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

Phylogenetic review of Alligatoroidea (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
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Orientadora: Prof^a. Dr^a. 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 descendants. 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 is 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 remanescant 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 aligatorioideos 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

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 Paleontológicas, 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 Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina.

MCNC-PAL: Museo de Ciencias 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 Orocal’ collection of the Instituto Venezolano de Investigaciones Científicas, San Antonio 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 für Naturkunde, Stuttgart, Germany.

SMNK: Staatliches Museum für Naturkunde, Karlsruhe, Germany.

Spa: Naturhistorisches Museum Basel, Basilea, Switzerland.

STUS: Departamento de Paleontología, “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, Munich, 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 antibacterial substances that can be used as antibiotics for human patients (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 larger 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 *Rauisuchus tiradentes* von Huene, 1942, *Poposaurus gracilis* Mehl, 1915,

Gracilisuchus stipanicorum 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 went 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 crocodylomorphs 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 *Hylaeochampsia 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 Eosuchia is exactly that of *H. vectiana*, from the Early Cretaceous of the Isle of Wight, United Kingdom (Owen, 1874; Brochu, 2003).

Within Eosuchia 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 crocodylian 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-aquatic 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. rollinatti* (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 basal 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. cairensis* from Egypt, although the assignment of the species to this genus is challenged due to its phylogenetic placement outside the other members 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 that 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 Osteolaeminae, an exclusively African group that comprises the extant genus *Osteolaemus* (with two species, *O. tetrapis* 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. chechchiae* 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 Uzbekistan (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; Kälin, 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 animals 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 in 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 *Acrasuchus* (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 olsenii* 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-osteological 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 dataset 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 specifically 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 dataset 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 furnished 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 redescrptions (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 medium-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 biogeography 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 assessment 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, formerly 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).

3. Materials and Methods

3.1. Taxa

3.1.1. List of visited collections and examined specimens

Museo Argentino de Ciencias 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: *Acrasuchus 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: *Stangerochampsia 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 Landesmuseum, 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, holotype; 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); *Brachychampsia 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 brasiliensis*); *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 Ciencias 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)

Hylaeochampsia 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).

Eothoracosaurus mississippiensis

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.

Albertochampsia langstoni (Fig. 6)

Specimen analyzed: SMM-P67.15.3, holotype.

Bibliography consulted: Erickson (1972).

Figure 6: Skull of the holotype of *Albertochampsia 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.

Allognathosuchus 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 analyzed: 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.

Bottosaurus 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 deposits across the Late Cretaceous and the Paleocene of New Jersey, United States (Cossette & Brochu, 2018).

Brachychampsia 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 *Brachychampsia 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.

Brachychampsia sealeyi (Fig. 19)

Bibliography consulted: Williamson (1996).

Figure 19: Skull of the holotype of *Brachychampsia 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)

Bibliography 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 lateral 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: Kålin (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 Gérard-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, holotype (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 brasiliensis*.

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.

Stangerochampsia 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 *Stangerochampsia 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.

7. References

Abel, O. 1928. *Allognathosuchus*, ein an de cheloniphage Nahrungsweise angepaßter Krokodiltypus des nordamerikanischen Eozäns. *Paläontologisches Zeitschrift*, 9:367–374.

Aguilera, O.A., Riff, D. & Bocquentin-Villanueva, J. 2006. A new giant *Purussaurus* (Crocodyliformes, Alligatoridae) from the upper Miocene Urumaco Formation, Venezuela. *Journal of Systematic Palaeontology*, 4:221–232.

Ambrosetti, J.B. 1887. Observaciones sobre los reptiles fósiles Oligocenos de los terrenos Terciarios del Paraná. *Boletín de la Academia Nacional de Ciencias de Córdoba*, 4:409–426.

Angielczyk, K.D. & Gingerich, P.D. 1998. New specimen of cf. *Asiatosuchus* (Crocodyloidea) from the Middle Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan). *Contributions from the Museum of Paleontology, The University of Michigan*: 30(5):163–189.

Antunes, M.T. 1961. *Tomistoma lusitanica*, crocodilien du Miocène du Portugal. *Revista da Faculdade de Ciências Universidade de Lisboa, Serie IIc*, 9:3–88.

Antunes, M.T. 1987. Affinities and taxonomical status of Miocene longirostrine crocodilians from Western Europe with remarks on phylogeny, paleoecology and distribution. *Comunicações dos Serviços Geológicos de Portugal*, 73:49–58.

Antunes, M.T. 2017. Huge Miocene Crocodilians from Western Europe: predation, comparisons with the “false gharial” and size. *Anuário do Instituto de Geociências – UFRJ*, 40(3): 117–130.

Aureliano, T., Ghilardi, A.M., Guilherme, E., Souza-Filho, J.P., Cavalcanti, M. & Riff, D. 2015. Morphometry, bite-force, and paleobiology of the Late Miocene Caiman *Purussaurus brasiliensis*. *Plos One*, 10(2):e0117944. doi.org/10.1371/journal.pone.0117944

Baez, A.M. & Gasparini, Z.B. 1977. Origen y evolución de los anfibios y reptiles del cenozoico de América del Sur. *Acta Geológica Lilloana*, 14:149–232.

Baez, A.M. & Gasparini, Z.B. 1979. The South America herpetofauna: an evaluation of the fossil record. The South American Herpetofauna: Its Origin, Evolution, and Dispersal. *University of Kansas Museum of Natural History Monograph*, 7:29–54.

Barbosa-Rodrigues, B. 1892. Les Reptiles fossiles de la vallée de l’Amazone. *Vellosia*, 2:41–46.

Barrios, F. 2011. Nuevos restos de Alligatoridae Cuvier, 1807 (Eusuchia, Crocodylia) del Neógeno del Sur de la provincia de Salta. Implicancias sistemáticas. Licenciature Thesis,. Universidad Nacional de Salta.

Bartels, W.S. 1983. A transitional Paleocene-Eocene reptile fauna from the Bighorn Basin, Wyoming. *Herpetologica*, 39(4):359–374.

Bartels, W.S. 1984. Osteology and systematic affinities of the horned alligator *Ceratosuchus* (Reptilia, Crocodilia). *Journal of Paleontology*, 58:1347–1353.

Benton, M.J. & Clark, J.M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pp. 295–338 In M.J. Benton (ed.). *The phylogeny and classification of the tetrapods. Vol. 1. Amphibians and reptiles*. Clarendon Press, Oxford.

Berg, D.E. 1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*?, aus dem Eozän von Messel bei Darmstadt/Hessen. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, 52:1–105.

Berg, D.E. 1969. *Charactosuchus kugleri*, von Jamaica. *Eclogae Geologicae Helvetiae*, 62:731–735.

Bezuijen, M.R., Shwedick, B.M., Sommerlad, R., Stevenson, C. & Steubing, R.B. 2010. *Tomistoma schlegelii*. Pp. 133–138 In S.C. Manolis and C. Stevenson (eds.). *Crocodiles, Status Survey and Conservation Action Plan*. Crocodile Specialist Group, Darwin.

Bezuijen, M.R., Shwedick, B., Simpson, B.K., Staniewicz, A. & Stuebing, R. 2014. *Tomistoma schlegelii*. *The IUCN Red List of Threatened Species*, e.T21981A2780499. doi:10.2305/IUCN.UK.2014-1.RLTS.T21981A2780499.en

Bocquentin-Villanueva, J. 1984. Um nuevo Nettosuchidae (Crocodylia, Eusuchia) proveniente de la Formación Urumaco (Mioceno Superior), Venezuela. *Ameghiniana*, 21:3–8.

Bocquentin-Villanueva, J., Souza-Filho, J.P., Buffetaut, E. & Negri, F. R. 1989. Nova interpretação do gênero *Purussaurus* (Crocodylia, Alligatoridae). *Anais do XI Congresso Brasileiro de Paleontologia, Curitiba, Brasil*, 1:427–438.

Bona, P. 2007. Una nueva especie de *Eocaiman* Simpson (Crocodylia, Alligatoridae) del Paleoceno Inferior de Patagonia. *Ameghiniana*, 44(2):435–445.

Bona, P. & Barrios, F. 2015. The Alligatoroidea of Argentina: an update of its fossil record. Pp. 143–158 In: Fernández, M., Herrera, Y. (eds.). *Reptiles Extintos - Volumen en Homenaje a Zulma Gasparini*. Publicación Electrónica de la Asociación Paleontológica Argentina.

Bona, P. & Carabajal, A.P. 2013. *Caiman gasparinae* sp. nov., a huge alligatorid (Caimaninae) from the late Miocene of Paraná, Argentina. *Alcheringa*, 37(4):462–473.

Bona, P., Riff, D., & Gasparini Z. 2012. Late Miocene crocodylians from Northeast Argentina: new approaches about the austral components of the Neogene South American crocodylian fauna. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103:1–20. doi.org/10.1017/S175569101300042X

Bona, P., Fernandez-Blanco, M.V., Scheyer, T.M. & Foth, C. 2017. Shedding light on the taxonomic diversity of the South American Miocene caimans: the status of *Melanosuchus fisheri* (Crocodylia, Alligatoroidea). *Ameghiniana*, 54:681–687.

