal view and extant *Caiman*: *C. venezuelensis* (OR-1677, holotype, A); *C. crocodilus apaporiensis*, premaxillae (FMNH-69812, holotype, B); *C. crocodilus*, premaxillae (MCT-148-RR, C); *C. yacare*, premaxillae (MACN-30595, D). Taken from Cidade et al. (2019e). m = maxilla, n = nasal, pm = premaxilla, pms = suture between both premaxillae. Scale bars = 1 cm.

As for OR-1677 having an 'incisive foramen long, reaching the fourth premaxillary alveolus', this feature is actually rather common in all species of living Caimaninae, being observed in many of the specimens of living caimanines analyzed by this study: all specimens of *C. crocodilus apaporiensis*; *C. crocodilus* non-*apaporiensis* (AMNH-43291, AMNH-R-137179, MN-1030, MN-1031, MCT-148-RR, MCT-155-RR, MCT-300-RR, MN-25461); *C. latirostris* (MN-1041, MN-1254, MN-1255, MN-1455, MN-2078, MN-2333, MN-9756, MN-11254, MN-24588, AMNH-R-143183, MACN-30566, MACN-30567, MACN-30572, MACN-30610, MCT-156-RR,); *C. yacare* (MN-68, MN-1259, MN-9755, MN-12127, AMNH-R-97305, MACN-30542, MACN-30558, MACN-30593, MACN-30595, MACN-30601, MACN-30602, MACN-8267); *C. niger* (MN-61, MN-63, MN-64, MN-81, MN-3174, AMNH-R-58130, MCT-

286-RR); *P. palpebrosus* (MN-317, AMNH-R-93812, MCT-269-RR, MCT-291-RR) and *P. trigonatus* (MN-65, MN-2491, MN-9757, AMNH-R-66391).

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

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

This taxonomic review has been published in Cidade et al. (2019e).

4.2.7. *Eocaiman itaboraiensis*

Eocaiman itaboraiensis is a species of the Paleocene Itaboraí Basin of Brazil proposed by Pinheiro et al. (2013) based on four specimens: three anterior portion of left mandibular rami (MCT-1791-R, holotype; MCT-1792-R; MCT-1793-R; Fig. 101) and an isolated tooth (MCT-1974-R).

The genus *Eocaiman* has a unique synapomorphy and diagnostic feature that is the dentary being linear from the first to the tenth alveoli, with an elevation posterior to the 11th alveolous (Character 46-2). This feature is not exhibited by any of the three specimens of *E. itaboraiensis* that are mandibular remains. In the holotype (MCT-1791-R, Fig. 101-A), the tooth row is preserved only until the tenth alveolus, and in fact between the fifth and the tenth alveoli there is a slightly curve that can be interpreted as being the morphology described in state 0 of Character 46. The status of MCT-1792-R and MCT-1793-R about this character is inconclusive: in the first, the tooth row is preserved until the 14th alveolous, but there is no sign of the elevation described in state 2 of Character 46. In fact, this specimen also exhibits a very slight curve between the fifth and the tenth alveoli that may be the morphology described in the state 0, similarly to what is observed for the holotype (MCT-1791-R). However, as MCT-1792-R is severely damaged from the eight alveolous on (see Fig. 101-B), a definitive statement regarding the morphology of the specimen in this character is refrained from being made. In the other specimen, MCT-1793-R, the tooth row is preserved until the 12th alveolous and exhibits no difference in height between the 11th and the 12th alveolous and the first ten alveoli (Fig. 101-C), as seen in *E. cavernensis* and *E. palaeocenicus* (Character 46-2). However, at a first glance the specimen exhibits a morphology not observed in any other crocodylian: the dentary from the first to the fourth alveolous is lower than from the fifth alveolous on (Fig. 101-C). Nevertheless, given the small size of the specimen (less than 2.5 mm in length) and its rather not good preservation, caution is needed before stating that this was a natural morphology of the specimen. It is also possible that the morphology seen in MCT-1793-R is a taphonomical artifact, and that the specimen had the dentary linear from the fourth to the tenth alveolous (Character 46-3) or that it had a slight curve in the same area (Character 46-0). As such, a definitive statement about the morphology of this specimen regarding Character 46 is refrained from being made as well.

Figure 101: Main specimens of "*Eocaiman*" *itaboraiensis*: MCT-1791-R, holotype, in medial view; MCT-1792-R, in dorsomedial view; MCT-1793-R, in dorsomedial view. Scale bars = 1 cm.

Three characters are shared between the three specimens: the first dentary tooth being procumbent (Character 44-1; Fig. 67-B), the mandibular symphysis extending until the level between the sixth and eight dentary alveoli (Character 45-1), and the splenial participating in the mandibular symphysis (Character 50-0). The first character is also seen in *E. cavernensis*, but not in *E. palaeocenicus* and most alligatoroids, in which the first dentary tooth is dorsally oriented. The second character is not seen in either *E. cavernensis* or *E. palaeocenicus* (in which the symphysis extends to the level between the fourth and fifth alveoli, the state 0 of Character 45) but is shared with other alligatoroids: the basal form *Leidyosuchus canadensis*, the caimanines "*Caiman*" *brevirostris*, "*Caiman*" *wannlangstoni*, *Culebrasuchus mesoamericanus*, *Globidentosuchus brachyrostris* and *Kuttanacaiman iquitosensis*, and several alligatorines. The third character is not present in *E. palaeocencius*, in which the splenial does not participate in the symphysis and exhibits that state 2 of Character 50, while in *E. cavernensis* the character is not visible. However, it is shared with *Leidyosuchus canadensis*, several alligatorines and with the caimanines *Gnatusuchus pebasensis* and *Globidentosuchus brachyrostris*. Based on these shared characters, it is considered here that the three specimens belong to a single taxon, although the difference seen in MCT-1793-R regarding Character 46 still has to be analyzed with the hopeful finding of more complete, better preserved specimens. Additionally, MCT-1792-R exhibits the 12th alveolous as the largest of the dentary tooth row, which fits into the state 2 of Character 47 and is shared with most caimanines but differs from *E.*

cavernensis, which exhibits state 0 (the specimens of *E. palaeocenicus* are too incomplete for this character to be scored).

The other specimen, an isolated tooh (MCT-1794-R), has no differences compared to a typical crocodylian tooth, and as such must be assigned as “Crocodylia indet.”.

Regarding the taxonomic status of *Eocaiman itaboraiensis*, it is here considered that the specimens MCT-1791-R, MCT-1792-R and MCT-1793 belong at least initially to a single taxon (see previous observation MCT-1793-R), but that it does not belong to the genus *Eocaiman*. As such, a new genus must be created for the species “*Eocaiman*” *itaboraiensis*. The diagnosis of the new genus is the following unique combination of characters: an alligatoroid crocodylian with the first dentary tooth procumbent (shared with *E. cavernensis* and *Leidyosuchus canadensis*); differs from *L. canadensis* for having the fourth dentary alveolous larger than the third, with these alveolous being not confluent; differs from *E. cavernensis* for having the mandibular symphysis extending to the level of the sixth to the eighth alveolous and for having the 12th alveolous as the largest of the dentary.

4.2.8. *Necrosuchus ionensis*

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

Two characteristics indicate that *Necrosuchus ionensis* is a caimanine alligatoroid: the presence of a slender process ventrally to the basioccipital tubera (Brochu, 2011, Character 157-2; Fig. 102), which is found only in caimanines, among Crocodylia, 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 tip of splenial passing dorsal to the Meckelian groove (Brochu, 2011, Character

50-2; Fig. 103). This last feature is present in all caimanines except *Globidentosuchus brachyrostris*, *Gnatusuchus* and "*Eocaiman*" *itaboraiensis*. The scapulocoracoid synchondrosis of the holotype seems to be closing (see Brochu, 2011; fig. 104), and as 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 *Necrosuchus ionensis* belongs to Caimaninae (see Brochu, 1995 and Brochu, 1997a, Character 24, equivalent to Character 23 of the present analysis). In fact, the species has been consistently recovered within the Caimaninae clade by phylogenetic analyses that have included it (Brochu, 2011; Fortier et al., 2014; Hastings et al., 2016).

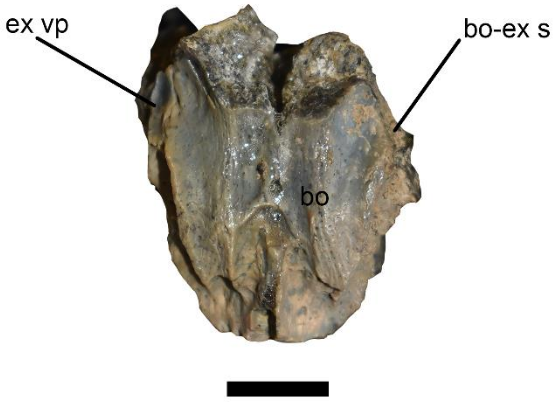

Figure 102: *Necrosuchus ionensis* (AMNH-3219, holotype) basioccipital (bo), left exoccipital ventral process (**ex vp**) and the suture between the basioccipital and the ventral process of the right exoccipital (**bo-ex s**), in occipital view. Taken from Cidade et al. (2019d). Scale bar: 1 cm.

The differential diagnosis proposed by Brochu (2011) for *Necrosuchus ionensis*, however, requires revision. Two of the characters used – the presence of slender process ventrally to the basioccipital tubera and the dentary symphysis extending back to a level just 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 at least 18 dentary alveoli is shared with taxa such as *Eocaiman cavernensis* and *Caiman* (see Brochu, 2011). Upon commenting on the last character, Brochu (2011) also notes that the dentary of *Necrosuchus ionensis* is slender. A slender dentary can also be seen in several caimanines, such as *Paleosuchus* (pers. obs.), *E. cavernensis*, *Centenariosuchus* and *Tsoabichi* (see Simpson, 1933; Brochu, 2010; Hastings et al., 2013). Additionally, the possibility that the width of the dentary may be subject to ontogenetic or individual variations makes this character not useful for taxonomy.

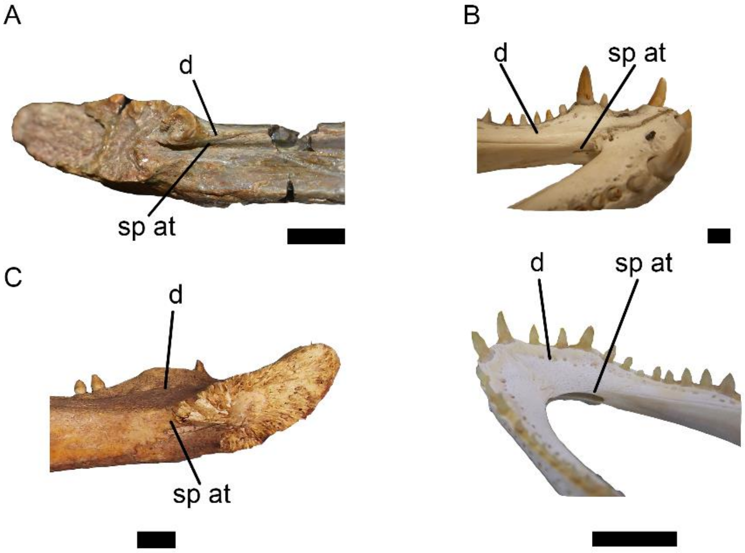

Figure 103: Comparison between the proximity of the splenial anterior tip to the mandibular symphysis in *Necrosuchus ionensis* and extant *Caiman*. *Necrosuchus ionensis*, right mandibular ramus in medial view (AMNH-3219, holotype, A). *Caiman crocodilus*, left mandibular ramus in medial view (AMNH-R-43291, B); *Caiman latirostris*, left mandibular ramus in medial view (MN-2395, C). *C. crocodilus*, right mandibular ramus in medial view (MN-1031, D). Taken from Cidade et al. (2019d). d = dentary; sp at = splenial anterior tip. Scale bar = 1 cm.

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 *Necrosuchus 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. 103). However, how close the splenial gets to the symphysis is variable in at least two extant caimanines: *Caiman crocodilus* and *C. latirostris*. Some specimens of *C. crocodilus* exhibit splenials whose anterior tip is very close to the symphysis (AMNH-R-43291, AMNH-R-137179, FMNH-69817, FMNH-69821, FMNH-69824, FMNH-69825, FMNH-69831, FMNH-69842; Fig. 103) while in others the anterior tip is more distant (FMNH-69819, FMNH-69832, FMNH-69854, FMNH-69855, FMNH-69865, FMNH-73700, MN-1031; Fig. 103). The same difference is observed for *C. latirostris*, in which some specimens exhibit the anterior tip of the splenial close to the symphysis (MN-1255, MN-2078, MN-69, MN-1257, MN-2395; Fig. 103), while in others the anterior tip is more distant (MN-1041, MACN-30566, MCT-156-RR). The specimens that exhibit the splenial anterior tip more distant from the symphysis are juveniles or sub-adults, which raises the possibility of an ontogenetic variation in this character. However, detailed studies about the relation 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.

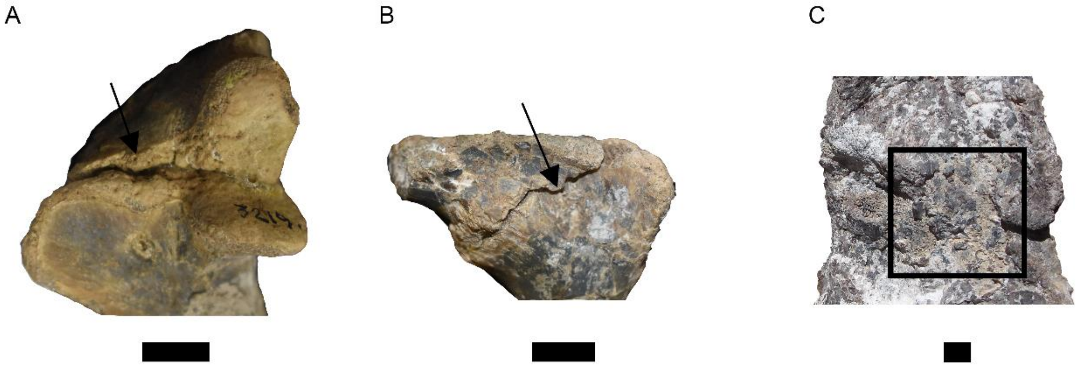

Figure 104: Comparison between the possible beginning of the closure (indicated by arrows) of the left scapuloracoid synchondrosis in *Necrosuchus ionensis* (AMNH-3219; A, lateral view; B, medial view) and the beginning of the closure of the same structure (black square) in the left scapuloracoid of the holotype of *Mourasuchus arendsi* (CIAAP-1297) in medial view (C; see also Cidade et al., 2018). Taken from Cidade et al. (2019d). Scale bars = 1 cm.

There is, however, one character that differs *Necrosuchus ionensis* from most other caimanines: the 13th dentary alveolus as the largest immediately caudal to the fourth dentary alveolus (Fig. 105), which had already been noted by Simpson (1937) and which fits *N. ionensis* into the state 0 (the 13th or the 14th dentary alveolus as the largest immediately caudal to the fourth) of the Character 47. 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): *Caiman crocodilus*, *C. latirostris*, *C. yacare*, *C. niger*, *Centenariosuchus* and *Paleosuchus* (even though there is individual variation in this last genus, as detailed below; see Fig. 105). "*Caiman*" *brevirostris* has the ninth alveolous as the largest, together with a series of a large teeth behind it (state 8 of the same character).

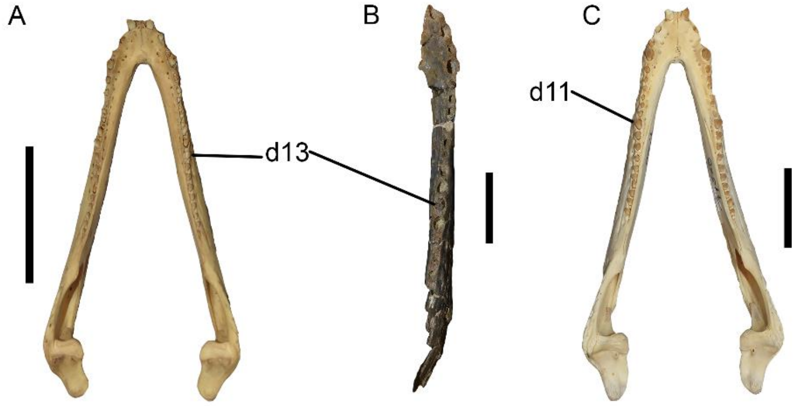

Figure 105: Comparison of the size of the 13th dentary alveolus relative with the other alveoli in *Necrosuchus ionensis* and *Paleosuchus*: *Paleosuchus palpebrosus*, mandibular rami in dorsal view (AMNH-R-137170, A); *Necrosuchus ionensis*, right mandibular ramus in dorsal view (AMNH-3219, holotype, B); *P. palpebrosus*, mandibular rami in dorsal view (AMNH-R-97328, C). Taken from Cidade et al. (2019d). d11 = 11th dentary alveolus; d13 = 13th dentary alveolus. Scale bars: 5 cm.

In other taxa of Caimaninae, a series of large posterior alveoli starts with a large 12th alveolus ("*Caiman*" *wannlangstoni* and *Kuttanacaiman*). In *Necrosuchus ionensis*, the 14th alveolus is only slightly smaller than the 13th, but the alveoli posterior to it are progressively slightly smaller instead. In *Notocaiman stromeri* the largest alveoli are the 15th and 16th. In *Mourasuchus*, the first to the seventh alveoli are the largest of the tooth row, after which the alveoli become progressively slightly smaller (see Character 47, state 7 and Langston, 1965). At least two *Purussaurus* specimens – *P. brasiliensis* specimens DGM-527-R (see Price, 1967) and UFAC-4559 (pers. obs.) –exhibit the 13th alveolus as the largest; most alveoli are not preserved in the holotype of *P. neivensis* (Mook, 1941b), while in the holotype of *P. mirandai* this morphology cannot be clearly seen (see Aguilera et al., 2006) and the most complete specimen of *Purussaurus* sp. nov. (UCMP-39704) does not have mandibles. However, *Necrosuchus ionensis* is markedly distinct from *Purussaurus* by overall mandibular morphology. In the latter, the mandibles are remarkably massive in accordance with the large size *Purussaurus* had (see Langston, 1965; Aguilera et al., 2006; Aureliano et al., 2015) and also for the fact that 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), while 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 (*P. palpebrosus*: AMNH-R-137170, AMNH-R-137174, AMNH-R-145071, AMNH-R-93812, FMNH-69874, MCT-291-RR; *P. triognatus*: MN-65; MN-2491; AMNH-R-129259; AMNH-R-129260; AMNH-R-66391; USNM-234047; Fig. 105), thus varying from the standard in the genus (Fig. 105), which is the state 2 of Character 51 of Brochu (2011). This alone would raise the possibility that *Necrosuchus* could 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 Character 7); the dorsal margin blade of the iliac blade of *Necrosuchus* is rounded, with a modest dorsal indentation (Character 31-1; Fig. 106), similar to *Caiman* (e.g. *C. crocodilus*, Fig. 5-B) but different from *Paleosuchus*, in which the dorsal margin of the iliac blade is narrow, with a dorsal indentation (Character 31-3; Fig. 106); and, most notably, the posterior alveoli and teeth of *Paleosuchus* are lateromedially compressed, while those of *Necrosuchus* are circular (Brochu, 2011, Character 73; Fig. 106.

The alveolar pattern of the dentary of the fossil caimanine *Tsoabichi greenriverensis* has some similarities with that of *Necrosuchus*. The alveolar counting of *Tsoabichi* is not known since the only more 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 since *Necrosuchus* preserve only four alveoli posterior to the two largest posterior alveoli (Fig. 105), while the holotype of *Tsoabichi* preserves from six to seven (see Brochu, 2010, fig. 1).

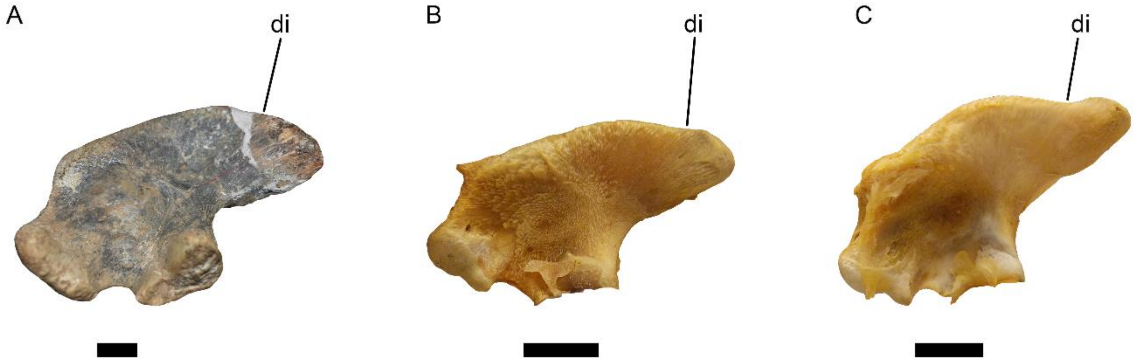

Figure 106: Comparison between the left ilia in lateral view of *Necrosuchus ionensis* (AMNH-3219; A), *Caiman crocodilus* (AMNH-R-137179; B) and *Paleosuchus palpebrosus* (AMNH-R-97326; C), showing the rounded dorsal margin of the iliac blade with modest dorsal indentation (di; A and B) and the narrow dorsal margin with di in C. Taken from Cidade et al (2019d). Scale bar = 1 cm.

Additionally, *Necrosuchus ionensis* differs from *Eocaiman* for having the dentary at the level of the first and fourth teeth at the same level than at the 11th and 12th teeth, while in *Eocaiman* the dentary at the first level is lower than in the second (Character 50-2). It also differs from "*Eocaiman" itaboraiensis* as in the last species the splenial participates in the mandibular symphysis (Pinheiro et al., 2013). *Necrosuchus* also differs from *Gnatusuchus* due to the presence of an extensive mandibular symphysis and the "shovel-like" process in the anterior portion of the mandible in the last taxa, aside from the participation of the splenial in the mandibular symphysis in *Gnatusuchus* (see Salas-Gismondi et al., 2015). From *Culebrasuchus*, *Necrosuchus* differs by having the dentary slightly curved between the fourth and tenth alveoli, while the same portion of the dentary which in *Culebrasuchus* is linear (see Character 46 and Hastings et al., 2013); additionally, the external mandibular fenestra in *Necrosuchus* is small, while in *Culebrasuchus* is large (see Character 59; 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 Character 157; Hastings et al., 2013). Comparisons between *Necrosuchus* and *Protocaiman peligrensis* are limited as the only bone present in both species is the quadrate, which exhibits no systematically relevant differences between them.

As such, *Necrosuchus ionensis* is considered here 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, *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, which is based in comparisons with extant and extinct caimanines.

The emended diagnosis of *Necrosuchus ionensis* is: a caimanine with the following unique combination of characters: differs from all other caimanines (except *Purussaurus brasiliensis* and some specimens of *Paleosuchus*) for having the 13th dentary alveolus as the largest immediately caudal to fourth; differs from *Purussaurus* for having a slender mandibular ramus and for not having the first four alveoli as the largest of the mandibular ramus; differs from *Paleosuchus* for having an atlantal rib without a thin laminae in the anterior end and the posterior mandibular alveoli and teeth not lateromedially compressed.

This taxonomic review was published in Cidade et al. (2019d).

4.2.9. ***Notocaiman stromeri***

The holotype and only known specimen of *Notocaiman stromeri* is PVL-752 (Fig. 107), an isolated, robust left mandibular fragment with 16 alveoli preserved. Originally described by Rusconi (1937) as a distinct, ‘huge’ alligatoroid, the assessment of further authors about the taxonomic validity of the species has varied. While Langston (1965), Brochu (2011) and Bona & Barrios (2015) considered *Notocaiman stromeri* a valid species, Gasparini (1973) in her PhD thesis considered it not valid and assigned the specimen as a “Eusuchia indet.”. This perspective would be followed by other works (Gasparini & Báez, 1975; Báez & Gasparini, 1977, 1979; Gasparini, 1981), but as the data of Gasparini’s 1973 thesis on *Notocaiman* has never been published, the species has never left to be formally valid. Fortier (2011) suggested that *Notocaiman* could be a junior synonym of *Eocaiman* due to similarities between the two taxa, but this perspective as well as a detailed comparison between the two has also never been published. In order to clarify these issues, a taxonomic review of *Notocaiman stromeri* was performed in this study.

Figure 107: Holotype and only known specimen of *Notocaiman stromeri* (PVL-752) in dorsal view. Scale bar = 5 cm.

The holotype (PVL-752) consists of an isolated left mandibular fragment comprised of the most anterior portion of the dentary and the splenial, with 16 alveoli preserved, with the 16th alveolous being preserved only in its anterior portion (Fig. 107).

The fourth to the seventh alveoli are lateromedially compressed; this may be either due to taphonomical effects or a natural morphology. The alveoli posterior to the seveth are roughly circular, and the first three alveoli are severely eroded to the point that their shape cannot be observed. The specimen has a brownish colour and is poorly preserved, exhibiting several distortions, probably of taphonomical origin, especially on the medial side. The fourth alveolus bears an almost complete tooth, which is roughly conical and eroded to the point that the carinae are not evident. The eight, ninth, 10th, 11th, 13th, 14th, 15th and 16th alveoli bear only the most basal portions of broken teeth. Among the ten first alveoli, the fourth alveolous is the largest (which is in accordance with the measurements of Rusconi, 1937). Posteriorly, the 14th, 15th are noticeably larger either lateromedially or anteroposteriorly, being roughly of the same size and the largest of the entire tooth row; the 16th alveolous is the smaller, and the 14th and the 15th are larger and roughly of the same size. It is possible that these three last alveoli bore globular teeth, like the posterior teeth of taxa such as *Brachychampsa*, *Stangerochampsa*, *Globidentosuchus, Kuttanacaiman,* "*Caiman*" *wannlangstoni* and the teeth assigned to *Balanerodus* (see Langston, 1965; Erickson, 1976; Langston & Gasparini, 1997; Brochu, 2004a; Scheyer et al., 2013; Salas-Gismondi et al., 2015).

In medial view, the mandibular symphysis is severely eroded, but its presence can be noticed. It extends to the level of the fifth mandibular alveolous. The splenial is present, comprising most of the medial wall of the mandibular ramus posterior to the mandibular symphysis, but without participating in the symphysis. It is not possible, however, to state whether the anterior tip of the splenial would be situated dorsal or ventral to the Meckelian groove (Character 50).

Among systematically important characteristics, the mandibular symphysis reaching the level of the fifth alveolous fits *Notocaiman* into the state 0 of Character 45, which encompass also the taxa in which the symphysis reaches the level of the fourth alveolous. The morphology of most alligatoroids fit into the state 0 of Character 45, except *Mourasuchus* (in which the symphysis extends only to the level of the first alveolous) and those in which the symphysis goes to the level of the sixth alveolous and beyond. These last taxa include many that are considered durophagous, like *Ceratosuchus, Allognatosuchus, Gnatusuchus, Globidentosuchus, Kuttanacaiman, Eocaiman* and "*Caiman*" *wannlangstoni* (see Brochu, 2004a; Salas-Gismondi et al., 2015; Cidade & Hsiou, 2018). In fact, a long mandibular symphysis (reaching the level of the sixth alveolous or beyond) has been associated with a durophagous feeding habit by Salas-Gismondi et al. (2015). The fact that the 14th dentary alveolous and a series behind it (the 15th and the 16th) are the largest of the dentary fits *N. stromeri* into the state 1 of Character 47. Furthermore, these posteriormost teeth are large and globular, which fits the taxon into the state 2 of Characer 171; this feature indicates that *N. stromeri* is an alligatoroid, as the character is found only among members of this group in Crocodylia. However, the presence of this feature also precludes *N. stromeri*, in a first assessment, to be assigned to Caimaninae, since it is only present in alligatorines (*Allognathosuchus wartheni*, *Brachychampsa sealeyi*, *Ceratosuchus, Hassiacosuchus* and *Wannaganosuchus*).

The morphology seen in the two characters point that *N. stromeri* is an alligatoroid. And all taxa that share with *N. stromeri* large globular teeth (*Allognathosuchus wartheni*, *Brachychampsa sealeyi*, *Ceratosuchus*, *Hassiacosuchus* and *Wannaganosuchus*) have mandibular symphysis that extends itself to the level between the sixth and eighth alveolous (Character 45-1), differently from *N. stromeri* which has the state 0 of the same character as stated previously.

As such, *Notocaiman stromeri* Rusconi, 1937 is considered here a valid species. The diagnosis is as follows: an alligatoroid crocodylian that differs from other alligatoroids for having posteriormost dentary teeth large and globular (shared with *Allognathosuchus wartheni*, *Brachychampsa sealeyi*, *Ceratosuchus, Hassiacosuchus* and *Wannaganosuchus*); differs from those taxa for having the mandibular symphysis extending until the level between the fourth and fifth alveolous.

4.2.10. Caimaninae sp. nov. (UCMP-39978)

UCMP-39978 is a fossil specimen comprised of an incomplete skull in which the following portions are lacking: the skull table, the dorsal portion of the area immediately anterior to the orbits, both quadrates and quadrato-jugals, the right jugal and all the area posterior to the left jugal (Fig. 25). The specimen is from the Honda Group, middle Miocene of Colombia, which was described and assigned by Langston (1965) to "*Caiman* cf. *C. lutescens*". Salas-Gismondi et al. (2015) suggested an affinity of the specimen with *Caiman wannlangstoni*, from the middle Miocene Pebas Formation of Peru. However, as mentioned previously, *C. lutescens* (Rovereto, 1912) is a junior synonym of *C. latirostris*, and as such the taxonomic assignment of UCMP-39978 must be reexamined.

The specimen UCMP-39978 has one autapomorphy that differentiates it from almost all other caimanines: a large circular external naris that occupies almost all of the dorsal surface of the premaxillae, reaching the anterior portion of the nasals. *Mourasuchus amazonensis* and *M. pattersoni* also have large external naris occupying most of the dorsal surface of the premaxillae, but in these the external naris is wider than long rather than circular (see Cidade et al., 2017). Additionally, the overall cranial morphology of *Mourasuchus* is markedly different from that of more 'typical' caimanines such as UCMP-39978. The only caimanine that shares with it UCMP-39978 is *Protoalligator huningensis*, from the Paleocene of China; however, this specimen lacks developed *canthi rostralii* (see Wang et al., 2016), in contrast with UCMP-39978. As such, the presence of these traits allows the specimen UCMP-39978 to be considered as a new caimanine species.

Furthermore, the developed *canthi rostralli* present in the specimen are shared with *Purussaurus mirandai, P. brasiliensis, Caiman latirostris, C. crocodilus, "Caiman" wannlangstoni* and the specimen MCNC-243 (*Caiman* cf. *C. niger* or *Caiman* sp.). However, those present in *P. mirandai* and *P. brasiliensis* have an associated lateral depression, which is absent in UCMP-39978. Additionally, the specimen can be distinguished from *C. niger* for not having an exposure of the vomer between the premaxillae and the maxillae, in the ventral portion of the skull. The phylogenetic analysis performed in this study found the specimen within the clade Globidentosuchidae, forming a clade with "*Caiman*" *wannlangstoni* (Fig. 90), corroborating the suggestion of Salas-Gismondi et al. (2015). As this last species is likely to represent a new genus, the specimen UCMP-39978 may be eventually considered a new species of that same genus. The diagnose of this new species within the new genus is based on the large size of the external naris, occupying almost all of the dorsal surface of the premaxillae, which differentiates it from "*Caiman*" *wannlangstoni*, which exhibits a circular external naris that does not occupy a large portion of the dorsal surface of the premaxillae.

4.2.11. *Purussaurus*

The first mention to *Purussaurus* fossils in the literature is by Giebel (1870), who proposed the species *Dakosaurus amazonicus* based on an isolated tooth and a vertebra (both not illustrated) from the Purus river in the Amazonas state of Brazil. *Dakosaurus* is a genus of thalattosuchian crocodylomorph currently known only for the Jurrasic and Cretaceous of Europe, Russia, Argentina and Mexico (see Steel, 1973; Ochev, 1981; Vignaud & Gasparini, 1996; Buchy et al., 2007). The tooth described by Giebel (1870) is located at the SMNK (Fig. 108). The vertebra was not found, but the morphology of the tooth is congruent with the teeth morphology seen in *Purussaurus* (see Langston, 1965; Aguilera et al., 2006; Aureliano et al., 2015, and below), which is also congruent with the provenance of the tooth being a river from the north of Brazil, which is known for Cenozoic deposits with a large crocodylian fauna, including *Purussaurus* (Cidade et al., 2019a).

The proposal of *Dakosaurus amazonicus* by Giebel (1870) has been totally overlooked by previous works that dealt with *Purussaurus* taxonomy (e.g. Nopcsa, 1924; Langston, 1965; Bocquentin-Villanueva et al., 1989). All of these have considered the work of Gervais (1876) as the first mention of *Purussaurus* in the literature. In it, the species *Dinosuchus terror* is proposed based on a large isolated vertebra (Fig. 109) from the Purus river in the Amazonas state of Brazil. In fact, Giebel (1876) proposed *Dinosuchus terror* to be a junior synonym of *Dakosaurus amazonicus* based on the similarity he perceived between the vertebrae assigned to the taxa.

The species *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892 was described based on the most anterior portion of a right mandibular ramus with the first nine alveoli preserved. The holotype (Fig. 110) was deposited in the Museu Botânico do Amazonas in the Brazilian city of Manaus, but after the closing of the museum in 1890 the whereabouts of the specimen are unknown: hypotheses are that it was taken to Italy after the closing of the museum, or that it was in the possession of Barbosa-Rodrigues' relatives until at least 1945 (see Price, 1967 for details). As no further news have erupted about the holotype ever since, it can be now considered as lost. Nevertheless, *P. brasiliensis* remains as a valid species as the holotype can be sufficiently differentiated from other crocodylomorphs.

Brachygnathosuchus braziliensis was described by Mook (1921e) based on an incomplete portion of a right dentary, two vertebral centra, another tentative vertebral centrum an a tentative osteoderm (AMNH-3855). The type material of this species does not exhibit significant differences with the holotype of *P. brasiliensis*, and thus *B. braziliensis* must be considered as a junior synonym of *P. brasiliensis*. Nopcsa (1924) considered *D. terror*, *P. brasiliensis* and *B. braziliensis* as synonyms, giving priority to *D. terror* as a valid name. Later, Patterson (1936, 1943) considered *Dinosuchus terror* and *Purussaurus brasiliensis* as valid species, *Brachygnathosuchus braziliensis* as a junior synonym of *D. terror* and *Purussaurus brasiliensis* as a member of *Caiman*.

Figure 108: Isolated tooth of the type material of *Dakosaurus amazonicus* (SMNK without number), assigned here as *Purussaurus* sp. Scale bar = 1 cm.

Mook (1941b) erected the species *Dinosuchus neivensis* based on remains (an incomplete mandible, see part of it in Fig. 66, fragmented ribs and six vertebrae) from the middle Miocene Honda Group of Colombia, although Mook (1941b) considered the fossils to be from Cretaceous deposits. Patterson (1943) did not agree with Mook (1941b) assignment of *D. neivensis* to *Dinosuchus* but did not assign it to another genus.

Langston (1965) considered *Dinosuchus terror* a non-valid species (a *nomen vanum*) but considered both *Purussaurus brasiliensis* and *Brachygnathosuchus* *braziliensis* as valid and distinct from each other. Additionally, he changed *D. neivensis* of Mook (1941b) to *Caiman neivensis*, based on much more complete specimens from the middle Miocene Honda Group of Colombia (UCMP-39704, Fig. 59, UCMP-39657, UCMP-45719, UCMP-41101), all of which are reanalyzed in this study. Shortly posteriorly, Price (1967) described new mandibular material of *P. brasiliensis* from the late Miocene Solimões Formation of Brazil.

Bocquentin-Villanueva et al. (1989) described new specimens of *Purussaurus brasiliensis*, including a complete skull (UFAC-1403, Fig. 57) from the late Miocene Solimões Formation of Brazil and followed Langston (1965) in considering *Dinosuchus terror* as a *nomen vanum* and *P. brasiliensis* and *B. braziliensis* as valid (and distinct) species, but reclassified *Caiman neivensis* as *P. neivensis*. This perspective was followed by Aguilera et al. (2006) upon erecting a new species, *P. mirandai*, from the late Miocene Urumaco Formation of Venezuela (Fig. 58); these authors, however, did not compare the holotype of the new species with the holotype of *P. neivensis* described by Mook (1941b) and only with a specimen assigned to that species deposited at Ingeominas, in Colombia (Ingeominas-DHL-45).

Despite the complicate taxonomical history of *Purussaurus*, no study to this day has performed a comparison between the holotypes of all species that have already been either assigned or considered closely related to the genus, including between those of the species currently assigned to *Purussaurus* (*P. brasiliensis*, *P. neivensis* and *P. mirandai*). This is the main objective of the study of *Purussaurus* in this thesis.

The tooth of the type material of *Dakosaurus amazonicus* Giebel, 1870 (Fig. 108) is robust and with serrated carinae, the same morphology seen in *Purussaurus* sp. nov. (see Langston, 1965, and below) and *P. mirandai* (Aguilera et al., 2006) and in isolated teeth assigned to *P. brasiliensis* (see Aureliano et al., 2015; Souza et al., 2016). In fact, teeth with this morphology may be considered a synapomorphy of the genus (see Souza et al., 2016). As such, *D. amazonicus* may be considered a *nomen dubium*, with the isolated tooth at SMNK being assigned as *Purussaurus* sp. However, an eventual finding and reanalysis of the vertebra that also makes part of the type material of the species may change this scenario, in spite of the fewer systematically relevant characters in the crocodylian post-cranium in comparison with cranial characters (see Brochu, 1999, 2011; this study).