Bona, P., Ezcurra, M.D., Barrios, F. & Fernandez-Blanco, M.V. 2018. A new Palaeocene crocodylian from southern Argentina sheds light on the early history of caimanines. *Proceedings of the Royal Society B*, 285:20180843. doi.org/10.1098/rspb.2018.0843

Buchy, M.-C., Stinnesbeck, W., Frey, E. & Gonzalez, A.H.G. 2007. First occurrence of the genus *Dakosaurus* (Crocodyliformes, Thalattosuchia) in the Late Jurassic of Mexico. *Bulletin de la Société Géologique de France*, 178(5):391–397.

Buffetaut, E. 1975. Sur l'anatomie et la position systématique de *Bernissartia fagesii* Dollo, L., 1883, crocodilien du Wealdien de Bernissart, Belgique. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (sci. Terre)*, 51:1–20.

Buffetaut, E. 1983. Sur la persistance tardive d'un crocodilien archaïque dans le Pleistocene de l'Ile des Pins (Nouvelle-Calédonie) et sa signification biogéographique. *Comptes Rendus de l'Academie des Sciences de Paris*, 297:89–92.

Buffetaut, E. 2016. From Charles Darwin's comments to the first mention of South American giant fossil birds: Auguste Bravard's catalogue of fossil species from Argentina (1860) and its significance. *Bulletin de la Société géologique de France*, 187:41–53.

Burmeister, G. 1883. Reprint of Bravard, 1858: monografía de los terrenos marinos terciarios del Paraná. *Annales del Museo Público de Buenos Aires*, 3:45–94.

Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por Don Augusto Bravard y mencionados en su obra precedente. *Annales del Museo Nacional de Buenos Aires*, 3:95–173.

Busbey, A.B. 1994. The structural consequences of skull flattening in crocodilians. Pp. 173–192 in J.J. Thomason (ed.). *Functional morphology in vertebrate paleontology*. Cambridge University Press, New York.

Bravard, A. 1858. *Monografía de los terrenos marinos terciarios de las cercanías del Paraná, Buenos Aires*. Reimpresión de la Cámara de Diputados de la Nación 1995, Buenos Aires.

Bravard, A. 1860. *Catalogue des espèces d'animaux fossiles recueillies dans l'Amerique du Sud de 1852–1860*. Lithographic brochure, Paris.

Brinkmann, W. & Rauhe, M. 1998. *Diplocynodon ratelii* Pomel, 1847 (Crocodylia, Leidyosuchidae) aus dem Unter-Oligozän von Céreste (Südfrankreich). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 209:295–321.

Brochu, C.A. 1995. Heterochrony in the crocodylian scapulocoracoid. *Journal of Herpetology*, 29(3):464–468.

Brochu, C.A. 1997a. Phylogenetic Systematics and Taxonomy of Crocodylia. PhD Dissertation. University of Texas, 467 pp.

Brochu, C.A. 1997b. A review of ‘*Leidyosuchus*’ (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. *Journal of Vertebrate Paleontology*, 17:679–697.

Brochu, C.A. 1999. Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Memoir Society of Vertebrate Paleontology*, 6:9–100.

Brochu, C.A. 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. *Copeia*, 2000:657–673.

Brochu, C.A. 2003. Phylogenetic approaches toward crocodilian history. *Annual Review of Earth and Planetary Sciences*, 31:357–397.

Brochu, C.A. 2004a. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. *Journal of Vertebrate Paleontology*, 24:856–872.

Brochu, C.A. 2004b. A new gavialoid crocodylian from the Late Cretaceous of eastern North America and the phylogenetic relationships of thoracosaurids. *Journal of Vertebrate Paleontology*, 24:610–633.

Brochu, C.A. 2006. Osteology and phylogenetic significance of *Eosuchus minor* (Marsh 1870), new combination, a longirostrine crocodylian from the Late Paleocene of North America. *Journal of Paleontology*, 80:162–186.

Brochu, C.A. 2007a. Morphology, relationships and biogeographic significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. *Zoological Journal of the Linnean Society*, 150:835–63.

Brochu, C.A. 2007b. Systematics and taxonomy of Eocene tomistomine crocodylians from Britain and Northern Europe. *Palaeontology*, 50(4):917–928.

Brochu, C.A. 2010. A new alligatoroid from the Lower Eocene Green River Formation of Wyoming and the origin of caimans. *Journal of Vertebrate Paleontology*, 30:1109–1126.

Brochu, C.A. 2011. Phylogenetic relationships of *Necrosuchus ionensis* Simpson, 1937 and the early history of caimanines. *Zoological Journal of the Linnean Society*, 163:S228–S256.

Brochu, C.A. 2013. Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103:521–550.

Brochu, C.A. & Storrs, G.W. 2012. A giant crocodile from the Plio–Pleistocene of Kenya, the phylogenetic relationships of Neogene African crocodylines, and the antiquity of *Crocodylus* in Africa. *Journal of Vertebrate Paleontology*, 32:587–602.

Brochu, C.A., Njau, J., Blumenschine, R.J. & Densmore, L.D. 2010. A new horned crocodile from the Plio-Pleistocene hominid sites at Olduvai Gorge, Tanzania. *Plos One*, 5(2):e9333. doi:10.1371/journal.pone.0009333.

Brochu, C.A., Parris, D.C., Grandstaff, B.S., Denton, R.K., Jr., & Gallagher, W.B. 2012. A new species of *Borealosuchus* (Crocodyliformes, Eusuchia) from the Late Cretaceous–early Paleogene of New Jersey. *Journal of Vertebrate Paleontology*, 32(1):105–116. doi:10.1080/02724634.2012.633585

Brownstein, C.D. 2019. First record of a small juvenile giant Crocodyliform and its ontogenetic and biogeographic Implications. *Bulletin of the Peabody Museum of Natural History*, 60(1):81–90. doi.org/10.3374/014.060.0104

Buscalioni, A.D., Sanz, J.L. & Casanovas, M.L. 1992. A new species of the eusuchian crocodile *Diplocynodon* from the Eocene of Spain. *Neues Jahrbuch für Geologie und Palaontologie Abhandlungen*, 187(1):1–29.

Buscalioni, A.D., Ortega, F. & Vasse, D. 1997. New crocodiles (Eusuchia: Alligatoroidea) from the Upper Cretaceous of southern Europe. *Comptes Rendus de l'Academie des Sciences de Paris, Sciences de la Terre et des Planètes*, 325:525–530.

Buscalioni, A.D., Ortega, F., Weishampel, D.B. & Jianu, C.M. 2001. A revision of the crocodyliform *Allodaposuchus precedens* from the Upper Cretaceous of the Hateg Basin, Romania. Its relevance in the phylogeny of Eusuchia. *Journal of Vertebrate Paleontology*, 21:74–86.

Carpenter, K. 1983. *Thoracosaurus neocesariensis* (De Kay, 1842) (Crocodylia: Crocodylidae) from the Late Cretaceous Ripley Formation of Mississippi. *Mississippi Geology*, 4(1):1–10.

Carpenter, K. & Lindsey, D. 1980. The dentary of *Brachychampsa montana* Gilmore (Alligatorinae; Crocodylidae), a Late Cretaceous turtle-eating alligator. *Journal of Paleontology*, 54:1213–1217.

Carvalho, A. L. 1951. Os jacarés do Brasil. *Arquivos do Museu Nacional*, 43:127–152.

Case, E.C. 1925. Note on a new species of the Eocene crocodilian *Allognathosuchus*, *A. wartheni*. *Contributions from the Museum of Geology, University of Michigan*, 2:93–97.

Cidade, G.M. & Hsiou, A.S. 2018. New morphological, evolutionary and paleoecological interpretations on the genus *Eocaiman* (Crocodylia, Caimaninae) from the Cenozoic of South America. P. 46 In: M. Marzola, O. Mateus & M. Moreno-Azanza. (eds.). *Abstract book of the XVI Annual Meeting of the European Association of Vertebrate Palaeontology*. Departamento de Ciências da Terra, Faculdade Ciências e Tecnologia, Universidade Nova de Lisboa, Caparica.

Cidade, G.M., Solórzano, A., Rincón, A.D., Riff, D. & Hsiou, A.S. 2017. A new *Mourasuchus* (Alligatoroidea, Caimaninae) from the late Miocene of Venezuela, the phylogeny of Caimaninae and considerations on the feeding habits of *Mourasuchus*. *PeerJ*, 5:e3056. doi.org/10.7717/peerj.3056

Cidade, G.M., Solórzano, A., Rincón, A.D., Riff, D., & Hsiou, A.S. 2018. Redescription of the holotype of the Miocene crocodilian *Mourasuchus arendsi* (Alligatoroidea, Caimaninae) and perspectives on the taxonomy of the species. *Historical Biology*, online first. doi.org/10.1080/08912963.2018.1528246

Cidade, G.M., Fortier, D. & Hsiou, A.S. 2019a. The crocodylomorph fossil record of the Cenozoic of South America and its evolutionary history: a review. *Journal of South American Earth Sciences*, 90:392–411. doi:10.1016/j.jsames.2018.12.026

Cidade, G.M., Riff, D., Souza-Filho, J.P. & Hsiou, A.S. 2019b. A reassessment of the osteology of *Mourasuchus amazonensis* Price, 1964 with comments on the taxonomy of the species. *Palaeontologia Electronica*, 22.2.44A:1–23. doi.org/10.26879/893 palaeo-electronica.org/content/2019/2602-mourasuchus-amazonensis

Cidade, G.M., Souza-Filho, J.P., Hsiou, A.S., Brochu, C.A., & Riff, D. 2019c. New specimens of *Mourasuchus* (Alligatoroidea, Caimaninae) from the Miocene of Brazil and Bolivia and their taxonomic and morphological implications. *Alcheringa*, 43:261–278. doi.org/10.1080/03115518.2019.1566495

Cidade, G.M., Fortier, D. & Hsiou, A.S. 2019d. Taxonomic and phylogenetic review of *Necrosuchus ionensis* (Alligatoroidea, Caimaninae) and the early evolution and radiation of caimanines. *Zoological Journal of the Linnean Society*, online first.

Cidade, G.M., Fortier, D., Rincón, A.D. & Hsiou, A.S. 2019e. Taxonomic review of two fossil crocodylians from the Cenozoic of South America and its implications for the crocodylian fauna of the continent. *Zootaxa*, 4656(3):475–486.

Cidade, G.M., Riff, D. & Hsiou, A.S. In press. The feeding habits of the strange

crocodylian *Mourasuchus* (Alligatoroidea, Caimaninae): a revision, new hypotheses and perspectives. *Revista Brasileira de Paleontologia*, in press.

Clark, J.M. & Norell, M.A. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsia vectiana* from the Wealden of the Isle of Wight. *American Museum Novitates*, 3032:1–19.

Clark, J.M., Sues, H.D. & Berman, D.S. 2000. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. *Journal of Vertebrate Paleontology*, 20:683–704.

Clark, J.M., Xing, X., Forster, C.A. & Wang, Y. 2004. A Middle Jurassic ‘sphenosuchian’ from China and the origin of the crocodylian skull. *Nature*, 430:1021–1024.

Colbert, E.H. & Bird, R.T. 1954. A gigantic crocodile from the Upper Cretaceous beds of Texas. *American Museum Novitates*. 1688:1–22.

Cope, E.D. 1872. Notices of new Vertebrata from the upper waters of Bitter Creek, Wyoming Territory. *Proceedings of the American Philosophical Society*, 12:483–486.

Conrad, J.L., Jenkins, K., Lehmann, T., Manthi, F.K., Peppe, D.J., Nightingale, S., Cossette, A., Dunsworth, H. M., Harcourt-Smith, W. E. H. & McNulty, K. P. 2013. New specimens of "*Crocodylus*" *pigotti* (Crocodylidae) from Rusinga Island, Kenya, and generic reallocation of the species. *Journal of Vertebrate Paleontology*, 33(3):629–646. doi:10.1080/02724634.2013.743404

Cossette, A. P. & Brochu, C.A. 2018. A new specimen of the alligatoroid *Bottosaurus harlani* and the early history of character evolution in alligatorids. *Journal of Vertebrate Paleontology*, 38(4). doi:10.1080/02724634.2018.1486321.

Dal Sasso, C., Pasini, G., Fleury, G. & Maganuco, S. 2017. *Razanandrongobe sakalavae*, a gigantic mesoeucrocodylian from the Middle Jurassic of Madagascar, is the oldest known notosuchian. *PeerJ*, 5:e3481 <https://doi.org/10.7717/peerj.3481>

De Kay, J.E. 1842. *Zoology of New York*. White & Visscher, New York.

Del Favero, L. 1999. Un esemplare di *Diplocynodon* Pomel, 1847 (Crocodylia, Leidyosuchidae) conservato nel museo geopaleontologico dell' Università di Padova. *Lavori Società Veneta di Scienze Naturali*, 24:107–17.

Delfino, M. & Smith, T. 2009. A reassessment of the morphology and taxonomic status of '*Crocodylus*' *depressifrons* Blainville, 1855 (Crocodylia, Crocodyloidea) based on the Early Eocene remains from Belgium. *Zoological Journal of the Linnean Society*, 156:140–167. doi:10.1111/j.1096-3642.2008.00478.x

Delfino, M. & Smith, T. 2012. Reappraisal of the morphology and phylogenetic relationships of the middle Eocene alligatoroid *Diplocynodon deponiae* (Frey, Laemmert, and Riess, 1987) based on a three-dimensional specimen. *Journal of Vertebrate Paleontology*, 32(6):1358–1369. doi:10.1080/02724634.2012.699484.

Delfino, M., Martin, J.E. & Buffetaut, E. 2008a. A new species of *Acynodon* (Crocodylia) from the Upper Cretaceous (Santonian-Campanian) of Villaggio del Pescatore, Italy. *Palaeontology*, 51:1091–1106.

Delfino, M., Codrea, V., Folie, A., Dica, P., Godefroit, P. & Smith, T. 2008b. A complete skull of *Allodaposuchus precedens* Nopcsa 1928 (Eusuchia) and a reassessment of the morphology of the taxon based on the Romanian remains. *Journal of Vertebrate Paleontology*, 28:111–122.

Densmore, L.D. 1983. Biochemical and immunological systematics of the order Crocodilia. Pp. 397-465 In M.K. Hecht, B. Wallace and G.H. Prance (eds.). *Evolutionary Biology, Vol. 16*. Plenum Press, New York.

De Stefano, G. 1905. Appunti sui Batraci e rettili del Quercy appartenenti alla collezioni Rossignol. *Bolletino della Societa Geologia Italiana*, 24:17–67.

Dott, R. H. & Prothero, D.R. 1994. *Evolution of the Earth*, 5th edition. McGraw Hill, New York.

Efimov, M.B. 1982. New fossil crocodilians from the U.S.S.R. *Paleontological Journal*, 16:140–145.

Efimov, M.B. 1988. [Fossil crocodiles and champsosaurs of Mongolia and the USSR]. *Trudy Somestnaya Sovetsko-Mongolskya Paleontologicheskaya Expeditsiya*, 36:1–108.
[In Russian]

Erickson, B.R. 1972. *Albertochampsia langstoni*, gen. et sp. nov., a new alligator from the Cretaceous of Alberta. *Scientific Publications of the Science Museum of Minnesota, New Series*, 2:1–13.

Erickson, B.R. 1976. Osteology of the early eusuchian crocodile *Leidyosuchus formidabilis*, sp. nov. *Monographs of the Science Museum of Minnesota (Paleontology)*, 2:1–61.

Erickson, B.R. 1982. *Wannaganosuchus*, a new alligator from the Paleocene of North America. *Journal of Paleontology*, 56(2), 492–506.

Erickson, B. R. 1984. Chelonivorous habits of the Paleocene crocodile *Leidyosuchus formidabilis*. *Scientific Publications of the Science Museum of Minnesota, New Series*, 5:3–9.

Erickson, B.R. & Sawyer, G.T. 1996. The estuarine crocodile *Gavialosuchus carolinensis* n. sp. (Crocodylia: Eusuchia) from the Late Oligocene of South Carolina, North America. *Science Museum of Minnesota Monographs (Paleontology)*, 3:1–47.

Erickson, G.M., Gignac, P.M., Stepan, S.J., Lappin, A.K., Kent, A.V., Brueggen, J.D., Inouye, B.D., Kledzik, D. & Webb, G.J.W. 2012. Insights into the ecology and evolutionary success of crocodylians revealed through bite-force and tooth-pressure experimentation. *Plos One*, 7(3):e31781.

Escobedo-Galván, A.H., Cupul-Magaña, F.G. & Velasco, J.A. 2011. Misconceptions about the taxonomy and distribution of *Caiman crocodilus chiapasius* and *C. crocodilus fuscus* (Reptilia: Crocodylia: Alligatoridae). *Zootaxa*, 3015: 66–68. doi.org/10.11646/zootaxa.3015.1.7

Estes, R. 1988. Lower vertebrates from the Golden Valley Formation, Early Eocene of North Dakota. *Acta Zoologica Cracoviensia*, 31(20):541–562.

Farris, D. W., Jaramillo, C., Bayona, G., Restrepo-Moreno, S., Montes, C., Cardona, A., Mora, A., Speakman, R.J., Glasscock, M.D., Reiners, P. & Valencia, V. 2011. Fracturing of the Panamanian Isthmus during initial collision with South America. *Geology*, 39:1007–1010.

Ferguson, M.W.J. 1981. The structure and development of the palate in *Alligator mississippiensis*. *Archives for Oral Biology*, 26:427–443.

Ferguson, M.W.J. 1984. Craniofacial development in *Alligator mississippiensis*. Pp. 223–273 in M.W.J. Ferguson (ed.). *The Structure, Development and Evolution of Reptiles, Symposia of the Zoological Society of London 52*. Academic Press, New York.