The vertebra is illustrated in Gervais (1876; Fig. 109) and indeed resembles other vertebrae described for *Purussaurus*, such as those belonging to the holotype of *Brachygnathosuchus braziliensis* Mook, 1921 for the holotype of *P. neivensis* (Mook, 1941b). Although *Purussaurus* is the only taxon known from the Miocene of South America to possess vertebrae of the size of that described by Gervais (1876), a large size alone is not a diagnostic character and the illustration of the specimen provided in the work does not exhibit any diagnostic character in comparison with other crocodylians. As such, we cannot exclude the possibility that the isolated vertebra could belong to a still unknown taxon that is not *Purussaurus*. Furthermore, the vertebra described by Gervais (1876) was not accompanied by any other fossil that could be assigned to more complete and more diagnostic remains of *Purussaurus* that are known today, and an additional complication is that the specimen is now considered to be lost, preventing a thorough reanalysis to be performed. For these reasons, we consider *Dinosuchus terror* as a *nomen dubium*.

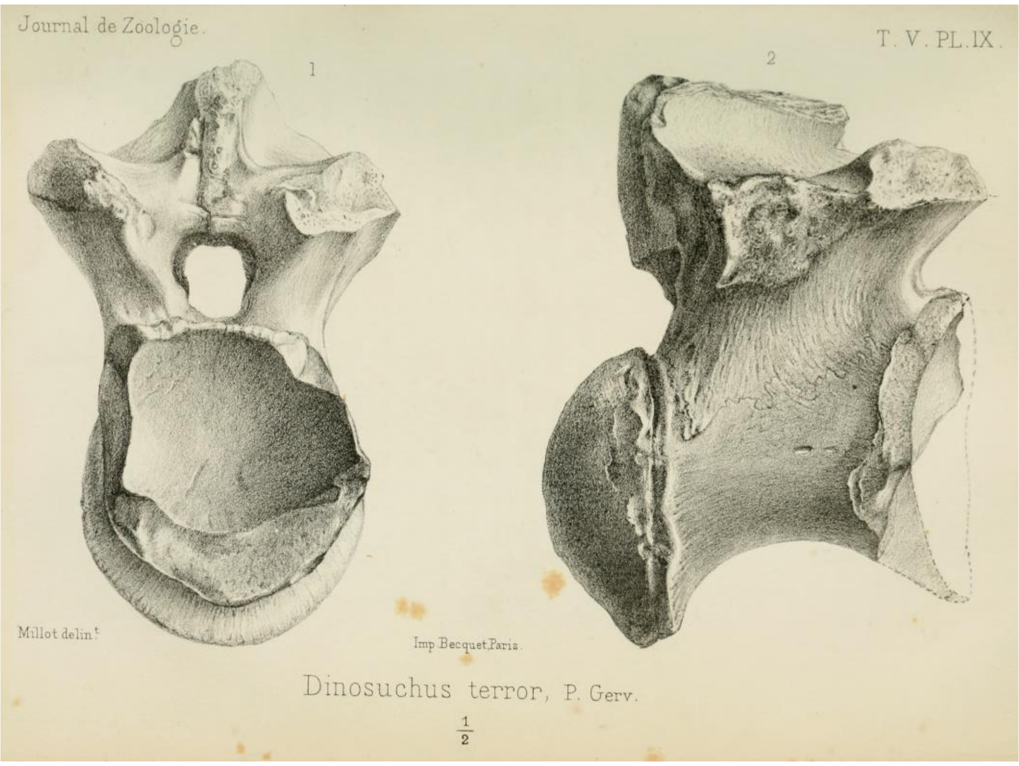

Figure 109: Holotype of *Dinosuchus terror*, an isolated vertebra, taken from Gervais (1876). In the original publication, the figure is reduzed to half of the size of the specimen.

Brachygnathosuchus braziliensis Mook, 1921e is considered here as a junior synonym of *P. brasiliensis* Barbosa-Rodrigues, 1892. There are no systematically relevant differences between the anterior portions of mandibular rami present in both holotypes: in both, the mandibular symphysis goes until the level of the fourth alveolous and the third and the fourth alveolous are largest of the preserved alveoli (from the first to the ninth in *P. brasiliensis*, from the third to the tenth in *B. braziliensis*). In figure 1 of Mook (1921e), the photograph of the mandibular ramus of *B. braziliensis* in dorsal view seems to exhibit a shorter mandibular symphysis that reaches only the third alveolous; however, when the specimen is seen in medial view, it is clear that the symphysis goes until the level of the fourth alveolous. This apparent difference is due to the presence of an intumescence in the anterior portion of the left size of the fossil, which has been previously interpreted as being pathological (Patterson, 1936; Langston, 1965), a perspective that is followed by this study.

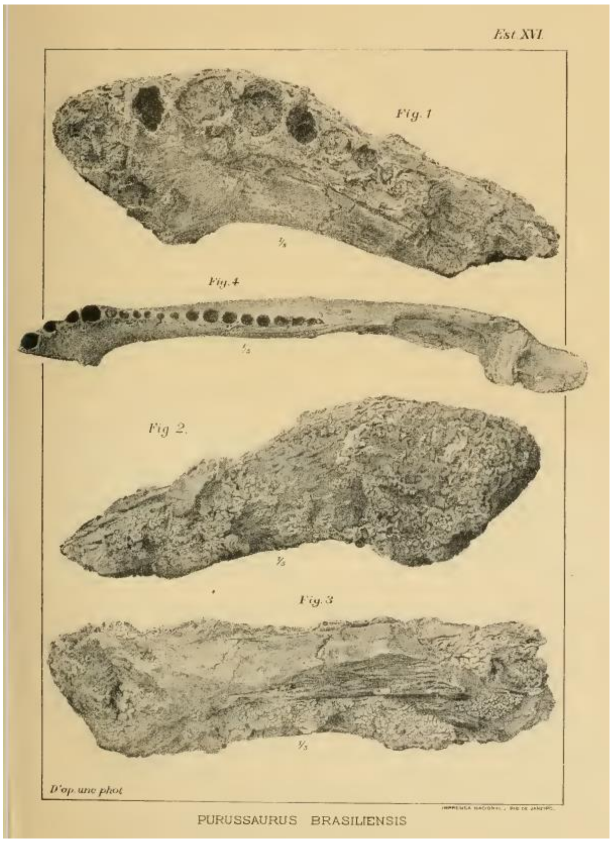

Figure 110: Holotype of *Purussaurus brasiliensis*, an incomplete right mandibular ramus, taken from Barbosa-Rodrigues (1892): dorsal view (“Fig. 1”), ventral view (“Fig. 2”) and medial vire (“Fig. 3”). “Fig. 4” is the right mandibular ramus of an indeterminate alligatoroid from the Amazon basin used for comparison. The

anteroposterior length of the specimen is 57 cm (Barbosa-Rodrigues, 1892; see also Price, 1967).

A taxonomic review of *P. neivensis* (Mook, 1941b) is a more complex scenario than those of the previously assessed species. The holotype of the species (USNM-10889) was only briefly described and scarcely illustrated in its original publication and, in fact, has never been thoroughly compared with the holotypes of the other two *Purussaurus* species: *P. brasiliensis* and *P. mirandai*.

When such study is performed, the first important comparison is that the holotypes of *Purussaurus brasiliensis* and *P. neivensis* cannot be compared regarding systematically relevant characters. The holotype of *P. brasiliensis* is the most anterior portion of a right mandibular ramus with the first nine alveoli preserved; the only part of the holotype of *P. neivensis* is the most anterior mandibular fragment, in which the dentary is firmly occluded with the maxilla. As such, it is unknown which alveoli are preserved in the anterior portion of the mandible of the holotype of *P. neivensis*. An eventual CT scan analysis may clarify this issue. In the meantime, however, *P. neivensis* cannot be distinguished from *P. brasiliensis* and thus may be considered a junior synonym of the last species.

Most complete specimens later assigned to *Purussaurus brasiliensis* (a complete skull, UFAC-1403, Fig. 57, a complete mandible, UFAC-1118, which are likely the same specimen but were collected in different time and thus given different catalogue numbers) do not exhibit systematically important differences with the holotype of *P. neivensis* either. The only systematically important character preserved in both the holotype of *P. neivensis* and UFAC-1118 is the position of the angular-surangular suture relative to the external mandibular fenestra; in both specimens, the suture contacts the fenestra at the posterior angle. As such, the holotype of *P. neivensis* does not exhibit systematically relevant differentes to the most complete referred specimens of *P. brasiliensis* to which it can be compared. Although vertebrae have been mentioned as belonging to *P. brasiliensis* (Aureliano et al., 2015), these have not been found associated with cranial material and thus cannot be assigned to the species.

Comparisons between the holotype of *Purussaurus neivensis* and the holotype of *P. mirandai* (CIAAP-1369, Fig. 58, a complete skull with associated mandibles, femur and ischium; see Aguilera et al., 2006) have the same issues as the comparison with the most complete *P. brasiliensis* specimens: the only systematically important character is the position of the angular-surangular suture relative to the external mandibular fenestra. In *P. mirandai*, however, this character cannot be seen due to poor preservation. As such, there ano systematically relevant differences between the holotypes of *P. neivensis* and *P. mirandai* as well.

Comparisons between the holotypes of *Purussaurus brasiliensis* (Fig. 110) and *P. mirandai* yielded more information. The two holotypes differ in the propotional size of the alveoli relative to the dentary bone: while in *P. brasiliensis* the alveoli are proportionally large (Fig. 110) in *P. mirandai* those are proportionally small (see Aguilera et al., 2006). As the holotype of *P. mirandai* is a large specimen (with a total skull length of 126 cm, see Aguilera et al., 2006), an ontogenetic variation is a ruled out as the cause of the difference, and as such *P. mirandai* may be considered a distinct species from *P. brasiliensis*. Likewise, the assignment of the specimen DGM-527-R, described by Price (1967) to *P. brasiliensis* is kept by this study as it also exhibits alveoli that are proportionally large relative to the dentary. Comparisons between the holotype of *P. mirandai* and the more complete specimens of *P. brasiliensis* (UFAC-1403 and UFAC-1118) reveals futher differences. The skull table of *P. mirandai* is more dorsoventrally concave than that of *P. brasiliensis* (Figs. 57 and 58); the external naris of *P. mirandai* is smaller in anteroposterior length than that of *P. brasiliensis*, and is also smaller in dorsoventral height (also this last difference is likely due to a dorsoventral flattening of the skull of *P. mirandai* that is probably of taphonomical origins; Figs. 57 and 58); the incisive foramen of *P. mirandai* is smaller than that of *P. brasiliensis*. These differences between the species fully allows *P. mirandai* to be considered valid.

However, upon the perspective that *Purussaurus neivensis* is a junior synonym of *P. brasiliensis*, there are two incomplete skulls (UCMP-39704, Fig. 59, and UCMP-45719) from the middle Miocene Honda Group described by Langston (1965) and assigned to the former species that need taxonomic revision. When compared with the holotype of *P. mirandai* and the most complete specimens of *P. brasiliensis*, both specimens exhibit a much smaller external naris and much longer nasal bones than both *P. mirandai* and *P. brasiliensis* and *canthi rostralli* with only a slight depression lateral to them, and not with a pronounced fossa as in *P. mirandai* and *P. brasiliensis* (Figs. 57, 58 and 59); additionally, UCMP-39704 exhibits a more dorsoventrally concave skull table than *P. mirandai* and *P. brasiliensis* (Figs. 57, 58 and 59; the skull table is not preserved in UCMP-45719). As such, both specimens represent a new species (*Purussaurus* sp. nov.) to be fully described in further assessments whose holotype would better be UCMP-39704. A preliminary diagnosis of the new species is as follows: a *Purussaurus* with significantly smaller external naris and longer nasal bones than both *P. brasiliensis* and *P. mirandai*; developed *canthi rostralli* with slight depression lateral to them, and not a developed fossa as in *P. brasiliensis* and *P. mirandai*; more dorsoventrally concave skull table than in *P. brasiliensis* and *P. mirandai*.

5. Discussion

5.1. Implications for paleoecology and morphological evolution

There are four ecomorphotypes in Alligatoroidea: generalist predator; durophagous; giant predator; gulp-feeder. The last two are represented only by *Deinosuchus* and *Purussaurus* (giant predator) and *Mourasuchus* (gulp-feeder), whereas the other two include a large number of taxa.

The phylogenetic results reveal new perspectives on the distribution, abundance and evolution of each of these ecomorphotypes. Regarding alligatoroid taxa included in this analysis, more than 50% can be considered generalist predators, whereas more than 30% can be considered as durophagous. The giant predator and gulp-feeder are less frequent, comprising only the three species of *Purussaurus* and the four species of *Mourasuchus*, respectively (Fig. 111).

The inference of a taxa to be generalist or giant predator is practically self-evident; *Mourasuchus* was previously defined as a “filter-feeder” (see Riff et al., 2010; Bona et al., 2012), but more recent assessments define their feeding habit as being “gulp-feeder”, with their prey being captured with the inferior part of the rostrum, without mastication, and presumably in large amounts (see Cidade et al., 2017; Cidade et al., in press). Durophagous taxa have been so classified due to a combination of features such as posterior globular teeth, long mandibular symphysis and anteroposteriorly short rostra (see Harlan, 1824; Case, 1925; Abel, 1928; Kälin, 1933, 1936a, 1939; Carpenter & Lindsay, 1980; Erickson, 1984; Brochu, 2004a; Fortier et al., 2014; Salas-Gismondi et al., 2015; Souza-Filho et al., 2019).

The basalmost alligatoroids (*Leidyosuchus* and *Diplocynodon*) can be considered as generalist taxa (Fig. 111). As this ecomorphotype is also the most common in the sister-group Crocodyloidea, it may be considered as plesiomorphic for Alligatoroidea. All durophagous alligatoroids are within Globidonta, a clade incidentally named after the posterior globular teeth exhibited by durophagous as well as non-durophagous forms. The topology of the clade reveals a relatively simple scenario for the origin and evolution of durophagy in Alligatoroidea, with most durophagous forms being concentrated in only two clades: all durophagous alligatorines are concentrated in the clade Brachychampsidae, whereas most durophagous caimanines are concentrated in the clade Globidentosuchidae (Fig. 111). Exceptions are *Arambourgia*, which is the sister-taxon of Alligatoridae; *Gnatusuchus*, the basalmost caimanine; and *Bottosaurus*, recovered in a basal polytomy in the Caimaninae clade (Fig. 111).

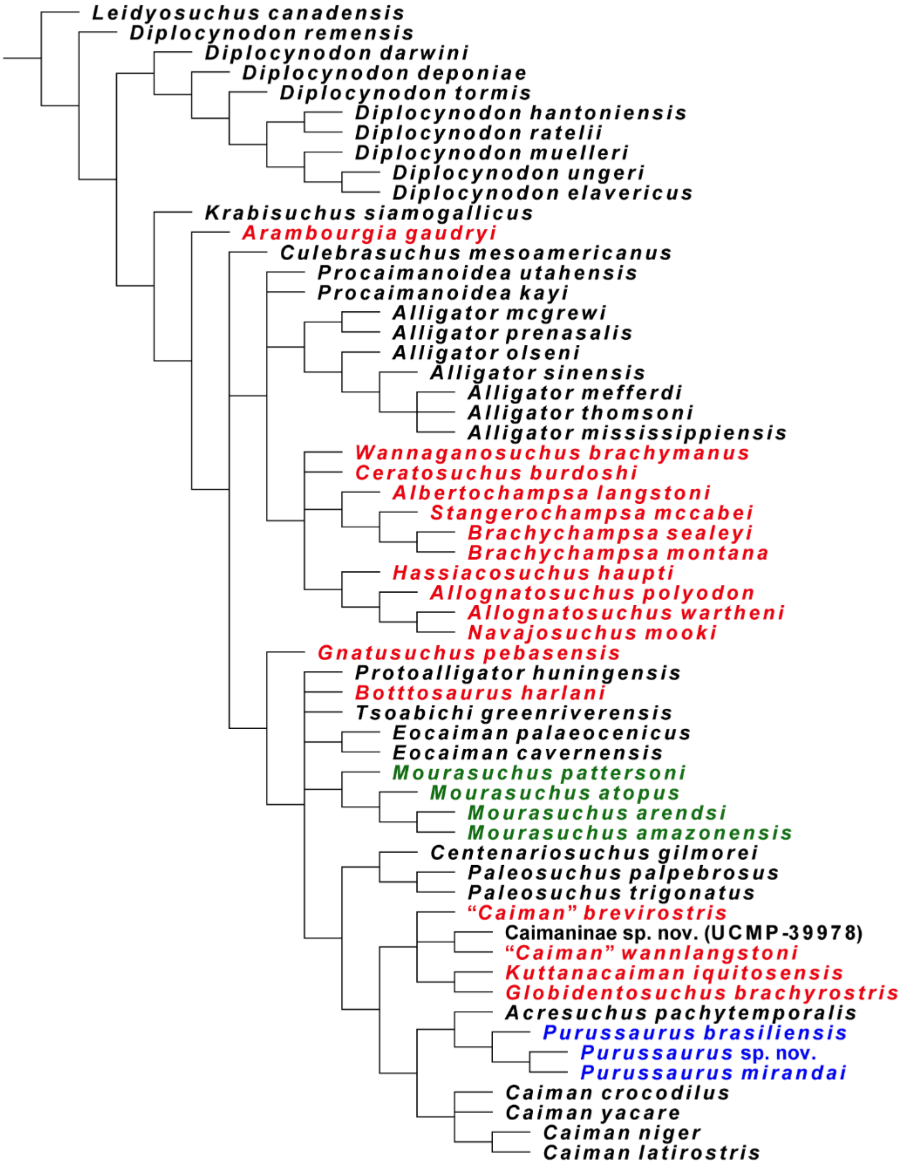

Figure 111: Topology of the strict consensus of the Alligatoroidea clade obtained in this study showing the distribution of the ecomorphotypes. Black: generalists; Red: durophagous; Green: gulp-feeders; Blue: giant predators.

This evidences that, in spite of the fact that most durophagous taxa are concentrated into two clades, the durophagous ecomorphotype may still have evolved several in Alligatoroidea (Fig. 111). Such hypothesis is not surprising when the cranial morphology of alligatoroids as a whole is taken into account. Although a specially anteroposteriorly short rostrum in typical of durophagous forms (Character 180-1), the rostra of most globidontans is proportionally shorter than other eusuchian groups, most notably Gavialoidea and Crocodyloidea (the sister-group of Alligatoroidea). Additionally, posterior globular teeth occur frequently in the fittingly named Globidonta clade in taxa not usually considered as durophagous, such as *Acresuchus, Caiman niger, C. latirostris, Eocaiman cavernensis*, in some individuals of *C. crocodilus* and *C. yacare* (see Character 171) and allegedelly in *Purussaurus* (Salas-Gismondi et al., 2015), whereas the shape of posterior teeth of basal alligatoroid *Diplocynodon hantoniensis* at least approach a globular shape (see Rio et al., 2019). This evidences that these two features, linked with a durophagous ecomorphotype, are not limited to the taxa possessing the ecomorphotype in Alligatoroidea, which in its turn suggest that multiple evolutions of durophagy cannot be considered an unlikely scenario in Alligatoroidea, exactly as the phylogenetic results point out. In a sense, it can be argued that alligatoroids in general and globidontans in particular are generally “pre-adapted” (or have a “potential”) to develop a durophagous feeding habit with the development of few features, such as a (compared with non-durophagous alligatoroids) shorter rostrum, more globular posterior teeth and a slightly longer mandibular symphyses.

One issue for which little is known is the evolution of the remarkably specialized morphology of the durophagous *Gnatusuchus*, from the middle Miocene of Peru, which includes a lateromedially expanded, anteroposteriorly short rostrum and mandibular with a “shovel-like” process (Salas-Gismondi et al., 2015). The shape of the rostrum bears some resemblance with the other alligatoroids *Brachychampsa sealeyi* and *Wannganosuchus*, but those were not recovered as close to *Gnatusuchus*. It is probable that only the finding of one or more “transitional forms” leading to the morphology of *Gnatusuchus* may shed light on the evolution of this taxa. Other taxa such as *Eocaiman* (Cidade & Hsiou, 2018) have been suggested to be durophagous, but more complete specimens are required to confirm this hypothesis.

Some authors have expressed doubts about whether the aforementioned features are indicative of durophagy (e.g. Bartels, 1984). This issue must be assessed in future studies; however, even if those traits are not adaptations to durophagy, one can still speak of a single morphology that evolved several times within Alligatoroidea.

On the evolution of the gulp-feeding habit of *Mourasuchus*, a previous assessment (Cidade et al., 2019 in press) proposed that this ecomorphotype can have evolved from a durophagous habit such as that of *Gnatusuchus*, in which the acquisition of small prey to be masticated and then swallowed would gradually evolve to the acquisition of small prey to be engulfed in large quantities, without mastication, with the use of the inferior part of the rostrum as a sort of "fishing net" and transport structure of the prey to be swallowed. The phylogenetic results of this work do not support this in the sense that it does not recover *Mourasuchus* as close to any durophagous taxon (except in the Pcr Prune semi-strict consensus, which shows *Bottosaurus* as possibly close to *Mourasuchus*, Fig. 91), and in fact the placement of *Mourasuchus* in a polytomy within Caimaninae in the strict consensus (Fig. 90) evidently indicates that the phylogenetic relationships of the taxon shall be subject to future assessments. Nevertheless, this phylogeny does not recover *Mourasuchus* as close to *Purussaurus*, a scenario that would be difficult to explain if the hypothesis of evolution from durophagy is considered. As such, this hypothesis still has to be thoroughly tested in future studies; additionally, an evolution of the gulp-feeding ecomorphotype from a generalist predator is also possibly, considering also the "potential" that alligatoroids have to evolve to a durophagous ecomorphotype from a generalist ecomorphotype. It is also probable that a thorough understanding on the evolution of *Mourasuchus* will only be achived with the discovery of one or more "transitional forms" that led to the morphology seen in this taxon, similarly for what is needed for *Gnatusuchus* and *à la* what *Acresuchus* has represented for *Purussaurus* (see below). A comprehensive assessment on the evolution of the gulp-feeder habit of *Mourasuchus* is offered in Cidade et al. (in press), available at the Appendix 5 in the form of an accepted manuscript.

Regarding giant predators, *Purussaurus* is recovered as close to the *Caiman* clade, whereas in many previous analyses it appeared as close to the gulp-feeder *Mourasuchus* (see Brochu, 1999; Aguilera et al., 2006; Bona, 2007; Bona et al., 2012; Scheyer et al., 2013; Fortier et al., 2014; Salas-Gismondi et al., 2015; Cidade et al., 2017). The topology of this study, upon recovering the clade formed by *Acresuchus* and *Purussaurus* as close to *Caiman* instead of *Mourasuchus*, reinforces the perspective of an evolution of gigantism from a “generalist” caimanine; this has been put forward originally by the description of *Acresuchus* itself, a medium-sized generalist predator that is the sister-taxon of *Purussaurus* and possess many features that allow it to be considered as a “transitional form” between a generalist small to medium caimanine and a giant form (Souza-Filho et al., 2019, available at the Appendix 6). The other alligatoroid giant predator, *Deinosuchus*, was not included in this analysis, but its general morphology (see Schwimmer, 2002) and previous assessments recovering it as a basal alligatoroid (Aguilera et al., 2006; Scheyer et al., 2013; Martin et al., 2014; Hastings et al., 2016) strongly suggest that it evolved independently of *Purussaurus*. Detailed accounts on the evolution of the gigantism of *Deinosuchus* in a phylogenetic framework are still lacking, but offer an interesting perspective as how alligatoroids, already in their “beginning” both stratigraphically and phylogenetically, managed to achive significantly large sizes, especially considering that it was contemporaneous with theropod dinosaurs (Colbert & Bird, 1954; Schwimmer, 2002).

5.2. Biogeographical implications

Alligatoroidea has been considered originally, upon the beginning of biogeographical considerations based on cladistic analysis, as having been originated in North America (Brochu, 1999). The results of this analysis corroborate this in the sense that a Late Cretaceous (the earliest epoch of occurrence of the clade) North American taxon, *Leidyosuchus canadensis*, is recovered as the basalmost alligatoroid. However, the fact that *Diplocynodon remensis*, the remaining *Diplocynodon* species, *Krabisuchus* and *Arambourgia* are recovered as successive sister-taxa to Alligatoridae (all taxa being from the Paleogene of Europe, except *Krabisuchus*, from the Eocene of Thailand) supports that Europe can be considered is at least as likely as North America as a possible origin area of Alligatoroidea. A similar proposition has been put forward by previous analyses (Martin, 2007, 2010b; Martin & Buffetaut, 2008; Delfino et al., 2008a), but these analyses recover Late Cretaceous European taxa such as *Acynodon*, *Allodaposuchus* and *Massaliasuchus* as alligatoroids, and mostly as basal within the clade. In the analysis of this study, *Acynodon* and *Allodaposuchus* were recovered as basal eusuchians, whereas *Massaliasuchus* was not included in this analysis, but was also recovered as a basal eusuchian in posterior assessments (Smith et al., 2015). Additionally, the inclusion and eventual recovering of *Deinosuchus* as a basal alligatoroid, as had been the case in previous analyses, may give support to a North American origin.

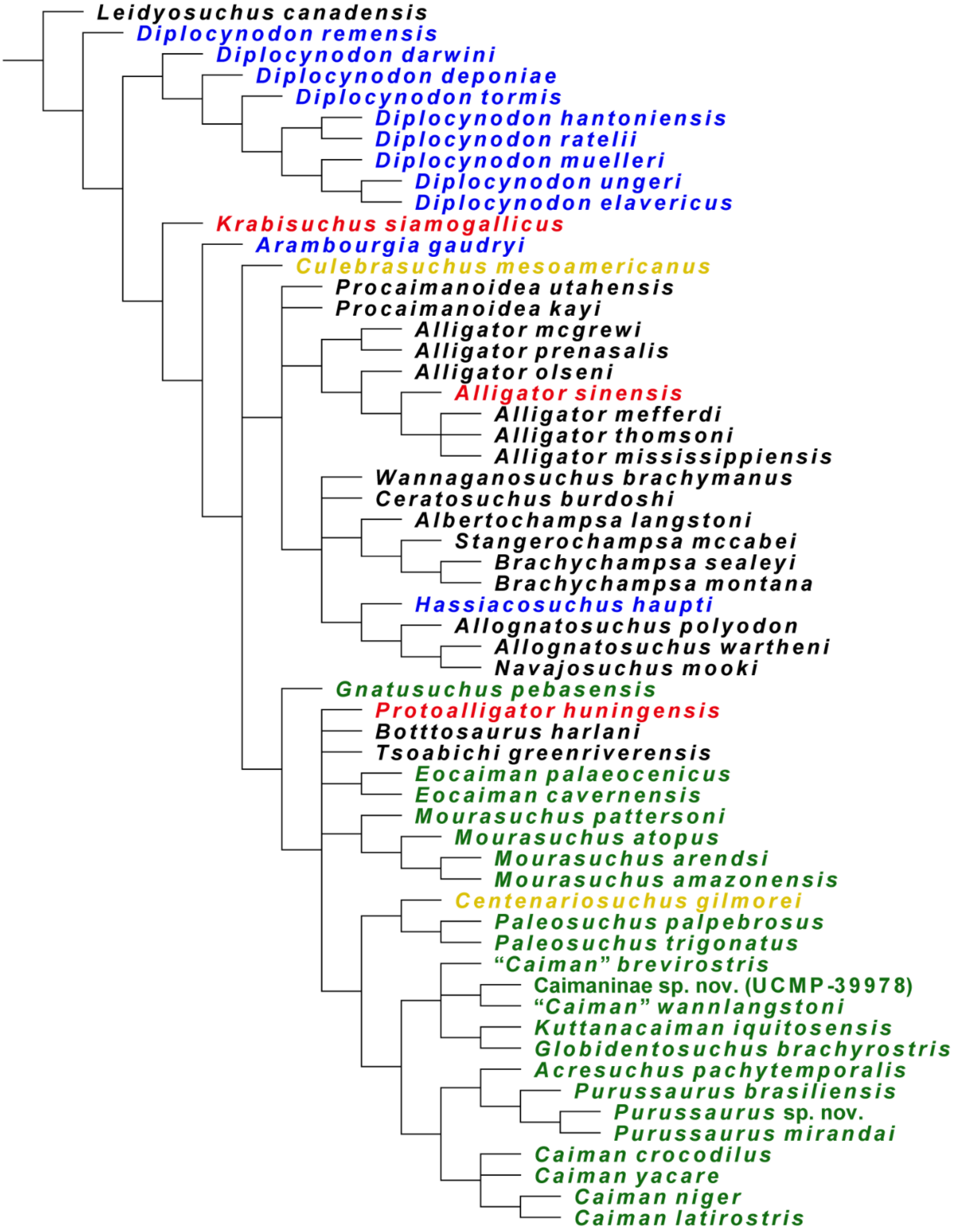

Figure 112: Topology of the strict consensus of the Alligatoroidea clade obtained in this study showing the distribution of the taxa by continent. Black: North America; Green: South America; Blue: Europe; Red: Asia; Yellow: Central America.

As such, regarding the biogeography as alligatoroids basal to Alligatoridae, considering a North American origin would imply in a dispersion towards Europe in the Late Cretaceous, whereas a European origin would imply a dispersion in the same epoch towards North America. According to Brochu (1999), such dispersions may have taken place through land connections that existed between North America and Eurasia, through both the Bering strait and North Atlantic, throughout the Cretaceous, Paleogene and Neogene (see Dott & Prothero, 1994; Martin, 2007); the same routes may have been used for later dispersions of alligatoroids from North America towards either Asia or Europe (see below). Regardless of the area of origin of the clade, a dispersion towards Asia among basal alligatoroids is needed to explain the occurrence of *Krabisuchus*, in the Eocene of Thailand; as this genus is the sister-taxon the clade formed by the European *Arambourgia* as the sister-taxon of Alligatoridae, the occurrence of *Arambourgia* may be explained either by a dispersion back towards Europe from Asia or from a stock that remained in Europe. The last hypothesis is considered as more likely as it is more parsimonious, but future assessments and, definitely, future fossil fidings are needed to give support to either scenario. Additionally, fossil remains have been previously assigned to Alligatoroidea (genus *Tadzhikosuchus*) from the Late Cretaceous of Tadjikistan and Uzbequistan (Efimov, 1982, 1988; Nesov et al., 1989; Storrs & Efimov, 2000), in Central Asia. Although these cannot be assigned to the group to the group (C.A. Brochu, pers. comm.; see also Brochu, 1999), eventual finding of alligatoroids in that time and space would help to explain the dispersion of basal alligarotoids between Asia and Europe during the Late Cretaceous and the Paleogene.

Alligatoridae is recovered in this analysis as consisting of three clades: the predominantely North American Alligatorinae, the predominantely South American Caimaninae, and a clade comprised solely by the Central American *Culebrasuchus mesoamericanus*, from the early Miocene of Panama. Upon taking the whole scenario into account, a more parsimonious place of origin for Alligatorinae is North America. It concurs with the predominantly North American occurrence of Alligatorinae and offers a more parsimonious origin area for the dispersions towards Central America (*Culebrasuchus*) and South America (Caimaninae) than either Asia or Europe, the other continents to have occurrences of basal alligatoroids. The dispersion towards South America that originated Caimaninae must have occurred between the Late Cretaceous and Paleocene. North and South America were separated for most of the time between the Jurassic and the rise of the Isthmus of Panama in the Pliocene (see Iturralde-Vinent, 2006; O'Dea et al., 2016), and as such the dispersion may have happened either through a relatively short-lasting land bridge existent between the two continents during the Late Cretaceous (Rage, 1978, 1986; Lucas & Hunt, 1989; Brochu, 1999, 2010; 2011; Newbrey et al., 2009), or through islands or archipelagos that existed between the two landmasses in the period (see Brochu, 1999, 2010, 2011; for the islands and archipelagos that existed during the time, see Iturralde-Vinent, 2006).

A dispersion from North America towards Central America to explain the occurrence of *Culebrasuchus* in Panama is also congruent with reconstruction of the land masses during the Cenozoic (e.g. Iturralde-Vinent, 2006) and with the fact that mammalian fauna from the Miocene of Panama has marked North American affinities (MacFadden, 2006; Hastings et al., 2013). However, a dispersion from South America can also be cogitated, as the distance between the continent and Panama during the Miocene has been suggested to be relatively short (around 200 km; see Farris et al., 2011; Montes et al., 2012; Hastings et al., 2013).

Regarding Alligatorinae biogeography, few are the taxa recovered in the group in this analysis that are not from North America: *Hassiacosuchus*, from the Eocene of Europe, and *Alligator sinensis*, an extant species from China. *Hassiacosuchus* is better seen as a result of a transoceanic dispersion through the Atlantic towards Europe during the Paleocene or the Eocene. *Alligator sinensis* is more parsimoniously seen as the result of a dispersion towards Asia through the Bering strait occurred during times with higher temperatures, given the low latitude of the Bering strait area and crocodylians intolerance to cold temperatures (see Brochu, 1999). The hypothesis of a dispersion first to Europe than to Asia would not require hotter climates or more tolerance to cold temperatues, but would be a significantly more complicated scenario regarding the distance involved; as such, it may be considered less parsimonious, even if possible (see Brochu, 1999). Regarding Asian alligatorids, however, the scenario may change considerably upon the inclusion of Chinese forms not considered in this cladistic analysis, such *Lianghusuchus* and the Maoming crocodylian, from the Eocene, and *Alligator lucius*, from the middle Miocene. If these forms are eventually found to be alligatorids not related to *A. sinensis*, they may invoke a scenario of multiple dispersions from North America towards Asia, and in the case of the first two forms, in periods as early as the Paleocene or the Eocene. If any of all of these three forms are recovered as basal to Alligatoridae, then dispersal events from Europe to Asia may be considered as alternatives. Additionally, *Protoalligator huningensis*, also from the Eocene of China, is recovered in this study as a Caimaninae, but may represent an alligatorine (see below) and thus may represent a similar issue to that of the other Chinese fossil alligatoroids.

Regarding Caimaninae, the biogeographic issue involve the North American taxa *Bottosaurus*, from the Late Cretaceous and the Paleocene and *Tsoabichi*, from the Eocene, which are both from the United States; the Asian taxon *Protoalligator*, from the Eocene of China; and the Central American taxon *Centenariosuchus*, from the early Miocene of Panama. Regarding the first three taxa, the strict consensus topology recovers each of them as independent lineages in a basal caimanine clade (Fig. 90), whereas the Pcr Prune semi-strict consensus recover the three taxa in a polytomy together with *Mourasuchus,* but in which *Bottosaurus* and *Tsoabichi* form a distinct clade (Fig. 91). These last two taxa were recovered as a clade in previous assessment (Cidade et al., 2019d), although *Bottosaurus* was found close to *Paleosuchus* instead in another previous analysis (Cossette & Brochu, 2018), whereas had been recovered in the single previous assessment to include it within a large polytomty of the clade Globidonta (Wang et al., 2016). Evidently, future assessments are needed to establish well-supported phylogenetic placements for the three taxa and the biogeographic inferences that can be made from those. Nevertheless, these results bring an interesting biogeographic issue upon recovering *Protoalligator* as a caimanine, creating an initially complex scenario where an Asian taxon from the Eocene is into a predominantely South American taxon, invoking the possibility of a dispersion event from South American towards Asia in the early Paleogene.

A much more parsimonious scenario, however, is considering that if *Protoalligator* is indeed a caimanine, it would be closer to *Bottosaurus* and *Tsoabichi* (and the Pcr Prune analysis hints), and then that its dispersal occurred from North America instead. This is congruent to the ages of all taxa: while *Protoalligator* and *Tsoabichi* are from the Eocene, *Bottosaurus* is from the Late Cretaceous and the

Paleocene. Regarding the biogeographic history of *Bottosaurus* and *Tsoabichi* themselves, they can either be seen as the result of a remanescent population of caimanines that stayed in North America after the dispersion of other populations of the clade to South America, or as a result of a “returning” dispersion from South America towards North America. The first hypothesis is more congruent with the Late Cretaceous/Paleogene occurrence of *Bottosaurus*, which places it as the most ancient Caimaninae (no other caimanines have records in the Late Cretaceous, see Cidade et al., 2019a), but the second hypothesis is more congruent with the topology of this study, in which an South American taxon, *Gnatusuchus* from the middle Miocene of Peru, appears as the basalmost caimanine. Additionally, characters of *Protoalligator* and *Tsoabichi* suggest that they might be alligatorines (see below), whereas a placement withing Alligatorinae would be more congruent with geographic-stratigraphic distribution of both taxa. Regarding *Bottosaurus*, an alligatorine or basal alligarotoid affinity which also be more congruent with its geographic-stratigraphic placement. More analyses on these taxa are definitely advised for a thorough understanding on these issues.

Regarding *Centenariosuchus*, the most parsimonious scenario is considered this taxon the result of a dispersion from South America towards the area of current Panama, contrary to the scenario of *Culebrasuchus* (see above). This is due to *Centenariosuchus* occupying a more derived position within Caimaninae, making a dispersion from South America a more parsiminuous scenario a dispersion from North America. The aforementioned suggestion that the distance between Panama and South America may not have been large during the Miocene is congruent with this hypothesis. However, a North American dispersion can also be hypothesized, due to the existence of North American caimanines and the aforementioned reconstruction of the land masses of North and Central Americas during the Cenozoic and the affinities between the mammalian from the Miocene of Panama with North American taxa.

5.3. Taxonomic, systematic and phylogenetic perspectives

There are several taxonomic and systematic perspectives arising from the results of this study. The strict consensus recovers *Diplocynodon remensis* as basal to the remaining species of *Diplocynodon*, which creates the possibility of the erection of a new genus for that species (see also Rio et al., 2019). However, such revision is precluded from being performed in this study as it is clear that a thorough taxonomic review if *Diplocynodon*, at a species and specimen level, needs to be performed. This genus very abundant in species. This study has included all nine species considered valid by Rio et al. (2019) which is the largest dataset ever used for *Diplocynodon* (together with Martin et al., 2014 and Rio et al., 2019), although Macaluso et al. (2019) implied that *D. monsvialensis* (Fabiani, 1914), from the Oligocene of Italy, might be a valid species, which was not included in this analysis. Other species already proposed for the genus, *D. dalpiazi* (Fabiani, 1915) apparently does not correspond to a valid species (Macaluso et al., 2019).