Ferguson, M.W.J. 1985. Reproductive biology and embryology of the crocodilians. Pp. 329–492 in C. Gans, F. Billett, and P.F.A. Maderson (ed.). *Biology of the Reptilia, vol. 14*. John Wiley and Sons, New York.

Fernández-Blanco, M.V., Cassini, G.H. & Bona, P. 2018. Skull ontogeny of extant caimans: a three-dimensional geometric morphometric approach. *Zoology* 129(2018):69–81.

Fortier, D. 2011. O registro fóssil de crocodilianos na América do Sul: estado da arte, análise crítica e registro de novos materiais para o Cenozóico. PhD Thesis. Universidade Federal do Rio Grande do Sul, 360 pp.

Fortier, D. & Rincón, A. 2012. Pleistocene crocodylians from Venezuela, and the description of a new species of *Caiman*. *Quaternary International*, 305:141–148. doi.org/10.1016/j.quaint.2012.03.018

Fortier, D., Brochu, C.A. & Souza-Filho, J.P. 2009. The oldest record of *Caiman yacare*. *Journal of Vertebrate Paleontology*, 29(3):97A.

Fortier, D.C., Souza-Filho, J.P., Guilherme, E., Maciente, A. & Schultz, C.L. 2014. A new specimen of *Caiman brevirostris* (Crocodylia, Alligatoridae) from the Late Miocene of Brazil. *Journal of Vertebrate Paleontology*, 34(4), 820–834. doi.org/10.1080/02724634.2014.838173

Foth, C., Fernandez-Blanco, M.V., Bona, P., Scheyer, T.M. 2018. Cranial shape variation in jacarean caimanines (Crocodylia, Alligatoroidea) and its implications in the taxonomic status of extinct species: the case of *Melanosuchus fisheri*. *Journal of Morphology*, 279(2):259–273. doi.org/10.1002/jmor.20769.

Fourtau, R. 1920. Contribution à l'étude des vertèbres miocènes de l'Égypte. Egypt Survey Department, Cairo.

Gasparini, Z. 1973. *Revisión de los Crocodylia (Reptilia) fósiles del territorio Argentino. Su evolución, sus relaciones filogenéticas, su clasificación y sus implicancias estratigráficas*. PhD Thesis, Facultad de Ciencias Naturales La Plata.

Gasparini, Z. 1981. Los Crocodylia fósiles de la Argentina. *Ameghiniana*, 18:177–205.

Gasparini, Z. & Baez, A.M. 1975. Aportes al conocimiento de la herpetofauna terciaria de la Argentina. *Actas I Congreso Argentino de Paleontología y Bioestratigrafía*, 2:377–415.

Gatesy, J., de Salle, R. & Wheeler, W. 1993. Alignment-ambiguous nucleotide sites and the exclusion of systematic data. *Molecular Phylogenetics and Evolution*, 2:152–157.

Gatesy, J., Amato, G., Norell, M., Desalle, R. & Hayashi, C. 2003. Combined support for wholesale taxic atavism in gavialine crocodylians. *Systematic Biology*, 52:403–422.

Gervais, P. 1876. Crocodile gigantesque fossile du Brésil. *Journal of Zoology*, 5:232–236.

Giebel, C.G.A. 1870. Ueber *Dakosaurus amazonicus* n. sp. *Zeitschrift für die gesammten Naturwissenschaften*, 35:170–171.

Giebel, C.G.A. 1876. *Dakosaurus amazonicus* ist neuerdings von Gervais als *Dinosuchus terror* beschrieben. *Zeitschrift für die gesammten Naturwissenschaften*, 48:307

Gilmore, C.W. 1910. *Leidyosuchus sternbergii*, a new species of crocodile from the Cretaceous Beds of Wyoming. *Proceedings of the United States National Museum*, 38(1762):485–502.

Gilmore, C.W. 1911. A new fossil alligator from the Hell Creek beds of Montana. *Proceedings of the United States National Museum*, 41:297–302. doi: 10.5479/si.00963801.41-1860.297

Gilmore, C.W. 1942. A new fossil reptile from the Upper Cretaceous of Utah. *United States National Museum Proceedings*, 1:109–114.

Gilmore, C.W. 1946. A new crocodilian from the Eocene of Utah. *Journal of Paleontology*, 20:62–67.

Ginsburg L, Buffetaut E. 1978. *Euthecodon arambourgii* n. sp., et l'évolution du genre *Euthecodon*, crocodilien du Néogène d'Afrique. *Géologie Méditerranéenne*, 5:291–302.

Gold, M.E., Brochu, C.A. & Norell, M.A. 2014. An expanded combined evidence approach to the *Gavialis* problem using geometric morphometric data from crocodylian braincases and eustachian systems. *Plos One*, 9:e105793. doi:10.1371/journal.pone.0105793

Goloboff, P. A. & Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32:221–238.

Goloboff, P.A. & Szumik, C.A. 2015. Identifying unstable taxa: Efficient implementation of triplet-based measures of stability, and comparison with Phyutility and RogueNaRok. *Molecular Phylogenetics and Evolution*, 88:93–104.

Goloboff, P.A., Farris, J.S. & Nixon, K.C. 2008. TNT: a free program for tree analysis using new technology. *Cladistics*, 24(5):774–786.

Gorman, G.C., Wilson, A.C. & Nakanishi, M. 1971. A biochemical approach towards the study of reptilian phylogeny: evolution of serum albumin and lactic acid dehydrogenase. *Systematic Zoology*, 20:167–185.

Gray, J.E. 1862. A synopsis of the species of alligators. *Annals and Magazine of Natural History*, 10:327–331.

Green, R. E., Braun, E. L., Armstrong, J., Earl, D., Nguyen, N., Hickey, G., Vandeweghe, M. W., St John, J. A., Capella-Gutiérrez, S., Castoe, T. A., Kern, C., Fujita,

M. K., Opazo, J. C., Jurka, J., Kojima, K. K., Caballero, J., Hubley, R. M., Smit, A. F., Platt, R. N., Lavoie, C. A., Ramakodi, M. P., Finger, J. W., Suh, A., Isberg, S. R., Miles, L., Chong, A. Y., Jaratlerdsiri, W., Gongora, J., Moran, C., Iriarte, A., McCormack, J., Burgess, S. C., Edwards, S. V., Lyons, E., Williams, C., Breen, M., Howard, J. T., Gresham, C. R., Peterson, D. G., Schmitz, J., Pollock, D. D., Haussler, D., Triplett, E. W., Zhang, G., Irie, N., Jarvis, E. D., Brochu, C. A., Schmidt, C. J., McCarthy, F. M., Faircloth, B. C., Hoffmann, F. G., Glenn, T. C., Gabaldón, T., Paten, B. And Ray, D. A. 2014. Three crocodilian genomes reveal ancestral patterns of evolution among archosaurs. *Science*, 346:1254449.

Guest, R.L. 2014. *Description and phylogenetic analysis of a new alligatoroid from the Eocene of Laredo, Texas*. Master's degree Dissertation, University of Iowa.

Harlan, R. 1824. On an extinct species of Crocodile not before described; and some observations on the Geology of West Jersey. *Journal of the Academy of Natural Sciences of Philadelphia*, 4:15–24.

Hastings, A.K., Bloch, J.I., Jaramillo, C.A., Rincon, A.F. & MacFadden, B.J. 2013. Systematics and biogeography of crocodylians from the Miocene of Panama. *Journal of Vertebrate Paleontology*, 33(2):239–263. doi.org/10.1080/02724634.2012.713814

Hastings, A. K., Reisser, M. & Scheyer, T.M. 2016. Character evolution and the origin of Caimaninae (Crocodylia) in the New World Tropics: new evidence from the Miocene of Panama and Venezuela. *Journal of Paleontology*, 90:317–332.

Hastings, A.K., Bloch, J.I. & Jaramillo, C.A., 2015. A new blunt-snouted dyrosaurid, *Anthracosuchus balrogus* gen. et sp. nov. (Crocodylomorpha, Mesoeucrocodylia), from the Paleocene of Colombia. *Historical Biology*, 8:998–1020.

Hill, R.V. & Lucas, S.G. 2006. New data on the anatomy and relationships of the Paleocene crocodylian *Akanthosuchus langstoni*. *Acta Palaeontologica Polonica*, 51:455–464.

Holliday, C.M. & Witmer, L.M. 2009. The epipterygoid of crocodyliforms and its significance for the evolution of the orbitotemporal region of eusuchians. *Journal of Vertebrate Paleontology*, 29(3), 715–33.

Huxley, T.H. 1875. On *Stagonolepis robertsoni*, and on the evolution of the Crocodilia. *Quarterly Journal of the Geological Society*, 31, 423–438.

Irmis, R.B., Nesbitt, S.J. & Sues, H.D. 2013. Early Crocodylomorpha. Pp. 275–302 In S.J. Nesbitt, J.B. Desojo, R.B. Irmis (eds.). *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. Geological Society of London Special Publication, London.

Iturralde-Vinent, M.A. 2006. Meso-Cenozoic Caribbean Paleogeography: Implications for the Historical Biogeography of the region. *International Geology Review*, 48:791–827.

Joleaud, L. 1920. Sur la présence d'un Gavialide du genre *Tomistoma* dans le Pliocène d'eau douce de l'Ethiopie. *Comptes Rendus de l'Académie des Sciences*, 70:816–818.

Jouve, S., Bardet, N., Jalil, N.-E., Suberbiola, X.P., Bouya, B. & Amaghazaz, M. 2008. The oldest African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine reptiles through the Cretaceous-Tertiary boundary. *Journal of Vertebrate Paleontology*, 28(2):409–421. doi:10.1671/0272-4634(2008)28[409:TOACPP]2.0.CO;2

Kälin, J.A. 1933. Beiträge zur vergleichenden Osteologie des Crocodilidenschädels. *Zoologisches Jahrbucher*, 57:535–714.

Kälin, J.A. 1936a. *Hispanochampsa mülleri* nov. gen. nov. sp., ein neuer Crocodilide aus dem unteren Oligocän von Tarrega (Catalonien). *Abhandlungen der Schweizerische Paläontologische Gesellschaft*, 58:1–40.

Kälin, J.A. 1936b. Über Skeletanomalien bei Crocodiliden. *Zeitschrift für Morphologie und Ökologie der Tiere*, 32:327–347.

Kälin, J.A. 1939. Ein extrem kurzschnauziger Crocodilide aus den Phosphoriten des Quercy, *Arambourgia* (nov. gen.) *gaudryi* de Stefano. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft*, 62:1–18.

Kälin, J.A. 1940. *Arambourgia* nov. gen. *gaudryi* de Stefano sp., ein kurzschnauziger Crocodilide aus den Phosphoriten des Quercy. *Eclogae Geologicae Helvetiae*, 32:185–186.

Kellner, A.W.A., Pinheiro, A.E.P. & Campos, D.A. 2014. A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K–Pg boundary. *Plos One*, 9:e81386.

Kommanee, J., Preecharram, S., Daduang, S., Tamsiripong, Y., Dhiravisit, A., Yamada, Y. & Thammasirirak, S. Antibacterial activity of plasma from crocodile (*Crocodylus siamensis*) against pathogenic bacteria. *Annals of Clinical Microbiology and antimicrobials*. 11(1):22. doi: 10.1186/1476-0711-11-22.

Lambe, L.M. 1907. On a new crocodilian genus and species from the Judith River Formation of Alberta. *Transactions of the Royal Society of Canada*, 4:219–244.

Lang, J.W., Andrews, H. & Whitaker, R. 1989. Sex determination and sex ratios in *Crocodylus palustris*. *American Zoologist*, 29:935–952.

Langston, W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University of California Publications in Geological Sciences*, 52:1–168.

Langston, W. 1975. Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), New Combination, from the Eocene of North America. *Fieldiana: Geology*, 33(16):291–314.

Langston, W. 2008. Notes on a partial skeleton of *Mourasuchus* (Crocodylia, Nettosuchidae) from the Upper Miocene of Venezuela. *Arquivos do Museu Nacional*, 66:125–143.

Langston, W. & Gasparini, Z. 1997. Crocodilians, *Gryposuchus*, and the South Americans gavials. Pp: 113-154 In R.F. Kay, R.H. Madden, R.L. Cifelli & J.J. Flynn (eds.). *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution, Washington.

Lee, M.S. & Yates, A.M. 2018. Tip-dating and homoplasy: reconciling the shallow molecular divergences of modern gharials with their long fossil record. *Proceedings of the Royal Society B*, 285(1881):20181071. doi10.1098/rspb.2018.1071

Li, J. 1976. Fossil of Sebecosuchia discovered from Nanxiong, Guangdong. *Vertebrata Palasiatica*, 14:169–74.

Li, J. 1984. A new species of *Planocrania* from Hengdong, Hunan. *Vertebrata Palasiatica*, 22:123–33.

Loomis, L.B. 1904. Two new river reptiles from the Titanotheres beds. *American Journal of Science (ser. 4)*, 18:427–432.

Lucas, S.G. & Hunt, A.P. 1989. *Alamosaurus* and the Sauropod Hiatus in the Cretaceous of the North American Western Interior. Geological Society of America Special Publication, 238:75–85.

Lucas, S.G. & Sullivan, R.M. 2004. The taxonomic status of *Chrysochampsia*, an Eocene crocodylian from North Dakota, USA and the paleobiogeography of *Allognathosuchus*. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 2004:461–472.

Ludwig, R. 1877. Fossile Crocodiliden aus der Tertiärformation des mainzer Beckens. *Paleontographica Supplement*, 3:1–52.

Macaluso, L., Martin, J.E., Del Favero, L. & Delfino, M. 2019. Revision of the crocodylians from the Oligocene of Monteviale, Italy, and the diversity of European eusuchians across the Eocene-Oligocene boundary. *Journal of Vertebrate Paleontology*, online first, e1601098:1–13.

MacFadden, B.J. 2006. North American Miocene land mammals from Panama. *Journal of Vertebrate Paleontology*, 26:720–734.

Maddison, W.P. & Maddison, D.R. 2017. Mesquite: a modular system for evolutionary analysis. Version 3.2. <http://mesquiteproject.org/>.

Malone, B. 1979. The systematics, phylogeny and paleobiology of the genus *Alligator*. PhD Dissertation, City University of New York.

Man, Z., Yishu, W., Peng, Y. & Xiaobing, W. 2011. Crocodilian phylogeny inferred from twelve mitochondrial protein-coding genes, with new complete mitochondrial genomic sequences for *Crocodylus acutus* and *Crocodylus novaeguineae*. *Molecular Phylogenetics and Evolution*, 60:62–67.

Mannion, P.D., Chiarenza, A.A., Godoy, P.L. & Cheah, Y.N. 2019. Spatiotemporal sampling patterns in the 230 million year fossil record of terrestrial crocodylomorphs and their impact on diversity. *Palaeontology* 62(4):615–637. doi:10.1111/pala.12419

Martin, B. G. & Bellairs, A.D'.A. 1977. The narial excrescence and pterygoid bulla of the gharial, *Gavialis gangeticus* (Crocodylia). *Journal of Zoology*, 182:541–558.

Martin, J.E. 2007. New material of the Late Cretaceous globidontan *Acynodon iberoccitanus* (Crocodylia) from southern France. *Journal of Vertebrate Paleontology*, 27:362–372.

Martin, J.E. 2010a. A new species of *Diplocynodon* (Crocodylia, Alligatoroidea) from the Late Eocene of the Massif Central, France, and the evolution of the genus in the climatic context of the Late Palaeogene. *Geological Magazine*, 147:596–610. doi:10.1017/S0016756809990161.

Martin, J.E. 2010b. *Allodaposuchus* Nopsca, 1928 (Crocodylia, Eusuchia), from the Late Cretaceous of southern France and its relationships to Alligatoroidea. *Journal of Vertebrate Paleontology*, 30:756–767.

Martin, J.E. 2019. The taxonomic content of the genus *Gavialis* from the Siwalik Hills of India and Pakistan. *Papers in Palaeontology*, 5(3):483–497. doi:10.1002/spp2.1247

Martin, J.E. & Gross, M. 2011. Taxonomic clarification of *Diplocynodon* Pomel, 1847 (Crocodylia) from the Miocene of Styria, Austria. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, 261:177–193.

Martin, J.E. & Lauprasert, K. 2010. A new primitive alligatorine from the Eocene of Thailand: relevance of Asiatic members to the radiation of the group. *Zoological Journal of the Linnean Society*, 158:608–628.

Martin, J.E., Smith, T., Lapparent-Broin, F., Escuillié, F. & Delfino, M. 2014. Late Palaeocene eusuchian remains from Mont de Berru, France, and the origin of the alligatoroid *Diplocynodon*. *Zoological Journal of the Linnean Society*, 172:867–891.

Mateus, O., Puértolas-Pascual, E. & Callapez, P.M. 2018. A new eusuchian crocodylomorph from the Cenomanian (Late Cretaceous) of Portugal reveals novel implications on the origin of Crocodylia. *Zoological Journal of the Linnean Society*, 186 (2):501–528. doi:10.1093/zoolinnea/zly064

Mead, J.I., Steadman, D.W., Bedford, S.H., Bell, C.J. & Spriggs, M. 2002. New extinct mekosuchine crocodile from Vanuatu, South Pacific. *Copeia*, 2002:632–641.

Mehl, M.G. 1916. *Caimanoidea visheri*, a new crocodilian from the Oligocene of South Dakota. *Journal of Geology*, 24:47–56.

Medem, F.J. 1958. The crocodilian genus *Paleosuchus*. *Fieldiana: Zoology*, 39(21):227–247.

Medem, F. 1981. Los Crocodylia de Sur America, Volume 1: Los Crocodylia de Colombia. Universidad Nacional de Colombia, Bogota.

Medem, F. 1983. Los Crocodylia de Sur America, Volume 2. Universidad Nacional de Colombia, Bogota.

Medina, C.J. 1976. Crocodilians from the Late Tertiary of Northwestern Venezuela: *Melanosuchus fisheri* sp. nov. *Breviora*, 438:1–14.