Some species of *Diplocynodon*, however, and in particular *D. darwini*, are known from an unusually large number of specimens, with many of them (again particularly for *D. darwini*) being very complete and well-reserved (see Ludiwg, 1877; Rio et al., 2019). Although this evidently a good aspect about this taxon, this also means that *D. darwini* and eventually other species may actually be a complex of several "cryptic" species still unknown, which may change significantly the phylogeny of the genus as a whole. As such, a thorough revision at a specimen level of the species of *Diplocynodon*, like the one recently performed for *D. hantoniensis* (Rio et al., 2019) is advised. Taxonomic revisions are a specific level also need to be considered; for example, Macaluso et al. (2019) suggest a possible synonymy between *D. monsvialensis*, *D. muelleri* and *D. tormis*.

Another perspective in taxonomic revision regards the clade within the genus *Alligator* uniting *A. mississippiensis*, *A. mefferdi* and *A. thomsoni*. Both *Alligator thomsoni* (see Malone, 1979; Brochu, 1999; Whiting et al., 2016) and *A. mefferdi* (see Snyder, 2007; Whiting et al., 2016) have been proposed as junior synonyms of *A. mississippiensis*. The topology of this analysis reinforces these perspectives, but taxonomic revisions regarding those two species are refrained to be performed in this study pending detailed assessments of both *A. mefferdi* and *A. thomsoni*. Another prospect regarding *Alligator* is the inclusion of *A. lucius*, from the middle Miocene of China, in phylogenetic analyses, which may have biogeographic implications (see below).

Another Asian taxon, *Lianghusuchus hengyangensis* Young, 1948 from the Eocene of China, has been suggested to be an alligatoroid (Brochu, 1999), but was not included in this analysis as no previous assessment included it and material of the species could not be analyzed. Its inclusion may also have biogeographic implications. Similarly, the "Maoming crocodylian", a fossil specimen from the Eocene of China described and recovered as an alligatorid by Skutschas et al. (2014) was not included in this analysis due to not being a distinct taxon, but future analyses may consider its inclusion for biogeographical reasons, even if its taxonomic eventually remains unclear.

Another genus that is in need of taxonomic revision is *Allognathosuchus*. Both species included in this analysis, *A. polyodon* and *A. wartheni*, are based on very fragmentary holotypes, and the assigned specimens are the ones that are most informative to the scoring used here. Whether these specimens can be assigned to those species needs to be thoroughly evaluated (see Brochu, 2004a). Additionally, *A. mlynarskii*, which is considered a distinct species of *Allognathosuchus* by Lucas & Sullivan (2004), or a distinct genus, *Chrysochampsa* (Estes, 1988; Brochu, 2004a), was not included in the analysis as it is not present in any published dataset and the specimens assigned to it were not analyzed directly. Another species, *A. heterodon*, is considered by Brochu (2004a) and indistinguishable from *A. polyodon*, but a thorough taxonomic revision of this species is advised as well.

The fact that both species are not recovered in a monophyletic group, but rather "in between" *Hassiacosuchus* and *Navajosuchus* in the clade Allognathosuchinae, also invites at a first glance for taxonomic revisions, especially considering the fact that both *Hassiacosuchus* and *Navajosuchus* were already considered as synonymous to *Allognathosuchus* (see Brochu, 2004a). However, caution is recommended regarding any revision of these generic assignments pending the taxonomic revision of the species currently included in *Allognathosuchus*. This notwithstanding, reconsideration of all these issues may change significantly the assessments of the phylogeny of this genus.

Regarding the Caimaninae clade, the placement of "*Caiman*" *brevirostris* and "*Caiman*" *wannlangstoni* in the clade Globidentosuchidae, separated from the clade *Caiman*, points to the creation of new genera for each of the species. Additionally, the new species represented by the specimen UCMP-39978 may belong to the same new genus as "*Caiman*" *wannlangstoni*, as the two taxa form a distinct clade. Another taxonomic revision indicated by the phylogenetic results, and that has been performed in this study, is the synonym of *Melanosuchus* with *Caiman*, with the reassignment of the black caiman extant species as *Caiman niger*.

Regarding the specifics of the strict consensus of the present analysis (and the perspectives of the Pcr Prune analysis and the 50% majority consensus), the main challenges of the phylogeny of Alligatoroidea to be tackled are: the placement of *Culebrasuchus* within Alligatoridae; of *Procaimanoidea* and *Ceratosuchus* within Alligatorinae; and of *Bottosaurus*, *Tsoabichi* and *Protoalligator* within Caimaninae. The caso fo the taxa in Caimaninae is more intriguing in that they have biogeographic implications: *Bottosaurus* and *Tsoabichi* are the only North American caimanines, whereas *Protoalligator* is the only Asian one, therefore an accuracy in their phylogenetic placements is critical to our understanding on the biogeographical dynamics of the Caimanianae clade and of Alligatoroidea as a whole. Alternative phylogenetic placements for these taxa can be cogitated: both *Protoalligator* and *Tsoabichi* have a septum in the external naris, a feature otherwise seen only in *Alligator* among Alligatoroidea (see Character 76), which would suggest an affinity of both taxa with the predominantly North American clade Alligatorinae, whereas in *Protoalligator* the scoring of character 48 with state 1 (which can be one of the characters putting this taxon in Caimaninae) could not be revised through publications. Regarding *Bottosaurus*, its stratigraphic distribution between the Late Cretaceous and the Paleocene of North America also suggests an affinity with either a basal alligatoroid clade from North America, where the group is thought to have originated during the Late Cretaceous (see below), or with Alligatorinae. Future analyses with focus on the relationship of these taxa are necessary.

Some species that have been assigned or suggested to belong to Caimaninae were not included in the analysis of this study for being based on very incomplete specimens: "*Caiman*" *australis*, *Caiman gasparinae*, "*Eocaiman*" *itaboraiensis, Necrosuchus ionensis, Notocaiman stromeri* and *Protocaiman peligrensis*. Out of these six taxa, however, two have specimens that can be considered to have a reasonable minimum amount of preservation that can yield phylogenetic and systematic relevant information upon eventual reassessments: *Caiman gasparinae* and *Necrosuchus ionensis* (see Simpson, 1937; Brochu, 2011; Bona & Carabajal, 2013; Cidade et al., 2019d). In the case of the other four species, the specimens currently known have a higher degree of incompleteness, which hinders more seriously assessments on their phylogenetic placements. This notwithstanding, future analysis with focus on these taxa are also recommended, as however incomplete these taxa may be, they also contribute to the understanding of the evolution of Alligatoroidea and Caimaninae. This is especially true as all of these taxa (except "*Caiman*" *australis and Caiman gasparinae*) are from the Paleocene of South America, which represents the beginning of the radiation of Alligatoroidea in the continent and yet has a sparse fossil record of the group (see Cidade et al., 2019a).

Regarding North American alligatoroids, two taxa that must be included in phylogenetic analysis, but were not so in the present study as they are undergoing thorough taxonomic reviews, are *Deinosuchus* and *Orthogenysuchus*. The first, one of the largest crococylomorphs ever discovered, is from the Late Cretaceous of several American states (Brochu, 1999; Schwimmer, 2002; Brownstein, 2019) whereas the second is from the Eocene of the American state of Wyoming (Mook, 1924). In previous analyses that did include them, *Deinosuchus* appears as a basal alligatoroid (Aguilera et al., 2006; Scheyer et al., 2013; Martin et al., 2014; Hastings et al., 2016), whereas *Orthogenysuchus* appears as a caimanine, as the sister-taxon of *Mourasuchus* e.g. (Brochu, 1999, 2010, 2011).

The phylogenetic relationships of the clade Alligatoroidea as a whole within Crocodylia also deserve a careful consideration. Molecular analyses recurrently recover Alligatoroidea as the basalmost clade within Crocodylia, with *Gavialis* close to *Tomistoma* and these two taxa as close to the remaining crocodyloids (Gatesy et al., 2003; Man et al., 2011; Oaks, 2011; Green et al., 2014), a contrastant result with most morphological analysis such as the results of this study. As such, a revision of Alligatoroidea may well be the key to solve the so-called *Gavialis*-*Tomistoma* debate (see Piras et al., 2010; Gold et al., 2014; Lee & Yates, 2018) if morphological analyses eventually recover similar topologies as those of molecular studies. Taxa considered in this analysis as basal eusuchians have been recovered as alligatoroids in other assessments (Martin, 2007, 2010b; Martin & Buffetaut, 2008; Delfino et al., 2008a), which brings the possibility of an affinity between "transitional" alligatoroids with these most basal forms, thus "pushing" Alligatoroidea to a more basal position within Crocodylia and offering different hypotheses for the evolution of the clade.

6. Conclusions

This study has performed the most comprehensive review of the phylogenetic dataset of Brochu (1997a, 1999, 2011) for the clade Alligatoroidea, including characters proposed by other studies (Bona, 2007; Barrios, 2011; Bona et al., 2012; Brochu, 2013; Pinheiro et al., 2013; Salas-Gismondi et al., 2015; Cidade et al., 2017). Ten new characters were proposed, and several characters previously proposed were changed, with many new states being created and others having their texts modified. Several scoring for previous characters were changed. Additionally, several clade names were proposed. As such, this study has assembled the largest ever phylogenetic dataset for the clade Alligatoroidea, consisting of 183 characters and 58 alligatoroid taxa, as well as 38 taxa as outgroups. The use of type specimens for state characters, in order to help identification and lessen ambiguity, is proposed experimentally.

The results of the phylogenetic analysis showed *Leidyosuchus* and *Diplocynodon* as the basalmost alligatoroids. There are followed by the clade Globidonta, which is comprised by the Asian *Krabisuchus* and the European *Arambourgia* as successive sister-taxa to Alligatoridae. This clade in its turn if formed by a three lineage polytomy: the predominantly North American Alligatorinae, the predominantly South American Caimaninae and one lineage formed exclusively by the Central American *Culebrasuchus*. The main clades within Alligatorinae are *Alligator* and Brachychampsidae, whereas the main clades are *Eocaiman*, *Mourasuchus*, the clade formed by *Centenariosuchus* and *Paleosuchus*, and Caimanini, which in its turn is formed by the clades Globidentosuchidae, Purussauria and *Caiman*.

Regarding the evolution of ecomorphotypes in Alligatoroidea, this analysis indicates that the durophagous ecomorphotype may have arisen up to five times during the evolutionary history of the clade, although the analysis shows that most durophagous taxa are concentrated in two clades: in Brachychampsidae (Alligatorinae) and Globidentosuchidae (Caimaninae). The analysis reinforces previous suggestions on the evolution of the giant predator ecomorphotype in *Purussaurus* (Souza-Filho et al., 2019) in showing the clade formed by this taxon and *Acresuchus* as the sister-group of *Caiman*, suggesting that the gigantism in *Purussaurus* evolved from the morphology of a small to medium-sized, generalist caimanine. The other giant alligatoroid, *Deinosuchus*, was not included in the analysis, but previous assessments recover it as a basal alligatoroid, indicating that the gigantism origined independently in this taxon. Regarding the "gulp-feeder" ecomorphotype of *Mourasuchus*, from a phylogenetic point of view further scrutinity is needed due to the non-resolved placement of the group within Caimaninae. However, the result of this analysis is more congruent with previous suggestions that this ecomorphotype evolved from a durophagous feeding habit (Cidade et al. in press) in the sense that it recovers *Mourasuchus* not closely related to *Purussaurus*, as in previous analyses.

A biogeographical assessment of Alligatoroidea exhibits several relevant perspectives. North America and Europe are considered as equally parsimonious places of origin for Alligatoroidea; however, the origin of Caimaninae is still more parsimoniously seen as a dispersion from North America between the Late Cretaceous and the Paleocene. A dispersion from Europe to Asia is the more likely explanation for the occurrence of *Krabisuchus* in Thailand. Dispersions from North America throughout the Cenozoic towards Asia (*Alligator sinensis* and possible related forms, such as the species *A. lucius*) and Europe (*Hassiacosuchus*) are also likely scenarios. The topology of Caimaninae suggests a dispersion "back" to North America already during the Late Cretaceous to explain the occurrences of *Bottosaurus* (Late Cretaceous-Paleocene) and *Tsoabichi* (Eocene), although the possibility of these two taxa being descendents of a remanescent caimanine population on North America can also be cogitated. The recovery of *Protoalligator* from the Paleocene of China within Caimaninae brings the possibility of a dispersion from South America towards Asia, but a more parsimonious scenario is a dispersion from North America to Asia, which is suggested by a possible affinity of this taxon with *Bottosaurus* and *Tsoabichi* as pointed out by the semi-strict consensus of the Pcr Prune analysis. Regarding the Miocene Central American (Panama) taxa, *Culebrasuchus* (one of the three lineages of the polytomy of Alligatoridae) may be the result of either a dispersion from North America or South America, whereas *Centenariosuchus* is more parsimoniously seen as a result of a dispersion from South America given its derived placement within Caimaninae.

The phylogenetic results also point out to possibilities of taxonomic revisions throughout the Alligatoridea clade, most notably that *Diplocynodon remensis* may represent a distinct genus, and that "*Caiman*" *brevirostris* and "*Caiman*" *wannlangstoni* may each represent a new genus. The results also reinforce the taxonomic perspective that *Melanosuchus niger* is a *Caiman* (Poe, 1997), which is adopted in this study (*Caiman niger*). Additionally, several taxonomic revisions not related to phylogenetic placements were performed by this study. A summary of all taxonomic revisions performed is as follows:

- *Balanerodus logimus* Langston, 1965 is a *nomen dubium*.
- *Caiman australis* (Burmeister, 1883) is a valid species that belongs to a distinct genus (to which the name *Proalligator* may probably be applied); the specific name that can be applied to the species, however, requires further scrutinity.
- *Caiman gasparinae* Bona & Carabajal, 2013 is a valid species.
- *Caiman lutescens* (Rovereto, 1912) is a junior synonym of *C. latirostris* (Daudin, 1802). Another specimen assigned to it, MACN-13551, is considered as Caimaninae indet.
- *Melanosuchus* Gray, 1862 is a junior syonym of *Caiman* Spix, 1825; hence the revision of *Melanosuchus niger* as *Caiman niger*. The holotype of Melanosuchus fisheri, MCNC-243, is preliminary assigned as *Caiman* sp., with affinities with the species *C. latirostris* and *C. niger*.
- *Caiman venezuelensis* Fortier & Rincón, 2012 is a junior synonym of *C. crocodilus* (Linnaeus, 1758).
- *"Eocaiman" itaboraiensis* Pinheiro et al., 2013 is a valid species, but that does not belong to *Eocaiman* and may be considered a new genus.
- *Necrosuchus ionensis* Simpson, 1937 is a valid species.
- *Notocaiman stromeri* Rusconi, 1937 is a valid species.
- The specimen UCMP-39978 is a new species that can be assigned to the same genus as "*Caiman*" *wannlangstoni*.
- *Purussaurus*: *Brachygnathosuchus braziliensis* Mook, 1921e and *P. neivensis* (Mook, 1941b) are junior synonyms of *P. brasiliensis* Barbosa-Rodrigues, 1892. *P. mirandai* Aguilera et al., 2006 is a valid species. Two specimens previously assigned to *P. neivensis* (UCMP-39704 and UCMP-45719) can be considered a new species of *Purussaurus*.

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Appendix 1

List of characters of Brochu (2011):

1. Ventral tubercle of proatlas more than one half (0) or no more than one half (1) the width of the dorsal crest

2. Fused proatlas boomerang-shaped (0), strapshaped (1), or massive and block-shaped (2)

3. Proatlas with prominent anterior process (0) or lacks anterior process (1)

4. Proatlas has tall dorsal keel (0) or lacks tall dorsal keel; dorsal side smooth (1)

5. Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0), or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1)

6. Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1)

7. Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end

8. Atlantal ribs lack (0) or possess (1) large articular facets at anterior ends for each other

9. Axial rib tuberculum wide, with broad dorsal tip (0) or narrow, with acute dorsal tip (1)

10. Axial rib tuberculum contacts diapophysis late in ontogeny, if at all (0) or early in ontogeny (1)

11. Anterior half of axis neural spine orientated horizontally (0) or slopes anteriorly (1)

12. Axis neural spine crested (0) or not crested (1)

13. Posterior half of axis neural spine wide (0) or narrow (1)

14. Axis neural arch lacks (0) or possesses (1) a lateral process (diapophysis)

15. Axial hypapophysis located toward the centre of centrum (0) or toward the anterior end of centrum (1)

16. Axial hypapophysis without (0) or with (1) deep fork

17. Hypapophyseal keels present on 11th vertebra behind atlas (0), 12th vertebra behind atlas (1), or tenth vertebra behind atlas (2)

18. Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1)

19. Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0) or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1)

20. Cervical and anterior dorsal centra lack (0) or bear (1) deep pits on the ventral surface of the centrum

21. Presacral centra amphicoelous (0) or procoelous (1)

22. Anterior sacral rib capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0), or anterior margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1)

23. Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1)

24. Deltoid crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1)

25. Scapulocoracoid synchondrosis closes very late in ontogeny (0) or relatively early in ontogeny (1)

26. Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1)

27. Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1)

28. M. teres major and M. dorsalis scapulae insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon; single insertion scar (1)

29. Olecranon process of ulna narrow and subangular (0) or wide and rounded (1)

30. Distal extremity of ulna expanded transversely with respect to long axis of bone; maximum width equivalent to that of proximal extremity (0) or proximal extremity considerably wider than distal extremity (1)

31. Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2)

32. Anterior end of interclavicle flat (0) or rod-like (1)

33. Iliac anterior process prominent (0) or virtually absent (1)

34. Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation (wasp-waisted; 2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4)

35. Supraacetabular crest narrow (0) or broad (1)

36. Limb bones relatively robust, and hindlimb much longer than forelimb at maturity (0) or limb bones very long and slender (1)

37. M. caudofemoralis with single head (0) or with double head (1)

38. Dorsal osteoderms not keeled (0) or keeled (1)

39. Dorsal midline osteoderms rectangular (0) or nearly square (1)

40. Four (0), six (1), eight (2), or ten (3) contiguous dorsal osteoderms per row at maturity

41. Nuchal shield grades continuously into dorsal shield (0) or differentiated from dorsal shield; four nuchal osteoderms (1) or differentiated from dorsal shield; six nuchal osteoderms with four central and two lateral (2) or differentiated from dorsal shield; eight nuchal osteoderms in two parallel rows (3)

42. Ventral armour absent (0) or single ventral osteoderms (1) or paired ventral ossifications that suture together (2)

43. Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth, without process (1)

44. Ventral scales have (0) or lack (1) follicle gland pores

45. Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two parallel enlarged rows (2)

46. Median pelvic keel scales form two parallel rows along most of tail length (0) or form single row along tail (1) or merge with lateral keel scales (2)

47. Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0), or fourth alveolus larger than third, and alveoli are separated (1), or 3 and 4 are nearly the same size and separated (2). Modificado por Salas-Gismondi *et al*. (2015).

49. Dentary symphysis extends to fourth or fifth alveolus (0) or sixth to eighth alveolus (1) or behind eighth alveolus (2) or to the first alveolous (3). Modificado por Cidade (2015).

Modificação deste caráter proposta por Salas-Gismondi *et al*. (2015): 49. Dentary symphysis extends to fourth or fifth alveolus (0) or sixth to eighth alveolus (1); or eighth to twelfth alveolus (2); or twelfth to sixteenth (3); beyond the sixteenth (4).

50. Dentary gently curved (0), deeply curved (1), or linear (2) between fourth and tenth alveoli

51. Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, (2) 11 or 12, or (3) no differentiation, or (4) behind 14

52. Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1)

53. Mandibular ramus of cranial nerve V exits splenial anteriorly only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1) or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2)

54. Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from mandibular symphysis;

anterior tip of splenial passes ventral to Meckelian groove (1) or splenial excluded from mandibular symphysis; anterior tip of splenial passes dorsal to Meckelian groove (2) or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide V within symphysis (3) or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within symphysis and forms narrow V (4)

55. Coronoid bounds posterior half of foramen intermandibularis medius (0) or completely surrounds foramen intermandibularis medius at maturity (1) or obliterates foramen intermandibularis medius at maturity (2)

56. Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1)

57. Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1)

58. Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1)

59. Process of splenial separates angular and coronoid (0) or no splenial process between angular and coronoid (1)

60. Angular–surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1)

61. Anterior processes of surangular unequal (0) or subequal to equal (1)

62. Surangular with spur bordering the dentary tooth row lingually for at least one alveolus length (0) or lacking such spur (1)

63. External mandibular fenestra absent (0) or present (1) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (2)

64. Surangular–dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) or at posterodorsal corner (1)

65. Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis; anterior tip acute (0) or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis; anterior tip very blunt (1)

66. Surangular–angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1)

67. Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1)

68. Articular–surangular suture simple (0) or articular bears anterior lamina dorsal to lingual foramen (1) or articular bears anterior lamina ventral to lingual foramen (2) or bears laminae above and below foramen (3)

69. Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1)

70. Foramen aereum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1)

71. Retroarticular process projects posteriorly (0), projects posterodorsally, not higher than the posterior edge of the articular fossa (1), or projects posterodorsally higher than the posterior edge of the articular fossa (2). Modificado por Salas-Gismondi *et al*. (2015).

72. Surangular extends to posterior end of retroarticular process (0) or pinched off anterior to tip of retroarticular process (1)

73. Surangular–articular suture orientated anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa

74. Sulcus between articular and surangular (0) or articular flush against surangular (1)

75. Dorsal projection of hyoid cornu flat (0) or rodlike (1)

76. Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1)

77. Lingual osmoregulatory pores small (0) or large (1)

78. Tongue with (0) or without (1) keratinized surface

79. Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posterior teeth laterally compressed (1), or all teeth compressed (2)

80. Maxillary and dentary teeth with smooth carinae (0), or serrated (1), or with neither carinae nor serrations (2). Modificado por Salas-Gismondi *et al*. (2015).

81. Naris projects anterodorsally (0) or dorsally (1)

82. External naris bisected by nasals (0) or nasals contact external naris, but do not bisect it (1) or nasals excluded, at least externally, from naris; nasals and premaxillae still in contact (2) or nasals and premaxillae not in contact (3)

83. Naris circular or keyhole-shaped (0) or wider than long (1) or longer than wide (2) or anteroposteriorly long and prominently teardrop-shaped (3). Modificado por Cidade (2015).

84. External naris of reproductively mature males (0) remains similar to that of females or (1) develops bony excrescence (ghara)

85. External naris (0) opens flush with dorsal surface of premaxillae or (1) circumscribed by thin crest

86. Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1) or surrounded by a dorsoventrally developed intumescence (2). Modificado por Cidade (2015).

87. Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny

88. Incisive foramen small, less than half the greatest width of premaxillae (0) or large, more than half the greatest width of premaxillae (1) or large, and intersects premaxillary–maxillary suture (2)

89. Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0) or abuts premaxillary tooth row (1) or projects between first premaxillary teeth (2)

90. Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1)

91. Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1)

92. All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between seventh and eighth maxillary teeth; all other dentary teeth occlude lingually (1) or dentary teeth occlude in line with maxillary tooth row (2)

93. Largest maxillary alveolus is no. 3 (0), no. 5 (1), no. 4 (2), nos. 4 and 5 are same size (3), no. 6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6)

94. Maxillary tooth row curved medially or linear (0) or curves laterally broadly (1) posterior to first six maxillary alveoli

95. Dorsal surface of rostrum curves smoothly (0) or bears medial dorsal boss (1)

96. Canthi rostralii absent or very modest (0) or very prominent (1) at maturity

97. Preorbital ridges absent or very modest (0) or very prominent (1) at maturity

98. Antorbital fenestra present (0) or absent (1)

99. Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary–maxillary suture (1)

100. Vomer entirely obscured by maxillae and palatines (0) or exposed on palate between palatines (1)

101. Surface of maxilla within narial canal imperforate (0) or with a linear array of pits (1)

102. Medial jugal foramen small (0) or very large (1)

103. Maxillary foramen for palatine ramus of cranial nerve V small or not present (0) or very large (1)

104. Ectopterygoid abuts maxillary tooth row (0) or maxilla broadly separates ectopterygoid from maxillary tooth row (1)

105. Maxilla terminates in palatal view anterior to lower temporal bar (0) or comprises part of the lower temporal bar (1)

106. Penultimate maxillary alveolus less than (0) or more than (1) twice the diameter of the last maxillary alveolus

107. Prefrontal dorsal surface smooth adjacent to orbital rim (0) or bearing discrete knob-like processes (1)

108. Dorsal half of prefrontal pillar narrow (0) or expanded anteroposteriorly (1)

109. Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1)

110. Prefrontal pillar solid (0) or with large pneumatic recess (1)

111. Medial process of prefrontal pillar wide (0) or constricted (1) at base

112. Maxilla has linear medial margin adjacent to suborbital fenestra (0) or bears broad shelf extending into fenestra, making lateral margin concave (1)

113. Anterior face of palatine process rounded or pointed anteriorly (0) or notched anteriorly (1)

114. Anterior ectopterygoid process tapers to a point (0) or forked (1)

115. Palatine process extends (0) or does not extend (1) significantly beyond anterior end of suborbital fenestra

116. Palatine process generally broad anteriorly (0) or in form of thin wedge (1)

117. Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1)

118. Palatine–pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra

119. Pterygoid ramus of ectopterygoid straight, posterolateral margin of suborbital fenestra linear (0) or ramus bowed, posterolateral margin of fenestra concave (1)

120. Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing shelf (1)

121. Anterior border of the choana is comprised of the palatines (0) or choana entirely surrounded by pterygoids (1)

122. Choana projects posteroventrally (0) or anteroventrally (1) at maturity

123. Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form neck surrounding aperture (2) or everted from flat surface to form neck surrounding aperture (3)

124. Posterior rim of internal choana not deeply notched (0) or deeply notched (1)

125. Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2)

126. Ectopterygoid–pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1)

127. Ectopterygoid extends (0) or does not extend (1) to posterior tip of lateral pterygoid flange at maturity

128. Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) or maxilla with posterior process between lacrimal and prefrontal (2) or prefrontal extending an anterior process that separates the nasal from the lacrimal (3). Modificado por Aguilera *et al*. (2006).

Modificação proposta para este caráter por Salas-Gismondi *et al*. (2015): 128. No posterior process of maxilla within lacrimal or within lacrimal and prefrontal (0), or maxilla with posterior process within lacrimal (1), or maxilla with posterior process between lacrimal and prefrontal (2).

129. Prefrontals separated by the frontal and nasals, anterior process of frontal extending far anterior to the anterior margin of the orbit (0), prefrontals separated by the frontal and nasals, anterior process of frontal around the same level or posterior to the anterior margin of the orbit (1), or prefrontals meet medially, anterior process of frontal around the same level or posterior to the anterior margin of the orbit (2). Modificado por Salas-Gismondi *et al*. (2015).

130. Lacrimal longer than prefrontal (0), or prefrontal longer than lacrimal (1), or lacrimal and prefrontal both elongate and nearly the same length (2)

131. Anterior tip of frontal forms simple acute point (0), or forms broad, complex sutural contact either with the nasals or prefrontals (1). Modificado por Salas-Gismondi *et al*. (2015).

132. Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1)

133. Postorbital bar massive (0) or slender (1)

134. Postorbital bar bears process that is prominent, dorsoventrally broad, and divisible into two spines (0) or bears process that is short and generally not prominent (1)

135. Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1)

136. Postorbital bar continuous with anterolateral edge of skull table (0) or inset (1)

137. Margin of orbit flush with skull surface (0) or dorsal edges of orbits upturned (1) or orbital margin telescoped (2)

138. Anterior margin of orbit not upturned, ventral margin gently circular (0), or anterior margin upturned, ventral margin gently circular (1), or anterior margin upturned, ventral margin with a prominent notch (2). Modificado de Salas-Gismondi *et al*. (2015).

139. Palpebral forms from single ossification (0) or from multiple ossifications (1)

140. Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1)

141. Quadratojugal spine low, near posterior angle of infratemporal fenestra (0) or high, between posterior and superior angles of infratemporal fenestra (1)

142. Quadratojugal forms posterior angle of infratemporal fenestra (0) or jugal forms posterior angle of infratemporal fenestra (1) or quadratojugal–jugal suture lies at posterior angle of infratemporal fenestra (2)

143. Postorbital neither contacts quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3)

144. Quadratojugal bears long anterior process along lower temporal bar (0) or bears modest process, or none at all, along lower temporal bar (1)

145. Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra; quadrate participates in fenestra (1)

146. Postorbital–squamosal suture orientated ventrally (0) or passes medially (1) ventral to skull table

147. Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1)

148. Squamosal–quadrate suture extends dorsally along posterior margin of external auditory meatus (0) or extends only to posteroventral corner of external auditory meatus (1)

149. Posterior margin of otic aperture smooth (0) or bowed (1)

150. Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2)

151. Frontoparietal suture concavoconvex (0) or linear (1) between supratemporal fenestrae

152. Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae small, with a circular or nearly circular shape (1) or supratemporal fenestra closes during ontogeny (2) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae large, significantly longer than wide, with an oval shape (3). Modificado por Cidade (2015).

153. Shallow fossa at anteromedial corner of supratemporal fenestra (0) or no such fossa; anteromedial corner of supratemporal fenestra smooth (1)

154. Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1)

155. Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0) or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1) or parietal and squamosal meet along posterior wall of supratemporal fenestra (2)

156. Skull table surface slopes ventrally from sagittal axis (0) or planar (1) at maturity

157. Posterolateral margin of squamosal horizontal or nearly so (0) or upturned to form a discrete horn (1) or producing a high transversely oriented eminence at the posterior margin, late in ontogeny (2). Modificado por Salas-Gismondi *et al*. (2015).

158. Mature skull table with broad curvature; short posterolateral squamosal rami along paroccipital process (0) or with nearly horizontal sides; significant posterolateral squamosal rami along paroccipital process (1)

159. Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paraoccipital process

160. Supraoccipital exposure on dorsal skull table small (0), absent (1), large (2), or large such that parietal is excluded from posterior edge of table (3)

161. Anterior foramen for palatine ramus of cranial nerve VII ventrolateral (0) or ventral (1) to basisphenoid rostrum

162. Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1)

163. Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall anterior to trigeminal foramen

164. Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1)

165. Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process or palatine (1)

166. Capitate process of laterosphenoid orientated laterally (0) or anteroposteriorly (1) toward midline

167. Parietal with recess communicating with pneumatic system (0) or solid, without recess (1)

168. Significant ventral quadrate process on lateral braincase wall (0) or quadrate–pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1)

169. Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid at maturity

170. External surface of basioccipital ventral to occipital condyle orientated posteroventrally (0) or posteriorly (1) at maturity

171. Posterior pterygoid processes tall and prominent (0) or small and project posteroventrally (1) or small and project posteriorly (2)

172. Basisphenoid thin (0) or anteroposteriorly wide (1) ventral to basioccipital

173. Basisphenoid not broadly exposed ventral to basioccipital at maturity; pterygoid short ventral to median eustachian opening (0) or basisphenoid exposed as broad sheet ventral to basioccipital at maturity; pterygoid tall ventral to median eustachian opening (1)

174. Exoccipital with very prominent boss on paroccipital process; process lateral to cranioquadrate opening short (0) or exoccipital with small or no boss on paroccipital process; process lateral to cranioquadrate opening long (1)

175. Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal

176. Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust process ventrally and participate in basioccipital tubera (1) or send slender process ventrally to basioccipital tubera (2)

177. Quadrate foramen aereum on mediodorsal angle (0) or on dorsal surface (1) of quadrate

178. Quadrate foramen aereum is small (0), comparatively large (1), or absent (2) at maturity

179. Quadrate lacks (0) or bears (1) prominent, mediolaterally thin crest on dorsal surface of ramus

180. Attachment scar for posterior mandibular adductor muscle on ventral surface of quadrate ramus forms modest crests (0) or prominent knob (1)

181. Quadrate with small, ventrally reflected medial hemicondyle (0) or with small medial hemicondyle; dorsal notch for foramen aereum (1) or with prominent dorsal projection between hemicondyles (2) or with expanded medial hemicondyle (3)

Appendix 2

Character proposed by Bona (2007) in the revised version of Pinheiro et al. (2013):

Character 124: Dentary at level of 1st and 4th teeth equal height or teeth higher than at level of 11th-12th teeth (0) or dentary at level of 1st and 4th teeth lower than at level of 11th-12th teeth (1).

List of characters proposed by Barrios (2011):

104: Extremo anterior del frontal, largo y alcanzando o pasando el borde anterior de las órbitas (0), corto y no alcanza el borde anterior de las órbitas (1).

105: Sutura palatino-pterigoidea, recta (0), cóncavoconvexa (1), levemente ondulada (2), o profundamente ondulada (3).

106: Festonamiento lateral del hocico, ausente (0), ligero (1), marcado (2).

107: Pterigoides participa del borde posterior de la fenestra palatal (0), o excluido de la fenestra palatal (1).

108: Borde posterior de la tabla craneal transversalmente recto a levemente cóncavo (0), o profundamente cóncavo (1).

109: Cresta preorbital uniendo las órbitas anteriormente, ausente (0), o presente (1).

List of characters proposed by Bona et al. (2012):

165. Orbits equal or sub equal than infratemporal fenestrae (0); orbits larger than infratemporal fenestrae, supratemporal fenestrae smaller or obliterated (1); orbits smaller than infratemporal fenestrae, supratemporal fenestrae reduced (2) or orbits larger than infratemporal fenestrae, supratemporal fenestrae larger than orbits (3).

166. Supratemporal fenestra surrounded anteriorly by postorbital and parietal (0) or only by postorbital bones (1).

167. Prefrontal-frontal not thickened or thickened forming a flange (0) or thickened forming a marked knob (1) at the anterior-medial margin of the orbits.

List of characters of Brochu (2013):

182: Iris (0) greenish/yellowish or (1) brown.

183: Two or more (0) or one (1) row of postoccipital osteoderms.

184: Fewer than eight (0) or eight to 14 (1) or more than 14 (2) paired midline scale rows.

185: Ectopterygoid maxillary ramus forms less than (0) or more than (1) two-thirds of lateral margin of suborbital fenestra.

186: Ectopterygoid maxillary ramus terminates at lateral margin of suborbital fenestra (0) or lateral to it, with maxilla separating the ectopterygoid from fenestra for short distance.

187: Palatine–maxillary suture intersects suborbital fenestra at its anteromedial margin (0) or nearly at its anteriormost limit (1).

188: Frontal lacks (0) or bears (1) prominent midsagittal crest between orbits.

189: All cervical neural spines anteroposteriorly broad (0) or posterior neural spines thin and rod-like (1).

List of characters proposed by Salas-Gismondi et al. (2015):

198. Dentary teeth series behind to alveoli 12-13 are pointed to slightly blunt (0), globular, different in size among them (1), globular, at least four subequal in size (2), molariform multicusped (3) or absent (4).

199. First four alveoli in the dentary are the same size or smaller than other dentary alveoli (0) or are the largest within the dentary (1).

Character proposed by Cidade et al. (2017):

188. Jugal lateromedially slender and dorsoventrally low (0), or jugal lateromedially wide and dorsoventrally low, with a blade-like shape (1) or jugal lateromedially wide and dorsoventrally high, with a cylindrical shape (2).

Appendix 3

List of the characters used in the analysis of this study in telegraphic form:

1. Ventral tubercle of proatlas more than one half (0) or no more than one half (1) the width of the dorsal crest. From Brochu (2011), character 1.

2. Fused proatlas boomerang-shaped (0), strapshaped (1), or massive and block-shaped (2). From Brochu (2011), character 2.

3. Proatlas with prominent anterior process (0) or lacks anterior process (1). From Brochu (2011), character 3.

4. Proatlas has tall dorsal keel (0) or lacks tall dorsal keel; dorsal side smooth (1). From Brochu (2011), character 4.

5. Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0), or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1). From Brochu (2011), character 5.

6. Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1). From Brochu (2011), character 6.

7. Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end. From Brochu (2011), character 7.

8. Atlantal ribs lack (0) or possess (1) large articular facets at anterior ends for each other. From Brochu (2011), character 8.

9. Axial rib tuberculum wide, with broad dorsal tip (0) or narrow, with acute dorsal tip (1). From Brochu (2011), character 9.

10. Axial rib tuberculum contacts diapophysis late in ontogeny, if at all (0) or early in ontogeny (1). From Brochu (2011), character 10.

11. Anterior half of axis neural spine orientated horizontally (0) or slopes anteriorly (1). From Brochu (2011), character 11.

12. Axis neural spine crested (0) or not crested (1). From Brochu (2011), character 12.

13. Posterior half of axis neural spine wide (0) or narrow (1). From Brochu (2011), character 13.

14. Axis neural arch lacks (0) or possesses (1) a lateral process (diapophysis). From Brochu (2011), character 14.

15. Axial hypapophysis located toward the centre of centrum (0) or toward the anterior end of centrum (1). From Brochu (2011), character 15.

16. Axial hypapophysis without (0) or with (1) deep fork. From Brochu (2011), character 16.

17. Hypapophyseal keels present on 11th vertebra behind atlas (0), 12th vertebra behind atlas (1), or tenth vertebra behind atlas (2). From Brochu (2011), character 17.

18. Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1). From Brochu (2011), character 18.

19. Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0) or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1). From Brochu (2011), character 19.

20. Anterior sacral rib capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0), or anterior margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1). From Brochu (2011), character 22.

21. Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1). From Brochu (2011), character 23.

22. Deltoid crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1). From Brochu (2011), character 24.

23. Scapulocoracoid synchondrosis closes very late, if at all, in ontogeny (0) or relatively early in ontogeny (1). Modified from Brochu (2011), character 25.

24. Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1). From Brochu (2011), character 26.

25. Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1). From Brochu (2011), character 27.

26. M. teres major and M. dorsalis scapulae insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon; single insertion scar (1). From Brochu (2011), character 28.

27. Olecranon process of ulna narrow and subangular (0) or wide and rounded (1). From Brochu (2011), character 29.

28. Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2). From Brochu (2011), character 31.

29. Anterior end of interclavicle flat (0) or rod-like (1). From Brochu (2011), character 32.

30. Iliac anterior process prominent (0) or virtually absent (1). From Brochu (2011), character 33.

31. Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation (wasp-waisted; 2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4). From Brochu (2011), character 34.

32. Supraacetabular crest narrow (0) or broad (1). From Brochu (2011), character 35.

33. Limb bones relatively robust, and hindlimb much longer than forelimb at maturity (0) or limb bones very long and slender (1). From Brochu (2011), character 36.

34. Dorsal osteoderms not keeled (0) or keeled (1). From Brochu (2011), character 38.

35. Dorsal midline osteoderms rectangular (0) or nearly square (1). From Brochu (2011), character 39.

36. Four (0), six (1), eight (2), or ten (3) contiguous dorsal osteoderms per row at maturity. From Brochu (2011), character 40.

37. Nuchal shield grades continuously into dorsal shield (0) or differentiated from dorsal shield; four nuchal osteoderms (1) or differentiated from dorsal shield; six nuchal

osteoderms with four central and two lateral (2) or differentiated from dorsal shield; eight nuchal osteoderms in two parallel rows (3). From Brochu (2011), character 41.

38. Ventral armour: absent (0) or comprised by single ventral osteoderms (1) or comprised by paired ventral ossifications that suture together (2). Modified from Brochu (2011), character 42.

39. Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth, without process (1). From Brochu (2011), character 43.

40. Ventral scales have (0) or lack (1) follicle gland pores. From Brochu (2011), character 44.

41. Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two parallel enlarged rows (2). From Brochu (2011), character 45.

42. Median pelvic keel scales form two parallel rows along most of tail length (0) or form single row along tail (1) or merge with lateral keel scales (2). From Brochu (2011), character 46.

43. Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0), or fourth alveolus larger than third, and alveoli are separated (1), or 3 and 4 are nearly the same size and separated (2). From Salas-Gimsondi et al. (2015), character 47, modified from Brochu (2011), character 47.

44. Two or three anterior dentary teeth strongly procumbent (0), only first anterior tooth strongly procumbent (1) or anterior teeth project anterodorsally (2). Modified from Brochu (2011), character 48.

45. Dentary symphysis extends to fourth or fifth alveolus (0) or sixth to eighth alveolus (1) or behind eighth alveolus (2) or symphysis very short, extending to the level of the first alveolous (3), or symphysis very long, extending behind sixth alveolous with a lateromedial expansion of the dentary area lateral to the symphysis (4). Modified from Cidade et al. (2017), character 49, modified from Brochu, character 49.

46. Dentary slightly curved between 4th and 10th alveoli (0), or deeply curved between 4th and 10th alveoli (1), or linear to the 10th alveolous and elevated after the 11th alveolous (2) or linear throughout the tooth row (3). Modified from Brochu (2011),

Character 50, fused with Pinheiro et al. (2013), Character 124, which is adapted from Bona (2007).

47. Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, (2) 11 or 12, or (3) no differentiation, or (4) behind 14, or (5) 12 and a series behind it, or (6) 17 and a series behind it, or (7) 5, 6 and 7, after which alveoli are smaller and approximately of the same size (8) 9 and a series behind it. Modified from Brochu (2011), Character 51.

48. Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1). From Brochu (2011), character 52.

49. Mandibular ramus of cranial nerve V exits splenial anteriorly only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1) or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2). From Brochu (2011), character 53.

50. Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove (1) or splenial excluded from mandibular symphysis; anterior tip of splenial passes dorsal to Meckelian groove (2) or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide V within symphysis (3), or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within symphysis and forms narrow V (4), or splenial excluded from mandibular symphysis; anterior tip of splenial does not approach Meckelian groove (5). Modified from Brochu (2011), character 54.

51. Coronoid bounds posterior half of foramen intermandibularis medius (0) or completely surrounds foramen intermandibularis medius at maturity (1) or obliterates foramen intermandibularis medius at maturity (2). From Brochu (2011), character 55.

52. Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1). From Brochu (2011), character 56.

53. Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1). From Brochu (2011), character 57.

54. Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1). From Brochu (2011), character 58.

55. Process of splenial separates angular and coronoid (0) or no splenial process between angular and coronoid (1). From Brochu (2011), character 59.

56. Angular–surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes along ventral margin of external mandibular fenestra late in ontogeny (1) or passes along dorsal margin of external mandibular fenestra late in ontogeny (2). Modified from Brochu (2011), character 60.

57. Anterior processes of surangular unequal (0) or subequal to equal (1). From Brochu (2011), character 61.

58. Surangular with spur bordering the dentary tooth row lingually for at least one alveolus length (0) or lacking such spur (1). From Brochu (2011), character 62.

59. External mandibular fenestra absent (0) or present (1) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (2) or present, dorsoventrally compressed and anteroposteriorly expanded (3). Modified from Brochu (2011), character 63.

60. Surangular–dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) or at or close to the posterodorsal corner (1). Modified from Brochu (2011), character 64.

61. Surangular–angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1). From Brochu (2011), character 66.

62. Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1). From Brochu (2011), character 67.

63. Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1). From Brochu (2011), character 69.

64. Foramen aereum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1). From Brochu (2011), character 70.

65. Retroarticular process projects posteriorly (0) or projects posterodorsally (1). From Brochu (2011), character 71.

66. Surangular extends to posterior end of retroarticular process (0) or pinched off anterior to tip of retroarticular process (1). From Brochu (2011), character 72.

67. Surangular–articular suture orientated anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa. From Brochu (2011), character 73.

68. Sulcus between articular and surangular (0) or articular flush against surangular (1). From Brochu (2011), character 74.

69. Dorsal projection of hyoid cornu flat (0) or rodlike (1). From Brochu (2011), character 75.

70. Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1). From Brochu (2011), character 76.

71. Lingual osmoregulatory pores small (0) or large (1). From Brochu (2011), character 77.

72. Tongue with (0) or without (1) keratinized surface. From Brochu (2011), character 78.

73. Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posteriormost teeth laterally compressed (1), or all teeth posterior to the fifth alveolous compressed (2) or all teeth compressed (3). Modified from Brochu (2011), character 79.

74. Maxillary and dentary teeth with smooth carinae (0), or serrated (1), or with pseudo-serrations (2) or with neither carinae nor serrations (3). Modified from Salas-Gismondi et al. (2015), character 80, modified from Brochu (2011), character 80.
75. Naris projects anterodorsally (0) or dorsally (1). From Brochu (2011), character 81.
76. External naris bisected by nasals (0) or not bisected (1). Modified from Brochu (2011), character 82.

77. Naris circular or keyhole-shaped (0) or wider than long (1) or longer than wide (2) or anteroposteriorly long and prominently teardrop-shaped (3). From Cidade et al. (2017), character 83, modified from Brochu (2011), character 83.

78. External naris of reproductively mature males (0) remains similar to that of females or (1) develops bony excrescence related to the ghara. Modified from Brochu (2011), character 84.

79. External naris (0) opens flush with dorsal surface of premaxillae or (1) circumscribed by thin crest. From Brochu (2011), character 85.

80. Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1) or surrounded by a dorsoventrally developed rim (2). From Cidade et al. (2017), character 86, modified from Brochu (2011), character 86.

81. Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny. From Brochu (2011), character 87.

82. Incisive foramen small, less than half the greatest width of premaxillae (0) or large, with more than or approximately half the greatest width of premaxillae (1) or large, and intersects premaxillary–maxillary suture (2). Modified from Brochu (2011), character 88.

83. Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0) or abuts premaxillary tooth row (1) or has anterior margin tapering anteriorly and projecting itself between first premaxillary teeth (2). Modified from Brochu (2011), character 89.

84. Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1). From Brochu (2011), character 90.

85. Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1). From Brochu (2011), character 91.

86. All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between seventh and eighth maxillary teeth; all other dentary teeth occlude lingually (1) or dentary teeth occlude in line with maxillary tooth row (2) or occlusion pits between fifth to the seventh or the eight teeth; all other dentary teeth occlude lingually (3). Modified from Brochu (2011), character 92.

87. Largest maxillary alveolus among the first ten alveoli is no. 3 (0), no. 5 (1), no. 4 (2), nos. 4 and 5 are same size (3), no. 6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6), nos. 3 and 4 are same size (7). Modified from Brochu (2011), character 93.

88. Maxillary tooth row curved medially or linear (0) or curves laterally broadly (1) posterior to first six maxillary alveoli. From Brochu (2011), character 94.

89. Canthi rostralii absent or very modest at maturity (0) or very prominent at maturity, with or without a depression lateral to it (1) or very prominent at maturity, with a developed fossa lateral to it (2). Modified from Brochu (2011), character 96.

90. Preorbital ridges absent or very modest (0) or very prominent (1) at maturity. From Brochu (2011), character 97.

91. Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary–maxillary suture (1). From Brochu (2011), character 99.

92. Surface of maxilla within narial canal imperforate (0) or with a linear array of pits (1). From Brochu (2011), character 101.

93. Medial jugal foramen small (0) or very large (1). From Brochu (2011), character 102.

94. Maxillary foramen for palatine ramus of cranial nerve V small or not present (0) or very large (1). From Brochu (2011), character 103.

95. Ectopterygoid abuts maxillary tooth row (0) or maxilla broadly separates ectopterygoid from maxillary tooth row (1). From Brochu (2011), character 104.

96. Maxilla terminates in palatal view anterior to lower temporal bar (0) or comprises part of the lower temporal bar (1). From Brochu (2011), character 105.

97. Penultimate maxillary alveolus less than (0) or more than (1) twice the diameter of the last maxillary alveolus. From Brochu (2011), character 106.

98. Dorsal half of prefrontal pillar narrow (0) or expanded anteroposteriorly (1). From Brochu (2011), character 108.

99. Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1). From Brochu (2011), character 109.

100. Prefrontal pillar solid (0) or with large pneumatic recess (1). From Brochu (2011), character 110.

101. Medial process of prefrontal pillar wide (0) or constricted (1) at base. From Brochu (2011), character 111.

102. Anterior ectopterygoid process tapers to a point (0) or forked (1). From Brochu (2011), character 114.

103. Palatine process extends (0) or does not extend (1) significantly beyond anterior end of suborbital fenestra. From Brochu (2011), character 115.

104. Palatine process generally broad anteriorly (0) or in form of thin wedge (1). From Brochu (2011), character 116.

105. Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1). From Brochu (2011), character 117.

106. Palatine–pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra. From Brochu (2011), character 118.

107. Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing shelf (1). From Brochu (2011), character 120.

108. Anterior border of the choana is comprised of the palatines (0) or choana entirely surrounded by pterygoids (1). From Brochu (2011), character 121.

109. Choana projects posteroventrally (0) or anteroventrally (1) at maturity. From Brochu (2011), character 122.

110. Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form neck surrounding aperture (2) or everted from flat surface to form neck surrounding aperture (3). From Brochu (2011), character 123.

111. Posterior rim of internal choana not deeply notched (0) or deeply notched (1). From Brochu (2011), character 124.

112. Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2). From Brochu (2011), character 125.

113. Ectopterygoid–pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1). From Brochu (2011), character 126.

114. Ectopterygoid extends (0) or does not extend (1) to posterior tip of lateral pterygoid flange at maturity. From Brochu (2011), character 127.

115. Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) or prefrontal with anterior expansion separating the lacrimal from the nasals (2) or lacrimal broadly separated from the nasals (3). Modified from Aguilera et al. (2006), from Brochu (2011), character 128, and from Brochu (1999), character 93.

116. Lacrimal longer than prefrontal (0), or prefrontal longer than lacrimal (1), or lacrimal and prefrontal both elongate and nearly the same length (2). From Brochu (2011), character 130.

117. Anterior tip of frontal visible in dorsal view forms simple acute point (0), or forms broad, complex sutural contact either with the nasals or prefrontals (1). Modified from Salas-Gimsondi et al. (2015), character 131, and from Brochu (2011), character 131.

118. Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1). From Brochu (2011), character 132.

119. Postorbital bar massive (0) or slender (1). From Brochu (2011), character 133.

120. Postorbital bar bears process that is prominent, dorsoventrally broad, and divisible into two spines (0) or bears process that is short and generally not prominent (1). From Brochu (2011), character 134.

121. Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1). From Brochu (2011), character 135.

122. Margin of orbit flush with skull surface (0) or dorsal edges of orbits highly upturned (1) or dorsal edges of orbits lowly upturned (2) or orbital margin telescoped (3). Modified from Brochu (2011), character 137.

123. Lateral margin of orbit (medial margin of the jugal): smooth (0) or with prominent notch (1). Modified from Brochu (2011), character 138.

124. Palpebral forms from single ossification (0) or from two ossifications (1) or from three ossifications (2). Modified from Brochu (2011), character 139.

125. Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1). From Brochu (2011), character 140.

126. Quadratojugal spine low, near posterior angle of infratemporal fenestra (0) or high, between posterior and superior angles of infratemporal fenestra (1). From Brochu (2011), character 141.

127. Quadratojugal forms posterior angle of infratemporal fenestra (0) or jugal forms posterior angle of infratemporal fenestra (1) or quadratojugal–jugal suture lies at posterior angle of infratemporal fenestra (2). From Brochu (2011), character 142.

128. Postorbital neither contacts quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3). From Brochu (2011), character 143.

129. Quadratojugal bears long anterior process along lower temporal bar (0) or bears modest process, or none at all, along lower temporal bar (1). From Brochu (2011), character 144.

130. Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra (1). Modified from Brochu (2011), character 145.

131. Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1). From Brochu (2011), character 147.

132. Squamosal–quadrate suture extends dorsally along posterior margin of external auditory meatus (0) or extends only to posteroventral corner of external auditory meatus (1). From Brochu (2011), character 148.

133. Posterior margin of otic aperture smooth (0) or bowed (1). From Brochu (2011), character 149.

134. Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2). From Brochu (2011), character 150.

135. Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra

near maturity; fenestrae small, with a circular or nearly circular shape (1) or supratemporal fenestra closes or nearly closes during ontogeny (2) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity; fenestrae large, significantly longer than wide, with an oval shape (3). Modified from Cidade et al. (2017), character 151, and from Brochu (2011), character 152.

136. Shallow fossa at anteromedial corner of supratemporal fenestra (0) or no such fossa; anteromedial corner of supratemporal fenestra smooth (1). From Brochu (2011), character 153.

137. Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1). From Brochu (2011), character 154.

138. Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0) or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1) or parietal and squamosal meet along posterior wall of supratemporal fenestra (2). From Brochu (2011), character 155.

139. Skull table surface slopes ventrally from sagittal axis (0) or planar (1) at maturity. From Brochu (2011), character 156.

140. Posterolateral margin of squamosal horizontal or nearly so (0) or upturned to form a discrete eminence (1) or producing a high transversely oriented eminence at the posterior margin, late in ontogeny (2) or highly upturned throughout the entire lateral margin, with a dorsoventral expansion in the posterior portion of the eminence (3) or highly upturned throughout the entire lateral margin, with a dorsoventral and lateromedial expansion in the posterior portion of the eminence (4). From Souza-Filho et al. (2019), character 156, modified from Salas-Gismondi et al. (2015) and Brochu (2011), character 157.

141. Mature skull table with broad curvature; short posterolateral squamosal rami along paroccipital process (0) or with nearly horizontal sides; significant posterolateral squamosal rami along paroccipital process (1). From Brochu (2011), character 158.

142. Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paraoccipital process. From Brochu (2011), character 159.

143. Supraoccipital exposure on dorsal skull table medium (0), absent, or with minimal exposure (1), large (2), or large such that parietal is excluded from posterior edge of table (3). Modified from Brochu (2011), character 160.

144. Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1). From Brochu (2011), character 162.

145. Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall anterior to trigeminal foramen. From Brochu (2011), character 163.

146. Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1). From Brochu (2011), character 164.

147. Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process of the pterygoid (1). Modified from Brochu (2011), character 165.

148. Capitate process of laterosphenoid orientated laterally (0) or anteroposteriorly (1) toward midline. From Brochu (2011), character 166.

149. Parietal with recess communicating with pneumatic system (0) or solid, without recess (1). From Brochu (2011), character 167.

150. Significant ventral quadrate process on lateral braincase wall (0) or quadrate–pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1). From Brochu (2011), character 168.

151. Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid at maturity. From Brochu (2011), character 169.

152. Posterior pterygoid processes tall and prominent (0) or small and project posteroventrally (1) or small and project posteriorly (2). From Brochu (2011), character 171.

153. Basisphenoid thin (0) or anteroposteriorly wide (1) ventral to basioccipital. From Brochu (2011), character 172.

154. Basisphenoid not broadly exposed ventral to basioccipital at maturity; pterygoid short ventral to median eustachian opening (0) or basisphenoid exposed as broad sheet

ventral to basioccipital at maturity; pterygoid tall ventral to median eustachian opening (1). From Brochu (2011), character 173.

155. Exoccipital with very prominent boss on paroccipital process; process lateral to cranioquadrate opening short (0) or exoccipital with small or no boss on paroccipital process; process lateral to cranioquadrate opening long (1). From Brochu (2011), character 174.

156. Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal. From Brochu (2011), character 175.

157. Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust process ventrally and participate in basioccipital tubera (1) or send slender process lateral to the basioccipital tubera (2). Modified from Brochu (2011), character 176.

158. Quadrate foramen aereum on mediodorsal angle (0) or on dorsal surface (1) of quadrate. From Brochu (2011), character 177.

159. Quadrate lacks (0) or bears (1) prominent, mediolaterally thin crest on dorsal surface of ramus. From Brochu (2011), character 179.

160. Attachment scar for posterior mandibular adductor muscle on ventral surface of quadrate ramus forms modest crests (0) or prominent knob (1). From Brochu (2011), character 180.

161. Quadrate with small, ventrally reflected medial hemicondyle (0) or with small medial hemicondyle; dorsal notch for foramen aereum (1) or with prominent dorsal projection between hemicondyles (2) or with expanded medial hemicondyle (3). From Brochu (2011), character 181.

162. Orbits equal or sub equal than infratemporal fenestrae (0) or orbits larger than infratemporal fenestrae (1) or orbits smaller than infratemporal fenestrae (2). From Souza-Filho et al. (2019), character 181, modified from Cidade et al. (2017), character 181, and Bona et al. (2012), character 165. Rephrased.

163. Prefrontal-frontal not thickened or thickened forming a flange (0) or thickened forming a marked knob (1) at the anterior-medial margin of the orbits. From Bona et al. (2012) character 167.

164. Anterior extremity of the frontal long and reaching or exceeding the anterior margins of the orbits (0), or short, not reaching the anterior margins of the orbits (1). From Barrios (2011) character 104, translated from Spanish.

165. Posterior margin of the skull table transversely straight to slightly concave (0) or deeply concave (1). From Barrios (2011) character 108, translated from Spanish.

166. Jugal lateromedially slender and dorsoventrally low (0), or jugal lateromedially wide and dorsoventrally low, with a blade-like shape (1) or jugal lateromedially wide and dorsoventrally high, with a cylindrical shape (2). From Cidade et al. (2017), character 188.

167. Iris (0) greenish/yellowish or (1) brown. From Brochu (2013), character 182.

168. Two or more (0) or one (1) row of postoccipital osteoderms. From Brochu (2013), character 183.

169. Ectopterygoid maxillary ramus forms less than (0) or more than (1) two-thirds of lateral margin of suborbital fenestra. From Brochu (2013), character 185.

170. Palatine–maxillary suture intersects suborbital fenestra at its anteromedial margin (0) or nearly at its anteriormost limit (1). From Brochu (2013), character 187.

171. Shape of the posteriormost five to six dentary teeth: exclusively pointed to slightly blunt (0); with the presence of globular teeth (1); with the presence of large globular teeth (2); with the presence of molariform multicusped (3). Modified from Salas-Gismondi et al. (2015), character 198.

172. Preorbital crest absent (0) or present (1). Modified from Barrios (2011), character 109, translated from Spanish.

173. Maxilla with strong festooning and dorsoventrally low (0), or with strong festooning and dorsoventrally high (1) or with rounded lateral margins (2) or with slight festooning (3) or no festooning, maxilla dorsoventrally flattened (4) or no festooning, maxilla making part of rostrum with tubular shape (5). Modified from Barrios (2011), character 106.

174. Secondary choana circular (0) or compressed lateromedially and anteroposteriorly (1). New character.

175. Secondary choana small (0) or large (1). New character.

176. Pattern of size in the maxillary teeth and alveoli: anteriormost with increasing size, those in the middle-length slightly smaller, and posteriormost with the same size or larger than those of middle-length (0); anteriormost with increasing size, those in the middle-length strongly smaller, and posteriormost with larger than those of middle-length (1); anteriormost with increasing size, followed by progressively smaller teeth and alveoli (2); teeth and alveoli approximately of the same size (3); anteriormost teeth and alveoli small, followed by progressively larger teeth and alveoli (4). New character.

177. Mid-length portion of the palatines lateromedially compressed (0) or expanded (1). New character.

178. Medial portion of the quadrate oriented dorsally (0) or medially (1). New character.

179. Retroarticular process anteroposteriorly long (0) or short (1). New character. 180. Anteroposteriorly length of the maxilla in dorsal view: long (0) or short (1). New character.

181. Laterocaudal bridge sectioning the trigeminal foramen: absent (0) or present (1). New character.

182. Osteoderms with low spines (0) or with high spines (1). New character.

183. Median crest of the parietal: absent or low (0) or high (1). New character.

Appendix 4

Complete matrix of scored characters used in this study:

Bernissartia fagesii

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Allodaposuchus precedens

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Acynodon iberoccitanus

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Acynodon adriaticus

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Iharkutosuchus makadii

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Hylaeochampsa venctiana

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Eothoracosaurus mississippiensis

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Eosuchus minor

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Eogavialis africanus

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Gryposuchus colombianus

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Gavialis gangeticus

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Borealosuchus sternbergii

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Borealosuchus formidabilis

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Borealosuchus acutidentatus

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Borealosuchus wilsoni

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Planocrania hengdongensis

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Planocrania datagensis

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Boverisuchus magnifrons

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Boverisuchus vorax

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Asiatosuchus germanicus

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Crocodylus affinis

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Crocodylus acer

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Kentisuchus spenceri

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Thecachampsa americana

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Tomistoma schlegelii

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Kambara implexidens

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Australosuchus clarkae

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Trilophosuchus rackhami

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Crocodylus megarhinus

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Rimasuchus lloydi

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Voay robustus

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110?0000?002100100100001101010110101000100001111 0?00101100121100 14111?1
101?111001000003100000??000000000100000?0

Osteolaemus tetraspis

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10111011111011000003100001100000000000?0000

Osteolaemus osborni

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011101?1110110000031000 01000?000000000?00

Mecistops cataphractus

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Crocodylus porosus

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Crocodylus acutus

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Crocodylus niloticus

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Prodiplocynodon langi

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Diplocynodon deponiae

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Diplocynodon darwini

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Diplocynodon ratelii

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Diplocynodon muelleri

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Diplocynodon tormis

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Ceratosuchus burdoshi

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Navajosuchus mooki

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Hassiacosuchus haupti

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Allognatosuchus polyodon

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Arambourgia gaudryi

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Alligator sinensis

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Alligator mississippiensis

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Alligator thomsoni

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Alligator prenasalis

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Alligator mefferdi

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Alligator olseni

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Alligator mcgrewi

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Stangerochampsa mccabei

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Albertochampsa langstoni

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Brachychampsa montana

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Brachychampsa sealeyi

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Purussaurus mirandai

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Purussaurus sp. nov.

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Mourasuchus arendsi

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Mourasuchus pattersoni

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Caiman yacare

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Caiman crocodilus

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Caiman latirostris

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Caiman niger

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Paleosuchus trigonatus

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Paleosuchus palpebrosus

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“*Caiman*” *brevirostris*

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Centenariosuchus gilmorei

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Globidentosuchus brachyrostris

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Eocaiman cavernensis

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Eocaiman palaeocenicus

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Gnatusuchus pebasensis

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Kuttanacaiman iquitosensis

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“*Caiman*” *wannlangstoni*

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Caimaninae sp. nov. (UCMP-39978)

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Acresuchus pachytemporalis

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Diplocynodon remensis

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Diplocynodon elavericus

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Diplocynodon ungeri

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Botttosaurus harlani

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Protoalligator huningensis

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Appendix 5

THE FEEDING HABITS OF THE STRANGE CROCODYLIAN *MOURASUCHUS* (ALLIGATOROIDEA, CAIMANINAE): A REVIEW, NEW HYPOTHESES AND PERSPECTIVES

GIOVANNE M. CIDADE[1], DOUGLAS RIFF[2], ANNIE SCHMALTZ HSIOU[1]

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ABSTRACT

The caimanine crocodylian from the Miocene of South America *Mourasuchus* is one of the most peculiar crocodylomorphs of all time. It exhibits an unusual long, wide and dorsoventrally flattened rostrum, long, slender mandibles and relatively short cervical vertebrae. These features have taken previous studies to propose that the feeding habits of *Mourasuchus* were very different from those of most crocodylomorphs. In order to significantly improve the knowledge on the feeding habits of *Mourasuchus*, we performed the most comprehensive review on this issue in order to offer the most complete assessment on the question to date and to propose new hypotheses that are coherent with our current knowledge on *Mourasuchus* and on the feeding habits of crocodylomorphs as a whole. As results, this study proposes that *Mourasuchus* was likely incapable of capturing and consuming large prey and specialized in eating small prey, such as mollusks, crustaceans and small fish. The rostrum of *Mourasuchus* possibly evolved to cover the largest possible area to allow more efficiency in the capture of large amounts of small prey. Whether *Mourasuchus* was capable to “select” the food from the material it ingested together with it is not yet known. As such, we follow “gulp-feeding” as a more proper name for the proposed feeding habits of the taxon. *Mourasuchus* was probably an inhabitant of quiet, shallow water bodies, which possessed the largest quantity of habitats in which the preferred prey of this taxon dwelled. It is also proposed that the habit of *Mourasuchus* evolved from the durophagous habit proposed for many fossil caimanines. This hypothesis, however, has to be addressed by future studies.

RESUMO

O crocodiliano caimaníneo do Mioceno da América do Sul *Mourasuchus* é um dos crocodilomorfos mais peculiares de todos os tempos. Ele possui um incomum rostro longo, largo e dorsoventralmente achatado, mandíbulas longas e esguias e vértebras cervicais relativamente curtas. Tais características levaram estudos prévios a propor que os hábitos alimentares de *Mourasuchus* eram muito diferentes dos da maioria dos crocodilomorfos. Com o objetivo de melhorar significativamente o conhecimento sobre os hábitos alimentares de *Mourasuchus*, realizamos a revisão mais abrangente sobre esta questão para oferecer a análise mais completa sobre ela até o momento e propor novas hipóteses que sejam coerentes com o conhecimento atual sobre *Mourasuchus* e sobre os hábitos alimentares dos crocodilomorfos como um todo. Como resultados, este estudo propõe que *Mourasuchus* era provavelmente incapaz de capturar e consumir grandes presas e se especializou em consumir presas pequenas, como moluscos, crustáceos e pequenos peixes. O rostro de *Mourasuchus* possivelmente evoluiu para abranger a maior área possível para permitir maior eficiência na captura de grandes quantidades de pequenas presas. Não se sabe ainda se *Mourasuchus* seria ou não capaz de “selecionar” a comida do material que ele ingeria junto com ela. Assim, seguimos “engolfamento” como o melhor nome para os hábitos alimentares propostos para o táxon. *Mourasuchus* habitava provavelmente corpos d’água quietos e rasos, que possuiriam em maior quantidade os hábitats em que viviam suas presas preferenciais. Também se propõe que

o hábito de *Mourasuchus* evoluiu do hábito durófago proposto para muitos caimaníneos fósseis. Esta hipótese, porém, precisa ser avaliada por estudos posteriores.

INTRODUCTION

The fossil crocodylomorphs of the Miocene of South America comprise one of the largest, most taxonomically diverse and morphologically disparate faunas of the Crocodylomorpha clade (Langston, 1965, 2008; Gasparini, 1996; Langston & Gasparini, 1997; Paolillo & Linares, 2007; Salas-Gismondi et al., 2007, 2015; Riff et al., 2010; Scheyer & Moreno-Bernal, 2010; Bona et al., 2013a; Scheyer et al., 2013; Bona & Barrios, 2015; Moreno-Bernal et al., 2016; Scheyer & Delfino, 2016; Souza et al., 2016; Cidade et al., 2017). This includes not only records of the extant genera *Paleosuchus* (Salas-Gismondi et al., 2007), *Melanosuchus* (Medina, 1976; Bona et al., 2017; Foth et al., 2017) and *Caiman* (Souza-Filho, 1987; Fortier et al., 2009; Bona & Carabajal, 2013; Bona et al., 2013a, 2014; Fortier et al., 2014; Salas-Gismondi et al., 2015), but perhaps the most impressive examples of such diversity are the crocodylomorphs whose morphology, ecological niche and feeding habits differ substantially from those of the extant crocodylians.

These include the terrestrial predators sebecids (Langston, 1965; Paolillo & Linares, 2007; Salas-Gismondi et al., 2007), the giant, semi-aquatic top predator *Purussaurus* (Barbosa-Rodrigues, 1892; Mook, 1941; Langston, 1965; Bocquentin-Villanueva et al., 1989; Aguilera et al. 2006; Aureliano et al., 2015), the durophagous caimanines *Gnatusuchus, Kuttanacaiman, Globidentosuchus, Balanerodus* and *Caiman wannlangstoni* (Langston, 1965; Salas-Gismondi et al., 2015) and the predominantely piscivorous, longirrostrine taxa represented by crocodyloids such as *Charactosuchus* and *Brasilosuchus* (Langston, 1965; Souza-Filho & Bocquentin-Villanueva, 1989; Souza-Filho, 1991, 1993; Souza-Filho et al., 1993) and gryposuchinae gavialoids (Gürich, 1912; Langston, 1965; Gasparini, 1968; Sill, 1970; Bocquentin-Villanueva & Buffetaut, 1981; Kraus, 1998; Brochu & Rincón, 2004; Riff & Aguilera, 2008; Salas-Gismondi et al., 2016).

One of the most strikingly disparate forms of the Miocene of South America is *Mourasuchus*, a caimanine crocodylian that exhibits a long, wide, dorsoventrally flattened rostrum (a “platyrostral-broad” rostrum according to the classification of Busbey, 1994) with a relatively small skull table (Fig. 1), slender, long mandibles (Figs. 2 and 3) and cervical vertebrae relatively short anteroposteriorly (Fig. 4) (see Price, 1964; Langston, 1965, 2008; Bocquentin-Villanueva, 1984; Bona et al., 2013a, 2013b; Cidade et al., 2017). The diversity of the genus is currently comprised by four species: *M. atopus* (Langston, 1965), from the middle Miocene Honda Group of Colombia and Pebas Formation of Peru (Langston, 1965; Salas-Gismondi et al., 2015); *M. amazonensis* Price, 1964, from the late Miocene Solimões Formation of Brazil (Price, 1964; Souza-Filho & Guilherme, 2011a); *M. arendsi* Bocquentin-Villanueva, 1984 from the late Miocene Urumaco Formation of Venezuela, Solimões Formation of Brazil and Ituzaingó of Argentina (Bocquentin-Villanueva, 1984; Gasparini, 1985; Souza-Filho & Guilherme, 2011b; Scheyer & Delfino, 2016); and *M. pattersoni* Cidade et al., 2017, also from the Urumaco Formation (Cidade et al., 2017).

There are also records of *Mourasuchus* for the early/middle Miocene Castilletes Formation of Colombia (Moreno-Bernal et al., 2016); for the middle Miocene units

Fitzcarrald Arch and Pebas Formation of Peru (Salas-Gismondi et al., 2007, 2015) and Socorro Formation of Venezuela (Scheyer et al., 2013) and for the late Miocene Solimões Formation, of Brazil (Souza-Filho & Kischlat, 1995; Oliveira & Souza-Filho, 2001; Scheyer & Moreno-Bernal, 2010), Urumaco, of Venezuela (Scheyer & Delfino, 2016) and Yecua, of Bolivia (Tineo et al., 2014).

Ever since the first descriptions, the unusual morphology *Mourasuchus* has sparked a debate about how this taxon would capture its prey, and about what exactly would comprise such prey. Many hypotheses have been put forward: the first ones were proposed by Langston (1965), which would later be called "filter-feeding" by later authors (Riff et al., 2010; Bona et al., 2013b) while a second hypothesis, briefly discussed by Cidade et al. (2017), is that *Mourasuchus* would perform a feeding behaviour named as "gulp-feeding". Additionally, different studies have proposed many distinct possible prey items for *Mourasuchus*, including fish, crustaceans, gastropod and bivalve mollusks and even herbivory.

Langston (1965) proposed three different foraging strategies for this taxon: *Mourasuchus* could stay stopped in the water surface with an open mouth, waiting that fish and arthropods ended up entering into the mouth unwary – a strategy that had been observed in living caimanines according to the author; or it could swim slowly through the water surface scooping up (presumably with the gular sac) small-sized animals; or that *Mourasuchus* could forage among the mud ("mud-grubbing"), either on the margins or on the floor of the water bodies, somewhat similarly to the behavior seen in modern-day ducks and according to Langston (1965) also in extant caimanines. In addition, Langston (1965), upon arguing that the teeth of *Mourasuchus* were too small to have a large role in food capture, stated that would only aid in "food straining". This expression was apparently taken by later authors (Riff et al., 2010; Bona et al., 2013b) to mean the same as "filter-feeding"; however, neither Langston (1965) nor the later authors explained what "straining" and "filter-feeding", respectively, would specifically mean.

The first feeding strategy could certainly be performed by *Mourasuchus*, but we consider unlikely that such a behavior by itself would provide all the food necessary for the animal due to the relative level of randomness in food capture that arises in this process; and additionally, it would not explain the peculiar cranial morphology evolved by the taxon. The second behavior could also be performed, but likely mostly in shallow water bodies in order to diminish the resistance the animal would face to close the jaws under water. A behavior similar to the third one proposed by Langston (1965) is in the opinion of this study the one that better fits with the known morphology of *Mourasuchus* and thus considered the most likely to be performed predominantly by the taxon (see an illustration in Figure 5), as will be detailed below.

Cidade et al. (2017) take from this third hypothesis of Langston (1965) to suggest that the most likely behavior of *Mourasuchus* for obtaining food would be foraging through bottoms and margins of shallow water-bodies, but emphasized briefly on the role of the platyrostral-broad (see Busbey, 1994) shape of the rostrum in capturing large amounts of small prey with the ventral portion of the rostrum serving as a "fishing net" or "gular sac". Additionally, Cidade et al. (2017) name this behavior proposed for *Mourasuchus* as "gulp-feeding", which would be more accurate than "filter-feeding" in describing the behavior, as the latter could imply the idea that *Mourasuchus* would perform techniques akin to baleen whales, for example. Regarding the foraging strategies and methods of ingestion of the food in *Mourasuchus*, this work develops on the perspectives put forward by Cidade et al. (2017) bur reviews thoroughly the hypothesis of those authors as well as those of Langston (1965, 2008).

Regarding the diet items of *Mourasuchus*, Langston (1965) suggested that these would be comprised by small fish and arthropods. The same author would posteriorly (Langston, 2008) propose that the main diet items would be fish of slow movement, such as *Lepidosiren* (Lepidosireniformes) and members of the Siluriformes group (catfish), and freshwater crabs, all of which are found in the Amazonian area of the Miocene of South America (Langston, 2008). Additionally, Langston (1965) cogitated the hypothesis that *Mourasuchus* could be an herbivore, since plants and algae would be easier to handle with the anatomical features of the skull and vertebrae present in the taxon.

Another interesting scenario is the notable anatomical convergence between *Mourasuchus* and the Cretaceous crocodyliforms from the north of Africa *Stomatosuchus*, *Laganosuchus*, *Aegyptosuchus* and *Aegisuchus*, especially in the morphology of the skull, which is also platyrostral-broad in the two first two taxa and is inferred to have the same morphology in the other two (Stromer, 1925; Sereno & Larsson, 2009; Holliday & Gardner, 2012). This fact meant that some similar hypothesis have been proposed regarding the feeding habits of *Mourasuchus* and the taxa from the African Cretaceous, most notably the ventral portion of the rostrum serving as a “fishing net” or “gular sac” for collecting and swallowing prey(see Nopcsa, 1926; Langston, 1965; Sereno & Larsson, 2009).

Given these different hypothesis and scenarios, the objective of this paper was to perform the most comprehensive revision on the studies about the feeding habits of *Mourasuchus* to date and to present which hypothesis is more congruent with our current knowledge of the taxon, the paleoenvironment in which it lived and the biota with which it co-existed during the Miocene. Specifically, the three questions this study addresses are the following: how *Mourasuchus* did to capture its food; what exactly *Mourasuchus* ate; and how its unusual morphology and feeding strategy evolved, diverging from more “traditional” caimanine morphology and foraging habits.

In accordance with these objectives, comprehensive revisions were performed on the *Mourasuchus* anatomy that is related to the feeding habits, the convergence between *Mourasuchus* and the Cretaceous crocodyliforms from northern Africa, and the historical on the research on *Mourasuchus* feeding habits. As a result of these revisions, the hypothesis defended by this work on the feeding habits of *Mourasuchus* are presented, along with perspectives to be looked forward to regarding the paleoecology of this peculiar taxon.

Institutional Abbreviations

CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; MCNC-PAL, Museo de Ciéncias Naturales de Caracas, Caracas, Venezuela; MNN IGU Muséum National du Niger, Niamey, Niger; UFAC, Universidade Federal do Acre, Rio Branco, Brazil.