Megirian, D., Murray, P.F. & Willis, P. 1991. A new crocodile of the gavial ecomorph morphology from the Miocene of northern Australia. *Beagle*, 8:135–158.

Molnar, R.E. 2010. A new reconstruction of the skull of *Sebecus icaeorhinus* (Crocodyliformes: Sebecosuchia) from the Eocene of Argentina. *Brazilian Geographical Journal: Geosciences and Humanities research medium*, 1:314–330.

Montefeltro, F.C. Revisão filogenética de Mesoeucrocodylia: irradiação basal e principais controvérsias. PhD Thesis, Universidade de São Paulo, 285 pp.

Montes, C., Cardona, A., McFadden, R.R., Moron, S., Silva, C.A., Restrepo-Moreno, S., Ramirez, D., Hoyos, N., Wilson, J., Farris, D.W., Bayona, G., Jaramillo, C.,

Valencia, V., Bryan, J. & Flores, J.-A. 2012. Evidence for middle Eocene and younger emergence in Central Panama: implications for Isthmus closure. *Geological Society of America Bulletin*, 124:780–799. doi:10.1130/B30528.1.

Mook, C.C. 1921a. The skull of *Crocodylus acer* Cope. *Bulletin of the American Museum of Natural History*, 44:117–121.

Mook, C.C. 1921b. Description of a skull of a Bridger crocodilian. *Bulletin of the American Museum of Natural History*, 44:111–116.

Mook, C.C. 1921c. Skull characters and affinities of the extinct Florida gavial *Gavialosuchus americana* (Sellards). *Bulletin of the American Museum of Natural History*, 44:33–41.

Mook, C.C. 1921d. *Allognatosuchus*, a new genus of Eocene crocodilians. *Bulletin of the American Museum of Natural History*, 44:105–110.

Mook, C.C. 1921e. *Brachygnathosuchus braziliensis*, a new fossil crocodilian from Brazil. *Bulletin of the American Museum of Natural History*, 44(6):43–49.

Mook, C.C. 1923. A new species of Alligator from the Snake Creek Beds. *American Museum Novitates*, 73:1–13.

Mook, C.C. 1924. A new crocodilian from the Wasatch Beds. *American Museum Novitates*, 137:1–4.

Mook, C.C. 1927. The skull characters of *Crocodylus megarhinus* Andrews. *American Museum Novitates*, 289:1–8.

Mook, C.C. 1932. A study of the osteology of *Alligator prenasalis* (Loomis). *Bulletin of the Museum of Comparative Zoology*, 74:19–41.

Mook, C.C. 1940. A new fossil crocodilian from Mongolia. *American Museum Novitates*, 1097:1–3.

Mook, C.C. 1941a. A new crocodilian from the Lance Formation. *American Museum Novitates*, 1128:1–5.

Mook, C.C. 1941b. A new fossil from Colombia. *Proceedings of the United States National Museum*, 91(31–22):55–61.

Mook, C.C. 1941c. A new crocodilian, *Hassiacosuchus kayi*, from the Bridger Eocene Beds of Wyoming. *Annals of the Carnegie Museum*, 28:207–220.

Mook, C.C. 1942. A new crocodilian from the Belly River Beds. *American Museum Novitates*, 1202:1–5.

Mook, C.C. 1946. A new Pliocene alligator from Nebraska. *American Museum Novitates*, 1311:295–304.

Mook, C.C. 1955. Two new genera of Eocene crocodilians. *American Museum Novitates*, 1727:1–4.

Mook, C.C. 1959. A new species of fossil crocodile of the genus *Leidyosuchus* from the Green River Beds. *American Museum Novitates*, 1933:1–6.

Müller, L. 1924. Beiträge zur osteologie der rezenten Krokodilier. *Zeitschrift für Morphologie und Ökologie der Tiere*, 2:427–460.

Nesbitt, S.J. 2011. The early evolution of Archosauria: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, 352:1–292.

Nesov, L.A., Kaznyshkina, L.F. & Cherepanov, G.O. 1989. [Mesozoic Ceratopsian dinosaurs and crocodiles of Central Asia]. Pp. 144–155 In: T.N. Bogdanova & L.I. Khozatsky (eds.). *Theoretical and Applied Aspects of Modern Paleontology. Proceedings of the XXXIII Session of the All-Union Paleontological Society*. Nauka, St. Petersburg. [In Russian]

Newbrey, M.G., Murray, A.M., Wilson, M.V.H., Brinkman, D.B. & Neuman, A.D. 2009. Seventy-five-million-year-old tropical tetra-like fish from Canada tracks Cretaceous global warming. *Proceedings of the Royal Society B*, 276(1674):3829–3833. doi.org/10.1098/rspb.2009.1047.

Nopcsa, F. 1924. Über die Namen einiger brasilianischer fossiler Krokodile. *Centralblatt für Mineralogie, Geologie und Palaeontologie*, 12:378.

Norell, M.A. 1988. Cladistic approaches to paleobiology as applied to the phylogeny of alligatorids. PhD Dissertation, Yale University.

Norell, M.A. 1989. The higher level relationships of the extant Crocodylia. *Journal of Herpetology*, 23:325–335.

Norell, M.A. & Clark, J.M. 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 60:115–128.

Norell, M.A., Clark, J.M. & Hutchison, J.H. 1994. The Late Cretaceous alligatoroid *Brachychampsa montana* (Crocodylia): new material and putative relationships. *American Museum Novitates*, 3116:1–26.

Oaks, J.R. 2011. A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *Evolution*, 65:3285–3297.

Ochev, V.G. 1981. [Marine crocodiles in the Mesozoic of Povolzh'e]. *Priroda* 1981:103. [In Russian]

O'Dea, A., Lessios, H.A., Coates, A.G., Eytan, R.I., Restrepo-Moreno, S.A., Cione, A.L., Collins, L.S., de Queiroz, A., Farris, D.W., Norris, R.D., Stallard, R.F., Woodburne, M.O., Aguilera, O., Aubry, M.P., Berggren, W.A., Budd, A.F., Cozzuol, M.A., Coppard, S.E., Duque-Caro, H., Finnegan, S., Gasparini, G.M., Grossman, E.L., Johnson, K.G., Keigwin, L.D., Knowlton, N., Leigh, E.G., Leonard-Pingel, J.S., Marko, P.B., Pyenson, N.D., Rachello-Dolmen, P.G., Soibelzon, E., Soibelzon, L., Todd, J.A., Vermeij, G.J., Jackson, J.B.C., 2016. Formation of the Isthmus of Panama. *Science Advances*, 2:e1600883. doi.org/10.1126/sciadv.1600883.

O'Neill, F.M., Lucas, S.G. & Kues, B.S. 1981. *Akanthosuchus langstoni*, a new crocodilian from the Nacimiento Formation (Paleocene, Torrejonian) of New Mexico. *Journal of Paleontology*, 55:340–352.

Ösi, A., Clark, J.M. & Weishampel, D.B. 2007. First report on a new basal eusuchian crocodyliform with multicusped teeth from the Upper Cretaceous (Santonian) of Hungary. *Neues Jahrbuch für Geologie und Palaontologie Abhandlungen*, 243:169–177.

Owen, R. 1850. Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds. Part II. Crocodilia. *Palaeontographical Society Monographs*, 3:5–50.

Owen, R. 1874. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. VI. *Hylaeochampsia*. *Palaeontographical Society Monographs*, 27:1–7.

Parrish, J.M. 1991. A new specimen of an early crocodylomorph (cf. *Sphenosuchus* sp.) from the Upper Triassic Chinle Formation of Petrified Forest National Park, Arizona. *Journal of Vertebrate Paleontology*, 11:198–212.

Patterson, B. 1936. *Caiman latirostris* from the Pleistocene of Argentina, and a summary of South American cenozoic crocodilia. *Herpetologica*, 1(29):43–54.

Patterson, B. 1943. Remarks on south American crocodiles. *Copeia*, 1943:123–124.

Phosri, S., Jangpromma, N., Chang, L.C., Tan, G.T., Wongwiwatthanakul, S., Maijaroen, S., Anwised, P., Payoungkiattikun, W. & Klaynongsruang, S. 2018. Siamese

crocodile white blood cell extract inhibits cell proliferation and promotes autophagy in multiple cancer cell lines. *Journal of Microbiology and Biotechnology*, 28(6):1007–1021.

Pinheiro, A.E.P., Fortier, D.C., Pol, D., Campos, D.A. & Bergqvist, L.P. 2013. A new *Eocaiman* (alligatoridae, crocodylia) from the Itaboraí Basin, paleogene of Rio de Janeiro, Brazil. *Historical Biology*, 25(3):327–337. doi.org/10.1080/08912963.2012.705838.

Piras, P. & Buscalioni, A.D. 2006. *Diplocynodon muelleri* comb. nov., an Oligocene diplocynodontine alligatoroid from Catalonia (Ebro Basin, Lleida Province, Spain). *Journal of Vertebrate Paleontology*, 26:608–620.

Piras, P., Delfino, M., Del Favero, L. & Kotsakis, T. 2007. Phylogenetic position of the crocodylian *Megadontosuchus arduini* and tomistomine palaeobiogeography. *Acta Palaeontologica Polonica*, 52(2):315–328.