RESULTS

Mourasuchus **unusual anatomy related to feeding habits**

Both the cranial and the postcranial anatomy of *Mourasuchus* exhibit remarkable differences if compared to most crocodyliforms, even if considered the unusual morphological disparity exhibited by the group in the Miocene of South America. Many of these peculiarities were linked by previous studies to the feeding behaviour of the taxon (see Langston, 1965, 2008; Bona et al., 2013b; Tineo et al., 2014; Cidade et al., 2017), which were reviewed by this study.

The *Mourasuchus* skull has a remarkably long, wide, dorsoventrally flattened, "duck-like" platyrostral-broad rostrum (Fig. 1). In accordance with the shape of the rostrum, the mandibles are long, but also lateromedially slender, with a short mandibular symphysis that does not extend beyond the level of the first mandibular alveolus (Cidade et al., 2017; Figs. 2 and 3). Such skull most likely precluded *Mourasuchus* to capture, hold or ingest large prey, in the way that many of the current crocodylians do, especially those of large size (e.g. Busbey, 1994) as it would not provide the bite force required for such activity (Langston, 1965). In addition, the shape of the rostrum would disturb the movement of the skull in water bodies with swift currents, while being met with great resistance if the animal tried to close the "duck-like" rostrum under water (Langston, 1965).

Most of the teeth of *Mourasuchus* are very small relative to the size of the skull. Whereas the first to the fourth alveoli are the biggest in the mandibulary tooth row and are comparable to the extant *Crocodylus acutus*, from the fifth alveolous on the alveolar size of *Mourasuchus* tends to be smaller than those of other crocodilians (see Langston, 1965, fig. 29). This suggests that the teeth did not have a proeminent role in the capture or handling of the prey in the mouth. As such, the morphologies of the skull and the teeth indicate that *Mourasuchus* was not capable of capturing or handling large or middle-sized prey, which are a prominent diet item in the adult individuals of current large crocodylians whose body length approaches that of *Mourasuchus* (estimated in 6.6m by Langston, 2008), such as *Crocodylus porosus, C. niloticus, Alligator mississippiensis* and *Melanosuchus niger*, among others.

The postcranial anatomy features of *Mourasuchus* that have relation to the feeding behavior corroborate these hypotheses. The cervical vertebrae of *Mourasuchus arendsi* and *M. pattersoni* are relatively anterposteriorly shorter than those of extant crocodylians (Bocquentin-Villanueva, 1984; Langston, 2008; Fig. 4), while Tineo *et al.* (2014) described a cervical vertebra of "*Mourasuchus* sp." with a short vertebral centrum from the Late Miocene of Bolivia. This suggests that the neck of *Mourasuchus* was "relatively weak and less motile" than that of extant crocodylians, as proposed by Langston (2008).

Langston (2008) also linked some postcranial features to biomechanical consequences related to the feeding behavior of *Mourasuchus*. These are the "nearly vertical" trochlear surfaces on the odontoid bone, which would indicate a shorter vertical excursion of the head than that of extant crocodylians; the small, non-hooked hypapophyses of the cervical vertebrae suggest less development of the *M. longus colli*, which is involved with flexing and lateral movement of the neck; and the low cervical neural spines suggest that the epaxial antagonist muscles would be less powerful that in extant taxa (see Langston, 2008, p. 139). These features, associated with the proportionally small size of the cervical vertebrae as whole, took the same author to propose that the cervical area ("neck") of *Mourasuchus* would be relatively weaker and less motile than that of extant crocodylians.

All these suggestions still require proper biomechanical analyses to be throroughly tested, but this work considers that the features noted by Langston (2008) indicate in the least that *Mourasuchus* was not capable of accentuated head movements, as pointed out the same author. Thus, the vertebral anatomy agrees with the skull anatomy in indicating that this taxon was very probably not capable of holding and dismembering large prey in the way many modern crocodylians do, with behaviors such as the 'death roll' (see Blanco et al., 2015) being unlikely to be performed by *Mourasuchus*.

Furthermore, Tineo *et al*. (2014) also propose that *Mourasuchus* would have a reduced length of the vertebral column in comparison with extant crocodilians, which would result in a skull-length-to-body ratio hydrodynamically adverse to a typical aquatic crocodylian. This would be in agreement with the known features of vertebral anatomy of the taxon, but as no complete vertebral column of *Mourasuchus* has been found so far, this hypothesis needs to be seen with caution. Nevertheless, Tineo et al. (2014) also proposed that *Mourasuchus* would be a preferential inhabitant of "lentic, shallow aquatic habitats" (Tineo *et al*., 2014), such as swamps and quiet lakes. This agrees with the aforementioned proposition of Langston (1965) about the shape of the rostrum of *Mourasuchus* disturbing the movement of the skull in swift waters and the great resistance the animal would face to close the rostrum under water. These proposals are in agreement with the feeding habits and lifestyle proposed for *Mourasuchus* in this study, which are detailed below. Additionally, swamps and lakes were known to exist in the paleoenvironements *Mourasuchus* lived in during the Miocene (e.g. Latrubesse *et al*., 2010; Scheyer & Moreno-Bernal, 2010).

Convergence with North African forms of the Cretaceous

The unusual skull morphology of *Mourasuchus* is convergently shared with five species of four genera from the Late Cretaceous of north Africa: *Stomatosuchus inermis* Stromer, 1925, from the Baharyia Formation of Egypt; *Laganosuchus thaumastos* Sereno & Larsson, 2009, from the Echkar Formation of Niger (Fig. 3) and *L. maghrebensis* Sereno & Larsson, 2009 from the Late Cretaceous Kem Kem Formation of Morocco; *Aegisuchus witmeri* Holliday & Gardner, 2012, also from the Kem Kem Formation; *Aegyptosuchus peyeri* Stromer, 1933, also from the Baharyia Formation. *Stomatosuchus* and *Laganosuchus* have been grouped together in Stomatosuchidae Stromer, 1925, whereas *Aegyptosuchus* and *Aegisuchus* have been grouped within Aegyptosuchidae Kuhn, 1936 (Holliday & Gardner, 2012). *Stomatosuchus* and *Laganosuchus* share with *Mourasuchus* a long, wide, dorsoventrally flattened skull and slender mandibles with short symphyses (see Stromer, 1925; Nopcsa, 1926; Sereno & Larsson, 2009). While skull and mandibles were described for *Stomatosuchus* (Stromer, 1925; Nopcsa, 1926), only mandibles were described for *Laganosuchus*, but a platyrostral-broad rostrum can be safely inferred for this taxon due to the long, slender mandibles that strongly resemble those of *Stomatosuchus* (Sereno & Larsson, 2009; Fig. 3). *Aegisuchus* and *Aegyptosuchus* do not have complete skulls or mandibles preserved, but estimations made for *Aegisuchus* by Holliday & Gardner (2012) indicate that this taxon likely had a long, wide rostrum similar to that of stomatosuchids, and the phylogenetic proximity and morphological similarities between *Aegyptosuchus* and *Aegisuchus* suggest that the former possessed a similar platyrostral-broad rostrum (see

Holliday & Gardner, 2012), but further specimens of *Aegyptosuchus* are required for this issue to be settled.

The convergent nature of these similarities is evident for the fact that Stomatosuchidae (represented only by *Laganosuchus* in phylogenetic analysis, since the holotype of *Stomatosuchus* was destroyed during the Second World War, see Holliday & Gardner, 2012) is phylogenetically placed as a neosuchian basal to Eusuchia (Sereno & Larsson, 2009; Holliday & Gardner, 2012), and Aegyptosuchidae is placed either as a sister-taxon of Crocodylia or as a clade within Crocodylia but unrelated to Alligatoroidea, the clade within *Mourasuchus* is situated (Holliday & Gardner, 2012).

The morphological similarities between *Mourasuchus* and the Cretaceous taxa has meant that similar paleoecological hypotheses to be proposed for both. Sereno & Larsson (2009) proposed that the mandibles of *Laganosuchus* could not be adducted or abducted with great force. Langston (1965) had also described the mandibles of *Mourasuchus* as “mechanically inefficient”. Consistent with this, Sereno & Larsson (2009) suggested that *Laganosuchus* was a low-lying, sit-and-wait predator, while Langston (2008) described *Mourasuchus* as a “lie in wait” predator that inhabited quiet waters. Additionally, Langston (1965) had already suggested that *Mourasuchus* could have an ambush behaviour of staying immobile in the water with the mouth opened, waiting for small fish and other animals entered it, a behaviour that has been observed in extant taxa (Langston, 1965), a behaviour that can also be proposed for *Laganosuchus*. Most remarkable, however, is the proposal that the musculature of the ventral part of the rostrum that could perform as a ““fishing net” that would allow these taxa to “collect” the prey for subsequent swallowing, presumably without any large participation of the teeth in the process. The suggestion was first made for *Stomatosuchus* by Nopcsa (1926) and later proposed for *Mourasuchus* as well (Langston, 1965; Cidade et al., 2017).   Upon suggesting this mechanism for *Stomatosuchus*,

Nopcsa (1926) proposed that the ventral portion of that taxon could be a contractible structure analogous to the gular sac found in pelicans, based on features such as the length and slenderness of the mandible, the presence of a “wing-like” process ventral to the posterior portion of the same element (that would serve as attachment area for the ligaments of the “gular sac) and the fact that the “post-articular process” (interpreted here as the retroarticular process) being bent inwards relative to the mandible. In the figures of *Stomatosuchus*, the inward bending of the retroarticular process is not evident, but a ventral expansion in the posterior portion of the mandible that may be what Nopcsa names “wing-like” process is (see Stromer, 1925, figs. 1 and 1a; Sereno & Larsson, 2009, figs. 2-B and 2-C). Neither of these two features, however, are present in *Laganosuchus* (see Sereno & Larsson, 2009) or in *Mourasuchus* (see Langston, 1965; Cidade et al., 2017, 2018); but the long, slender mandibles are shared between the three taxa. However, no specific studies to determine how contractible the ventral portion of the skull was in these taxa has ever been performed. In addition, the exact role that such contraction ability could perform in the feeding process of *Mourasuchus* has never been thoroughly reviewed and discussed, for example through comparison with observations made in extant crocodylians about the musculature of the ventral portion of the rostrum. The latter issue is also one of the objectives of this study.

Hypotheses defended in this work for the feeding habits of *Mourasuchus*

The anatomy of both the skull and the cervical vertebrae makes it very unlikely that *Mourasuchus* was able to hold, dismember and ingest larger prey, especially if these are capable of fast movements. The only large prey *Mourasuchus* could eat would be those not capable of fast movements, such as the aforementioned *Lepidosiren* fish, but even these slow-moving prey were likely to require some strength of the skull and mandibles, as well as large and sharp teeth, to be properly manipulated; all characteristics that *Mourasuchus* lacks. As such, it is here considered more likely that the prey of *Mourasuchus* would be mostly comprised of small animals.

The most consumed small animais were most likely small fish and crustaceans (e.g. fresh water crabs and shrimps), as proposed by Langston (1965, 2008) and Cidade et al. (2017), but also gastropod and bivalve mollusks (Cidade et al., 2017; Fig. 5) which are also find in the Miocene formations of South America and which comprise the main diet items of several durophagous caimanines (see Salas-Gismondi et al., 2015), whose possible relation to the feeding habits of *Mourasuchus* will be discussed posteriorly. Insects could also make part of the diet of *Mourasuchus*, although presumably to a lesser extent than the eminently aquatic gastropods, bivalves and crustaceans. The consumption of these groups of invertebrates by extant crocodilians has been continuously recorded, inclusive in living Caimaninae (e.g. Carvalho, 1951; Medem, 1981, 1983; Monteiro, et al., 1997), especially when juvenile (e.g. Monteiro, et al., 1997), whilst *Caiman latirostris* is considered to rely mainly on ampularid gastropods also during adulthood (Diefenbach, 1979, 1987; Vanzolini & Gomes, 1979; Ayarzagueña, 1983; Monteiro, et al., 1997; Ösi & Barrett, 2011).

The possibility that *Mourasuchus* could be an herbivore is not considered here as likely, but further evidence may point to an opposite direction. Consumption of vegetal matter has been observed in living crocodilians, being it either of foliage, seeds or fruits (e.g. Brito et al., 2002; see Platt et al., 2013 for a revision); additionally, some capacity of digestion of plant carbohydrates, proteins and lipids has been detected in *Alligator mississipiensis* (Coulson et al., 1987; Staton, 1988; Platt *et al*., 2013). Herbivory has also been suggested for other fossil crocodyliforms, such as *Chimaerasuchus paradoxus* from Early Cretaceous of China (Wu et al., 1995), and *Simosuchus clarki*, from the Late Cretaceous of Madagascar (Buckley *et al*., 2000). As far as it concerns *Mourasuchus*, however, there are no evidences yet to support an herbivorous habit for this taxon, such as those that could be obtained through the finding and analysis of stomach contents or an analysis of coprolite content, for example.

The extinct caimanines *Kuttanacaiman*, *Caiman wannlangstoni*, *Balanerodus*, *Globidentosuchus* and *Gnatusuchus* are considered to be durophagous taxa, feeding mainly of hard-shelled invertebrates such as bivalves and gastropods (see Langston, 1965; Langston & Gasparini, 1997; Salas-Gismondi *et al*., 2015). They are described as durophagous mainly due to the presence of posterior globular teeth and large mandibular symphysis, among other cranial features. *Gnatusuchus*, specifically, is considered by Salas-Gismondi *et al*. (2015) to have a foraging strategy of a “head burrowing” activity in which the animal predated infaunal bivalves of unconsolidated bottoms of lakes and rivers. Even though *Gnatusuchus* was a very specialized form for this kind of behavior, counting with a unique “shovel-like” structure in the lower jaws that helped to “scrape” the bottom of the water bodies (Salas-Gismondi *et al*., 2015), it is possible that such a strategy could be performed by all the other extinct durophagous Caimaninae taxa. The bivalve infauna in the water bodies of Miocene of South America, where all of the aforementioned extinct taxa lived, was very rich (Wesselingh *et al*., 2002; Wesselingh, 2006; Salas-Gismondi *et al*., 2015), providing and abundant diet source for durophagous crocodilians. Given the possibility that the main prey of *Mourasuchus* would be the same as that of durophagous caimanines such as *Gnatusuchus*, we consider that the foraging behavior of *Mourasuchus* could be somewhat similar to that of those taxa, although exhibiting a specialization toward the swallowing of large quantities of prey without the necessity to crunch them with the teeth.

If durophagous Caimaninae such as *Gnatusuchus* fed themselves by burrowing the margins and floors of the water-bodies to collect its prey (especially bivalve mollusks but also gastropods, as well as crustaceans and other arthropods) and subsequently crunch them with their posterior globular teeth, *Mourasuchus* could use of a similar way to capture the prey but would not crunch them with its teeth, since most of those are not only very small in its taxa, while also lacking the globular shape seen in the typical durophagous crocodylians. Instead, *Mourasuchus* would swallow the prey entirely, preferably in large quantities that could be captured with the inferior part of the rostrum and then ingested all together. Such behavior would explain not only the small size of most of the teeth in *Mourasuchus* (Langston, 1965), as it would also explain the long, wide, dorsoventrally flattened, platyrostral-broad rostrum of this taxon, as such morphology significantly increases the area occupied by the rostrum, consequently increasing the efficiency and the probability of capturing large amounts of the invertebrate prey on which *Mourasuchus* preferably fed on (Cidade et al., 2017). It explains, furthermore, the not very efficient musculature involved in the opening of the mouth as inferred in previous works (Langston, 1965, 2008; Tineo *et al*., 2014). Additionally, the use of the inferior part of the rostrum to collect prey would allow the taxon to capture large amounts of prey in a more efficient way than if the capture of the prey relied more on the use of the teeth, as it is frequently observed in extant crocodylians.

The use of the inferior part of the rostrum to collect prey is directly linked with some capacity of contraction of the ventral portion of the rostrum. Such capacity has been observed in the extant *Alligator mississippiensis*, which is achieved probably by the activation fo the muscles *M. genioglossus* and *M. hyoglossus*, located underneath the tongue (Busbey, 1989). As such, this contraction can also be present in *Mourasuchus* – pending biomechanical studies that may confirm or not its existence in this taxon – and would aid in the “gulping” of the prey in the fashion proposed above. Such contraction is reminiscent of the idea of the presence of a “gular sac”, as proposed by Langston (1965). Although the expression “gular sac” could be used to denote only a contractible inferior part of the rostrum being presumably involved in the capture of the prey by *Mourasuchus,* we recommend that this expression should not be used to describe this structure for this taxon unless future studies eventually show the inferior part of the rostrum of *Mourasuchus* to have striking similarities with the gular skins found in birds like pelicans, for example. However, the role of the ventral portion of the rostrum as a contractable collecting tool for food (as a “fishing net”), regardless of the fact that it may be called a “gular sac” or not, is proposed here as a likely possibility given the inferred foraging behavior and diet items of *Mourasuchus*, as well as the presence of contraction of the musculature of this area seen in *A. mississippiensis*.

Walmsley et al. (2013) state that the crocodilian skull exhibited a “trade-off” along its evolutionary history between a long, slender rostrum that provided speediness, and a shorter, yet more robust rostrum that provide strength in biting and consequently in the capture of prey. In this context, as argued by Cidade et al. (2017), *Mourasuchus* presents an interesting case in which the rostrum does not provide either speediness or strength to the biting of the living individual; instead, an increase in area – to optimize the capture of preferentially a large amount of small prey – seem to be the great advantage this rostral morphology provided to the individuals of *Mourasuchus*.

This foraging strategy aforementioned described for *Mourasuchus* has been named as “gulp-feeding” (Cidade et al., 2017) to emphasize the process of collecting and swallowing the food that were performed by the taxon, instead of the term “filter-feeding”, which denotes the performing of a selection process on the food for which there is no evidence yet in *Mourasuchus*. However, the small invertebrate animals on which *Mourasuchus* would mainly feed would not be found separate from the microenvironment in which they live in, either biotic – plants, algae – or abiotic – water, mud, sand, etc (Cidade et al., 2017). As such, *Mourasuchus* could rarely obtain its food in the aforementioned described way without also carrying into its mouth a certain amount of any of these materials, and thus it would be useful for the animal to develop a selection procedure to separate the edible matter from the non-edible matter (mud, water, etc.) that came with the former (Cidade et al., 2017). Such selection procedure may be what Langston (1965) described as “straining technique”, which later authors (e.g. Riff *et al*., 2010; Bona et al., 2013b) would refer to as a filtering or “filter-feeding” technique, even though none of this works give a detailed description of how these techniques would function.

Nevertheless, the possibility that *Mourasuchus* performed a procedure akin to a “selection” of the material put in the mouth before swallowing is considered here as plausible. Langston (1965) suggested that the tongue could be used to perform this procedure, as it could be elevated pressuring the water against the upper palate until the water could be expelled between the teeth, leaving the edible material concentrated for swallowing. Another possibility is that this movement proposed for the tongue by Langston (1965) could be performed by the muscles positioned between both mandibular rami in the inferior part of the rostrum. Living crocodylians have been observed to use such behavior exactly to expel water from the mouth between the teeth (Daniel C. Fortier, personal communication). Nevertheless, our current knowledge on *Mourasuchus* does not allow inferring whether this taxon was really capable of performing such selection or not (Cidade et al., 2017), and as such we favorable “gulp-feeding” as a better term to name the proposed feeding habits of *Mourasuchus*.

The proposed similarities allow the suggestion that the feeding behavior of *Mourasuchus* would have evolved directly from the durophagous feeding habit of caimanines such as *Gnatusuchus*. However, Caimaninae phylogenetic analyses that include the durophagous taxa and *Mourasuchus* (Salas-Gismondi et al., 2015; Cidade et al., 2017) do not recover the latter as closely related to any of the former. These topologies indicate that the feeding habits of *Mourasuchus* have evolved independently from that of the durophagous Caimaninae. Future analyses may reveal different scenarios, as the evolution of such a complex habit as that of *Mourasuchus* is more likely to have arisen from a pre-existent durophagous habit than from a generalist ancestor.

Nevertheless, a durophagous habit is already known to have arisen more than once in the Alligatoroidea clade, with basal alligatoroids such as *Brachychampsa* and alligatorines such as *Allognathosuchus* also being described as having been durophagous (see Carpenter & Lindsay, 1980; Brochu, 2004; Salas-Gismondi et al., 2015). As such, a possible scenario for the independent evolution of the “gulp-feeding” habit of *Mourasuchus* within Caimaninae is that it may have evolved from the habit of swallowing prey without masticating (which is plesiomorphic within crocodyliformes), which gradually evolved with the enlargement of the rostrum to allow a large number of small prey to be captured simultaneously, whereas the durophagy of the other Caimaninae could be seen as a specialization of the use of the posterior globular teeth against hard-bodied prey, having evolved probably from an ancestor that exhibit a feeding behavior similar to the extant *Caiman latirostris* (see Monteiro et al., 1997; Ösi & Barrett, 2011).

DISCUSSION

Perspectives

The comprehensive revision and the detailed hypotheses presented in this study comprise the most complete assessment on the feeding habits of *Mourasuchus* published to date. However, both the hypotheses presented in this study and those presented by previous ones still need to be properly tested and assessed empirically.

The proposed reduced capacity of movement of the neck by *Mourasuchus* inferred by Langston (2008) still needs to be properly assessed in a biomechanical analysis. Similarly, even if the slender mandibles of *Mourasuchus* have low mechanical capacities in all likelihood, a quantitative measurement of such mechanical capacities is also still in need to be done by proper biomechanical studies. Additionally, biomechanical studies in addition with muscular reconstructions may examine how elastic the musculature of the inferior part of the rostrum of *Mourasuchus* could be so to test whether (or to which level) it could act as analogous to a “gular sac”. The same studies are necessary to investigate whether (and if yes, how) *Mourasuchus* could select the edible from the edible-matter that it introduced into its mouth in order not to ingest a significant amount of water, mud, sand, plants or other materials.

Additionally, more fossil findings and further phylogenetic analyses are required to clarify where *Mourasuchus* exactly fits in the phylogeny of Caimaninae. This is fundamental to understand how the unusual feeding habits of the taxon evolved. The hypothesis that the habit of *Mourasuchus* evolved from a durophagous one exhibited by several caimanine taxa has been put forward by this study, but further phylogenetic studies must find a close relationship between *Mourasuchus* and those taxa (which has not been recovered in the analyses performed to date; see Brochu, 2011; Salas-Gismondi et al., 2015; Cidade et al., 2017) in order for this hypothesis to be more plausible. Additionally, the search for more fossils may bring some direct evidence of the dietary items of *Mourasuchus*, such as stomach contents or remains of food in coprolites, any of which have not been found to date.

The historical paleoecology of South American crocodylomorphs

The evolution the peculiar feeding of *Mourasuchus* is another consequence of the environmental conditions that allowed the establishment of an especially rich, morphologically diverse community of crocodylomorphs in the Miocene of South America. In this context, it is interesting to notice that from the four lineages that comprised such Miocene diversity (Sebecidae, Caimaninae, Gavialoidea and Crocodyloidea), two of them were already inhabiting South America by the Paleocene (Sebecidae and Caimaninae; see Bona, 2007; Riff et al., 2010; Brochu, 2011; Pol & Powell, 2011; Kellner et al., 2014; Cidade et al., 2019), while the first record of Gavialoidea for the continent is from the late Oligocene/early Miocene (Moraes-Santos et al., 2011) and the first records of Crocodyloidea (the putative tomistomine genera *Charactosuchus* and *Brasilosuchus*) are from the Miocene (see Riff et al., 2010), while the genus *Crocodylus* that currently inhabits the continent has its record beginning only in the Pliocene (Scheyer et al., 2013).

Of all these four lineages, Caimaninae is the one that exhibits the largest and most conspicuous morphological disparity in the Miocene, possessing morphotypes ranging from generalist predators (*Melanosuchus, Paleosuchus*), predominately durophagous (*Gnatusuhcus, Kuttanacaiman, Globidentosuchus, Caiman brevirostris*), the giant generalist predator *Purussaurus* and the gulp-feeding *Mourasuchus* (Cidade et al., 2019). These two taxa were also especially large crocodylians, with *Mourasuchus* reaching up to 6.6 meters (Langston, 2008) and *Purussaurus* up to 12.5 meters (Aureliano et al., 2015). Some gavialoids and sebecids also reached large sizes, with *Gryposuchus croizati* estimated to have reached between 9 and 10 meters (Riff & Aguilera, 2008) and *Barinasuchus arveloi* between 6.3 to over 10 meters (Molnar & Vasconcellos, 2016). However, Gavialoidea, putative tomistomines and *Crocodylus* exhibited basically the same bauplan along their evolutionary history in the South American Cenozoic, including the Miocene. Sebecidae is an exception, in which the species *Lorosuchus nodosus* exhibits a platyrostral skull that denotes a semi-aquatic habit, different from the terrestrial habit possessed by the other members of the taxa (Pol & Powell, 2011). Nevertheless, this still contrasts deeply with the large morphological disparity exhibited among the Caimaninae taxa.

Gavialoids and crocodyloids probably did not develop a similar morphological disparity in the Miocene of South America due to having arrived later in the continent if compared to caimanines and sebecids. Additionally, not only the gavialoids but also the crocodyloids that inhabited the South American Miocene were longirrsotrine, and it is possible that such skull shape would be less evolutionary “plastic” than a brevirrostrine one, thus precluding these taxa of exhibiting a larger morphological disparity. These hypotheses, however, requires further, detailed research to be properly addressed.

The differences in morphological disparity between caimanines and sebecids may be related to the semi-aquatic habits of the former and the terrestrial habits of the latter. The northern part of the South America, equivalent to the area of the current Amazon rainforest and which houses the largest crocodylomorph diversity during the Cenozoic of the continent, including the Miocene, underwent gradual geomorphological changes during the Paleogene and the Neogene that gradually increased the size of the water-bodies form a series of rivers from systems of mega-lakes (see Hoorn et al., 2010).

As such, semi-aquatic crocodylomorphs had not only an ever-growing habitable space but they also had ever-growing different kinds of habitats in the aquatic systems of the Cenozoic of South America which, together with the generally hot climate and high biodiversity (which generated a vast array of prey items), were the factors that allowed the Caimaninae clade to evolve the distinctly different morphotypes it exhibited in the Miocene, including the “gulp-feeding” habit of *Mourasuchus*. In this context, it is interesting to notice that the reduction in the size of the water systems of the Amazon area during and after the late Miocene are coincident with the extinction of all the large and specialized crocodylomorphs, such as *Mourasuchus*, *Purussaurus*, durophagous caimanines, gavialoids and the longirrostrine crocodyloids *Charactosuchus* and *Brasilosuchus* (see Riff et al., 2010; Scheyer et al., 2013; Cidade et al., 2019), which reinforces the importance of large water systems for the survival and evolution of large, specialized semi-aquatic crocodylomorphs. Additionally, it is also possible that the sebecid terrestrial-oriented morphology was also less “plastic” that that of the semi-aquatic, brevirrostrime caimanines, but this issue must also be addressed by future, detailed studies on this issue.

CONCLUSIONS

As a result of the comprehensive revision and reassessment of the literature and morphological characters relevant to the understanding of the feeding habits of *Mourasuchus*, this study concludes that the taxon was likely unable of capturing and consuming large prey, especially those capable of fast movements such as mammals. As such, *Mourasuchus* has likely specialized in eating small prey, such as crustaceans, bivalves and gastropod mollusks, and small fish. Large prey would only be consumed if they were slow-moving, like the *Lepidosiren* fish, and likely only occasionally. There are no evidences that *Mourasuchus* could be herbivorous.

We propose that the long, wide, dorsoventrally flattened rostrum of *Mourasuchus* evolved as to make the rostrum cover the largest possible area to allow a maximum efficiency in the capture of large amounts of small prey. The use of the inferior part of the rostrum would be more efficient in the capture of large amounts of prey the relying on teeth to capture and handle the small animals that likely comprised the diet items of *Mourasuchus*. In spite of the inferred proeminent role that the inferior part of the rostrum played in the foraging of *Mourasuchus*, it is recommended that the term “gular sac” should not be used to describe this structure for this taxon until eventual further studies determine whether it was contractible and expansible, functioning in an analogous manner to the gular skin present in extant birds, for example.

As the small animals proposed to have comprised the main diet items of *Mourasuchus* would nearly always be found immersed into the micro-habitat they lived in (water, mud, sand or plants, among others), it is probable that *Mourasuchus* also captured quantities of these materials together with the prey. As such, some sort of “selection” of the edible from the non-edible matter somewhat akin to the “filtering” mentioned by previous authors (Langston, 1965; Riff et al., 2010; Bona et al., 2013b) would be advantageous to *Mourasuchus*, but with our current knowledge there are no evidences that such a selection could be performed by this taxon. As such, we follow Cidade et al. (2017) in naming the presumable feeding habits of *Mourasuchus* as “gulp-feeding", and not "straining" or "filtering" feeding as in those previous studies. *Mourasuchus* was most probably a inhabitant of quiet, shallow water bodies, not only due to the presumable mechanical inefficiency of its jaws, skull and cervical vertebrae, but also because water bodies such as those possessed the largest quantity of habitats in which the preferred prey of the taxon – mollusks, crustaceans and small fish – dwelled.

This study proposed the hypothesis that the "gulp-feeding" habit of *Mourasuchus* evolved from the durophagous habit proposed for many fossils caimanines, particularly the highly adapted *Gnatusuchus*. This hypothesis, however, needs to be properly addressed by future studies, and no phylogenetic analysis performed to date showed a close relationship between *Mourasuchus* and any durophagous taxa, which means a hindrance to the acceptance of this hypothesis. Additionally, many hypothesis of this and previous studies about the inferred limited movements and lack of strength of the bones, osseous structures and muscles of the mandibles, skull and the cervical vertebrae still need to be properly assessed by biomechanical and muscular reconstruction studies so a thorough and more empirically-based understanding of the feeding habits of *Mourasuchus* can be reached.

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Figures

Figure 1

Figure 2

Figure 3

Figure 4

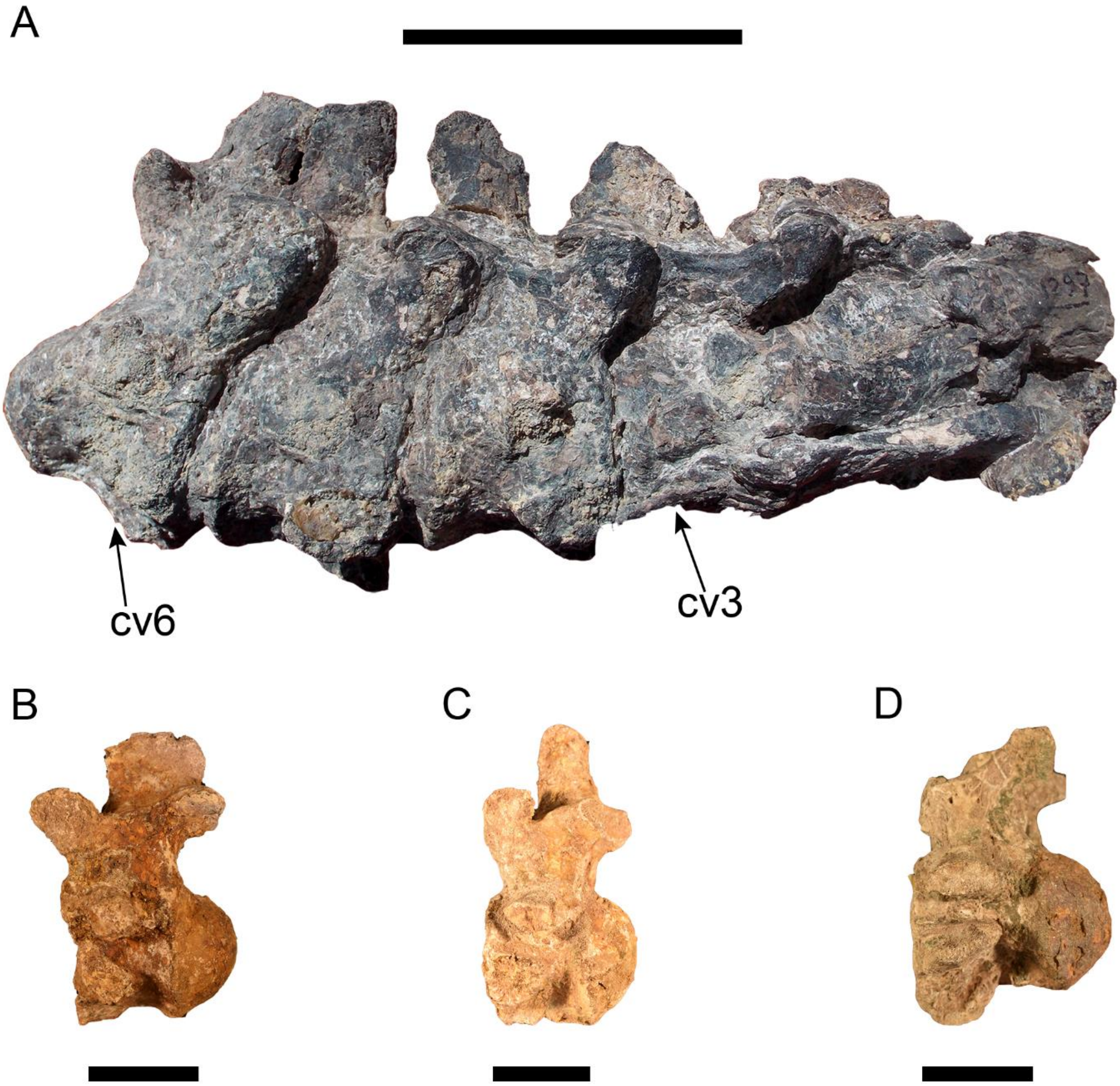

Figure 5

Captions

Figure 1: The platyrostral-broad skull morphology of *Mourasuchus*: the skull of the holotypes of *M. arendsi* (CIAAP-1297; A) and *M. pattersoni* (MCNC-PAL-110-72V; B) in dorsal view. B is taken from Cidade et al. (2017, fig. 2). Scales = 10 cm.

Figure 2: The long, slender mandibles of *Mourasuchus*: the articulated right and left hemimandibles of the holotype of *M. pattersoni* (MCNC-PAL-110-72V; A) in dorsal view and the right hemimandible of the holotype of *M. arendsi* (CIAAP-1297; B) in dorsolateral view. A is taken from Cidade et al. (2017, fig. 4). Scales = 20 cm (A) and 10 cm (B).

Figure 3: A right hemimandible (UFAC-2283) and a left hemimandible (UFAC-1669) of *Mourasuchus* (A) in dorsal view and the articulated mandibles of the holotype of *Laganotushcus thaumastos* (MNN IGU13; Niger; B) in dorsal view, evidencing the similarities of the mandibular morphology of the two taxa. Scales = 5 cm (A) and 10 cm (B).

Figure 4: First six cervical vertebrae of the holotype of *Mourasuchus arendsi* (CIAAP-1297) in right lateral view (A) and the tentative third (B), fifth (C) and sixth (D) cervical vertebrae of the holotype of *M. pattersoni* (MCNC-PAL-110-72V, following the position of the vertebrae proposed by Langston, 2008; B). Scales = 10 cm (A) and 5 cm (B, C and D).

Figure 5: Paleoartistic reconstruction of *Mourasuchus* feeding on invertebrate prey by paleoartist Renata Cunha.

Appendix 6 – Article: Souza-Filho, J.P., Souza, R.G., Hsiou, A.S., Riff, D., Guilherme, E., Negri, F.R., & Cidade, G.M. 2019. A new caimanine (Crocodylia, Alligatoroidea) species from the Solimões Formation of Brazil and the phylogeny of Caimaninae. *Journal of Vertebrate Paleontology,* online first. doi.org/10.1080/02724634.2018.1528450

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ARTICLE

A NEW CAIMANINE (CROCODYLIA, ALLIGATOROIDEA) SPECIES FROM THE SOLIMÕES FORMATION OF BRAZIL AND THE PHYLOGENY OF CAIMANINAE

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ABSTRACT—The Miocene deposits of South America are notable for their diverse crocodyliform fauna, of which the giant caimanine *Purussaurus* is a well-known example. This contribution describes a new caimanine, *Acresuchus pachytemporalis*, gen. et sp. nov., based on an almost complete skull and mandible from the late Miocene Solimões Formation of the southwestern Brazilian Amazonia. This new taxon is based on a unique combination of characters, of which the presence of an upturned posterolateral margin of the squamosal throughout the entire lateral margin of the bone (a 'horn'), with a dorsoventral expansion in the posterior portion of the eminence, stands out. We conducted a phylogenetic analysis of Eusuchia, which showed the new taxon as sister to *Purussaurus*. This placement allows discussion about the evolution of gigantism in the *Acresuchus-Purussaurus* clade, which reveals several characters that may be related to gigantism. Additionally, *Acresuchus* was probably a medium-sized generalist caimanine that had an ecological niche similar to the extant *Melanosuchus niger*. Until now, crocodyliforms that had such niches were unknown from the Solimões Formation.

http://zoobank.org/urn:lsid:zoobank.org:pub:F40D1084-AD76-44C6-92D1-8CEB7718E605

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

All living crocodylian species are nested within crown group Crocodylia Gmelin, 1789, which is divided into three main lineages: Gavialoidea Hay, 1930, Crocodyloidea Fitzinger, 1826, and Alligatoroidea Gray, 1844. This latter clade is stem based (sensu Cantino and de Queiroz, 2000), defined by Brochu (1999, 2003) as including all species of Crocodylia more closely related to *Alligator mississippiensis* (Daudin, 1802) than to *Gavialis gangeticus* (Gmelin, 1789) or *Crocodylus niloticus*. Within Alligatoroidea is the less inclusive clade Caimaninae Brochu, 1999, which is also stem based, defined as being formed of the species closer to *Caiman crocodilus* (Linnaeus, 1758) than to *Alligator mississippiensis* (sensu Brochu, 1999, following Norell et al., 1994).