Piras, P., Colangelo, P., Adams, D. C., Buscalioni, A., Cubo, J., Kotsakis, T., & Raia, P. 2010. The Gavialis–Tomistoma debate: the contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships. *Evolution & Development*, 12(6):568–579.

Poe, S. 1997. Data set incongruence and the phylogeny of crocodilians. *Systematic Biology*, 45(4):393–414.

Pol, D. & Escapa, I.H. 2009. Unstable taxa in cladistic analysis: identification and the assessment of relevant characters. *Cladistics*, 25:515–527.

Pomel, A. 1847. Note sur les animaux fossiles découverts dans le département de l'Allier. *Bulletin de la Société Géologique de France*, 4:378–385.

Pough, F. H., Andrews, R. M., Cadle, J. E., Crump, M. L., Savitzky, A. H. & Wells, K. D. 2004. *Herpetology, third edition*. Pearson Prentice-Hall, Upper Saddle River, New Jersey.

Prasad, G.V.R. and de Broin, F.L. 2002. Late Cretaceous crocodile remains from Naskal (India): Comparisons and biogeographic affinities. *Annales de Paléontologie*, 88:19–71. doi.org/10.1016/S0753-3969(02)01036-4

Price, L. I. 1964. Sobre o crânio de um grande crocodilídeo extinto do Alto de Rio Juruá, Estado do Acre. *Anais da Academia Brasileira de Ciências*, 56:59–66.

Price, L.I. 1967. Sobre a mandíbula de um gigantesco crocodilídeo extinto do alto rio Juruá, Estado do Acre. *Atas do Simpósio sobre a Biota Amazônica, Geociências*, 1:359–371.

Rage, J.C. 1978. Une connexion continentale entre Amerique du Nord et Amerique du Sud au Cretace superieur? L'exernple des vertebres continentaux. *Comptes rendus sommaires des seances de la Societe geologique de France*, 6:281–285.

Rage, J.C. 1986. South American/North American terrestrial interchanges in the latest Cretaceous: short comments on Brett-Surman and Paul (1985), with additional data. *Journal of Vertebrate Paleontology*, 6(4):382–383

Remy, J.-A. 1972. Etude du crâne de *Pachynolophus lavocati* n. sp. (Perissodactyla, Palaeotheriidae) des Phosphorites du Quercy. *Palaeovertebrata*, 5:45–78.

Renne, P.R., Deino, A.L., Hilgen, F.J., Kuiper, K.F., Mark, D.F., Mitchell, W.S., Morgan, L.E., Mundil, R. & Smit, J. 2013. Time scales of critical events around the Cretaceous Paleogene boundary. *Science*, 339(6120):684–687. doi.org/10.1126/science.1230492.

Riff, D. & Aguilera, O. 2008. The world's largest gharials *Gryposuchus*: Description of *G. croizati* n. sp. (Crocodylia, Gavialidae) from the Upper Miocene Urumaco Formation, Venezuela. *Palaeontologische Zeitschrift*, 82:178–95.

Riff, D. & Kellner, A.W.A. 2011. Baurusuchiid Crocodyliforms as theropod mimics: clues from the skull and appendicular morphology of *Stratiosuchus maxhecti* (Upper Cretaceous of Brazil). *Zoological Journal of the Linnean Society*, 163:37–56.

Riff, D., Romano, P.S.R., Oliveira, G.R. & Aguilera, O.A. 2010. Neogene Crocodile and Turtle Fauna in Northern South America. Pp. 259-280 In C. Hoorn & F. Wesselingh (eds.). *Amazonia, Landscape and Species Evolution: A Look into the Past*. Wiley-Blackwell, London.

Rio, J.P., Mannion, P.D., Tschopp, E., Martin, J.E. & Delfino, M. 2019. Reappraisal of the morphology and phylogenetic relationships of the alligatoroid crocodylian *Diplocynodon hantoniensis* from the Late Eocene of the United Kingdom. *Zoological Journal of the Linnean Society*, zlz034. doi.org/10.1093/zoolinnean/zzz034

Rovereto, C. 1912. Los crocodilos fósiles en las capas del Paraná. *Anales de Museo Nacional de Buenos Aires*, 22:339–369.

Rossmann, T. 2000a. Skelettanatomische Beschreibung von *Pristichampsus rollinatti* (Gray) (Crocodilia, Eusuchia) aus dem Paläogen von Europa, Nordamerika und Ostasien. *Courier Forschungsinstitut Senckenberg*, 221:1–107.

Rossmann, T. 2000b. Studien an känozoischen Krokodilen: 5. Biomechanische Untersuchung am postkranialen Skelett des paläogenen Krokodils *Pristichampsus rollintii* (Eusuchia: Pristichampsidae). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 217:289–330.

Rusconi, C. 1933. Observaciones críticas sobre reptiles Terciarios de Paraná (Familia Alligatoridae). *Revista de la Universidad Nacional de Córdoba*, 20:1–52.

Rusconi, C. 1937. Nuevo aligatorio del Paleoceno Argentino. *Boletín Paleontológico de Buenos Aires*, 8:1–5.

Salas-Gismondi, R., Antoine, P.O., Baby, P., Brusset, S., Benammi, M., Espurt, N., De Franceschi, D., Pujos, F., Tejada, J. & Urbina, M. 2007. Middle Miocene Crocodiles from the Fitzcarrald Arch, Amazonian Peru. *Cuadernos del Museo Geominero*, 8:355–360.

Salas-Gismondi, R., Flynn, J.J., Baby, P., Tejada-Lara, J.V., Wesselingh, F.P. & Antoine, P.-O. 2015. A Miocene hyperdiverse crocodilian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proceedings of the Royal Society B*, 282:20142490. [dx.doi.org/10.1098/rspb.2014.2490](https://doi.org/10.1098/rspb.2014.2490)

Salas-Gismondi, R., Flynn, J.J., Baby, P., Tejada-Lara, J.V., Claude, J. & Antoine, P.-O. 2016. A new 13 million year old gavialoid crocodylian from proto-amazonian megawetlands reveals parallel evolutionary trends in skull shape linked to longirostry. *Plos One*, 11(4):e0152453. doi.org/10.1371/journal.pone.0152453.

Salisbury, S.W. & Willis, P.M.A. 1996. A new crocodylian from the Early Eocene of southeastern Queensland and a preliminary investigation of the phylogenetic relationships of crocodyloids. *Alcheringa*, 20:179–227.

Scalabrini, P. 1887. *Cartas científicas al General Eduardo Racedo*. Museo de la Provincia de Entre Ríos, Tipografía y Encuadernación La Velocidad, Paraná.

Scheyer, T.M. & Delfino, M. 2016. The late Miocene caimanine fauna (Crocodylia:Alligatoroidea) of the Urumaco Formation, Venezuela. *Palaeontologia Electronica*, 19.3.48A:1–57. doi.org/10.26879/657 palaeo-electronica.org/content/2016/1625-caimanines-from-urumaco-formation

Scheyer, T.M., Aguilera, O.A., Delfino, M., Fortier, D.C., Carlini, A. A., Sánchez, R., Carrillo-Briceño, J.D., Quiroz, L. & Sánchez-Villagra, M.R. 2013. Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nature Communications*, 4:1907.

Schmidt, K.P. 1938. New crocodilians from the upper Paleocene of western Colorado. *Geological Series of the Field Museum of Natural History*, 6(21):315–321.

Schmidt, K.P. 1941. A new fossil alligator from Nebraska. *Fieldiana: Geology*, 8:27–32.

Schwimmer, D. R. 2002. *King of the crocodylians: the paleobiology of Deinosuchus*. Indiana University Press, Bloomington.

Sellards, E.H. 1915. A new gavial from the Late Tertiary of Florida. *American Journal of Science*, 40:135–138.

Sereno, P.C. 2005. Stem Archosauria – taxon search: <http://www.taxonsearch.org/Archive/stem-archosauria-1.0.php> (version 1.0, 2005 November 7).

Sereno, P.C. & Larsson, H.C.E. 2009. Cretaceous crocodyliforms from the Sahara. *ZooKeys*, 28:1–143.

Sereno, P.C., & Wild, R. 1992. Procompsognathus: theropod, “thecodont” or both? *Journal of Vertebrate Paleontology*, 12:435–458.

Sereno, P.C., Larsson, H.C.E., Sidor, C.A. & Gado, B. 2001. The giant crocodyliforms *Sarcosuchus* from the Cretaceous of Africa. *Science*, 294:1516–1519.

Shan, H.-Y., Cheng, Y.-N. & Wu, X.-C. 2013. The first fossil skull of *Alligator sinensis* from the Pleistocene, Taiwan, with a paleogeographic implication of the species. *Journal of Asian Earth Sciences*, 69:17–25.

Sideleau, B.M. & Britton, A.R.C. 2013. An analysis of crocodilian attacks worldwide for the period of 2008–July 2013. Pp. 110–113 in *Proceedings of the 22nd Working Meeting of the IUCN-SSC Crocodile Specialist Group*. IUCN, Gland.