The extant diversity of Caimaninae comprises three genera—*Caiman* Spix, 1825, *Melanosuchus* Gray, 1862, and *Paleosuchus* Gray, 1862, with a total of six species recognized: *C. crocodilus*, *C. latirostris* (Daudin, 1802), *C. yacare* (Daudin, 1802), *M. niger* (Spix, 1825), *P. palpebrosus* (Cuvier, 1807), and *P. trigonatus* (Schneider, 1801). All extant species exclusively occur in South America, with the exception of *Caiman crocodilus*, which is also naturally present in Central America and the Caribbean (Medem, 1983; Thorbjarnarson, 1992; Brochu, 1999). However, the fossil record of the group is much more rich and diverse (e.g., Langston, 1965; Brochu, 1999, 2010, 2011; Riff et al., 2010; Bona et al., 2013b), tracing back unequivocally to the early Paleocene of Argentina, with the species *Eocaiman palaeocenicus* Bona, 2007, *Necrosuchus ionensis* Simpson, 1937, and *Notocaiman stromeri* Rusconi, 1937 (Bona, 2007; Brochu, 2011). Additionally, there is a putative record from the Upper Cretaceous of the U.S. state of Montana (Bryant, 1989). As seen for the extant species, the fossil diversity of Caimaninae is predominantly South American, with the notable exceptions of *Orthogenysuchus olseni* Mook, 1924, and *Tsoabichi greenriverensis* Brochu, 2010, both from the Eocene of the United States (Brochu, 1999, 2010, 2011), and *Culebrasuchus mesoamericanus* Hastings, Bloch, Jaramillo, Rincon, and MacFadden, 2013, and

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Centenariosuchus gilmorei Hastings, Bloch, Jaramillo, Rincon, and MacFadden, 2013, from the early Miocene of Panama in Central America (Hastings et al., 2013, 2016).

The fossil record shows the Miocene as the period when Caimaninae reached the apex of both their diversity and their morphological disparity (Riff et al., 2010; Salas-Gismondi et al., 2015; Souza et al., 2016; Cidade et al., 2017). The middle Miocene fauna of La Venta, in Colombia (Langston, 1965; Langston and Gasparini, 1997), and the late Miocene rocks of the Ituzaingó Formation, in Argentina (Bona et al., 2013b), the Urumaco Formation, in Venezuela (Aguilera, 2004; Riff et al., 2010), and the Solimões Formation, in Brazil (Riff et al., 2010; Souza et al., 2016) stand out as yielding the richest and most diverse fossil records of the group. Specifically, the Urumaco and Solimões formations, located in the Amazon region, are regarded as having two of the richest crocodylian fossil faunas of the world (Riff et al., 2010).

Aside from the living genera *Caiman*, *Melanosuchus*, and *Paleosuchus*, the caimanine fossil record from the Miocene of South America comprises three distinctive, peculiar morphotypes: the 'duck-faced,' putative gulp-feeding *Mourasuchus* Price, 1964 (Price, 1964; Langston, 1965; Bocquentin-Villanueva, 1984; Gasparini, 1985; Bona et al., 2013a, 2013b; Cidade et al., 2017), the durophagous taxa *Balanerodus*, *Globidentosuchus*, *Gnatusuchus*, *Kuttanacaiman*, and *Caiman wannlangstoni* (Langston, 1965; Langston and Gasparini, 1997; Scheyer et al., 2013; Salas-Gismondi et al., 2015), and the giant, top predator *Purussaurus* Barbosa-Rodrigues, 1892 (Barbosa-Rodrigues, 1892; Mook, 1941; Langston, 1965; Price, 1967; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006), which could have reached as much as 12 m in total body length (Riff and Aguilera, 2008; Riff et al., 2010; Aureliano et al., 2015). The Solimões Formation has a high crocodylian diversity with eight proposed species, including four caimanines (Fortier, 2011). Occurrences of *Caiman*, *Mourasuchus*, and *Purussaurus* have been recorded from this formation, the latter being represented only by *P. brasiliensis* Barbosa-Rodrigues, 1892 (Bocquentin-Villanueva et al., 1989; Riff et al., 2010).

In this work, a new caimanine species is described from the Solimões Formation and from the *Purussaurus* lineage. This new taxon may offer meaningful insight into the diversity of the crocodylian fauna of the South American Miocene and also provide a new perspective on the evolution of gigantism in the well-known predator *Purussaurus*.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; **CIAAP**, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **MCT**, Museu de Ciências da Terra, Rio de Janeiro, Brazil; **MN**, Museu Nacional, Rio de Janeiro, Brazil; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UFAC**, Universidade Federal do Acre, Rio Branco, Brazil.

Anatomical Abbreviations—af, adductor fossa; **an**, angular; **ar**, articular; **bo**, basioccipital; **bs**, basisphenoid; **cr**, coronoid; **d**, dentary; **da**, dentary alveolous; **emf**, external mandibular fenestra; **en**, external naris; **ex**, exoccipital; **f**, frontal; **fic**, foramen intermandibularis caudalis; **fm**, foramen magnum; **fv**, foramen vagus; **if**, incisive foramen; **itf**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **ls**, laterosphenoid; **m**, maxilla; **ma**, maxillary alveolous; **ms**, mandibular symphysis; **n**, nasal; **o**, orbit; **oc**, occipital condyle; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **pma**, premaxillary alveolus; **po**, postorbital; **pt**, pterygoid; **ptf**, posttemporal fenestra; **q**, quadrate; **qj**, quadratojugal; **san**, surangular; **sfo**, supratemporal fossa; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **stf**, supratemporal fenestra.

REMARKS ON NOMENCLATURE

Prior to this work, two other species names have been proposed based on the specimen here described as the holotype (UFAC-2507): '*Caiman niteroiensis*' (Souza-Filho and Bocquentin, 1991) and '*Caiman pachytemporalis*' (Souza-Filho, 1998). These names created some confusion about the taxonomic affinities of UFAC-2507 since recent publications treated '*Caiman niteroiensis*' as valid species (e.g., Riff et al., 2010). However, because neither of these names has been proposed in an official publication, with Souza-Filho and Bocquentin (1991) being a conference abstract and Souza-Filho (1998) a Ph.D. dissertation, both violate articles from Chapter 3 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). As such, neither is a valid species name for UFAC-2507. Therefore, the only taxonomically valid name for this taxon is the one proposed in this work: *Acresuchus pachytemporalis*.

MATERIALS AND METHODS

The phylogenetic data matrix was created with the software Mesquite, version 2.75 (Maddison and Maddison, 2011). The phylogenetic analysis was made with the software Tree Analysis Using New Technology (TNT version 1.5; Goloboff et al., 2008; Goloboff and Catalano, 2016). The analysis was performed using traditional search for RAS (random addition sequences) with a 'random seed' value of zero, 20,000 replications, and 10 cladograms saved per replication. The branch swapping algorithm used was 'Tree Bisection Reconnection' (TBR) and the existing trees were replaced in the analysis. After this first analysis, a second round of TBR with the trees in memory (RAM) from the first analyses was conducted. The trees in both analyses were collapsed after the search. The characters were unordered.

The phylogenetic analysis was performed with a modified version of the matrix of Cidade et al. (2017) that includes 93 eusuchian taxa in the ingroup and the non-eusuchian crocodyliform *Bernissartia fagesii* Dollo, 1883, as outgroup. The phylogenetic characters are listed in Appendix S1 in Supplementary Data 1. This matrix is based mainly on that of Brochu (2011), with additional input from other work (see Appendix S2 in Supplementary Data 1 for details). Of the ingroup taxa, 88 were already included in the matrix of Cidade et al. (2017). The scoring of *Necrosuchus ionensis*, *Melanosuchus fisheri* Medina, 1976, *Caiman gasparinae* Bona and Carabajal, 2013, *Purussaurus brasiliensis*, and specimen UCMP-39997 was based on other previous work (Barrios, 2011; Brochu, 2011; Bona et al., 2013b; Pinheiro et al., 2013; Salas-Gismondi et al., 2015) with complimentary scorings by the authors (see Appendix S2), whereas the scoring of *Acresuchus pachytemporalis* was made entirely by the authors. *Bernissartia fagesii* was also included in Brochu (2011) and Cidade et al. (2017). The analysis of this study included the 187 morphological characters by Cidade et al. (2017) and Brochu (2011), with one character being rephrased (Character 156) and several scorings revised (see Appendix S2). The fossil specimen UCMP-39978, from the middle Miocene of La Venta (Colombia) described by Langston (1965), was assigned to '*Caiman lutescens*' (Rovereto, 1912) in all previous analyses except Brochu (2011); consistent with this, we follow Bona et al. (2013b) in considering that this specimen cannot be assigned to *C. lutescens*. Codings for all taxa form Appendix S3 in Supplementary Data 1. A Nexus file of the matrix is available as Supplementary Data 2.

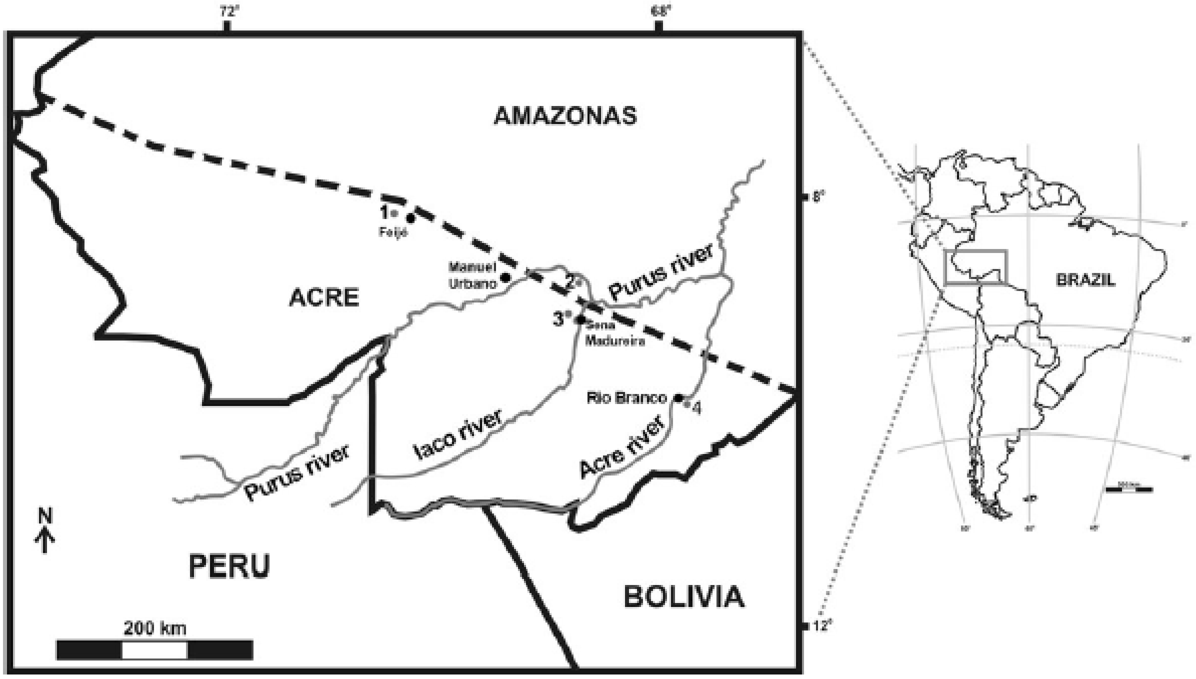

FIGURE 1. Map of the Brazilian state of Acre (modified from Hsiou, 2010) showing the localities from which the material of *Acresuchus pachytemporalis* is known. Gray dots represent the localities; black dots represent municipalities. The dashed line represents the border between Brazilian states and continuous lines represent borders between countries. **Key:** **1**, Morro do Careca; **2**, Talismã; **3**, Lula; **4**, Niteroi.

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789 (sensu Benton and Clark, 1988)
ALLIGATOROIDEA Gray, 1844 (sensu Brochu, 2003, following Norell et al., 1994)
CAIMANINAE Brochu, 1999 (following Norell, 1988)
ACRESUCHUS, gen. nov.

Type Species—*Acresuchus pachytemporalis*, gen. et sp. nov.

Etymology—'Acre' from the name of the Brazilian state where the holotype was found, and 'suchus' from the ancient Greek word for 'crocodile.'

Diagnosis—Same as the type species.

ACRESUCHUS PACHYTEMPORALIS, gen. et sp. nov.

Holotype—UFAC-2507, a nearly complete skull with both hemimandibles.

Referred Material—UFAC-1187, UFAC-1379, UFAC-1486, UFAC-3142, UFAC-4153, UFAC-4154, UFAC-4183, UFAC-4678, UFAC-5256, UFAC-6384, all posterior portions of the skull table with variable sizes and degrees of preservation.

Etymology—The specific epithet '*pachytemporalis*' alludes to the accentuated pachyostosis present in the squamosals of the holotype.

Occurrence—Solimões Formation, late Miocene (equivalent to the Huayquerian land mammal age according to Latrubesse et al., 2010, based on paleontological content [vertebrates and palynology] and facies analysis), Acre Basin, Brazil. The holotype and four referred specimens (UFAC-4153, UFAC-4154, UFAC-4183, and UFAC-4678) come from the fossiliferous locality 'Niteroi' (10°8′2.27″S, 67°48′48.84″W: Bona et al., 2013b; UTM 19L 629983E, 8879539S, datum WGS84: Kerber et al., 2017), which is located on the east bank of the Acre River (Fig. 1), between the cities of Rio Branco and Senador Guiomard, in the Brazilian state of Acre (Bona et al., 2013b). Two referred specimens (UFAC-1187, UFAC-1379) are from the 'Lula' locality, one (UFAC-5256) from the 'Morro do Careca' locality (Fig. 1), one (UFAC-6384) from an unknown locality on the margins of the BR-364 highway in the municipality of Feijó, in Acre (Fig. 1), one (UFAC-3142) from the 'Talismã' locality, located in the right margin of the Upper Purus River, in the Amazonas state (Fig. 1), and one (UFAC-1486) from an unknown locality in the upper portion of the Acre River (Fig. 1).

Diagnosis—Caimanine with a medium-sized body, teeth with smooth (non-serrated) carinae, orbits large in comparison with other caimanines, having roughly straight margins that are larger than the infratemporal fenestrae, circular external naris, posterior margin of the skull table transversely straight to slightly concave, *posterolateral margin of squamosal upturned throughout the entire dorsal lateral margin with a dorsoventral expansion in the posterior portion of the eminence (*autapomorphy within Caimaninae).

GEOLOGICAL SETTING

The sediments of the Solimões Formation, outcropping within the Acre and Solimões basins (Caputo et al., 1971; Eiras et al., 1994), are continental in origin and composed mainly of claystones, with calcareous concretions and calcite as well as gypsum veins, lying in horizontal to subhorizontal beds that can

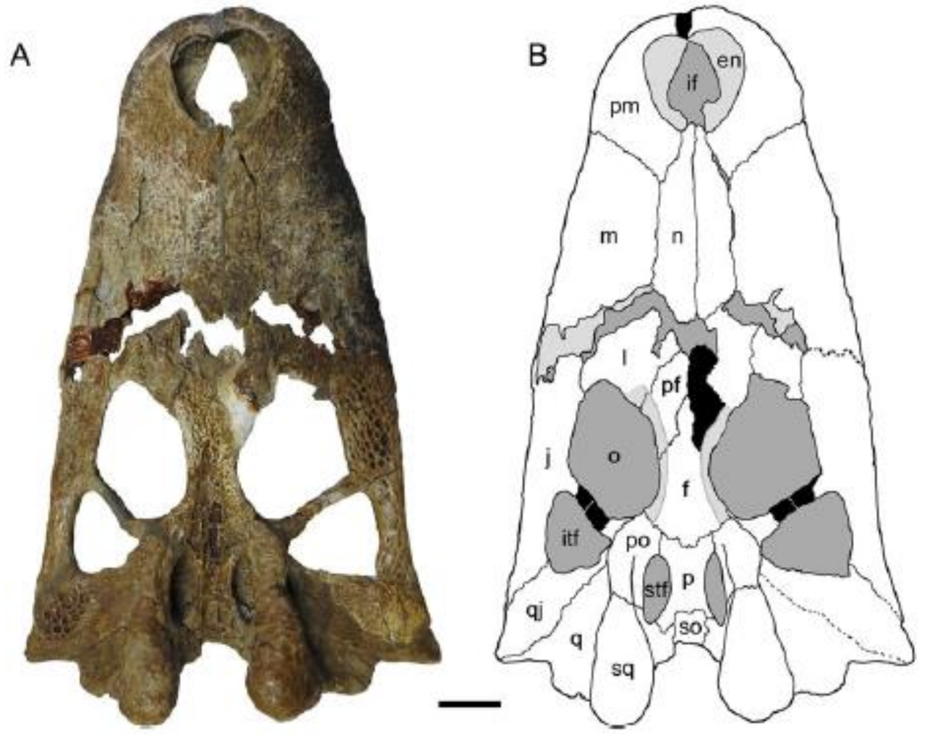

FIGURE 2. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype. **A**, dorsal view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 5 cm.

reach thicknesses of over 1000 m (Latrubesse et al., 2010). The depositional environment of the formation is described as being predominantly floodplain-lacustrine-paludal (Latrubesse et al., 2010), having the Andes chain as the main source of the sediments (Latrubesse et al., 1997). Although previous works assign the Solimões Formation to a late Miocene—Pliocene age (e.g., Latrubesse, 1992; Latrubesse et al., 1997), recent geological, palynological, and sedimentological data (Cozzuol, 2006; Latrubesse et al., 2010) and absolute dating using radioisotopes (Bissaro-Junior et al., 2019) have indicated a late Miocene age for the Formation. (Cozzuol, 2006; Latrubesse et al., 2010), corresponding to the Huayquerian (?9–6.8 Ma) South American Land Mammal Age (SALMA; Fortier et al., 2014).

The Niteroi locality, specifically where the holotype of *Acresuchus pachytemporalis* was collected, consists of moderately consolidated claystone layers, as well as sandstones and siltstones in smaller quantities, deposited in a low-energy environment (Campbell et al., 2006; Latrubesse et al., 2007, 2010). An absolute dating via U-Pb radioisotopes dating of detrital zircon of the Niteroi locality showed an age of 8.5 ± 0.5 Ma for it, corresponding to the Tortonian stage of the late Miocene (Bissaro-Junior et al., 2019).

DESCRIPTION

General Preservation Status of the Holotype

The skull of the holotype is nearly complete, with a rupture in front of the orbits (Figs. 2–5) along the surfaces of the jugal, the maxilla, the prefrontal, and the lacrimal, separating the rostrum from the posterior portion of the skull. The skull has a total length (measured from the tip of the snout to the posterior extremity of the quadrate) of 51.5 cm. It is generally well preserved, with many portions of the skull having notable ornamentation, such as on the dorsal portion of the skull table (Fig. 6), especially on the frontal bone at its most posterior portion, the left quadratojugal, the right jugal, and the anterior portion of the dorsal surface of the left jugal. The dorsal surfaces of the nasals, the maxillae, and the premaxillae also bear relatively well-preserved ornamentation, although not as marked as those on the posterior portion of the skull.

In occipital view, the specimen is fully preserved from the dorsal margin of the supraoccipital and the highly elevated squamosals (see Squamosals, below) to the ventral margin of the basioccipital. Ventral to this, there is only a small fragment of the pterygoid (Fig. 4).

In ventral view, neither the palatines nor the prefrontal pillars are preserved (Fig. 3), whereas the basisphenoid is partially preserved, including part of the basisphenoid rostrum. Ventrally, both premaxillae are preserved, but with a wide rupture between them posterior to the incisive foramen (Fig. 3). Both maxillae are incompletely preserved, mainly due to the fact that the rupture between the two premaxillae is also present between the two maxillae (Fig. 3).

The left and right hemimandibles were preserved unsutured. The right hemimandible is almost entirely preserved (Figs. 7, 8). The main missing parts are the anterior-most portion of the splenial; the anterior-most portion of the surangular that surrounds the dentary in medial view; the medial portion of the angular, which is missing from the anterior margin of the foramen intermandibularis caudalis to the sutural connection of the angular with the articular and surangular bones; and most

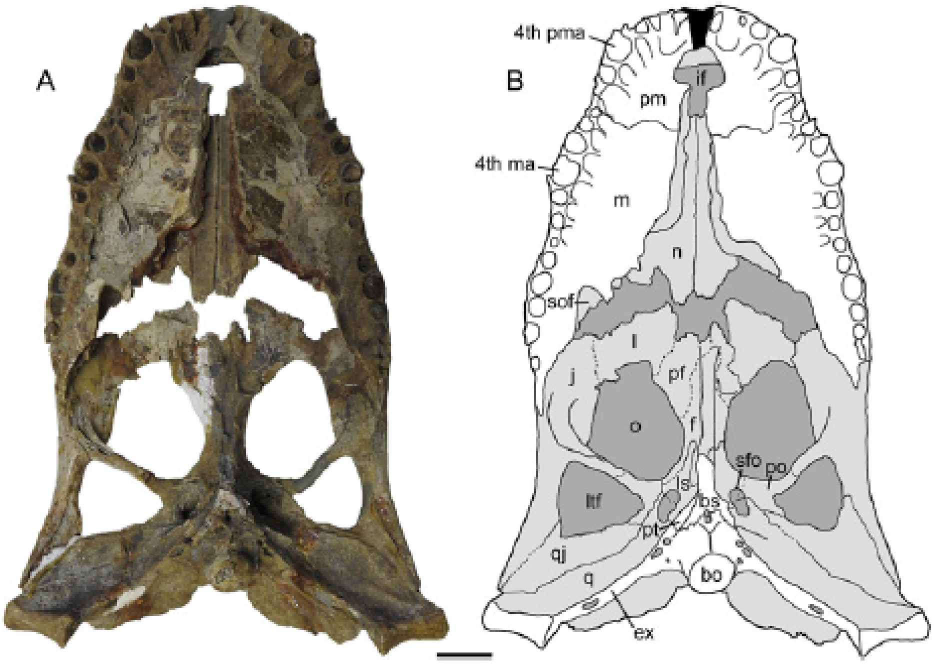

FIGURE 3. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype. **A**, ventral view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 5 cm.

of the coronoid. The missing parts of the left hemimandible are (all in medial view; Fig. 9) the anterior extremity of the splenial and the posterior-most part of the splenial, along with the most anterior portion of the dorsal ramus of the angular, including most of the dorsal margin of the foramen intermandibularis caudalis, and there are no remains that can be identified as belonging to the coronoid.

Despite the damage observed and described in the holotype, no breakage and/or weathering was found that could have been the result of transport or long exposure (for the relation between bone weathering and transport/exposure, see Behrensmeyer, 1978). The specimen does not present any deformation, such as compression, and the outer bone surface is entirely preserved. The main rupture observed in the rostrum of the holotype most likely occurred after burial, but this hypothesis still needs to be properly assessed by future taphonomic work. This preservation may be considered good, which is congruent with the depositional environment of the Niteroi site, described as a low-energy environment in which vertebrate fossils typically exhibit good preservation due to little or no transport between the place of death and the place of burial (Campbell et al., 2006). However, it is important to note that well-preserved fossil crocodyliforms may also come from different depositional environments than low-energy ones (e.g., Syme and Salisbury, 2014), and that a proper, comprehensive taphonomic analysis of the assembly of the Niteroi locality has yet to be made.

Skull of the Holotype

Premaxillae—The premaxillae are almost completely preserved; the anterior-most portion of the medial suture between the two bones is missing, specifically from the tip of the snout to the anterior margin of the external naris. This separation was covered by resin, in both dorsal and ventral views (Figs. 2, 3), during the preparation of the holotype. In ventral view, the posterior-most portion of the suture is also separated; as described above, in ventral view, the areas between both premaxillae and both maxillae are ruptured from the posterior margin of the incisive foramen to the posterior-most extent of the preserved maxillae (Fig. 3).

Posteriorly, each premaxilla meets its corresponding maxilla and nasal bone in dorsal view, but they do not meet each other posterior to the external naris, allowing the nasal bones to reach the posterior margin of the external naris (Fig. 2). Each premaxilla also meets each corresponding maxilla in ventral view (Fig. 3).

Both premaxillae have five alveoli (Fig. 3). In both elements the fourth alveolus is the largest, followed by the third, and then by the first, with the second and the fifth being the smallest. In the right premaxilla, only the three posterior alveoli have preserved teeth. The first two are completely preserved, whereas the third one has its crown broken near the apex. Additionally, the first tooth preserved is smaller than the other two, likely being a more recently erupted tooth in its first stages of growth. In the left premaxilla, only the last two alveoli have teeth preserved. In the first, the apical crown is broken and only a basal portion of the tooth is preserved, whereas the second tooth is complete. These premaxillary teeth are conical, with a circular cross-section and with apices more robust than pointed.

Both premaxillae preserve four occlusion pits lingual to the upper tooth row ventrally (Fig. 3). The first and fourth occlusion pits are the deepest, in accordance with the fact that the first and fourth dentary teeth are largest among those that occlude with the premaxilla. Additionally, both of the last occlusion pits are situated between the sutures of each premaxilla with each maxilla. The fourth pit demonstrates that the fourth dentary tooth occludes in a pit, rather than in a notch, in *Acresuchus*.

The external naris is large (Fig. 2), with a roughly circular shape, and projects dorsally. In dorsal view, the incisive foramen may be seen in entirety through the external naris

(Fig. 2). Both nasal bones reach the external naris at its posterior margin, although not bisecting it (Fig. 2).

The premaxillary surface lateral to the external naris is smooth (i.e., without a notch), although this area shows a slight elevation (Fig. 2), mainly on the posterior margin, when compared with the remaining dorsal surface of the premaxillae. This area of the premaxillae also exhibits a roughly rugose surface—without marked ornamentation—in contrast to the marked ornamentation seen on the remaining surface of these bones. The dorsal premaxillary processes do not extend beyond the third maxillary alveoli.

Ventrally, the incisive foramen is small (i.e., less than half the greatest width of premaxillae sensu Brochu 2011, character 88-0), with a roughly 'teardrop-like' shape, i.e., with the anterior margin more lateromedially compressed than the posterior one (Fig. 3), although its posterior margin is discontinuous given the aforementioned rupture of the interpremaxillary suture seen in this specimen. Although the incisive foramen is situated far from the premaxillary tooth row at the level of the second or third alveolus, the rupture of the interpremaxillary suture in the region between the tip of the snout and the anterior margin of the incisive foramen leaves it unclear whether the foramen did or did not project between the first premaxillary teeth.

Maxillae—In ventral view, the maxillae have their most medial portion preserved until the level of the sixth maxillary alveolus. In both maxillae, the missing portion of the bones increases in a mediolateral direction until the most lateral portion of both bones reaches approximately the level of the 12th maxillary alveolus, a point after which both bones are no longer preserved (Fig. 3). Because the most posterior portions of the tooth rows of both maxillae are not preserved, the total number of maxillary alveoli was probably more than 12, but the exact number cannot be known.

In dorsal view, there is no rupture between the premaxillae and the maxillae as there is in ventral view. Posteriorly, however, the rupture between the maxillae and the rest of the skull comprises practically the same region as that visible in ventral view. The maxillae contact the premaxillae anteriorly and the nasals medially. Due to this fracture, none of the sutures of the maxillae with the bones they contact posteriorly are preserved (Fig. 2).

The maxillae of *Acresuchus pachytemporalis* form most of the snout, whereas their ventral (palatal) portions constitute a considerable part of the secondary palate, as in all living Crocodylia (Fig. 2). There is no sign of a possible ventral exposure of the vomer between the premaxillae and the maxillae in the holotype. Even though the area where the vomer could be exposed is fragmented, the visible arrangement of the bones in the area does not indicate a possible ventral exposure of the vomer between them.

The teeth (and alveoli) of both maxillae and dentaries are circular in cross-section (Figs. 3, 8). Occlusion pits of the dentary teeth located in the maxillae show that all dentary teeth occluded lingual to the maxillary teeth (Fig. 3). The fourth alveolus is the largest in the maxillary tooth row.

Dorsally in the maxillae, there are no signs of preorbital ridges. Very prominent 'canthi rostralli' are also absent in the new taxon. In the most posterior portions of both maxillae, in the area that would contact the lacrimals, there are several small depressions. The poor preservation of the area, however, leaves some doubt about whether these are real anatomical structures or simply fractures left on the dorsal area of the maxillae.

Nasals—The nasals of *Acresuchus pachytemporalis* are anteroposteriorly short and relatively wide mediolaterally (Fig. 2), similar to the morphology described for these bones in alligatorids by Iordansky (1973). The nasals are not completely preserved: the posterior-most portions of both nasals, which would contact the prefrontals and possibly the lacrimals, are missing due to the transverse rupture present in the skull. Anteriorly, each nasal contacts each corresponding premaxilla anterolaterally. Posterior to this, each nasal contacts the ipsilateral maxilla in all the area in which they are preserved (Fig. 2). In ventral view, when viewing dorsally through the rupture between the two maxillae, it is possible to see the internal dorsal roof of the narial passage, which is preserved until the level of the 14th alveolus of both maxillae (Fig. 3).

Prefrontals—Neither element is completely preserved, and their most anterior portions are missing due to the fracture present in the skull (Fig. 2). The descending processes of the prefrontals (the prefrontal pillars) are not preserved complete in the holotype of *Acresuchus pachytemporalis* (see Fig. 3). Whereas the left prefrontal preserves most of its original ornamentation of the dorsal surface, the right prefrontal has its dorsal surface mostly damaged, with nothing of the original ornamentation preserved. The prefrontals meet medially (Fig. 2).

In the prefrontals, or in their contacts with the lacrimals, there is no sign of prominent preorbital ridges. The prefrontal surface adjacent to the orbital rim, as well as the orbital rim as a whole, is smooth, with no presence of knob-like processes. The orbital rims of *Acresuchus* are upturned.

Lacrimals—The lacrimals are only partially preserved; their most anterior portions are lacking, just as with the surfaces of the prefrontals (Fig. 2). Therefore, although it is possible that the lacrimals of the holotype contacted the nasals medially, this cannot be demonstrated.

Frontal—The frontal is completely preserved (Fig. 2), forming the roof of the anterior part of the braincase as in all living Crocodylia (Iordansky, 1973). Its dorsal surface is well preserved, conserving most of the ornamentation of the bone (see Fig. 6) except in the area adjacent to the right prefrontal. Ventrally, the frontal preserves the cristae cranii frontales, a pair of descending crests that protect the olfactory tract in living Crocodylia (Iordansky, 1973; Fig. 3).

As described for the prefrontals, the lateral margins of the frontal are upturned, forming the dorsal edges of the orbits. Dorsally, the frontal contacts both prefrontals anteriorly through an acute anterior process projected between them (Fig. 2). Posteriorly, the frontal contacts each postorbital laterally, and the parietal posteriorly. The frontoparietal suture is located entirely on the skull table, not contacting the supratemporal fenestrae, and is concavoconvex sensu Brochu (1997, character 139-0; equivalent to Brochu's [2011] character 151-0). Posteroventrally, the frontal also contacts the laterosphenoid.

Postorbitals—The postorbitals are completely preserved, with both conserving their dorsal flat plates, which form the anterolateral corners of the cranial roof (Figs. 2, 6), as well as their descending processes, which constitute the dorsal portion of the postorbital bars (Fig. 3). Dorsally, all the sutures of both postorbitals are visible: with the frontal anteriorly, with the parietal medially, and with each corresponding squamosal posteriorly. The dorsal surfaces of the postorbital plates are dorsoventrally elevated, except in their most lateral portions. These surfaces are continuous with the elevation present in both squamosal bones, and this constitutes an important diagnostic feature of *Acresuchus pachytemporalis*, as described below.

The descending processes of the postorbitals articulate ventrally with ascending processes of each corresponding jugal to form the postorbital bar (Fig. 3). It is also possible that the descending processes of the postorbitals of this species articulated with ascending processes of each

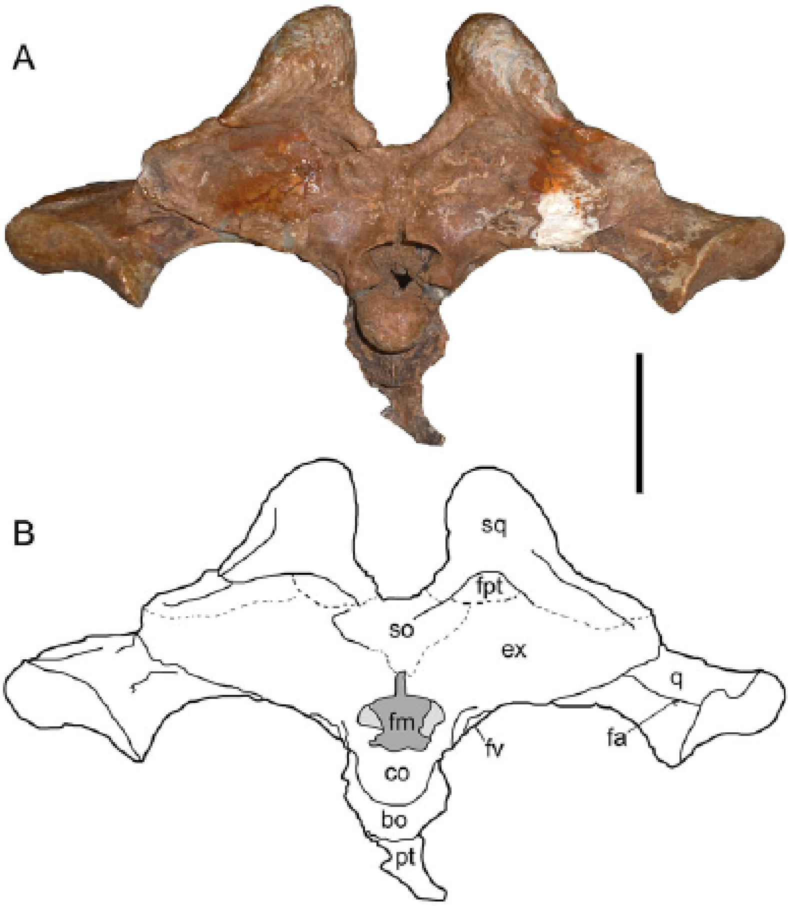

FIGURE 4. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype. **A**, occipital view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 5 cm.

ectopterygoid as well. The ectopterygoids are not preserved in *Acresuchus pachytemporalis*, but in the lateral portion of, and also in the area immediately anterior to, each postorbital bar, there is a concavity that may correspond, at least partially, to the place where the ectpterygoids were situated (Fig. 3). If this interpretation is correct, then it is probable that the postorbitals indeed articulated with the ectopterygoids ventrolaterally at the postorbital bar, even though the possible sutural contacts between these two bones are also not discernible in the holotype. The postorbital bar is slender and bears a short, anteriorly directed process in its dorsal portion while also being inset from the anterolateral edge of the skull table.

Parietal—The parietal is completely preserved, constituting most of the roof of the braincase, as in all Crocodylia (Iordansky, 1973), as well as the medial margins of the supratemporal fenestrae, which in *Acresuchus* are of large size and roughly oval in shape (Figs. 2, 6). The parietal preserves most of the original ornamentation on its dorsal surface (Fig. 6). Anteriorly, the parietal contacts the frontal; laterally, on each side, the parietal contacts the postorbital anteriorly and the squamosal posteriorly. Posteriorly, the parietal contacts the supraoccipital and the squamosals and does not contact the posterior margin of the skull table (Figs. 2, 6).

Squamosal—Both elements are nearly completely preserved (Figs. 2, 4, 5, 10). In dorsal view, each squamosal contacts each corresponding postorbital anteriorly, and both meet anteromedially with the parietal and medially with the supraoccipital (Fig. 2). In occipital view, each squamosal meets each corresponding exoccipital ventrally and the supraoccipital medioventrally (Fig. 4). In lateral view, the squamosal contacts the postorbital anteroventrally and the quadrate ventrally; the squamosal and the quadrate constitute the margins of the otic apertures, each of which has a bowed posterior margin (Fig. 10). The dorsal and ventral rims of the squamosal groove are parallel (Fig. 10).

The most striking feature of this bone in *Acresuchus pachytemporalis* is the large eminence present in its lateral and posterior portions, which forms a 'horn' in the posterior portion of the skull table (Figs. 6, 10). Although most of the squamosal is elevated (except for the most medial portion of the bone, adjacent to the supraoccipital), the eminence is markedly larger posteriorly than anteriorly, surpassing significantly the level of the posterior margin of the skull table (Fig. 6).

Jugals—Both jugals are nearly completely preserved; most of the anterior portion of the left jugal is absent due to the transverse fracture present in the region anterior to the orbits; the anterior portion of the right jugal is preserved, but eroded (due to the same transverse fracture), preventing the limit with the maxilla from being properly distinguished (Fig. 2). Posterior to the fracture, the jugals are almost completely preserved dorsally and ventrally, aside from some erosion, in the ventral portion of both jugals, of the region immediately posterior to the fracture (Fig. 3). The right jugal is better

FIGURE 5. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype in **A**, right and **B**, left lateral views. Scale bar equals 5 cm.

preserved, both in dorsal and ventral views, exhibiting some of the original ornamentation of its dorsal surface, whereas the left jugal exhibits a rather rough, slightly eroded surface in both dorsal and ventral views (Figs. 2, 3). The jugals are lateromedially slender and dorsoventrally low.

Anteriorly, the ascending process of the jugal contacts the ventrally descending process of the postorbital and, as such, constitutes the ventral portion of the postorbital bar (Fig. 3), which is ventrally inset to the jugal as is typical in Brevirostres (Brochu, 1997). As mentioned previously, the ectopterygoids are not preserved, but there are concavities in the areas close to the ventral portion of each postorbital bar that may, at least partially, correspond to the areas where the ectopterygoids would be positioned. If this interpretation is correct, that would mean that the jugals of *Acresuchus pachytemporalis* would contact each corresponding ectopterygoid ventromedially, as is common in Crocodylia (see Iordansky, 1973). Posteriorly, both jugals contact each corresponding quadratojugal, both dorsally and ventrally (Figs. 2, 3).

The jugal forms the lateral margin of the orbits and infratemporal fenestrae (Fig. 2). The medial jugal foramen is small (Brochu, 2011, character 102-0), as in most eusuchians (Brochu, 1997). In lateral view, the portion that forms the lateral margins of the orbits presents its dorsal margin as linear and more elevated than the dorsal margin of the jugal portion that forms the lateral margins of the infratemporal fenestrae. These latter margins are concave on their dorsal surfaces, giving a rounded aspect to the triangular shape of the infratemporal fenestrae.

Quadratojugals—Both elements are nearly completely preserved. In dorsal view, the left quadratojugal still preserves most of its original ornamentation (Fig. 2). The right quadratojugal, however, has a rather rough, slightly damaged surface (Fig. 3). The quadratojugals contact the jugal anterolaterally, projecting a long anterior process along the lower temporal bar (Fig. 2). Posteriorly, the quadratojugal contacts the quadrate (Figs. 2, 3).

FIGURE 6. *Acresuchus pachytemporalis*, UFAC-2507, dorsal surface of the skull table. Scale bar equals 5 cm.

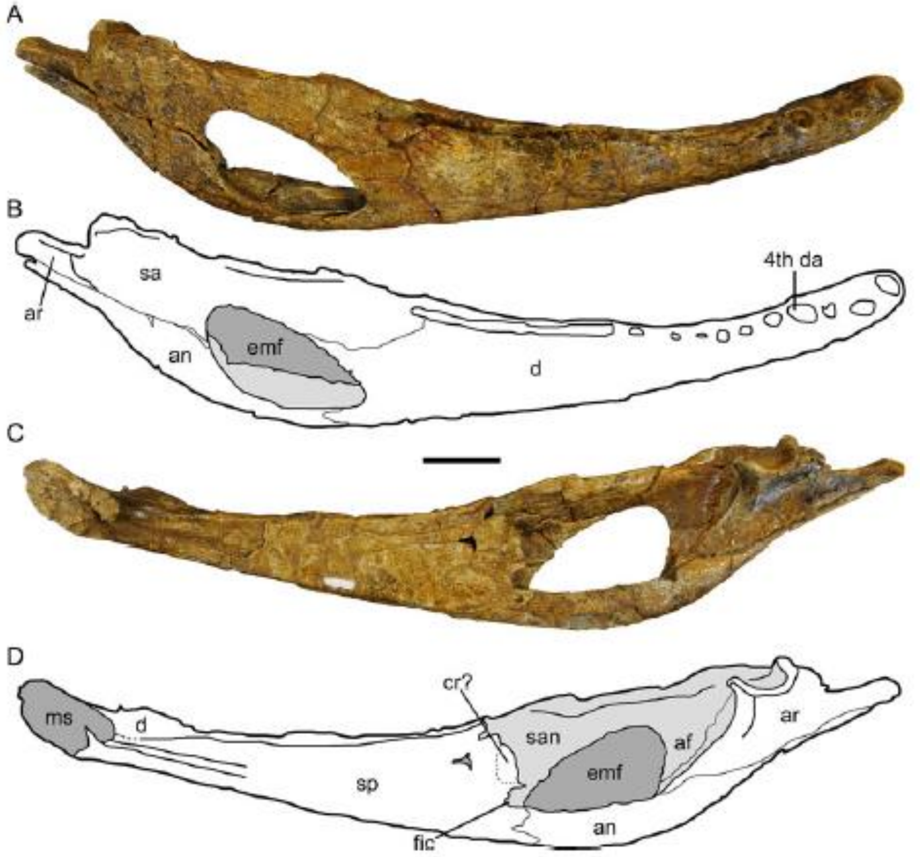

FIGURE 7. *Acresuchus pachytemporalis*, UFAC-2507, right mandibular ramus, photographs and schematic drawing illustrating bones and sutures in **A**, **B**, lateral and **C**, **D**, medial views. Scale bar equals 5 cm.

The quadratojugal constitutes the entire posterior angle of the infratemporal fenestra, preventing any participation of the jugal (Fig. 2). The quadratojugal spine is absent.

Quadrates—Both quadrates are completely preserved (Figs. 2, 3). The quadrate contacts the quadratojugal anterolaterally and the squamosal dorsomedially. In the anterior region of the braincase, the quadrate contacts the laterosphenoid and the pterygoid anteriorly and the postorbital dorsally.

In occipital view, the quadrate has a medial oblique contact with the exoccipital (Fig. 4). The foramen aereum is small and situated in a notch on the dorsal surface of the bone. On the ventral surface of the quadrate, crests for insertion of tendons and aponeuroses of the mandibular adductor muscles are present (Iordansky, 1973). On the left quadrate, crests that may correspond to crests 'A' and 'D' of Iordansky (1973) are remarkably evident.

The contact facet of the quadrate with the articular bone is a wide, convex, and smooth surface. The surface is slightly posteromedially displaced, with the small medial hemicondyle displaced in a more posteroventral direction (Fig. 4).

Supraoccipital—The supraoccipital is nearly completely preserved. In dorsal view, the bone has a large exposure on the skull table, contacting the parietal anteriorly (Fig. 2). The supraoccipital also contacts the squamosals laterally (in both dorsal and occipital views; Figs. 2, 4) and the exoccipitals laterally and ventrally (in occipital view only; Fig. 4).

Both posttemporal fenestrae are preserved. These structures are delimited dorsally and laterally by the squamosals, ventrolaterally by the exoccipitals, and ventromedially by the supraoccipital (Fig. 4). The dorsal, ventral, and medial borders of the fenestrae are surrounded by bony crests, which are absent in the lateral portion of the fenestrae.

Exoccipitals—The exoccipitals of *Acresuchus pachytemporalis* are nearly completely preserved, forming most of the occipital surface of the skull table. They contact the squamosals dorsally, the supraoccipital dorsomedially, and the quadrates laterally (Fig. 4) through a rather oblique contact in which the cranioquadrate canal exit is situated, as is common in Crocodylia (Iordansky, 1973). The cranioquadrate canal extends to the middle ear cavity, providing passage for the main branch of the facial nerve (cranial nerve VII), the orbitotemporal artery, and the lateral cephalic vein (Iordansky, 1973). The exoccipitals also meet each other medially (even though the area in which they meet is fractured) and dorsally at the foramen magnum, thus preventing the supraoccipital from contacting this foramen (Fig. 4) as is common in Crocodylia (Iordansky, 1973).

Ventrally, the exoccipital is not very well preserved lateral to the foramen magnum and occipital condyle. As a result, it is

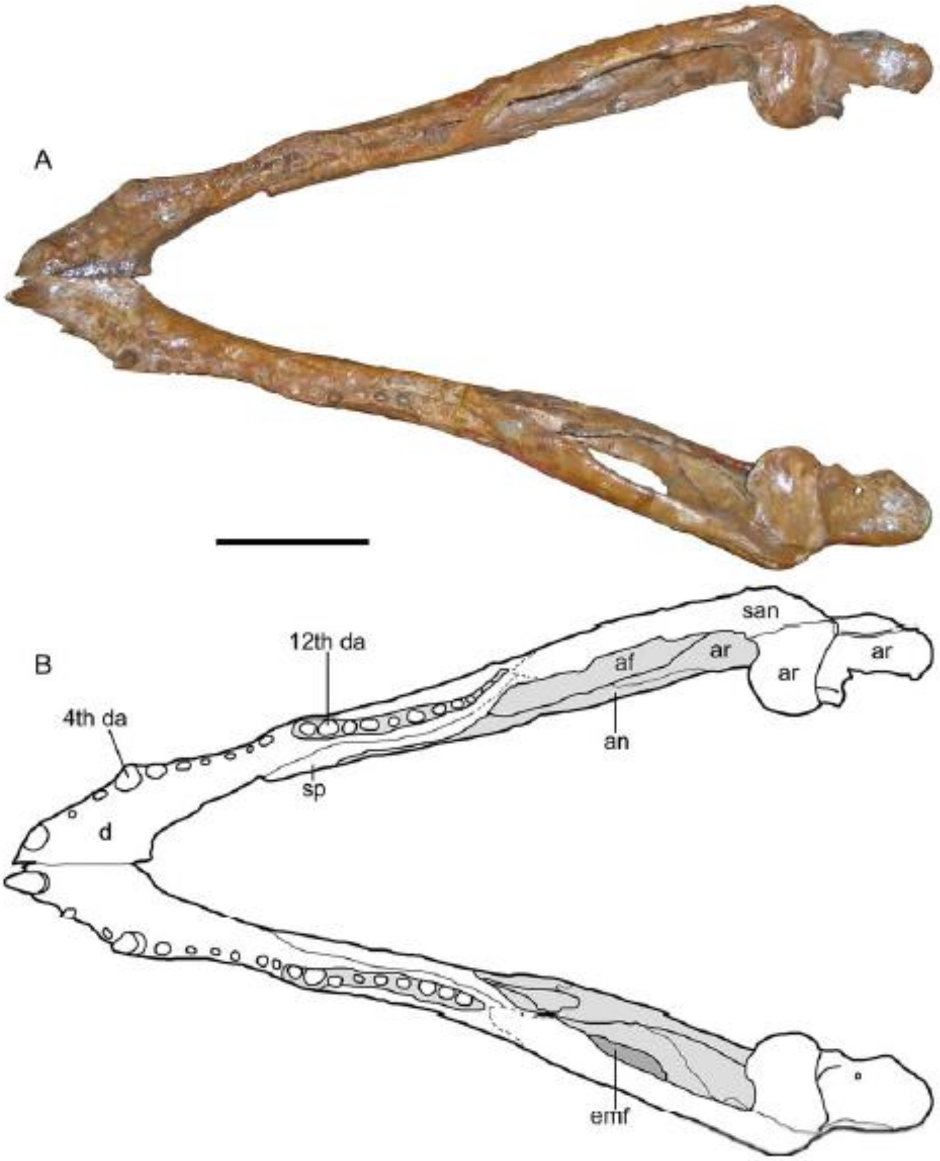

FIGURE 8. *Acresuchus pachytemporalis*, UFAC-2507, holotype, right (upper) and left (lower) mandibular rami. **A**, dorsal view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 10 cm.

not possible to assess whether the ventral processes of the exoccipitals lateral to the basioccipital were slender or robust (Brochu, 2011, character 176). Dorsal to this area, there are three circular openings. The ventral opening is here interpreted as the carotid foramen, for the passage of the internal carotid artery (Bona and Desojo, 2011; = foramen caroticum posterius of Iordansky, 1973). Dorsal to this, there are two openings: the medial one, smaller, is here interpreted as an opening for cranial nerve XII, following Iordansky (1973). The lateral, larger, one is here interpreted as being the foramen vagus, which contains cranial nerves IX and X, as well as the ramus communicans that connects cranial nerves VII and IX (Iordansky, 1973).

Basioccipital—The basioccipital is nearly completely preserved. The occipital condyle is complete (Fig. 4), formed exclusively by the basioccipital, as in all Crocodylia (Iordansky, 1973). Ventral to the condyle, the basioccipital plate (sensu Iordansky, 1973) is nearly complete (Figs. 4, 11) and is oriented posteriorly sensu Brochu (2011, character 170-1). The ventral and lateral margins of the plate, which form the basioccipital tubera (see Brochu, 1997, character 162, and the equivalent of Brochu's [2011] character 176) are slightly eroded, although the general morphology of the plate is preserved. The basioccipital tubera of *Acresuchus pachytemporalis* are not very developed. The medial crest of the basioccipital is preserved (Fig. 4). In living crocodylians, the tubera and the medial crest serve

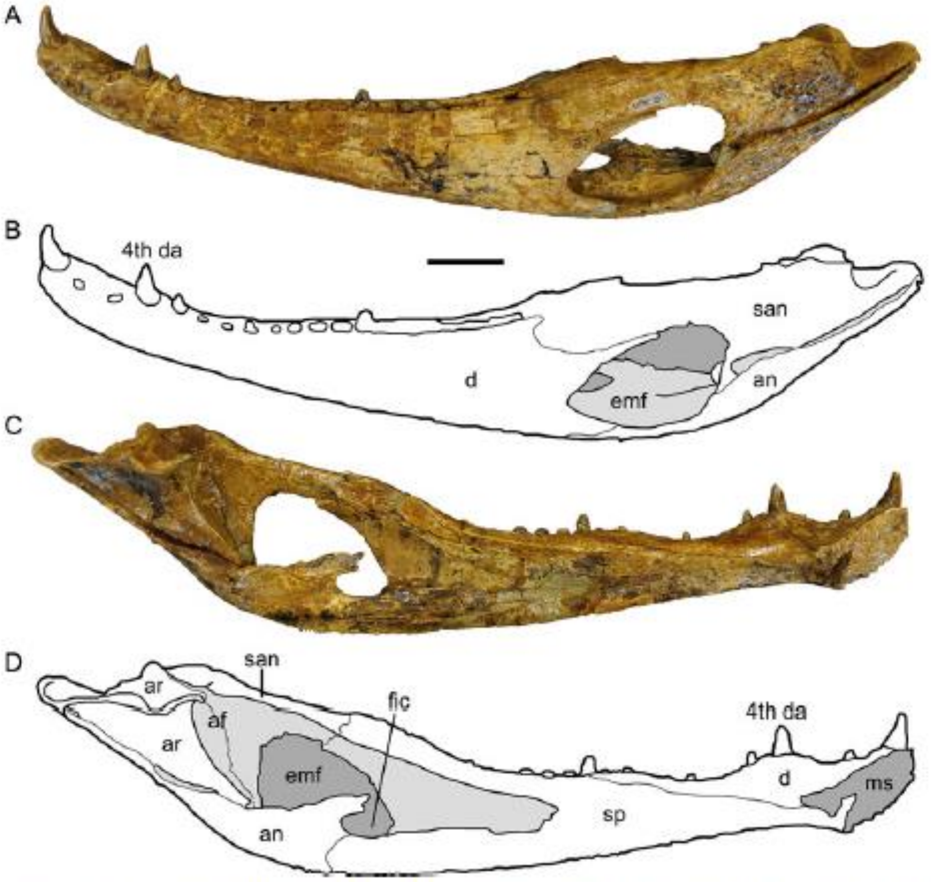

FIGURE 9. *Acresuchus pachytemporalis*, UFAC-2507, holotype, left mandibular ramus, photographs and schematic drawings illustrating bones and sutures in **A**, **B**, lateral and **C**, **D**, medial views. Scale bar equals 5 cm.

as attachments for the tendons of the muscles basioccipitovertebralis and occipitotransversalis profundus (Iordansky, 1973).

Basisphenoid—The basisphenoid is partially preserved (Fig. 11). It is possible to observe that the basisphenoid forms the anterior wall of the medial eustachian canal, because it contacts the basioccipital plate posteriorly. Only a proximal portion of the basisphenoid rostrum is preserved (Fig. 11).

Pterygoids—Only part of the pterygoids are preserved. In anterior view of the basicranium, the pterygoids contact the laterosphenoids dorsally and the basisphenoid anteromedially (Fig. 11). Ventral to the basisphenoid and the basioccipital, a small fragment of the pterygoids is preserved (Fig. 3), composed mostly of the right posteromedial ascending process of the bone (sensu Iordansky, 1973). No other portions of the pterygoids are preserved.

Laterosphenoid—Both bones are nearly completely preserved, forming the anterior parts of the lateral walls of the braincase and surrounding the foramen ovale, as is common in Crocodylia (Iordansky, 1973). It also extends dorsally to form the anteroventral area of the medial wall of the supratemporal fenestrae (Fig. 11), as described for *Caiman latirostris* by Bona and Desojo (2011). The laterosphenoid contacts the frontal and the postorbital dorsally, the quadrate posteriorly, and the basisphenoid and the pterygoid ventrally (Fig. 11). The laterosphenoids also contact each other medially through their anterodorsal portions. They, along with frontal bone dorsally, form the circular foramen for the olfactory tract of the forebrain.

Mandible of the Holotype

Dentary—Both dentaries of *Acresuchus pachytemporalis* are almost completely preserved, with some wear on their surfaces (Figs. 7–9). The dentaries form the greatest portion of the mandibular ramus, as in Crocodylia (Iordansky, 1973), specifically in lateral and dorsal view. The dentary contacts the splenial posteromedially and both the surangular and angular posteriorly, while also forming the anterior margin of the external mandibular fenestra. The dentary-surangular suture contacts the external mandibular fenestra anterior to the posterodorsal corner (Figs. 7, 9).

The mandibular symphysis of *Acresuchus* extends to the level of the fifth alveolus (character 49-0; Fig. 8). The anterior teeth project anterodorsally. The teeth and alveoli of the dentary, as well as those of the maxillae, are circular in cross-section. The first and fourth dentary teeth (only preserved in the left dentary) are noticeably the largest. The fourth alveolus is separated from—and larger than—the third. Between the fourth and the 10th alveoli, the dentary is 'gently curved'

FIGURE 10. *Acresuchus pachytemporalis*, UFAC-2507, skull table of the holotype in **A**, right and **B**, left lateral views. Scale bar equals 3 cm.

(sensu Brochu, 2011, character 50-0; see Fig. 8). The 12th alveolus is the largest of those situated posterior to the fourth (character 51-2).

Splenial—Both elements are nearly completely preserved (Figs. 7, 9), each forming a considerable part of the medial portion of the mandible. The left splenial is missing the posteriormost portion of its dorsal region (Fig. 9). The right splenial is also missing a portion in a similar area, although to a lesser degree than the left splenial. Additionally, the right splenial is also missing its anterior-most portion, which contacts the dentary dorsally and anteriorly, medially exposing the anterior portion of the Meckelian canal (Fig. 7). The splenial contacts the dentary dorsally and anteriorly, the surangular posterodorsally, and the angular and the coronoid, which are only preserved posteriorly on the right side (Fig. 7, 9). The splenial of *Acresuchus pachytemporalis* does not participate in the mandibular symphysis (Figs. 7, 9), with its anterior tip passing dorsal to the Meckelian groove.

Coronoid—Only a medial part of the most medial portion of the right coronoid is possibly preserved (Fig. 7), with the most dorsal and ventral parts of the medial portion being absent. This tentative portion of the coronoid is situated dorsal to the anterior margin of the incompletely preserved foramen intermandibularis caudalis (Fig. 7).

Surangular—Both surangulars of *Acresuchus pachytemporalis* are nearly completely preserved. The surangular forms the dorsal region of the adductor fossa in medial view, as well as the posterior portion of the dorsal margin and the dorsal portion of the posterior margin of the external mandibular fenestra in lateral view. It contacts the dentary anteriorly and anterolaterally, the splenial anteromedially, the articular posteriorly and medially, and the angular ventromedially and posteroventrally (Figs. 7–9).

Medially, the surangular-angular suture meets the articular dorsal to the latter's ventral tip. Additionally, in this view the surangular contacts the articular continuously, without a sulcus; it 'flushes' against the articular, sensu Brochu (2011, character 74-1).

Dorsally, the surangular continues to the dorsal tip of the lateral wall of the glenoid fossa, as in most eusuchians, whereas the surangular-articular suture is orientated anteroposteriorly within the fossa. Posterior to this, the left surangular extends to the posterior end of the retroarticular process, whereas the right surangular is broken at its posterior-most extent.

The external mandibular fenestra is present and is very large in the new taxon (Fig. 7, 9), allowing most of the foramen intermandibularis caudalis to be visible in lateral view (Brochu, 2011, character 63-2). Even though this foramen is not entirely preserved on either side, the position of this opening can be seen in the left mandibular ramus (Fig. 9). The angular-surangular suture passes broadly along the ventral margin of the external mandibular fenestra (Brochu, 2011, character 60-1; Figs. 7, 9).

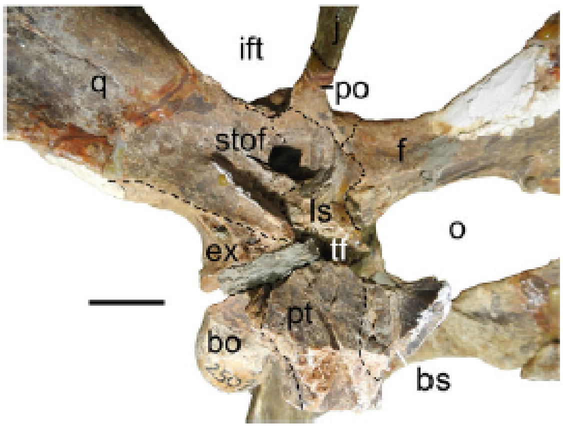

FIGURE 11. *Acresuchus pachytemporalis*, UFAC-2507, holotype, posterior portion of the skull in anterolateral view. Scale bar equals 5 cm.

Angular—The angulars are nearly completely preserved (Figs. 7–9). Both lack the dorsal part of their anterior-most portion in medial view, which would constitute the dorsal portion of the foramen intermandibularis caudalis (Figs. 7, 9). The right angular lacks this region completely (Fig. 7), implying that the posterior margin and most of the dorsal margin of the foramen intermandibularis caudalis are not preserved. Meanwhile, the left angular preserves only its posterior portion, in such a way that at least the posterior margin of the foramen is preserved, as well as the most posterior portion of the dorsal margin of the foramen (Fig. 9). In medial view, the bone contacts the splenial anteriorly, the coronoid dorsally, and the articular posterodorsally; in lateral view, it contacts the dentary anteriorly and the surangular dorsally (Figs. 7, 9). In dorsal view, the angular also has lateral contacts with the surangular anteriorly and the articular posteriorly (Fig. 8).

Articular—The articulars are completely preserved, including the retroarticular processes, the glenoid fossae, and the descending processes of both (Figs. 7–9). The only considerable damage is a circular hole near the medial margin of the retroarticular process of the left articular (Fig. 8). The glenoid fossa serves as the articular surface with the hemicondyles of the quadrate, as in all Crocodylia (Iordansky, 1973). The articular surface of the glenoid fossa is smooth, with the medial portion slightly more ventrally displaced than the lateral one. The retroarticular process projects posterodorsally. The articular contacts the surangular ventrolaterally (through its descending process) and dorsolaterally (through the glenoid fossa and the retroarticular process) and the angular ventromedially (through its descending process) and ventrally, in medial view (Figs. 7–9).

Teeth

The teeth of *Acresuchus pachytemporalis* have well-marked, non-serrated carinae, and the enamel presents some longitudinal lines parallel to the carinae.

Referred Specimens

The 10 referred specimens of *Acresuchus pachytemporalis* all consist of isolated skull tables with variable sizes and degrees of preservation (Fig. 12). All of the specimens preserve the parietal, both postorbitals (except UFAC-6384, which only preserves the right postorbital), the supraoccipital, and the most posterior portion of the frontals; three of these specimens preserve a larger part of the most posterior portion that the others (Fig. 12). Six of the specimens (UFAC-1486, UFAC-3142, UFAC-4153, UFAC-4154, UFAC-4183, and UFAC-4678) also preserve the squamosals and part of the quadrates and of the exoccipitals. Two specimens (UFAC-1187 and UFAC-5256) also preserve only part of the squamosals, the quadrates, and the exoccipitals. Specimen UFAC-1379 preserves the left squamosal and part of the right squamosal and the exoccipitals, and UFAC-6384 also preserves the right squamosal and part of the right exoccipital.

Seven of the referred specimens (UFAC-1486, UFAC-3142, UFAC-4153, UFAC-4154, UFAC-4183, UFAC-4678, and UFAC-6384) can be assigned to the new taxon because they exhibit the upturning on the posterolateral margin of the squamosal bone throughout the entire lateral margin, with a dorsoventral expansion of the posterior portion of the eminence that is an autapomorphy of *Acresuchus pachytemporalis* within Caimaninae. The other three (UFAC-1187, UFAC-1379, and UFAC-5256) have the posterior portions of their squamosals (the portion in which the eminence is larger in *A. pachytemporalis*) incomplete, except for the right squamosal of UFAC-1379, which is more complete and exhibits the eminence (Fig. 12I). However, the postorbitals and the anterior portions of the squamosals in these specimens are not elevated as in the other referred specimens and in the holotype (see Figs. 2, 4–6, 12). Nevertheless, the three specimens can be assigned to the new species for exhibiting supratemporal fenestrae that are large, significantly longer than wide, with an oval shape (which is a unique synapomorphy of the *Acresuchus* + *Purussaurus* clade) and for exhibiting a straight posterior margin of the skull table, which is present in *A. pachytemporalis* (Fig. 6) but absent in *Purussaurus* (Cidade et al., 2017). The differences observed between UFAC-1187, UFAC-1379, UFAC-5256, the holotype, and the other specimens referred to *A. pachytemporalis* raise the possibility that either the size of the eminence is intraspecifically variable or that the specimens may belong to another species of *Acresuchus*. Additionally, however, the three specimens have a relative small size when compared with the other referred specimens and the holotype (Figs. 2, 12). This in turn raises the possibility that the smaller size of the eminence may be related to a difference in ontogenetic development, which is observed in extant crocodylians (as it is in *Crocodylus niloticus* and other species of *Crocodylus* according to Brochu et al., 2010). Another possibility is that the difference is due to sexual dimorphism; the possibility that the eminences could be used in courtship or mating displays is examined in the discussion.

COMPARISONS

Skull

Premaxillae—The premaxillae of *Acresuchus pachytemporalis* exhibit the same general morphology as those of nearly all brevirostrine crocodylians (Fig. 2), including all caimanines except for *Mourasuchus*, which exhibits dorsoventrally flattened premaxillae that follow the overall aspect of the rostrum in this group (see Price, 1964; Bocquentin-Villanueva, 1984). The presence of five alveoli in each of the premaxillae is the morphology in all alligatoroids except for *Paleosuchus*, which has four alveoli (Brochu, 1999). The presence of tooth occlusal surfaces between the sutures of each premaxilla with each maxilla, on both sides, is considered a common feature among alligatorids by Iordansky (1973). The fourth dentary tooth occluding in a pit rather than in a notch in *Acresuchus* is a well-known feature of most alligatoroids, with exception of *Leidyosuchus canadensis* Lambe, 1907, and *Diplocynodon remensis* Smith, De Lapparent, and Delfino, 2014, which have the fourth and fifth dentary teeth occluding in a notch (Brochu, 1999, 2011; Wu et al., 2001; Smith et al., 2014).

The large, roughly circular shape of the external naris of *Acresuchus pachytemporalis* (Fig. 2) is a morphology shared with most Eusuchia, with the exceptions of *Mourasuchus amazonensis* Price, 1964, *M. pattersoni* Cidade, Solórzano, Rincón, Riff, and Hsiou, 2017, *Purussaurus mirandai* Aguilera, Riff, and Bocquentin-Villanueva, and *P. brasiliensis* (Price, 1964; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006; Cidade et al., 2017). The dorsal projection of the external naris in *Acresuchus* is also present in all caimanines except *Tsoabichi greenriverensis* and *Caiman wannlangstoni* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh, and Antoine, 2015 (Brochu, 2010; Salas-Gismondi et al., 2015). The nasal bones reaching the external naris in its posterior margin but not bisecting the naris is a feature observed in all caimanines except *Mourasuchus* (Price, 1964; Bocquentin-Villanueva, 1984), *Caiman gasparinae* (Bona and Carabajal, 2013), and *Globidentosuchus* Scheyer, Aguilera, Delfino, Fortier, Carlini, Sánchez, Carrillo-Briceño, Quiroz, and Sánchez-Villagra, 2013 (Scheyer et al., 2013), in which the nasals are excluded from the external naris, at least externally.

The smooth premaxillary surface lateral to the external naris, without the presence of a notch, is a feature shared with all caimanines except *Gnatusuchus* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh, and Antoine, 2015, *Mourasuchus atopus* (Langston, 1965), and *M. arendsi* Bocquentin-Villanueva, 1984. The presence of a slight elevation mainly in the posterior margin of the premaxillary surface lateral to the external naris, and its more rugose surface, is also seen in some specimens of caimanine taxa analyzed for this study, such as *Caiman crocodilus* (AMNH 43291), *Melanosuchus niger* (AMNH R-58130), and *Paleosuchus palpebrosus* (AMNH 93812). This elevation may correspond to the 'posterolateral ridge' that Bona and Desojo (2011) referred to as being present in *Caiman latirostris*. It is noteworthy that, although elevated, the lateral surface of the external naris in *Acresuchus* is not considered here to be similar to the thin crest reported in *Tsoabichi greenriverensis*

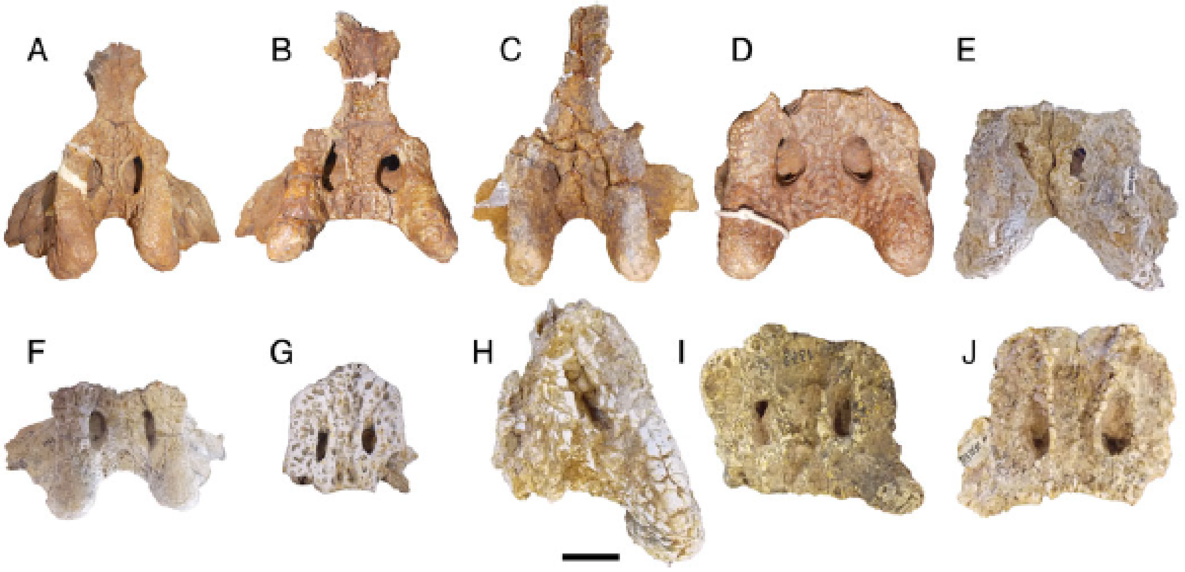

FIGURE 12. *Acresuchus pachytemporalis*, referred specimens in dorsal view. **A**, UFAC-4678; **B**, UFAC-4154; **C**, UFAC-4183; **D**, UFAC-4153; **E**, UFAC-1486; **F**, UFAC-3142; **G**, UFAC-5256; **H**, UFAC-6384; **I**, UFAC-1379; **J**, UFAC-1187. Scale bar equals 1 cm.

by Brochu (2010), while also being different from the marked knob seen around the external naris in *Mourasuchus arendsi* (Cidade et al., 2017). The condition of the dorsal premaxillary processes not extending beyond the third maxillary alveolus seen in *Acresuchus* is also the condition in all caimanines except *Mourasuchus* (Price, 1964; Bocquentin-Villanueva, 1984) and *Caiman brevirostris* Souza-Filho, 1987 (Fortier et al., 2014).

Maxillae—The absence of an exposure of the vomer between the premaxillae and the maxillae in *Acresuchus* is shared with most eusuchians, because such exposure occurs only and consistently in both species of *Melanosuchus* (Brochu, 1997, 1999).

The teeth and alveoli of both maxillae and dentaries being circular in cross-section differs from the laterally compressed posterior teeth seen in *Kuttanacaiman* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh, and Antoine, 2015, *Paleosuchus*, and *Mourasuchus*. All dentary teeth occluding lingually to the maxillary teeth is a morphology also seen in living alligatorids (Brochu, 1997). The fourth alveolus as the largest of the maxillary tooth row is a feature shared with all caimanines except *Culebrasuchus*, *Gnatusuchus*, and *Globidentosuchus*.

The absence of preorbital ridges seen in *Acresuchus* is a morphology shared with all alligatoroids (see Brochu, 1997), whereas the absence of very prominent 'canthi rostralli' is the same morphology present in most caimanines except *Purussaurus mirandai*, *Melanosuchus*, *Caiman latirostris*, *C. brevirostris*, and *C. wannlangstoni*. The tentative small depressions present in the most posterior portions of both maxillae may be homologous to the similar shallow depressions present in *P. neivensis* (Mook, 1941) and to the accentuated depressions of *P. mirandai* and *P. brasiliensis*. The presence of the accentuated depressions in *P. mirandai* and *P. brasiliensis* has been associated with the biting performance of these forms (Aureliano et al., 2015), as will be discussed below.

Nasals—The nasals of this taxon are longer than the remarkably short nasals present in *Purussaurus neivensis* and *Purussaurus brasiliensis* (Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006). The reduction of the nasals in these two *Purussaurus* species, however, is evidently related to the accentuated increase in the size of the external naris present in both, which is not so accentuated in *P. neivensis* (see Aguilera et al., 2006) or *Acresuchus*. These differences in the size of the external naris may be related to the evolution of gigantism in the *Purussaurus* lineage, as will be discussed later.

Prefrontals—The medial contact between the prefrontals is also present in many taxa within Caimaninae, such as *Purussaurus*, *Mourasuchus*, *Kuttanacaiman*, *Globidentosuchus*, *Melanosuchus fisheri*, *Caiman yacare*, *C. wannlangstoni*, and some individuals of *C. crocodilus* (Brochu, 1999, 2013; Cidade et al., 2017).

The absence of prominent preorbital ridges in *Acresuchus pachytemporalis* is a common feature among neosuchians (Brochu, 1997). The absence of knob-like processes in the prefrontal surface adjacent to the orbital rim is similar to the morphology of most eusuchians and all caimanines except for *Mourasuchus*, which has a marked knob in the anteromedial region of the orbits (Bona et al., 2013b). The upturning of the orbital rims is a morphology shared by all caimanines except *Gnatusuchus*, *Kuttanacaiman*, *Globidentosuchus*, and *Culebrasuchus* (Fig. 2).

Frontal—The placement of the frontoparietal suture entirely on the skull table is a morphology shared with all caimanines. The concavoconvex shape of the frontoparietal suture is a character shared with many caimanines, such as *Purussaurus*, *Gnatusuchus*, *Globidentosuchus*, *Caiman crocodilus*, *C. yacare*, *C. wannlangstoni*, and *C. brevirostris*.

Postorbitals—A slender postorbital bar inset from the anterolateral edge of the skull table with a short, not prominent, process is a set of a characters shared between *Acresuchus pachytemporalis* and most eusuchians (see Brochu, 1997).

Parietal—The parietal not contacting the posterior margin of the skull table is a feature common to all caimanines for which this part of the skull is known, except *Tsoabichi*, *Paleosuchus*, and what is described for *Purussaurus mirandai* (see Aguilera et al., 2006:fig. 7).

The large, roughly oval, supratemporal fenestrae of *Acresuchus pachytemporalis* are similar to the supratemporal fenestrae of the species of *Purussaurus* (see Aguilera et al., 2006; Aureliano et al., 2015). However, in all other eusuchians, the supratemporal fenestrae have a different morphology. In most non-caimanine eusuchians, these fenestrae are not overhung by the dermal bones delimiting it, exhibiting a 'fossa' in its surroundings (Brochu, 2011, character 152-0). Within Caimaninae, most fossil and extant species exhibit small fenestrae, of which most are rounded in shape, although some taxa exhibit oval supratemporal fenestrae, such as *Tsoabichi greenriverensis* (Brochu, 2010), *Caiman lutescens* (Bona et al., 2013b), and at least some specimens of *Melanosuchus niger* (AMNH R-58130, MN-3174, MCT-286-RR). These are strikingly smaller than those of *Acresuchus* and *Purussaurus* relative to the size of the skull table. Moreover, in *Paleosuchus*, the fenestrae close during ontogeny in most individuals (Brochu, 1997). The large size of the supratemporal fenestrae in *Acresuchus* and *Purussaurus* may be related to an increase of the insertion area of the M. adductor mandibulae externus profundus (Iordansky, 1973; Holliday and Witmer, 2007; = M. pseudotemporalis of Schumacher, 1973) or to a thermoregulation function of the brain, both of which may be related to increasing size in the *Acresuchus* + *Purussaurus* lineage, as will be discussed later.

Squamosal—The bowed posterior margin of the otic apertures is a morphology shared with most taxa of the clades Alligatoroidea and Crocodyloidea (see Brochu, 2011). The parallel dorsal and ventral rims of the squamosal groove are also present in most eusuchians (Brochu, 1997).

The most striking feature of this bone in *Acresuchus pachytemporalis* is the large eminence present in its lateral and posterior portions, which forms a 'horn' in the posterior portion of the skull table (Figs. 6, 10). Although most of the squamosal is elevated (except for the most medial portion of the bones, adjacent to the supraoccipital), the eminence is markedly larger posteriorly than anteriorly, surpassing significantly the dorsal level of the posterior margin of the skull table (Figs. 6, 10).

These highly hypertrophied, posterolaterally positioned 'horns' of *Acresuchus pachytemporalis* are also seen in the alligatorid *Ceratosuchus burdoshi* Schmidt, 1938 (Fig. 13C), from the Paleocene of the U.S.A. (Schmidt, 1938; Bartels, 1984). The morphology of these two taxa led to the creation of a new state for Character 156 that concerns this feature (see Appendix S1 in Supplementary Data 1). Within Caimaninae, both *Purussarus neivensis* and *P. mirandai* have the lateral margins of the squamosals upturned, but not to the degree seen in the new taxon. Additionally, the lateral margins of the squamosals of *P. neivensis* and *P. mirandai* are uniformly elevated, without the distinct 'second' elevation that occurs from the posterior portion of the supratemporal fenestrae in *Acresuchus pachytemporalis*. The species *Mourasuchus arendsi* also has hypertrophied squamosals (Gasparini, 1985; Bona et al., 2013a; Cidade et al., 2018; Scheyer and Delfino, 2016; Fig. 13B), but these differ from those of *Acresuchus pachytemporalis* by having the entire dorsal surface elevated, not only the lateral portion.