Sigler, L., Thorbjarnarson, J.B., Hinojosa-Falcon, O. & Henley, B. 2007. Searching for the Northern and Southern distribution limits of two crocodilian species: *Alligator mississippiensis* and *Crocodylus moreletii* in South Texas, US, and in Northern Tamaulipas, Mexico. *Crocodile Specialist Group Newsletter*, 26(3):6–7.

Simpson, G.G. 1930. *Allognathosuchus mooki*, a new crocodile from the Puerco Formation. *American Museum Novitates*, 445:1–16.

Simpson, G.G. 1933. A new crocodilian from the Notostylops Beds of Patagonia. *American Museum Novitates*, 623:1–9.

Simpson, G.G. 1937. An ancient eusuchian crocodile from Patagonia. *American Museum Novitates*, 965:1–20.

Skinner, M. F., Skinner, S.M. & Gooris, R.J. 1977. Stratigraphy and biostratigraphy of late Cenozoic deposits in central Sioux County, western Nebraska. *Bulletin of the American Museum of Natural History*, 158(5):263–370.

Skutschas, P.P., Danilov, I.G., Kodrul, T.M. & Jin, J. 2014. The first discovery of an alligatorid (Crocodylia, Alligatoroidea, Alligatoridae) in the Eocene of China. *Journal of Vertebrate Paleontology*, 34(2):471–476.

Smith, T., Narváez, I., Brochu, C.A., Escaso, F., Pérez-García, A., Ortega, F. 2015. New crocodyliforms from Southwestern Europe and definition of a diverse clade of European Late Cretaceous basal eusuchians. *Plos One*, 10(11): e0140679. doi:10.1371/journal.pone.0140679

Snyder, D. 2007. Morphology and systematics of two Miocene alligators from Florida, with a discussion of *Alligator* biogeography. *Journal of Paleontology*, 81:917–928.

Souza, R.G., Cidade, G.M., Campos, D.A. & Riff, D. 2016. New crocodylian remains from the Solimões Formation (Lower Eocene–Pliocene), state of Acre, southwestern

Brazilian Amazonia. *Revista Brasileira de Paleontologia*, 19(2):217–232.
doi.org/10.4072/rbp.2016.2.06

Souza-Filho, J.P. 1987. *Caiman brevirostris* sp. nov., um novo Alligatoridae da Formação Solimões (Pleistoceno) do Estado do Acre, Brasil. *Anais do X Congresso Brasileiro de Paleontologia*, 1:173–180.

Souza-Filho, J.P. 1991. *Charactosuchus sansaoi*, uma nova espécie de Crocodilidae (Crocodylia) do Neógeno do Estado do Acre, Brasil. Resumos do XII Congresso Brasileiro de Paleontologia, 1:36.

Souza-Filho, J.P. & Bocquentin-Villanueva, J.C. 1989. *Brasilosuchus mendesi*, n. g., n. sp., um novo representante da Família Gavialidae do Neógeno do Acre, Brasil. *Anais do XI Congresso Brasileiro de Paleontologia*, 1:457–463.

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

Spix, J.B. 1825. *Animalia nova sive species novae Lacertarum, quas in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavaria Regis suscepto collegit et descripsit D. J. B. De Pix. Typis Franc. Seraph. Hübschamanni, Munich.*

Steel, R. 1973. *Crocodylia: Handbuch der Paläoherpetologie, Teil 16*. Gustav Fischer Verlag, Stuttgart.

Storrs, G.W. & Efimov, M.B. 2000. Mesozoic crocodyliforms of north-central Eurasia. Pp. 402–419 In: M.J. Benton, M.A. Shishkin, D.M. Unwin & E.N. Kurochkin (eds.). *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge.

Taplin, L. E. & Grigg, C.G. 1989. Historical zoogeography of the Eusuchian crocodilians: a physiological perspective. *American Zoologist*, 29:885–901.

Thornbjarnason, J. 1992. Crocodiles: An Action Plan for Their Conservation. IUCN. Gland.

Toula, F. & Kail, J.A. 1885. Über einen Krokodil–Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich: eine paläontologische Studie. *Denkschriften der Kaiserlichen Akademie der Wissenschaften von Wien, Mathematisch–naturwissenschaftliche Klasse*, 50:299–355.

Tykoski, R.S., Rowe, T.B., Ketcham, R.A., Colbert, M.W. 2002. *Calsoyasuchus valliceps*, a new crocodyliform from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, 22 (3): 593–611.

Vélez-Juarbe, J. & Brochu, C.A. in press. Eocene crocodyliforms from Seven Rivers, Jamaica: implications for neotropical crocodyliform biogeography and the status of *Charactosuchus* Langston 1965. In: R.W. Portell & D.P. Domning (eds.). *The Eocene Fossil Site of Seven Rivers, Jamaica: Geology, Paleontology, and Evolutionary and Biogeographic Implications*. Springer Verlag, Dordrecht.

Vélez-Juarbe, J., Brochu, C.A. & Santos, H. 2007. A gharial from the Oligocene of Puerto Rico: transoceanic dispersal in the history of a non-marine reptile. *Proceedings of the Royal Society B*, 274:1245–1254.

Venegas-Anaya, M., Crawford, A.J., Escobedo-Galván, A.H., Sanjur, O.I., Densmore, L.D. & Bermingham, E. 2008. Mitochondrial DNA phylogeography of *Caiman crocodilus* in Mesoamerica and South America. *Journal of Experimental Zoology*, 309A, 614–627. doi.org/10.1002/jez.502

Vianna, A. & Moraes, A. 1945. Sur un crâne de crocodile fossile decouvert dans le Miocène de Lisbonne. *Boletim da Sociedade Geológica de Portugal*, 4:161–170.

Vignaud, P. & Gasparini, Z.B. 1996. New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) from the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences, Paris* 2:245–250.

Wang, Y., Sullivan, C. & Liu, J. 2016. Taxonomic revision of *Eoalligator* (Crocodylia, Brevirostres) and the paleogeographic origins of the Chinese alligatoroids. *PeerJ*, 4:e2356. doi.org/10.7717/peerj.2356

Wassersug, R.J. & Hecht, M.K. 1967. The status of the crocodylid genera *Procaimanoidea* and *Hassiacosuchus* in the New World. *Herpetologica*, 23:30–34.

Weems, R.E. 2018. Crocodilians of the Calvert Cliffs. *Smithsonian Contributions to Paleobiology*, 100:213–240. doi:10.5479/si.1943-6688.100.

Weitzel, K. 1935. *Hassiacosuchus haupti* n.g n.s. ein durophages Krokodil aus dem Mitteleozän von Messel. *Notizblatt des Vereins für Erdkunde und der hessischen geologischen Landesanstalt zu Darmstadt*, 16:40–49.

White, T. E. 1942. A new alligator from the Miocene of Florida. *Copeia*, 1942:3–7.

Whiting, E. T., Steadman, D.W. and Vliet, K. A. 2016. Cranial polymorphism and systematics of Miocene and living alligator in North America. *Journal of Herpetology*, 50:30–315.

Wilberg, E.W., Turner, A.H. & Brochu, C.A. 2019. Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. *Scientific Reports*, 9(514): 1–10. doi:10.1038/s41598-018-36795-1

Williamson, T.E. 1996. ?*Brachychampsia sealeyi*, sp. nov., (Crocodylia, Alligatoroidea) from the Upper Cretaceous (lower Campanian) Menefee Formation, northwestern New Mexico. *Journal of Vertebrate Paleontology*, 16(3):421–431.

Willis, P.M.A. 1993. *Trilophosuchus rackhami* gen et sp. nov., a new crocodilian from the early Miocene limestones of Riversleigh, northwestern Queensland. *Journal of Vertebrate Paleontology*, 13(1):90–98.

Willis, P.M.A. & Molnar, R.E. 1991. A new middle Tertiary crocodile from Lake Palankarinna, South Australia. *Records of the South Australian Museum*, 25:39–55.

Willis, P.M.A., Molnar, R.E. & Scanlon, J.D. 1993. An early Eocene crocodilian from Murgon, southeastern Queensland. *Kaupia*, 3:27–33.

Wood, S.V. 1846. On the discovery of an alligator and of several new Mammalia in the Hordwell Cliff; with observations upon the geological phenomena of that locality. *London Geological Journal*, 1:117–122.

Wu, X.-C. & Chatterjee, S. 1993. *Dibothrosuchus elaphros*, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia. *Journal of Vertebrate Paleontology*, 13:58–89.

Wu, X.C., Brinkman, D.B. & Russell, A.P. 1996. A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians. *Palaeontology*, 39(2):351–375.

Wu, X.-C., Russell, A.P. & Brinkman, D.B. 2001. A review of *Leidyosuchus canadensis* Lambe, 1907 (Archosauria: Crocodylia) and an assessment of cranial variation based upon new material. *Canadian Journal of Earth Sciences*, 38:1665–1687.

Young, C.C. 1982. A Cenozoic crocodile from Huaining, Anhui. Pp. 47–48 In *Selected Works of Yang Zhongjian*. Academia Sinica, China.