Outside Caimaninae, other crocodylians also exhibit hypertrophied squamosals. The extinct *Aldabrachampsus dilophus* Brochu, 2006, the extant *Crocodylus siamensis* Schneider, 1801 (Brochu et al., 2010) and *Crocodylus rhombifer* Cuvier, 1807 (Brochu, 2000; Fig. 13A), and some large individuals of most extant species of *Crocodylus* Laurenti, 1768, such as *C. niloticus* (Brochu et al., 2010; G.M.C., pers. observ.), have their lateral margins of the squamosals elevated, but not as prominently as in *Acresuchus pachytemporalis*. The extinct *Voay robustus* (Grandidier and Vaillant, 1872) has its squamosals more hypertrophied in the posterior portion of the bones (see Brochu, 2007), like in the new taxon, but differs from the latter by presenting a lateromedial expansion (Fig. 13D). This last morphology has also led to the creation of another new state for Character 156 (see Appendix S1). The extinct *Crocodylus anthropophagus* Brochu, Njau, Blumenschine, and Densmore, 2010, also has hypertrophied squamosals (Brochu et al., 2010), but the holotype material is too fragmented to allow a thorough comparison between the morphology of the squamosal, as a whole, and the squamosal of other species.

As such, the hypertrophied squamosals of *Acresuchus pachytemporalis*—with an eminence larger in the posterior portion of the lateral margins of the squamosals in which there is not a lateromedial expansion—may be seen as an unique feature of this species within Caimaninae and hence as a diagnostic feature of the new taxon, being shared only with the alligatorine *Ceratosuchus burdoshi*. Moreover, the evolution of these squamosal horns in the *Acresuchus* + *Purussaurus* clade may be related to the evolution of gigantism in this lineage, as will be detailed in Discussion, below.

Jugals—The mediolaterally slender and dorsoventrally low jugals of *Acresuchus pachytemporalis* are similar to those present in most eusuchians and all caimanines except *Mourasuchus amazonensis* and *M. pattersoni* (Cidade et al., 2017).

Quadratojugals—The long anterior process of the quadratojugal along the lower temporal bar (Brochu, 2011, character 144-0) observed in *Acresuchus pachytemporalis* is also present in most eusuchians and all alligatoroids for which the character is known (Brochu, 2011). The posterior angle of the infratemporal fenestra being composed entirely of the quadratojugal, preventing any participation of the jugal, is a morphology shared with most eusuchians and with all alligatoroids for which this character is known (Brochu, 2011; Fig. 2). The absence of the quadratojugal spine is shared with most alligatoroids (Brochu, 2011).

Quadrates—The small size of the foramen aereum is a morphology shared with most eusuchians, whereas its location on the dorsal surface and in a notch (Brochu, 2011, character 181-1) are features shared with most alligatoroids (Brochu, 2011).

Supraoccipital—The posttemporal fenestrae of *Acresuchus pachytemporalis*, which are delimited ventromedially by the supraoccipital, are not proportionally as large in this taxon as in *Purussaurus* and not as anteroposteriorly deep as in *Mourasuchus* (see Bona et al., 2013a, 2013b), resembling more those of living caimanines.

Basioccipital—The poor development of the basioccipital tubera observed in *Acresuchus pachytemporalis* is also present in most eusuchians except for some longirostrine forms such as *Gavialis* Oppel, 1811, and *Thoracosaurus* Leidy, 1852 (Brochu, 1997).

Mandible

Dentary—The dentary-surangular suture contacting the external mandibular fenestra anterior to the posterodorsal corner seen in *Acresuchus pachytemporalis* is a morphology shared with most eusuchians (see Brochu, 2011). The extension of the mandibular symphysis to the level of the fifth alveolus is a feature also present in most caimanines except *Mourasuchus*, *Eocaiman* Simpson, 1933, *Globidentosuchus*, and *Gnatusuchus*. The anterodorsal projection of the anterior teeth is shared with all alligatoroids except *Eocaiman cavernensis* Simpson, 1933, *E. itaboraiensis* Pinheiro, Fortier, Pol, Campos, and Bergqvist,

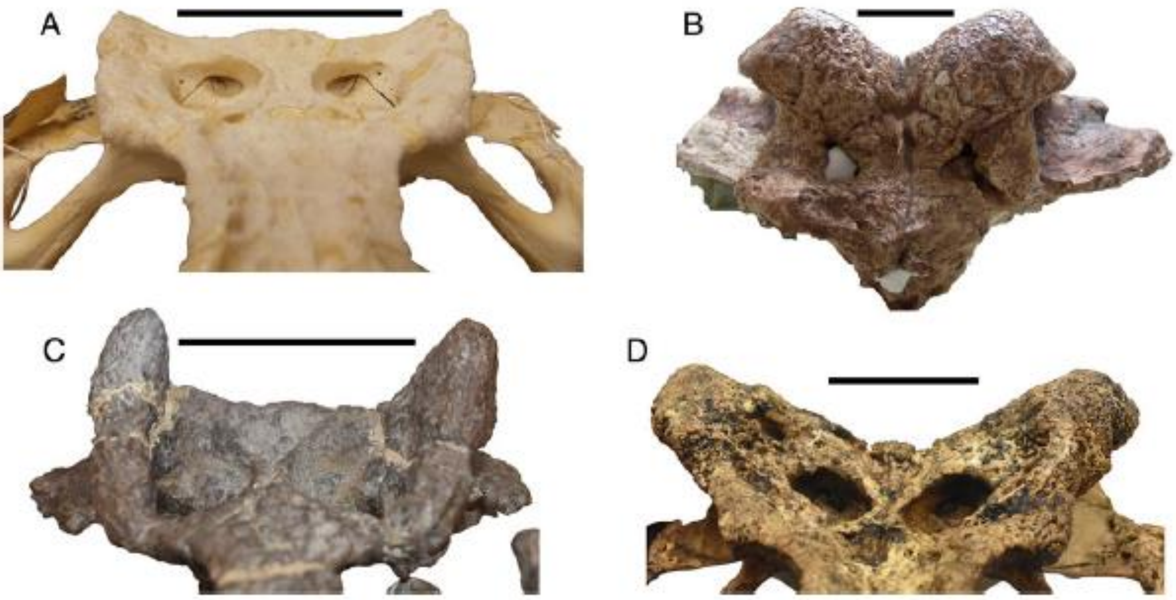

FIGURE 13. Crocodylian skull tables in anterodorsal view exhibiting the diversity in morphology of squamosal eminences. **A**, *Crocodylus rhombifer*, AMNH R-6178; **B**, *Mourasuchus arendsi*, UFAC-1431; **C**, *Ceratosuchus burdoshi*, FMNH P15576, holotype; **D**, *Voay robustus*, AMNH 3101. Scale bars equal 5 cm.

2013, and *Gnatusuchus* (Brochu, 2011; Pinheiro et al., 2013; Salas-Gismondi et al., 2015). The fourth alveolus separated from the third alveolus, while also being the larger of the two, is a character also observed in all alligatorids except *Gnatusuchus*, in which these alveoli are separated but nearly of the same size (Salas-Gimsondi et al., 2015), and *Leidyosuchus* and *Diplocynodon*, in which the two alveoli are confluent and nearly of the same size (Brochu, 2011). The 'gently curved' morphology of the dentary between the fourth and the 10th alveoli (sensu Brochu, 2011, character 50-0) is shared with all caimanines except *Mourasuchus* (see Langston, 1965; Bona et al., 2013b) and *Culebrasuchus mesoamericanus* (Hastings et al., 2013), in which it is linear. The 12th alveolus as the largest of those situated posterior to the fourth is a feature shared with all caimanines in which this character is known, except *Mourasuchus* and *Globidentosuchus*.

Splenial—The splenial of *Acresuchus pachytemporalis* not reaching the mandibular symphysis (Figs. 7, 9), with its anterior tip passing dorsal to the Meckelian groove, is a character shared with all caimanines except *Globidentosuchus* and *Gnatusuchus* (Scheyer et al., 2013; Salas-Gismondi et al., 2015).

Surangular—The surangular-angular suture meeting the articular dorsal to the latter's ventral tip in medial view as observed in *Acresuchus pachytemporalis* is a feature shared with all caimanines except *Gnatusuchus*. The surangular 'flushing' against the articular (sensu Brochu, 2011, character 74-1) is shared with most alligatoroids and all caimanines, except *Mourasuchus atopus*.

The surangular continuing dorsally to the dorsal tip of the lateral wall of the glenoid fossa is a morphology shared with most eusuchians, whereas the surangular-articular suture being orientated anteroposteriorly within the fossa is shared with all alligatoroids except *Globidentosuchus* (Scheyer et al., 2013). Additionally, the surangular extending until the posterior end of the retroarticular process is shared with all caimanines for which this character is known except *Globidentosuchus* (Scheyer et al., 2013).

The external mandibular fenestra being large to the point of allowing most of the foramen intermandibularis caudalis to be visible in lateral view is shared only with *Purussaurus* among Caimaninae. The angular-surangular suture passing broadly along the ventral margin of the external mandibular fenestra is a morphology also observed in most taxa within crown-group caimans, except *Mourasuchus*.

Articular—The posterodorsal projection of the retroarticular process observed in the new taxon is shared with most eusuchians.

Teeth

The teeth of *Acresuchus pachytemporalis* (with well-marked, non-serrated carinae and enamel with longitudinal lines parallel to the carinae) are similar to the typical morphology observed in most extant crocodylians (see Prasad and de Broin, 2002). The lack of serrations in the carinae distinguishes the teeth of this taxon from the marked pseudoziphodont serrations seen in *Purussaurus* (see Aureliano et al., 2015; Souza et al., 2016).

PHYLOGENETIC ANALYSIS

A strict consensus of 16,800 cladograms was constructed (Fig. 14; Fig. S1 in Supplementary Data 1), with a best score of 641 steps (ensemble consistency index = 0.387; ensemble retention index = 0.811). It shows *Acresuchus pachytemporalis* as the sister taxon of *Purussaurus*. This clade is supported by the following three synapomorphies: (1) external mandibular fenestra present and very large, with most of the foramen intermandibularis caudalis visible in lateral view (character 63-2), shared with *Boverisuchus magnifrons* Kuhn, 1938, and all the

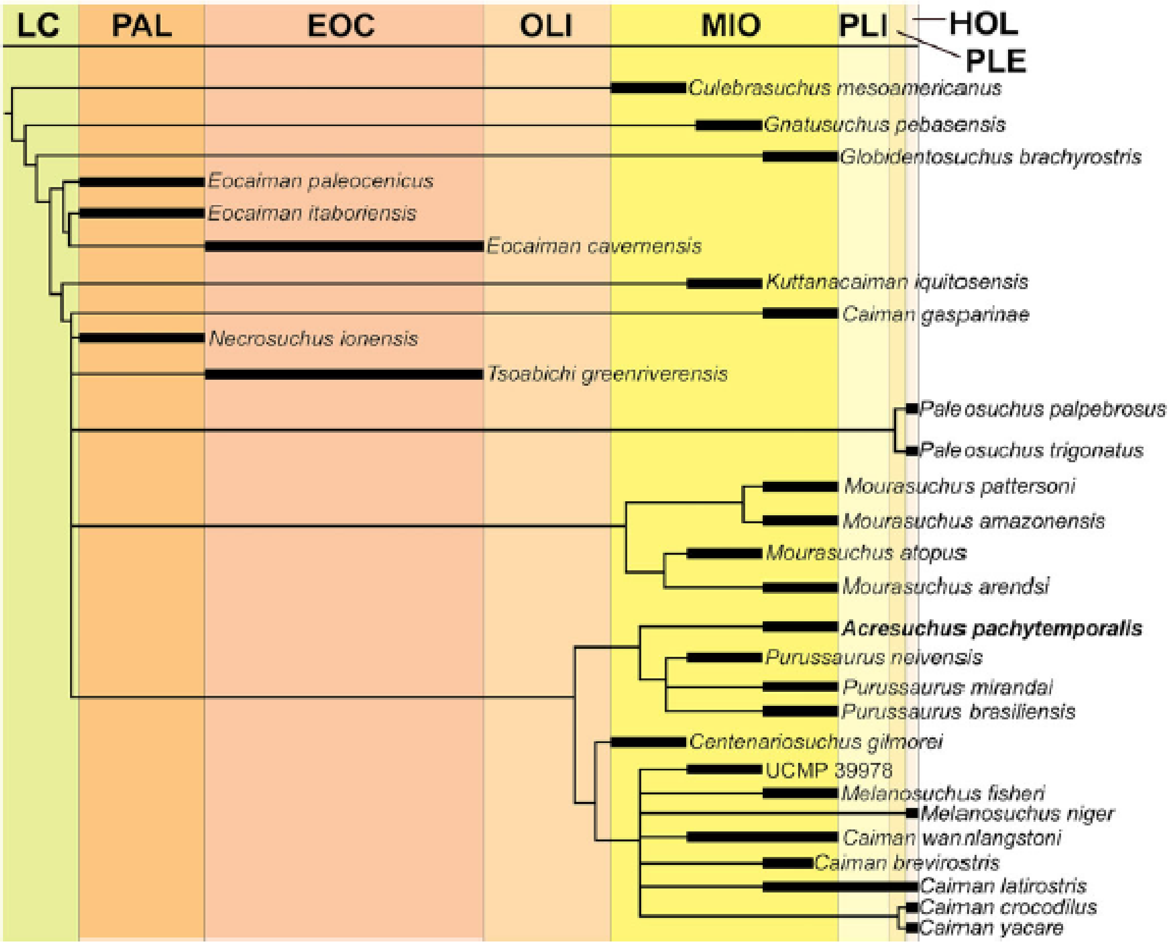

FIGURE 14. Detailed phylogeny of Caimaninae obtained in this study, highlighting the placement of *Acresuchus pachytemporalis* as the sister taxon to *Purussaurus*.

species of *Alligator* Cuvier, 1807, included in the analysis except *A. prenasalis* (Loomis, 1904) and *A. mcgrewi* Schmidt, 1941; (2) anterior tip of frontal forming simple acute point (character 130-0), a reversal within Alligatoroidea that is shared with *Kuttanacaiman*; and (3) dermal bones of the skull roof overhanging the rims of the supratemporal fenestrae near maturity, with the fenestrae large, significantly longer than wide and with an oval shape (character 151-3), which is a synapomorphy unique to this clade. *Purussaurus* is supported as a clade also by three synapomorphies: (1) external naris longer than wide (character 83-2), which is a unique synapomorphy; (2) orbits equal or subequal in size to the infratemporal fenestrae (character 181-0), a character shared convergently with *Acynodon iberoccitanus* Buscalioni, Ortega, and Vasse, 1997, *Kambara implexidens* Salisbury and Willis, 1996, *Brachychampsa montana* Gilmore, 1911, *Diplocynodon darwini* (Ludwig, 1877), *D. hantoniensis* (Wood, 1846), and *D. ratelii* Pomel, 1847; and (3) posterior margin of the skull deeply concave (character 185-1), a character shared with *Thecachampsa americana* (Sellards, 1915). The placement of *Acresuchus* relative to *Purussaurus* offers a previously unavailable opportunity to assess the evolution of *Purussaurus*, as will be discussed below.

The topology obtained for the basal caimanines does not differ from that of Cidade et al. (2017) upon recovering *Culebraushcus*, *Gnatusuchus*, *Globidentosuchus*, *Eocaiman*, as successive sister taxa to the remaining caimanines. The topology among the three species of *Eocaiman* is also similar to the previous works that included them (Pinheiro et al., 2013; Cidade et al., 2017). The placement of *Kuttanacaiman* as the sister taxon to crown-group caimanines (following Brochu, 1999) is different from that of Salas-Gismondi et al. (2015), which recovered it as the sister taxon of a two-lineage clade formed by crown-group caimans and a clade composed of *Purussaurus* and *Mourasuchus*, and from Cidade et al. (2017), which recovered it as the sister taxon of a clade formed by *Tsoabichi* and *Paleosuchus*.

The topology within crown-group caimanines presents itself as a polytomy, different from the more defined arrangement of Cidade et al. (2017). This is explained by the inclusion of two very fragmented taxa from Argentina, *Necrosuchus ionensis* from the Paleocene and *Caiman gasparinae* from the Miocene, which were not included in the analysis of those authors. These taxa represent two of the six lineages of the polytomy, the other four being *Tsoabichi*, *Paleosuchus*, *Mourasuchus*, and a more derived clade including *Acresuchus*, *Purussaurus*, *Centenariosuchus*, and Jacarea (sensu Brochu, 1999). *Tsoabichi* appears as the sister taxon of both extant species of *Paleosuchus* in many previous analyses (e.g., in the Adams consensus of Brochu, 2010, and in the strict consensus of Scheyer et al., 2013; Fortier et al., 2014; Salas-Gismondi et al., 2015; Cidade et al., 2017), but such an arrangement was not recovered in this work. Further studies of *Necrosuchus*, *Caiman gasparinae*, and *Tsoabichi* shall address these phylogenetic issues, but these are beyond the scope of the present contribution. *Mourasuchus* is recovered as a monophyletic group, as in previous analyses (Bona et al., 2013b; Salas-Gismondi et al., 2015; Cidade et al., 2017).

The topology among the species of *Mourasuchus* is similar to that recovered by Cidade et al. (2017). The placement of the *Acresuchus* + *Purussaurus* clade as the sister taxon of a clade formed by *Centenariosuchus* and Jacarea also differs from most previous analyses by showing *Purussaurus* as not closely related to *Mourasuchus*. Most previous phylogenies had recovered *Purussaurus* as the sister taxon of a clade composed of *Mourasuchus* and the North American Eocene taxon *Orthogenysuchus olseni* (Brochu, 1999; Aguilera et al., 2006; Bona, 2007; Bona et al., 2013b; Scheyer et al., 2013; Fortier et al., 2014) or as the sister taxon of *Mourasuchus* only (Salas-Gismondi et al., 2015; Cidade et al., 2017). Ongoing preparation of the holotype of *Orthogenysuchus* revealed significant changes in the scoring of the characters for this taxon that have not yet been published. As a result, previous works have excluded this taxon from their phylogenetic analyses (Salas-Gismondi et al., 2015; Cidade et al., 2017).

Centenariosuchus gilmorei is recovered as the sister taxon of the clade Jacarea, as in Salas-Gismondi et al. (2015), but different from Hastings et al. (2013), in which this taxon is not more closely related to Jacarea than *Purussaurus neivensis* or the clade formed by *Orthogenysuchus* and *Mourasuchus*, and from Cidade et al. (2017), in which it appears as the sister taxon to a clade formed by *Purussaurus* and *Mourasuchus*. The resolution within Jacarea is a seven-branch polytomy formed by *Caiman crocodilus* and *C. yacare* and each of the following units as an independent lineage: *Caiman latirostris*, *Caiman brevirostris*, *C. wannlangstoni*, *Melanosuchus fisheri*, *M. niger*, and UCMP-39978. This is the same topology recovered by Salas-Gismondi et al. (2015).

The placement of *Caiman brevirostris* differs from Fortier et al. (2014), which recovered it as the sister taxon of the clade formed by *Caiman latirostris*, UCMP-39978, and both species of *Melanosuchus*, and from Cidade et al. (2017), which placed it only as the sister taxon of a clade formed by *C. latirostris* and *M. niger*. Cidade et al. (2017) also recovered *C. wannlangstoni* in a much more basal position within the crown-group caimanines than Salas-Gismondi et al. (2015) and the present contribution. The placement of *C. crocodilus* and *C. yacare* as a monophyletic group closer to each other than to all other jacareans recovered by this work is a basic arrangement of Jacarea exhibited in many previous analyses (e.g., Brochu, 1999, 2010, 2011; Aguilera et al., 2006; Bona, 2007; Hastings et al., 2013; Scheyer et al., 2013; Fortier et al., 2014; Cidade et al., 2017). In-depth discussion regarding the phylogenetic relationships within Jacarea is beyond the scope of this work, but the main possible reasons for the lack of definition within this clade are the incompleteness of the remains of some operational taxonomic units, such as the specimen UCMP-39978 and *Caiman brevirostris*, as well as the lack of phylogenetic characters relative to the morphological differences and similarities of the taxa within Jacarea in the current phylogenetic data sets for Crocodylia (Brochu, 2011; Salas-Gismondi et al., 2015; Cidade et al., 2017; this paper). Future works must address these issues with a specific and thorough approach.

The topology of non-caimanine alligatoroids recovered in the analysis of this paper also shows some significant differences in comparison with previous analyses. The placement of *Leidyosuchus canadensis* as the basal-most alligatoroid is also seen in most of the phylogenetic analyses performed on Alligatoroidea to date (Brochu, 1999, 2004, 2010, 2011; Bona et al., 2013b; Pinheiro et al., 2013; Scheyer et al., 2013; Fortier et al., 2014; Martin et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Hastings et al., 2016; Wang et al., 2016; Cidade et al., 2017). *Diplocynodon* as the second most basal clade, after *Leidyosuchus*, is also recovered by most of these analyses (Brochu, 1999, 2004, 2010, 2011; Bona et al., 2013b; Pinheiro et al., 2013; Fortier et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Wang et al., 2016; Cidade et al., 2017), except for the analyses that include *Deinosuchus*, from the Upper Cretaceous of North America, which consistently appears as a basal alligatoroid (Aguilera et al., 2006; Scheyer et al., 2013; Martin et al., 2014; Hastings et al., 2016). The analysis of this paper did not obtain any resolution within the *Diplocynodon* clade, similar to Wang et al. (2016) and Cidade et al. (2017), but differently from several previous analyses that obtained resolutions between the taxa that constitute the clade (Brochu, 1999, 2004, 2010, 2011; Aguilera et al., 2006; Hill and Lucas, 2006; Scheyer et al., 2013; Martin et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Hastings et al., 2016). Future comprehensive analyses of basal alligatoroids shall address the issue of the placement of *Deinosuchus* and review the phylogeny of the species of *Diplocynodon*.

The placement of *Brachychampsa*, *Stangerochampsa*, and *Albertochampsa* as successive sister taxa to Alligatoridae is also seen in Brochu (2004) and Cidade et al. (2017). This topology differs from that of Brochu (2010), in which the three genera appear basal to Alligatoridae but in a polytomy, and from Brochu (2011, 2013), in which they appear within Alligatoridae but not forming a single clade. Additionally, Skutschas et al. (2014) recovered the three genera forming a single clade within Alligatoridae, whereas Salas-Gismondi et al. (2015) also recovered the three genera in a single clade that is the basal-most lineage of Caimaninae. These different placements of *Brachychampsa*, *Stangerochampsa*, and *Albertochampsa* indicate that an in-depth review of these three genera must be thoroughly addressed in other works. *Allognatosuchus*, *Procaimanoidea*, and *Arambourgia* forming a single clade in Alligatorinae is a topology also recovered by Brochu (2010, 2011), Scheyer et al. (2013), and Cidade et al. (2017). In Hastings et al. (2016), these three genera form a clade in Alligatoridae, but not in Alligatorinae, whereas in other analyses the genera were not recovered in a single clade.

Wannaganosuchus, *Hassiacosuchus*, *Navajosuchus*, and *Ceratosuchus* were all recovered in Alligatorinae, but as independent lineages, not forming part of any clade within that group. This topology is similar to that of Cidade et al. (2017), but different from most analyses, which recovered *Wannaganosuchus* as the sister taxon of *Alligator* (Brochu, 1999, 2004, 2010, 2011; Aguilera et al., 2006; Hastings et al., 2013; Scheyer et al., 2013; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Wang et al., 2016; Whiting et al., 2016; Cidade et al., 2017). *Ceratosuchus*, *Hassiacosuchus*, and *Navajosuchus* also appear in Alligatorinae as independent lineages in many previous analyses (Brochu, 1999, 2010; Aguilera et al., 2006; Hastings et al., 2013; Whiting et al., 2016), whereas

Brochu (2004) recovered the three taxa forming a single clade within Alligatorinae. Other analyses recovered these three genera as independent lineages in Alligatoridae, but not in Alligatorinae (Brochu, 2011; Scheyer et al., 2013; Skutschas et al., 2014; Hastings et al., 2016; Wang et al., 2016). These differences in the topology of these taxa also hint at the necessity of a comprehensive phylogenetic revision of these four genera.

Alligator appears as a clade without any immediate sister taxon within Alligatorinae. This absence of an immediate sister taxon is a topology similar to that in many analyses (Brochu, 1999; Aguilera et al., 2006; Hastings et al., 2013; Whiting et al., 2016; Cidade et al., 2017), but different from those in analyses that recovered *Wannaganosuchus* as the sister taxon of *Alligator* (Brochu, 1999, 2004, 2010, 2011; Aguilera et al., 2006; Hastings et al., 2013; Scheyer et al., 2013; Skutschas et al., 2014; Wang et al., 2016; Whiting et al., 2016; Cidade et al., 2017) and in other analyses that recovered the species *Allognatosuchus polyodon* as the immediate sister taxon of *Alligator* (Pinheiro et al., 2013; Fortier et al., 2014) or recovered *Procaimanoidea kayi* and *Wannaganosuchus* as successive sister taxa (Bona et al., 2013b). The topology among the species of *Alligator* is the same as in most analyses that included the same species (Brochu, 2011; Scheyer et al., 2013; Wang et al., 2016; Cidade et al., 2017), except for Skutschas et al. (2014), which recovered *A. mefferdi* as the sister taxon of the most derived clade formed by *A. mississippiensis* and *A. thomsoni*, Hastings et al. (2016), which only recovered *A. mefferdi*, *A. mississippiensis*, and *A. thomsoni* as a clade, and Salas-Gismondi et al. (2015), which recovered *Culebrasuchus mesoamericanus* (which appears in the analysis of this paper as the basal-most caimanine) within the species of *Alligator*, as the sister taxon of the clade formed by *A. mefferdi*, *A. mississippiensis*, and *A. thomsoni* in a polytomy. This polytomy also appears in the analysis of this paper. These perspectives suggest that the phylogenetic hypotheses between the species of *Alligator* have been relatively stable over time, although more comprehensive analysis involving the placement of *C. mesoamericanus* and the resolution of the polytomy involving *A. mefferdi*, *A. mississippiensis*, and *A. thomsoni* are perspectives to be explored in future analyses.

DISCUSSION

Acresuchus and the Evolution of Gigantism in *Purussaurus*

The skull length of the holotype of *Acresuchus pachytemporalis* is significantly smaller than those of the *Purussaurus* species. The skull of the holotype of *A. pachytemporalis* has an estimated snout-to-quadrate length of 51.5 cm; the same measurement in the species of *Purussaurus* according to Aguilera et al. (2006) are 80.1 cm in *P. neivensis* (UCMP-39704), 126.0 cm in *P. mirandai* (CIAAP-1369, holotype), and 140.0 cm in *P. brasiliensis* (UFAC-1403). As such, the phylogenetic placement of *Acresuchus pachytemporalis* as the sister taxon of *Purussaurus* raises the possibility that the new taxon can be seen as an evolutionary 'transitional form' between a 'medium-sized, generalized caimanine' and the giant, highly derived *Purussaurus*. This evolutionary perspective may have as its expression some characters that differentiate the two taxa as well as characters that are shared between them. For example, *Acresuchus* lacks an anteroposteriorly enlarged external naris (see Fig. 2) present in *Purussaurus* (see Langston, 1965; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006; Aureliano et al., 2015). This feature has been proposed to have either a thermoregulatory function in large-bodied crocodiles (Moreno-Bernal, 2007) or a stress-dissipating function associated with the bite force in *Purussaurus* (Aureliano et al., 2015), which in turn is also associated with the presence of deep dorsoventral depressions between the lacrimal and maxillary bones in *Purussaurus mirandai* and *P. brasiliensis* (see Aguilera et al., 2006; Aureliano et al., 2015). As mentioned previously, the holotype of *Acresuchus* exhibits small depressions in the posterior portions of the maxillae that could be homologous to the deep depressions of *Purussaurus*. If this interpretation is correct, the evolutionary increase in size of the external naris and of the dorsoventral depression could thus be correlated to the evolution of gigantism in the *Acresuchus*-*Purussaurus* clade.

Simultaneously, *Acresuchus pachytemporalis* exhibits some cranial characters that are also present in *Purussaurus* and might be adaptations for large size of both the skull and the body as a whole: the medial contact between the prefrontals (Fig. 2) allows either an anterior displacement of the nasals or a posterior displacement of the frontal when compared with other, non-gigantic caimanines, although some of these present prefrontals that meet medially, such as *Caiman yacare* (Brochu, 1999) or *Caiman crocodilus* (Medem, 1981; Brochu, 2013). Both *Acresuchus* (Figs. 2, 6) and *Purussaurus* exhibit larger supratemporal fenestrae compared with other caimanines; in the supratemporal fenestrae of extant crocodylians, there is an insertion area for the M. adductor mandibulae externus profundus (Iordansky, 1973; Holliday and Witmer, 2007; = M. pseudotemporalis of Schumacher, 1973). In longirostrine, this muscle is enlarged when compared with non-longirostrine ones (Schumacher, 1973; Holliday and Witmer, 2007), which is considered an adaptation for quick seizing of prey (Schumacher, 1973). Because longirostrine crocodylians also have larger supratemporal fenestrae as compared with non-longirostrine taxa (Iordansky, 1973; Langston, 1973; Holliday and Witmer, 2007), the enlargement of these fenestrae in the *Acresuchus*-*Purussaurus* clade may be related to an increase in the speed, efficiency, or strength of prey capture. Additionally, the supratemporal fenestrae are the exits for vascular vessels (the temporoorbital vessels) of the basicranium (see Holiday and Gardner, 2012; Bona et al., 2013a), and the enlargement of these structures may also be related to an increase of the vascularity of the area. Such increase may be related to a thermoregulatory function, as proposed for the other fossil crocodyliforms, *Aegisuchus* Holliday and Gardner, 2012 and *Mourasuchus* (e.g., Holliday and Gardner, 2012; Bona et al., 2013a). This thermoregulatory function would be especially interesting because gigantism in crocodylians implies higher and more stable body temperatures with the risk of overheating (Moreno-Bernal, 2007); thus, a greater capacity for thermoregulation could have contributed to the achievement of gigantism in the evolution of the *Acresuchus*-*Purussaurus* clade (see Aureliano et al., 2015). However, more detailed studies about this feature and this taxon need to be made to evaluate these last two concepts.

A squamosal 'horn' is also present, albeit with a significantly smaller size, in the two smaller species of the giant genus *Purussaurus*: *Purussaurus neivensis* and *P. mirandai*. In the largest species (*P. brasiliensis*), however, this structure is absent. The difference in sizes of these 'horns' in *Acresuchus* and *Purussaurus* indicates that they could have evolved in inverse proportion with respect to the increase in size that occurred in the evolution of the clade. Extant crocodylians that possess squamosal eminences, such as *Crocodylus rhombifer* and *C. siamensis*, have been observed to perform social displays in which the head is elevated in such a way that the squamosal 'horns' form the pinnacle of the angle (K. Vliet, pers. comm.). These displays are performed to attract the attention of other individuals and are most frequently performed by males; thus, males may attract females to courtship and mating through this behavior, but such displays are not a courtship/mating behavior per se (K. Vliet, pers. comm.). As such, these structures may serve to accentuate visual elements of those displays in these extant crocodylians, and a similar behavior could be performed by fossil crocodylians that present squamosal eminences, especially if these are large, like those of *Acresuchus*.

The false-ziphodont teeth observed in *Purussaurus* (Souza et al., 2016) and absent in *Acresuchus* could be a consequence of differences in enamel deposition during tooth development associated with increase in the size of the prey that could be captured by *Purussaurus* in comparison with the medium-sized *Acresuchus*. *Purussaurus* has also been suggested to perform the prey-capturing behavior known as 'death roll' (Blanco et al., 2015), and the false-ziphodont teeth may also have aided in making this specific behavior more efficient. This feature was possibly positively selected due to an increase in the predatory role of *Purussaurus* by facilitating the tearing or cutting of prey items, especially flesh.

Paleoecology of *Acresuchus*

The Solimões Formation possesses a remarkable diversity of crocodylian taxa, morphotypes, and feeding habits (see Riff et al., 2010, for a review). Such diversity consists of the giant, top predator *Purussaurus* (Barbosa-Rodrigues, 1892; Bocquentin-Villanueva et al., 1989; Aureliano et al., 2015); the 'duck'-snouted, putative gulp-feeding *Mourasuchus* (Cidade et al., 2017); the longirostrine piscivorous gavialoids *Gryposuchus* Gurich, 1912 and *Hesperogavialis* Bocquentin-Villanueva and Buffetaut, 1981; the longirostrine piscivorous crocodyloid *Charactosuchus* Langston, 1965 (Riff et al., 2010); and of medium-sized, generalist predators such as *Caiman* cf. *C. yacare* (Fortier et al., 2009, 2014) and *Caiman brevirostris*, a medium-sized, generalist predator that may have had an inclination toward durophagy, similar to the extant *Caiman latirostris* (Fortier et al., 2014).

It was not possible to assess whether the holotype of *Acresuchus pachytemporalis* was close to adult body size or even morphologically mature due to the absence of vertebrae (see Brochu, 1996), or osteoderms (Buffrénil, 1980) and long bones (Ikejiri, 2012) from which age estimates based on histology could be made. However, because all teeth present a rounded apex, we propose that this specimen had grown enough to change from the juvenile niche, with acute apex teeth, to the adult niche, with rounded apex teeth (see Erickson et al., 2003). Accordingly, if we assume that the skull is from a mature individual, its size implies that *Acresuchus* is a medium-sized caimanine (as compared with the giants *Purussaurus* and *Mourasuchus*), yet still larger than most other caimanines, including the extant species.

The skull length of a sample of 52 individuals of the largest extant caimanine, *Melanosuchus niger* (data available in Foth et al., 2013) had an average of ca. 31.5 cm; among these, the single largest skull had a length of 52.5 cm. As such, given the skull length of *Acresuchus pachytempralis*, this taxon may be considered as being at least as large as an extant *Melanosuchus*. Whether *Acresuchus* could reach even larger sizes must be addressed in future works, especially based on more complete specimens. The maxillary and mandibular dentitions of *Acresuchus* and *Melanosuchus* exhibit very similar morphologies, with most of the teeth being pointed except for the posterior-most teeth, which are blunt. In this scenario, based on the size and the morphological features already discussed, *Acresuchus* may be considered as having a diet similar to that of extant *Melanosuchus*, which consists of small invertebrates (insects, crustaceans, gastropods) for the juvenile (Silveira and Magnusson, 1999; Foth et al., 2013) and of fish and small- to medium-sized mammals for the adult (Foth et al., 2013).

Although generalist crocodylians have been known from the Solimões Formation, none have reached the size of *Acresuchus*, implying that it formed its own ecological niche, previously unknown for its environment. A similar ecological niche may have been held by different taxa in other Miocene units, such as *Melanosuchus fisheri* in the Urumaco Formation (Medina, 1976), *Caiman gasparinae* in the Ituzaingó Formation (Bona and Carabajal, 2013), and the taxon represented by the specimen UCMP-39978, formerly attributed to *Caiman* cf. *C. lutescens*, for the Honda Group (Langston, 1965; Bona et al., 2013b). The posterior-most blunt teeth of *Acresuchus* are similar to those of extant caimanines and several fossil taxa (see Fortier et al., 2014; Salas-Gismondi et al., 2015), the presence of which is a character that has been associated with both facultative and largely durophagous feeding habit, with the last being more associated specifically with the predominance of hard-shelled mollusks (see Harlan, 1824; Brochu, 2004; Salas-Gismondi et al., 2015) or turtles (Erickson, 1984; Ross and Garnett, 1989; Blanco et al., 2015). However, a largely durophagous habit for *Acresuchus* is considered unlikely. This species lacks other specific adaptations for a predominant durophagy, such as a large mandibular symphysis, extending at least beyond the level of the sixth alveolous, rostrum short relative to the total length of the skull, and posterior teeth globular (sensu Salas-Gismondi et al., 2015, character 198-1 and -2), that are present in *Globidentosuchus*, *Gnatusuchus*, *Kuttanacaiman*, and *Caiman wannlangstoni* (see Scheyer et al., 2013; Salas-Gismondi et al., 2015). It also lacks the 'shovel-like' mandible seen in *Gnatusuchus* (Salas-Gismondi et al., 2015). However, the presence of those teeth indicates that *Acresuchus* could have been a facultative durophage, performing some sort of processing of hard-shelled prey, as in the extant *C. latirostris* (Ősi and Barrett, 2011).

CONCLUSIONS

This work described *Acresuchus pachytemporalis* from the late Miocene Solimões Formation of the Acre Basin, Brazil, a new species that increases the already large crocodylomorph diversity of the Miocene of South America. This new species is diagnosed in particular by the presence of squamosal 'horns,' in which the squamosal has an upturned posterolateral margin throughout its entire lateral surface and a dorsoventral expansion toward the posterior end. This characteristic is not present in any other caimanine taxa, although it is present in the alligatorid *Ceratosuchus burdoshi*. However, *Acresuchus* differs from *Ceratosuchus* in other characteristics. The new taxon is phylogenetically placed as the sister taxon of *Purussaurus*, and some inferences about the morphological evolution of this clade are presented in this work. Some characters may be associated with the evolution of gigantism in *Purussaurus*, such as the size of the external naris and supratemporal fenestrae, although these perspectives have to be thoroughly assessed in detailed studies. Paleoecologically, *Acresuchus pachytemporalis* is proposed as a medium-sized generalist caimanine that had an ecological niche similar to the extant *Melanosuchus niger*.

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